Using Cultural Practices and Cultivar Resistance to Manage Phytophthora Crown Rot on Summer Squash

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Abstract. The effects of bed height, mulches, composted poultry litter, and cultivars on Phytophthora crown rot, caused by Phytophthora capsici Leonian, of summer squash (Cucurbita pepo L.) were evaluated in the absence of fungicide applications. The experimental design was a split-split-split plot arrangement of a randomized complete block. Bed height (flat or raised) was the main plot treatment. Mulches (bark meal, wheat straw, or plastic) were sub-plot treatments. Composted poultry litter applications (0 or 4.5 t ha−1) were sub-sub-plot treatments. Squash cultivars (Cougar or Payroll) were sub-sub-plot treatments. Incidence of plant death (%) was assessed from 0 to 35 days post-inoculation (dpi) with P. capsici. Plant death 35 dpi and area under the disease progress curve (AUDPC) differed significantly (P < 0.0001) between the cultivars Cougar and Payroll. Mean plant death 35 dpi was 87% for ‘Payroll’ and 99% for ‘Cougar’. The bed height × cultivar interaction was also significant (P = 0.0018) in the analyses of variance for plant death and AUDPC. Plant death at 35 dpi and AUDPC for ‘Payroll’ were greater in flat beds than raised beds. Disease was unaffected by the main effects of bed height, mulch type, or application of poultry litter. Thirty-two summer squash cultivars and 10 germplasm accessions were also evaluated for resistance to Phytophthora crown rot in a separate greenhouse trial. Crown rot severity was rated on a 1 (no symptoms) to 5 (plant death) scale at 18 dpi. Crown rot severity differed significantly (P < 0.0001) among cultivars and germplasm accessions. Crown rot severity averaged 4.3 on commercial cultivars and 2.2 on germplasm accessions. Crown rot was least severe on the commercial cultivar Spineless Beauty (mean rating = 2.9). No disease developed on four accessions of Cucurbita moschata previously reported to be crown rot-resistant.

Phytophthora capsici Leonian is an economically important soilborne pathogen of summer squash (Cucurbita pepo L.) and other vegetable crops in many areas of the world (Babadoost, 2004, 2005; Babadoost and Zitter, 2009; Hausbeck and Lamour, 2004; Hung and Kim, 1995). Phytophthora capsici causes fruit, crown, and root rot as well as foliar blight (Babadoost, 2004, 2005; Babadoost and Zitter, 2009; Hausbeck and Lamour, 2004). Phytophthora crown rot is particularly severe because infections result in plant death and significant crop loss. Management of Phytophthora crown rot requires an integrated approach (Babadoost, 2005; Hausbeck and Lamour, 2004; Hung and Kim, 1995; Ristaino and Johnston, 1999). Cultural management practices, including growing resistant cultivars, have been used to successfully manage other diseases caused by Phytophthora species including root rot of red raspberry (Rubus idaeus L.) caused by P. fragariae var. rubi (Wilcox et al., 1999), root rot of papaya (Carica papaya L.) caused by P. palmivora (Vavdrey et al., 2004), and leather rot of strawberry (Fragaria ×"ananaschema Duchesne) caused by P. cactorum (Madden and Ellis, 1990).

