Age-Related Resistance to Phytophthora Fruit Rot in 'Dickenson Field' Processing Pumpkin and 'Golden Delicious' Winter Squash Fruit

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Abstract

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Phytophthora fruit rot, caused by *Phytophthora capsici*, is a major constraint to cucurbit production for the processing industry in Michigan. Age-related resistance to Phytophthora fruit rot has been identified in pepper and some cucurbit fruit. In this study, 'Dickenson Field' processing pumpkin (*Cucurbita moschata*) and 'Golden Delicious' winter squash (*C. maxima*) were evaluated for age-related resistance to Phytophthora fruit rot. Hand-pollinated fruit were harvested 3, 7, 10, 14, 21, 28, 42, or 56 days post pollination (dpp), and inoculated with *P. capsici* isolate 12889. Susceptibility to Phytophthora fruit rot decreased with fruit age in Dickenson Field processing pumpkin, whereas Golden Delicious winter squash remained susceptible to fruit rot even as fruit reached full physiological maturity. Less than 15% of Dickenson Field fruit 21 dpp or older became diseased. Conversely, about 80% of Golden Delicious fruit 21 dpp or older became diseased. Lesion diameter and pathogen growth density ratings differed significantly ($P < 0.0001$) among fruit ages for both cultivars, and were negatively correlated ($\rho = -0.37$ to -0.87) with fruit age. Lesion diameter and pathogen growth were generally greater on younger fruit than older fruit. Lesion diameter was greatest on 7- and 10-dpp-old fruit of Dickenson Field and Golden Delicious, respectively. Pathogen growth density ratings were greatest on 3-dpp-old fruit of both cultivars. Several morphological and physiological changes were observed as fruit matured. Soluble solids content and exocarp firmness of both cultivars increased with fruit age. Lesion diameter and pathogen growth density ratings were negatively correlated ($\rho = -0.29$ to -0.73) with soluble solids content and exocarp firmness.

Phytophthora fruit rot, caused by *Phytophthora capsici* Leonian, is a major constraint to cucurbit production for processing and fresh-market consumption (3–6,13). Production of processing pumpkin (*Cucurbita moschata* Duchesne ex Poir.) for canned pie filling has recently increased in western Michigan due to production shortages elsewhere. Winter squash (*C. maxima* Duchesne) is also grown commercially in this region for use in baby food purees. Phytophthora fruit rot incidence was greater than 90% in a 32-ha field of 'NK 580' winter squash in Mason County, MI in 2010 (M. Meyer and M. Hausbeck, *personal observation*). Similarly, severe epidemics of Phytophthora fruit rot have occurred on processing pumpkin in Illinois, where a majority of the crop is produced (3).

Phytophthora fruit rot is initiated when fruit contact *P. capsici*-infested soil, or when propagules are splash dispersed to fruit during rain and irrigation events (5,19). Infected fruit eventually collapse and cannot be harvested (5,19). Processing pumpkin and winter squash plants have a vining growth habit and fruit are grown in direct contact with the soil, which favors fruit rot development. Management of Phytophthora fruit rot is particularly difficult because all commercial cucurbit cultivars are highly susceptible to *P. capsici* (3,4,6,13). Therefore, Phytophthora fruit rot is primarily managed with fungicides. Resistance to the fungicides metalaxyl and mefenoxam (metalaxyl-M) is widespread in *P. capsici* populations from the primary vegetable growing regions in Michigan (17). Furthermore, foliar fungicides can be ineffective when the crop canopy prevents adequate coverage of the fruit surface or when applications do not reach the undersides of fruit that are in direct contact with the soil.

Fruit age affects susceptibility to *P. capsici* in pepper (*Capsicum annuum*) and some cucurbit fruit (2,7,10,12). The degree of ontogenic or age-related resistance to *P. capsici* varies among cucurbit cultivar groups (squash cultivars of the same species that differ morphologically for fruit type) but taxonomic classes are not correlated with susceptibility to *P. capsici* (2). Age-related resistance to *P. capsici* is most apparent in cucumber (*Cucumis sativus*) (2,10,12). Immature, elongating cucumber fruit are more susceptible to *P. capsici* than mature fruit (2,10,12). Cucumber fruit harvested 14 days post pollination (dpp) and inoculated with *P. capsici* rarely developed symptoms (10). Seven cucurbit crops from four species, including *Cucumis melo, Citrullus lanatus, Cucurbita moschata,* and *C. pepo*, exhibited similar age-related responses to *P. capsici* inoculation using detached fruit under laboratory conditions (2). Wounding fruit prior to inoculation reduces age-related resistance to *P. capsici* (10,12).

The morphophysiological changes that convey age-related resistance to *P. capsici* are not well understood. Changes in exocarp color and waxiness during fruit development were associated with age-related resistance in acorn squash (*C. pepo*), butternut squash (*C. moschata*), and pumpkin (*C. pepo*) (2). In pepper, cuticle thickness was greater and lesion length was smaller on mature fruit than on immature fruit (7). However, *P. capsici* mycelial growth was greater in extracts from mature pepper fruit, which contained higher levels of sugar than immature fruit (7). Accumulation of dry matter increased and macroelement content decreased as pepper stems aged and became more resistant to *P. capsici* (15).