Host resistance is generally considered the most efficient means of controlling plant diseases. Resistance to P. capsici has been identified in pepper (Capsicum annuum L.) (Barksdale et al., 1984; Kimble and Grogan, 1960), and cultivars with resistance to Phytophthora crown rot are available. Unfortunately, few studies have screened unadapted cucurbit (Cucurbita spp.) germplasm for resistance to Phytophthora crown rot are available. Unfortunately, few studies have screened unadapted cucurbit (Cucurbita spp.) germplasm for resistance to Phytophthora crown rot are available. Unfortunately, few studies have screened unadapted cucurbit (Cucurbita spp.) germplasm for resistance to Phytophthora crown rot. At least one C. pepo and five C. moschata germplasm accesses with resistance to Phytophthora crown rot were recently identified using P. capsici isolates from Florida (Chavez et al., 2011; Padley et al., 2008). At least one C. pepo and five C. moschata germplasm accesses with resistance to Phytophthora crown rot were recently identified using P. capsici isolates from Florida (Chavez et al., 2011; Padley et al., 2008). Resistance to multiple P. capsici isolates was also identified in the Korean pumpkin cultivar Danmatmaedol (C. maxima) (Lee et al., 2001). Resistance to P. capsici from the wild species Cucurbita lundelliana was introgressed into 19 winter squash breeding lines (Kabelka et al., 2007). An inheritance study indicated that resistance to Phytophthora crown rot derived from C. lundelliana and C. okeechobensis subsp. okeechobensis is conferred by three dominant genes (Padley et al., 2009). Resistance to P. capsici has not been incorporated into commercial breeding lines, and all cucurbit cultivars are considered susceptible to Phytophthora crown rot (Babadoost, 2004, 2005; Hausbeck and Lamour, 2004). However, cultivars may differ slightly in their reactions to P. capsici, and growing less susceptible cultivars in combination with other cultural management practices could be used to improve management of Phytophthora crown rot.

Cultural management practices that reduce soil saturation or prevent splash dispersal of P. capsici propagules can affect Phytophthora crown rot development. Growing plants on raised beds improves water drainage, thereby limiting the conditions favorable for disease development. Phytophthora blight incidence on pepper was 18% in flat beds and 5% in beds raised 45 cm (Hung and Kim, 1995). Similarly, plant death of zucchini in a field naturally infested with P. capsici was greater in flat beds than raised beds (Hausbeck and Lamour, 2004). Covering planting beds with plastic mulch can reduce splash dispersal of P. capsici from the soil to susceptible plant tissues (Ristaino et al., 1997). However, in some cases, plastic mulches increased the spread of Phytophthora blight within a row because P. capsici propagules are readily dispersed in water on the surface of plastic mulches (Ristaino et al., 1997; Springer and Johnston, 1982). Organic mulches have also been effective at reducing splash dispersal of P. capsici. Chopped wheat straw dispersed between planting rows reduced the spread of Phytophthora blight on pepper (Ristaino et al., 1997). Altering cultural practices may not affect Phytophthora blight development on vining crops like watermelon, which grow off of raised beds and come in contact with the soil between rows (Kousik et al., 2011). Similarly, the costs associated with raised bed, plasticulture may not be feasible in crops grown for processing because crop values are lower.

Application of organic soil amendments such as composted animal manures has been used to suppress diseases caused by various soilborne pathogens including P. capsici (Zinat, 2005). Compost water extracts from livestock manures inhibited zoospore germination, germ tube formation, and mycelial growth of P. capsici (Sang et al., 2010). In a separate study, manure application reduced the viability of P. capsici oospores (Núñez-Zofiò et al., 2011). Applications of compost water extracts increased the expression of numerous pathogenesis-related genes in pepper plants and reduced disease caused by P. capsici (Sang et al., 2010). Amending potting mix with composted sewage sludge reduced the incidence of Phytophthora crown rot on pepper by 42% in a greenhouse trial.
(Lumsden et al., 1983). Application of semi-composted horse and poultry manure followed by plastic mulching increased soil microbial activity and reduced the incidence of Phytophthora crown and root rot on pepper in Spain (Nuñez-Zoﬁo et al., 2011).

Combining cultural management practices, including planting cultivars with resistance to P. capsici, could be used to improve the management of Phytophthora crown rot on summer squash. Few large-scale field trials have evaluated the integrated use of multiple cultural practices to manage Phytophthora crown rot of summer squash. The objective of this field study was to evaluate the effects of bed height, mulches, composted poultry litter, and cultivars on Phytophthora crown rot of summer squash in the absence of fungi-cides. Thirty-two summer squash cultivars and 10 germplasm accessions were also evaluated for their reaction to Phytophthora crown rot in a separate greenhouse study.

Materials and Methods

Inoculum preparation. Phytophthora capsici isolate 12889 (mating type A1) obtained from the culture collection of M.K. Hausbeck at Michigan State University was used to inoculate plants in this study. Phytophthora capsici isolate 12889 was originally collected from bell pepper and is insensitive to mefenoxam. Cultures were grown on unclarified V8 juice agar (UCV8) at room temperature (21 ± 2 °C) under constant fluorescent light. Phytophthora capsici-infested millet seed was produced as described by Quesada-Ocampo et al. (2009).

Field evaluation. Two separate field experiments were conducted at the Michigan State University Southwest Michigan Research and Extension Center in Benton Harbor. The previous crop was yellow straightneck summer squash (C. pepo L.). The soil type was Spinks Hapludalfs. The experimental design was a split-split-split plot arrangement of a randomized complete block with four replicates. Bed height, mulches, composted poultry litter, and cultivars were randomized within sub-sub-plots. These cultivars were selected based on previous studies of Phytophthora crown rot resistance (Chavez et al., 2011; Padley et al., 2008). Trials were conducted in May and June 2011 at the Michigan State University Horticulture Research and Teaching Center in Holt. The experimental design was completely randomized with eight replicates. An experimental unit was one plant grown in a 10-cm-diameter pot containing soilless potting mix (BACCTO High Porosity Professional Potting Mix; Michigan Peat Co., Houston, TX). Plants were inoculated with 1 g of P. capsici-infested millet seeds as previously described for field trials. Disease severity was assessed at 18 dpi. Each plant was visually assessed using a 1 to 5 scale, where 1 = no symptoms; 2 = lower leaves wilted with slight constriction of the stem; 3 = all leaves wilted with constriction and slight discoloration of the stem; 4 = all leaves wilted and crown rotted with visible sporulation on the stem surface; and 5 = plant dead.

Pathogen confirmation. Approximately 5% of symptomatic plants in field and greenhouse trials were sampled for pathogen confirmation. Symptomatic plants were arbitrarily selected and sheared at the soil line with hand pruners. Crown sections were surface-disinfested with a 70% ethanol solution and blotted dry with paper toweling. Four pieces of tissue were excised from each crown and plated on UCV8 amended with 25 ppm of benomyl, 100 ppm of ampicillin, 30 ppm of rifampicin, and 100 ppm of pentachloronitrobenzene. Colonies were identified as P. capsici using morphological characteristics and a key developed by Waterhouse (1963). Mating type and sensitivity to mefenoxam were also determined for each isolate and compared with the phenotype of isolate 12889.
Statistical analysis. All analyses were done using SAS, Version 9.2 (SAS Institute, Cary, NC). For field trials, final incidence of plant death 35 dpi and AUDPC were analyzed separately by analysis of variance (ANOVA) in the Proc Mixed procedure. Trials and blocks were considered random variables. Bed height, mulch type, poultry litter applications, and cultivars were considered fixed variables. For greenhouse trials, final crown rot severity ratings 18 dpi were analyzed by ANOVA using the Proc Mixed procedure. Cultivars were considered fixed variables. All effects were declared significant at P<0.01 unless otherwise stated. Slice statements were used to test simple main effects when two-way interactions were significant. Residuals were tested for normality using the Shapiro-Wilk statistic in the Proc Univariate procedure. Residuals were plotted against predicted values using the Proc Gplot procedure to assess homogeneity of error variance.

Results

Field evaluation. Plants were highly susceptible to P. capsici at all growth stages from expansion of the first true-leaf stage to full maturity. Plants with Phytophthora crown and root rot rapidly wilted and died (Fig. 1A). Crown rot symptoms were also observed in the absence of root rot. The primary growing point of plants with crown rot only was killed but lower leaves remained green and turgid (Fig. 1B). All plants with Phytophthora crown and root rot symptoms eventually died. Phytophthora capsici with the same phenotype as isolate 12889 was consistently isolated from symptomatic plants.