Phytophthora fruit rot is a major constraint to cucurbit production for the processing industry in Michigan, and growers have few options for managing this disease. Relatively little is known about the reactions of processing pumpkin and winter squash fruit to inoculation with *P. capsici*, and these fruit were not included in previous evaluations of age-related resistance to Phytophthora fruit rot. The objectives of this study were to determine the effect of fruit age on susceptibility to *P. capsici* in processing pumpkin and winter squash, and to determine whether susceptibility to *P. capsici* is associated with soluble solids content and exocarp firmness.

Materials and Methods

Inoculum. *P. capsici* isolate 12889 (mating type A1) obtained from the culture collection of M. K. Hausbeck at Michigan State

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University was used to inoculate fruit in this study. Isolate 12889 was originally isolated from bell pepper, and is highly virulent on fruit of various hosts (8,9). All cultures were grown on unclarified V8 juice agar (UCV8) at room temperature (21 ± 2°C) and under constant fluorescent light for 5 to 7 days.

Fruit production and measurement. Processing pumpkin and winter squash fruit were grown at the Michigan State University Plant Pathology Research Farm in East Lansing. Phytophthora blight had not previously occurred at this location. The soil type was a Capac loam (fine-loamy, mixed, active, mesic Aquic Glossudalfs). Seedlings of 'Dickenson Field' processing pumpkin (Rispens Seeds Inc.) and 'Golden Delicious' winter squash (Stokes Seeds Inc.) were transplanted at the second true-leaf stage into four raised beds covered with black plastic mulch. Beds were 30.5 m long and spaced 3.7 m apart. Plants were spaced 61 cm apart within beds. Female flowers were tagged at anthesis and hand pollinated. Fruit were harvested 3, 7, 10, 14, 21, 28, 42, or 56 dpp. Ages were selected based on previous research of age-related resistance in other cucurbit fruit (2,10). All replicates of a single fruit age were harvested on the same calendar date.

Fruit length was measured from the stem end to the blossom end of each fruit. Width was measured perpendicular to the stem–blossom axis at the greatest dimension of the fruit. Fruit weight and exocarp color also were determined. A 1.2-cm-diameter core was aseptically removed near the stem of each fruit using a cork borer. The resulting hole was covered with a piece of clear tape to prevent entry of environmental contaminants with the potential to compromise subsequent inoculation experiments. Fruit cores were placed into individual plastic bags and frozen at –20°C for 24 to 48 h. Fruit cores were thawed at room temperature (21 ± 2°C) for about 1.5 h and hand pressed to extract juices. Soluble solids content was determined using a temperature-compensated refractometer (model r^2 Mini; Reichert, Inc.). At the end of the experiment, firmness of an approximately 25-cm^2 exocarp (rind) section was determined using a penetrometer (model FT 327; QA Supplies LLC) mounted to a manual press and equipped with a 5-mm-diameter plunger. Firmness was expressed as the force in newtons (N) required to puncture the exocarp.

Experimental design and inoculation procedure. The same fruit used to determine soluble solids content and exocarp firmness were used for inoculation. The experimental design was completely randomized, with eight replicates of each fruit age. The experiment was conducted twice. Prior to the removal of sample cores and inoculation, fruit were surface disinfested in a 10% bleach solution (0.62% NaClO) for 5 min and rinsed with tap water for 1 min (8). Seven unwounded fruit were inoculated with a 7-mm-diameter agar plug removed from the edge of an actively growing culture of *P. capsici* isolate 12889. Agar plugs were placed with the *P. capsici*-colonized side in direct contact with the fruit surface. Fruit were inoculated near the center of the fruit to avoid any differences in susceptibility at the peduncle or blossom end of the fruit (2). One fruit was inoculated with a sterile agar plug as a control. Fruit were placed into 53-by-33-by-28-cm transparent, plastic moisture chambers and incubated at room temperature (21 ± 2°C). Moisture chambers were lined with moist paper toweling to maintain high humidity and exposed to constant fluorescent light. A WatchDog data logger (model A150; Spectrum Technologies Inc.) recorded temperature and relative humidity in the moisture chamber during incubation. Conditions in the moisture chambers during incubation were similar among experiments and favorable for disease development. Mean temperature was 23.9°C in experiment 1 and 23.5°C in experiment 2. Mean relative humidity was 97.7 and 99.0% in experiments 1 and 2, respectively.