No combination of cultural practices adequately controlled Phytophthora crown rot. Incidence of plant death caused by P. capsici approached 100% in all plots (Fig. 2). Plant death 35 dpi and AUDPC differed significantly (P<0.0001) among cultivars (Table 1). Disease was unaffected by bed height, mulches, or poultry litter applications. Plant death 35 dpi was 87% for ‘Payroll’ and 99% for ‘Cougar’ averaged across all other treatments (Table 2). The bed × cultivar interaction term also was significant (P = 0.0018) in the ANOVAs for plant death and AUDPC (Table 1). Complete death of ‘Cougar’ occurred regardless of bed height (Table 2). Plant death of ‘Payroll’ was greater in flat beds than in

Fig. 2. Plant death of summer squash cultivars Cougar and Payroll after inoculation with Phytophthora capsici. Plants were grown in flat or raised beds covered with no mulch (Bare), 8 cm of wheat straw (Straw), or black plastic (Plastic). Composted poultry litter was applied at a rate of 0 or 4.5 t·ha⁻¹ before mulch application.

Table 1. Mean squares for treatment sources of variation from analyses of variance of plant death incidence 35 d post-inoculation (dpi) and area under the disease progress curve (AUDPC) in field trials evaluating the effects of bed height, mulches, composted poultry litter, and cultivars on Phytophthora crown rot of summer squash.

| Source of variation | df | Plant death (%) 35 dpi | AUDPC² |
|---------------------|----|------------------------|--------|
| Bed¹                 | 1  | 954                    | 706,645|
| Mulch²               | 2  | 59                     | 201,433|
| Mulch × bed          | 2  | 396                    | 470,689|
| Litter³              | 1  | 9                      | 310,498|
| Litter × bed         | 2  | 101                    | 155,682|
| Litter × mulch       | 2  | 25                     | 64,856 |
| Cultivar⁴            | 1  | 7,154***               | 21,404,059*** |
| Cultivar × bed       | 1  | 1,045**                | 786,944** |
| Cultivar × mulch     | 2  | 15                     | 2,320  |
| Cultivar × mulch × bed | 2  | 320                    | 439,519|
| Cultivar × litter    | 1  | 2                      | 3,614  |
| Cultivar × litter × bed | 2  | 80                     | 92,796 |
| Cultivar × litter × mulch | 2  | 80                     | 89,820 |
| Cultivar × litter × mulch × bed | 2  | 20                    | 7,500  |
| Coefficient of variation (%) — 13 | 27 |

¹Corresponding mean square is statistically significant at ***P ≤ 0.01 or ****P ≤ 0.001.
²AUDPC was calculated for plant death incidence assessed at 7-d intervals from 0 to 35 dpi.
³Bed height (flat or raised) was the main plot treatment.
⁴Mulches (none, wheat straw, or black plastic) were the subplot treatment.
⁵Composted poultry litter application was the sub-subplot treatment.
⁶Squash cultivar (Cougar or Payroll) was the sub-sub-subplot treatment.
raised beds (Table 2). Yield data were not analyzed because almost all plants in both trials died before bearing fruit.

**Greenhouse evaluation of cultivars and germplasm accessions.** Disease symptoms began to develop by 7 dpi with *P. capsici*

Table 2. Effects of bed height and cultivar on incidence of plant death 35 d post-inoculation (dpi) with *Phytophthora capsici* and area under the disease progress curve (AUDPC) averaged over mulches and poultry litter applications.

| Bed h² | Plant death (%) 35 dpi | AUDPCw½ |
|--------|------------------------|----------|
| Flat   | 99 a                   | 92 a     | 2299 a 1760 a |
| Raised | 100 a                  | 83 b     | 2306 a 1510 b |
| Mean   | 99 87                  | 87 83    | 2303 1635     |

AUDPC was calculated for plant death incidence assessed at 7-d intervals from 0 to 35 dpi.

**Discussion**

No combination of cultural practices adequately controlled *Phytophthora* crown rot in this study. Differences in cultivar susceptibility to *P. capsici* accounted for the most variation in disease levels in the field. In a similar study, red raspberry cultivars had the greatest effect on *Phytophthora* root rot levels in field trials evaluating multiple disease management practices (Wilcox et al., 1999). Results of this study demonstrate the importance of breeding summer squash cultivars with resistance to *Phytophthora* crown rot and the difficulty of managing this disease without fungicides. Cucurbit growers could integrate the use of resistant cultivars and fungicide applications to improve control of *Phytophthora* crown rot, which has been effective for managing this disease on pepper (Foster and Hausbeck, 2010b; Hwang and Kim, 1995). Although raised bed and mulch treatments did not significantly affect disease development in this study, growers should continue to use these practices in fields naturally infested with *P. capsici* because they improve soil drainage (Hausbeck and Lamour, 2004; Hwang and Kim, 1995; Ristaino and Johnston, 1999), reduce splash dispersal of soilborne inoculum (Ristaino et al., 1997), and improve yield (Bhella and Kwolek, 1984).

Resistance to *P. capsici* is necessary for the successful long-term management of *Phytophthora* crown rot of summer squash. Potential sources of resistance to *P. capsici* have recently been identified in certain *Cucurbita* germplasm accessions (Chavez et al., 2011; Padley et al., 2008). Stem lesions developed after inoculation with *P. capsici* isolate 12889. Disease severity ratings were correlated ($r = 0.73, P < 0.0001$) among trials, and data were pooled before analysis. Crown rot severity differed significantly ($P < 0.0001$) among squash cultivars and germplasm accessions. None of the cultivars were completely resistant to *Phytophthora* crown rot. Crown rot was most severe on the cultivar Cougar (mean rating = 4.9), which is known to be highly susceptible to *P. capsici* (Table 3). Crown rot was least severe on the cultivar Spineless Beauty (mean rating = 2.9) (Table 3). Mean crown rot severity was 2.2 on germplasm accessions of *C. pepo* and *C. moschata* (Table 4). Crown rot severity ratings ranged from 2.9 to 3.8 among *C. pepo* accessions (Table 4). Most plants of *C. pepo* accessions had necrotic stem lesions, but leaves generally remained un wilted. No disease symptoms (rating = 1.0) developed on four *C. moschata* accessions previously reported to be resistant to *Phytophthora* crown rot (Table 4). *Phytophthora capsici* was not isolated from the crown sections of *C. moschata* plants.

| Cultivar          | Fruit type | Fruit color | Seed source | Crown rot severity 18 dpiw½ |
|-------------------|------------|-------------|-------------|-----------------------------|
| Cougar            | stra       | Y           | HM          | 4.9                         |
| Spineless Beauty  | stra       | G           | Rog         | 4.9                         |
| Golden Rod        | zuc        | Y           | HM          | 4.9                         |
| Payroll           | zuc        | G           | Rog         | 4.8                         |
| Golden Dawn III   | zuc        | Y           | Rog         | 4.8                         |
| Zucchini Elite    | zuc        | G           | HM          | 4.7                         |
| Fortune           | stra       | Y           | Rog         | 4.6                         |
| Multikap          | stra       | Y           | HM          | 4.6                         |
| Sunray            | stra       | Y           | Sem         | 4.6                         |
| Superkiss         | stra       | Y           | HM          | 4.6                         |
| Felix             | zuc        | G           | HM          | 4.6                         |
| Noche             | zuc        | G           | Rog         | 4.6                         |
| Golden Glory      | zuc        | Y           | Rog         | 4.6                         |
| Golden Delight    | zuc        | Y           | Rog         | 4.6                         |
| Cheetah           | stra       | Y           | Har         | 4.5                         |
| Paycheck          | zuc        | G           | Rog         | 4.5                         |
| Supersett         | croo       | Y           | HM          | 4.4                         |
| Radiant           | zuc        | G           | Sem         | 4.4                         |
| Tigress           | zuc        | G           | HM          | 4.4                         |
| Zucchini Select   | zuc        | G           | HM          | 4.4                         |
| Senator           | zuc        | G           | Sem         | 4.4                         |
| Jaguar            | zuc        | G           | Har         | 4.3                         |
| Ishihar           | mar        | G           | Sto         | 4.3                         |
| Lioness           | stra       | Y           | HM          | 4.2                         |
| Bobcat            | zuc        | G           | HM          | 4.2                         |
| Leopard           | zuc        | G           | HM          | 4.2                         |
| Gold Rush         | zuc        | Y           | Sem         | 4.0                         |
| Reward            | zuc        | G           | HM          | 3.6                         |
| Cashflow          | zuc        | G           | Rog         | 3.5                         |
| Black Beauty      | zuc        | G           | Sto         | 3.1                         |
| Clarita           | mar        | G           | Sto         | 3.1                         |
| Spineless Beauty  | zuc        | G           | Rog         | 2.9                         |
| Mean              | —          | —           | —           | 4.3                         |
| Standard deviation| —          | —           | —           | 0.53                        |
| FLSD* α = 0.05    | —          | —           | —           | 0.99                        |