Disease assessment and statistical analysis. Disease incidence was recorded for each fruit as a binary response, where 0 = not diseased and 1 = diseased. Lesion diameter and pathogen growth diameter were measured 4 days post inoculation (dpi). Pathogen growth density was visually assessed 4 dpi on a 1-to-4 scale, where 1 = no external signs of pathogen growth, 2 = light growth, 3 = moderate growth, and 4 = dense growth. Uninoculated control fruit were excluded from the analyses. Data from both experiments were combined before analysis. All analyses were performed using SAS (version 9.2; SAS Institute). Disease incidence was analyzed by logistic regression using the Proc Logistic procedure. Logistic regression was also used to calculate the predicted probability of disease for each cultivar. Lesion diameter, pathogen growth diameter, and pathogen growth density ratings were analyzed separately for each cultivar by analysis of variance using the Proc Mixed procedure. Fruit age was considered a fixed effect. Soluble solids content and exocarp firmness were regressed against fruit age using the Proc Reg procedure. Spearman-rank correlation coefficients were calculated between fruit measurements and disease assessments for each cultivar using the Proc Corr procedure.

Results

A range of reactions to *P. capsici* developed on Dickenson Field and Golden Delicious fruit differing in age (Figs. 1 and 2). Soft,

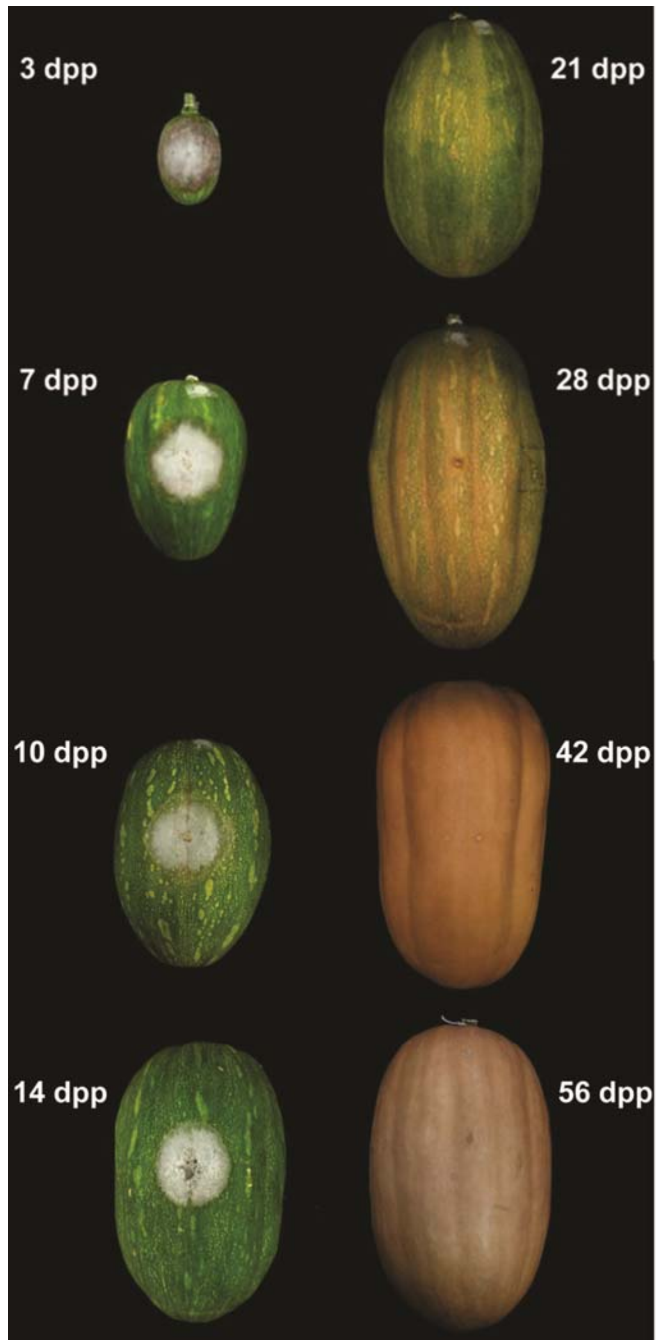

Fig. 1. Signs and symptoms 4 days post inoculation with *Phytophthora capsici* on 'Dickenson Field' processing pumpkin fruit harvested 3 to 56 days post pollination (dpp).

water-soaked lesions formed on 53 and 88% of Dickenson Field and Golden Delicious fruit, respectively. Most lesions contained visible signs of *P. capsici*, including mycelia and sporangiophores with sporangia. About 10% of lesions were water soaked but lacked external signs of pathogen growth. These lesions formed only on fruit that were 21 dpp or older.