Species and accession Origin Crown rot severity 18 dpiw½

| Cucurbita pepo | PI 209783 | Germany | 3.8    |
| C. pepo | PI 271209 | Spain | 3.7    |
| Cucurbita moschata | PI 615132 | Mexico | 3.2    |
| C. moschata | PI 169417 | Turkey | 3.0    |
| C. pepo | PI 181761 | Lebanon | 2.1    |
| C. moschata | PI 615142 | Kazakhstan | 1.9    |
| Cucurbita pepo | PI 442262 | Mexico | 1.0    |
| C. moschata | PI 458740 | Paraguay | 1.0    |
| Cucurbita pepo | PI 442266 | Mexico | 1.0    |
| C. moschata | PI 634693 | India | 1.0    |

Mean — 2.2  sd — 1.2  FLSD* α = 0.05 — 1.1

* Crown rot severity was rated 18 d post-inoculation (dpi) on a 1 to 5 scale, where 1 = no symptoms; 2 = lower leaves wilted with slight constriction of the stem; 3 = all leaves wilted with constriction and slight discoloration of the stem; 4 = all leaves wilted and crown rotted with visible sporulation on the stem surface; and 5 = plant dead. Values are the mean of two trials.

*FLSD = Fisher’s protected least significant difference.
on the six C. pepo accessions evaluated in this study. However, plants did not exhibit characteristic wilting symptoms. No symptoms developed after inoculation with P. capsici on four C. moschata (PI 442262, PI 458740, PI 442266, and PI 634693) accessions, which appear to possess high levels of Phytophthora crown rot resistance. Chavez et al. (2011) previously reported these accessions as potential sources of resistance to Phytophthora crown rot after inoculation with P. capsici isolates from Florida. Disease reactions can differ after inoculation with P. capsici isolates from different hosts as a result of physiological specialization (Lee et al., 2001; Ristaino, 1990). Plants in this study were inoculated with a single isolate of P. capsici originally recovered from pepper in Michigan. The accessions evaluated in this study could have different reactions to other isolates of P. capsici. Nevertheless, P. capsici isolate 12889 is highly virulent on multiple plant species and has been used in previous studies evaluating resistance to P. capsici in squash (Enzenbacher, 2011), pepper (Foster and Hausbeck, 2010a), tomato (Solanum lycopersicum L.) (Quesada-Ocampo and Hausbeck, 2010), and Fraser fir (Abies fraseri Pursh) (Quesada-Ocampo et al., 2009). Additional studies are necessary to identify additional sources of P. capsici resistance in multiple Cucurbita species under greenhouse and field conditions.

Commercial summer squash cultivars differed in their reactions to Phytophthora crown rot. The cultivars Cougar (yellow straightneck) and Spineless Beauty (green zucchini) were the most and least susceptible to P. capsici, respectively. Similar results were observed in a field evaluation of summer and winter squash cultivars in New York (Camp et al., 2009). Evaluating cultivar reactions to Phytophthora crown rot in the greenhouse required less labor and space than field evaluations, which could be a limiting factor when evaluating large, vining cucurbits. Although no squash cultivars had complete resistance to P. capsici, cucumber growers could use this information to select cultivars that are less susceptible to Phytophthora crown rot. Until resistant summer squash cultivars are available, growers should continue to combine fungicide applications and cultural practices to manage this disease.

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