Disease incidence varied among cultivars and fruit ages but generally decreased as age increased (Fig. 3A and B). The logistic regression of disease incidence on fruit age was significant ($P < 0.0001$) for both cultivars. On Dickenson Field, disease incidence was 100% when fruit were 3 dpp old and 0% when fruit were 56 dpp old (Fig. 3A). On Golden Delicious, disease incidence was 100% when fruit were 3 dpp old and 79% when fruit were 56 dpp old (Fig. 3B). Less than 15% of Dickenson Field fruit 21 dpp or older became diseased. Conversely, about 80% of Golden Delicious fruit 21 dpp or older became diseased. The predicted prob-

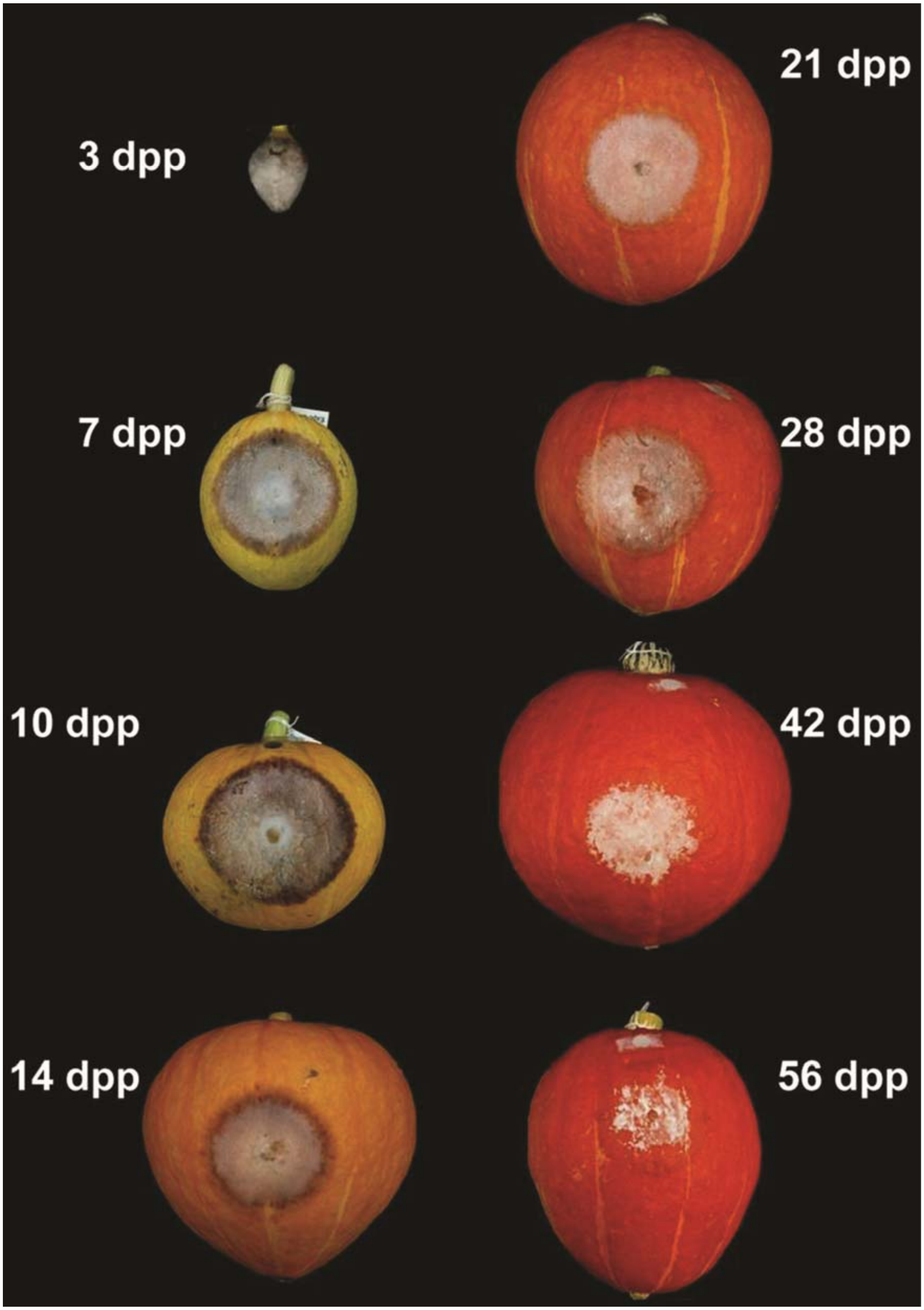

Fig. 2. Signs and symptoms 4 days post inoculation with *Phytophthora capsici* on ‘Golden Delicious’ winter squash fruit harvested 3 to 56 days post pollination (dpp).

ability of disease on Dickenson Field decreased substantially as fruit age increased, and was ≤0.45 when fruit were 21 dpp or older (Fig. 4). The predicted probability of disease on Golden Delicious was ≥0.60 regardless of fruit age (Fig. 4).

Results of analyses of lesion diameter and pathogen growth diameter were similar. Therefore, only lesion diameter results are presented. Lesion diameter and pathogen growth density ratings differed significantly ($P < 0.0001$) among fruit ages for both cultivars. Fruit age was negatively correlated ($\rho = -0.37$ to -0.87) with lesion diameter and pathogen growth density ratings (Table 1). Lesion diameter and pathogen growth were generally greater on younger fruit than on older fruit (Figs. 3C and D and 5). Lesion diameter was greatest on 7-dpp fruit of Dickenson Field and on 10-dpp fruit of Golden Delicious (Fig. 3C and D). Pathogen growth density was greatest on 3-dpp-old fruit of both cultivars (Fig. 5). Lesions that developed on Dickenson Field fruit 21 dpp or older were ≤1.0 cm in diameter and contained little or no pathogen growth (Figs. 3C and 5A). Lesions on Golden Delicious fruit 21 dpp or older were <5.0 cm and contained minimal pathogen growth (Figs. 3D and 5B).

Several morphological and physiological changes were observed during maturation in fruit of both cultivars. Fruit size and fresh weight generally increased as age increased (Table 2). Exocarp color changed from pale green to beige in Dickenson Field fruit and from pale yellow to dark orange in Golden Delicious fruit (Figs. 1 and 2). Soluble solids varied among fruit ages, ranging from 2.6 to 6.7°Brix in Dickenson Field and from 3.1 to 7.3°Brix in Golden Delicious. Soluble solids content slightly decreased after pollination and then increased when fruit were 14 dpp or older (Fig. 6A and B). Soluble solids content was negatively correlated with lesion diameter ($\rho = -0.33$ and -0.57) and pathogen growth density ($\rho = -0.29$ and -0.38) (Table 1). Exocarp firmness was 2.1 to 13.0 N in Dickenson Field and 2.9 to 13.0 N in Golden Delicious. Exocarp firmness increased linearly with fruit age (Fig. 6C and D). Exocarp firmness was also negatively correlated with lesion diameter ($\rho = -0.21$ and -0.73) and pathogen growth density ($\rho = -0.52$ and -0.75) (Table 1).

Discussion

This is the first evaluation of age-related resistance to Phytophthora fruit rot in pumpkin and winter squash cultivars grown

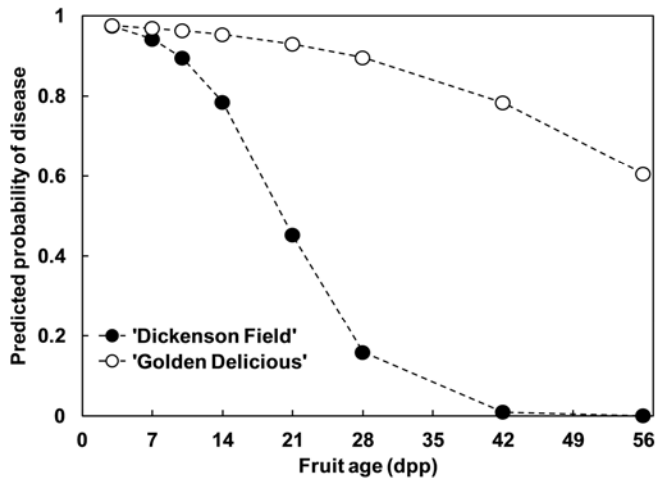

Fig. 4. Predicted probability of disease 4 days post inoculation with *Phytophthora capsici* on ‘Dickenson Field’ processing pumpkin and ‘Golden Delicious’ winter squash fruit harvested 3 to 56 days post pollination (dpp).

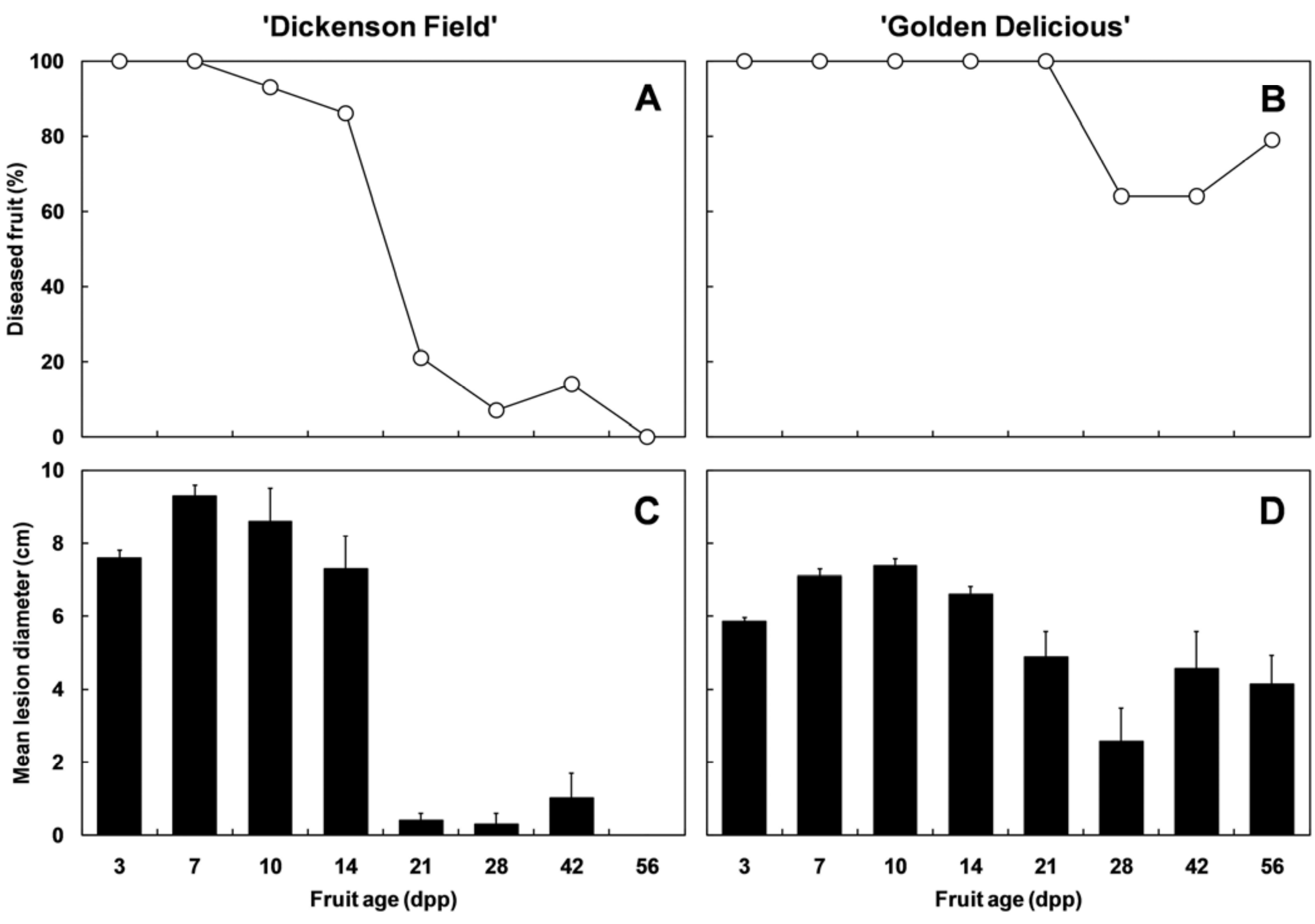

Fig. 3. Incidence of **A** and **B,** diseased fruit and **C** and **D,** mean lesion diameter 4 days post inoculation with *Phytophthora capsici* on ‘Dickenson Field’ processing pumpkin and ‘Golden Delicious’ winter squash fruit harvested 3 to 56 days post pollination (dpp). Values are the mean of 14 fruit. Error bars represent the standard error of the mean.

Table 1. Spearman-rank correlations between fruit characteristics and disease assessments in experiments evaluating age-related resistance to Phytophthora fruit rot caused by *Phytophthora capsici* in 'Dickenson Field' processing pumpkin and 'Golden Delicious' winter squash

	Spearman-rank correlation coefficient (ρ)[a]	
Cultivar, measurement[b]	Lesion diameter (cm)	Pathogen growth density rating
Dickenson Field		
Age (dpp)	–0.74**	–0.87**
Soluble solids (°Brix)	–0.57**	–0.38**
Exocarp firmness (N)	–0.73**	–0.75**
Golden Delicious		
Age (dpp)	–0.37**	–0.80**
Soluble solids (°Brix)	–0.33**	–0.29*
Exocarp firmness (N)	–0.21ns	–0.52**

[a] Asterisks indicate the correlation is significant at $P < 0.01$ (*) or $P < 0.0001$ (**); ns = not significant.
[b] Age in days post pollination (dpp) and firmness in newtons (N).

Table 2. Characteristics of 'Dickenson Field' processing pumpkin and 'Golden Delicious' winter squash fruit harvested 3 to 56 days post pollination (dpp)[a]

Cultivar, fruit age (dpp)	Length (cm)[b]	Width (cm)[c]	Fresh weight (kg)
Dickenson Field			
3	10.6	7.0	0.4
7	19.9	13.1	2.0
10	25.2	16.5	2.8
14	28.9	20.9	5.1
21	27.9	20.7	4.8
28	30.5	22.4	6.2
42	31.1	23.5	7.0
56	31.8	23.1	7.0
Golden Delicious			
3	6.0	4.9	0.1
7	10.6	9.8	0.8
10	13.6	13.1	2.1
14	15.8	14.5	2.3
21	19.1	18.4	2.8
28	19.2	18.8	2.6
42	22.1	19.7	3.1
56	22.0	19.6	3.1

[a] Values represent the mean of 14 fruit.
[b] Length was measured from the stem end to the blossom end of each fruit.
[c] Width was measured at the greatest dimension of the fruit at a 90° angle to the stem–blossom axis.

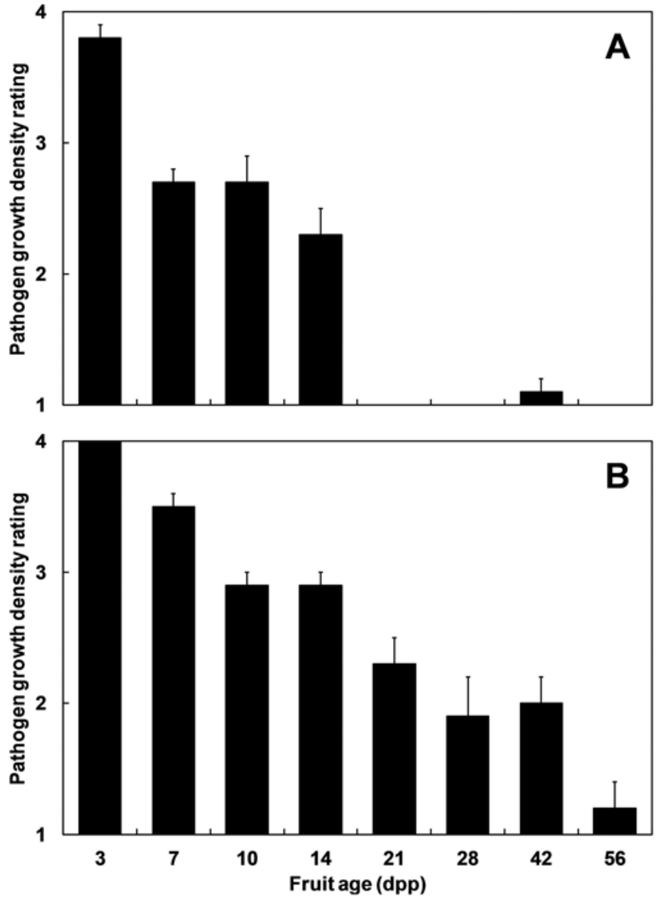

Fig. 5. Pathogen growth density ratings 4 days post inoculation with *Phytophthora capsici* on **A,** 'Dickenson Field' processing pumpkin and **B,** 'Golden Delicious' winter squash fruit harvested 3 to 56 days post pollination (dpp). Pathogen growth density was visually assessed on a 1-to-4 scale, where 1 = no external signs of pathogen growth, 2 = light growth, 3 = moderate growth, and 4 = dense growth. Values are the mean of 14 fruit. Error bars represent the standard error of the mean.

primarily for processing. Previously, age-related resistance to Phytophthora fruit rot was reported in eight cultivar-groups from five cucurbit species (2,10). Results from this experiment demonstrate that Dickenson Field processing pumpkin fruit become resistant to Phytophthora fruit rot as they mature. Conversely, Golden Delicious winter squash fruit remain susceptible to fruit rot even as they reach full maturity. Avoiding cultivars that are highly susceptible to Phytophthora fruit rot and scheduling fungicide applications according to host growth stage could be used to improve management of this disease. Additional studies are necessary to determine whether age-related resistance occurs under field conditions, and whether fungicide applications can be scheduled according to host growth stage on cultivars with age-related resistance.

Cucurbit fruit undergo numerous morphological and physiological changes as they mature. The onset of age-related resistance to Phytophthora fruit rot in multiple cucurbit species appears to occur when fruit reach maximum size (2,10). Large-fruited cucurbits reach maximum fruit size about 20 to 24 dpp, whereas small-fruited cucurbits reach full size about 15 to 20 dpp (18). In this study, <15% of Dickenson Field fruit 21 dpp or older became diseased. Cucumber fruit 14 dpp or older rarely became diseased in a similar study (10). Changes in nutrient content (15), cuticle thickness (7), and exocarp color and waxiness (2) have been associated with age-related resistance to *P. capsici* in various host fruit. In this study, soluble solids content was negatively correlated with lesion diameter and pathogen growth density. However, a significant correlation does not necessarily indicate a cause-and-effect relationship. Pathogen growth can be inhibited or enhanced by the sugar content of host tissues (14). The extracts of mature pepper fruit contained higher levels of sucrose and enhanced the growth of *P. capsici* (7). Thus, Phytophthora fruit rot may not be inhibited by increases in soluble solids content. Exocarp firmness also was negatively correlated with Phytophthora fruit rot development in this study. Thick cell walls can serve as a physical barrier to pathogen growth because they are more difficult for a fungus or oomycete pathogen to penetrate and colonize (1). Hard-rinded pumpkin (*C. pepo*) cultivars have recently been developed that are less susceptible to Phytophthora fruit rot (20). Incidence of Phytophthora fruit rot in field trials was 51% on 'HMX 5681' and 100% on 'Magic Lantern,' which are hard- and soft-rinded pumpkin cultivars, respectively (20). Unfortunately, exocarp firmness of these pumpkin cultivars was not determined. Breeding processing pumpkin and winter squash cultivars with the hard rind (*Hr*) gene could reduce the incidence of Phytophthora fruit rot in the field but it is unclear how this would affect the fruit's ability to be processed.

The effects of inoculum concentration, incubation period, and wounding on age-related resistance to Phytophthora fruit rot in processing pumpkin and winter squash are unknown. A similar inoculation method and a 4-day incubation period were used in this and previous experiments evaluating age-related resistance to Phytophthora fruit rot (2,10). Expression of age-related resistance to Phytophthora stem and foliar blight in pepper was affected by *P.*

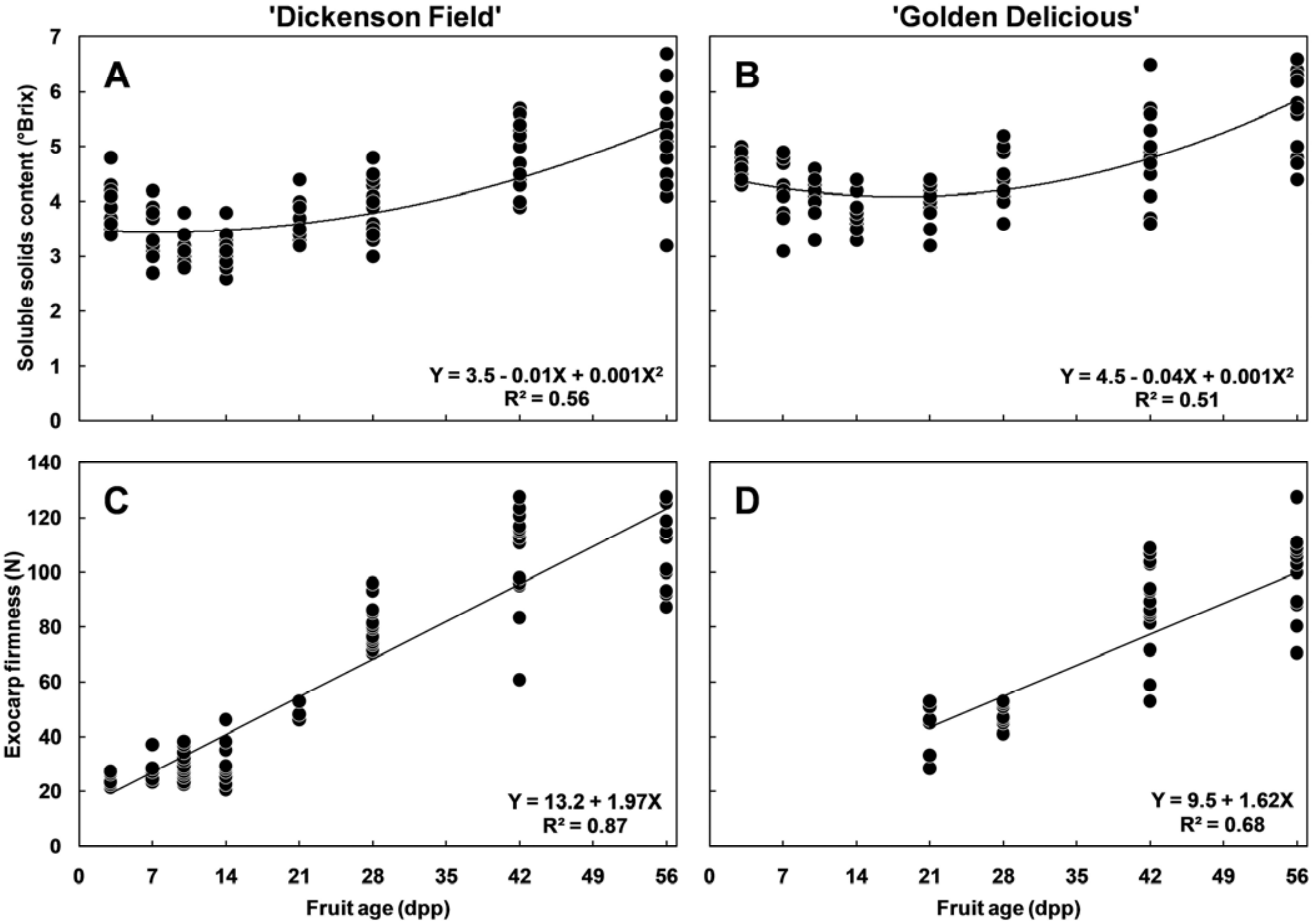

Fig. 6. A and **B,** Soluble solids content and **C** and **D,** exocarp firmness of healthy 'Dickenson Field' processing pumpkin and 'Golden Delicious' winter squash fruit regressed against fruit age. Soluble solids content was determined using a temperature-compensated refractometer. Exocarp firmness was determined using a handheld penetrometer, and is expressed as newtons (N) of force required to puncture the exocarp. Fruit age is expressed as days post pollination (dpp).

capsici zoospore concentration and inoculation method (16). Increasing *P. capsici* zoospore concentration resulted in greater levels of Phytophthora fruit rot on pickling cucumber fruit of similar age (11). Thus, increasing *P. capsici* inoculum concentration or using a different method of inoculation could affect age-related resistance to Phytophthora fruit rot in processing pumpkin and winter squash fruit. Similarly, wounding fruit could reduce age-related resistance, as has been demonstrated for cucumber (10,12). Additional studies are necessary to determine whether age-related resistance is overcome under high disease pressure associated with field conditions: for example, when fruit rest on *P. capsici*-infested soil for extended periods of time and when fields are flooded during heavy rainfall or irrigation events. Currently, management of Phytophthora fruit rot should include applications of fungicides with activity against *P. capsici* when conditions favor disease development in addition to ensuring that fields drain properly and are irrigated sparingly.

Acknowledgments

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