Field Response of Cucurbit Hosts to *Pseudoperonospora cubensis* in Michigan

M. C. Cespedes-Sanchez, Former Graduate Research Assistant, and R. P. Naegele, Research Associate, Department of Plant, Soil and Microbial Sciences, Michigan State University, East Lansing 48824; C. S. Kousik, Researcher, United States Department of Agriculture–Agricultural Research Service, U.S. Vegetable Laboratory, Charleston, SC 29414; and M. K. Hausbeck, Professor, Department of Plant, Soil and Microbial Sciences, Michigan State University

Abstract

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Downy mildew, caused by *Pseudoperonospora cubensis*, is a severe foliar disease of many cucurbit crops worldwide. Forty-one cucurbit cultigens (commercial cultivars and plant introductions) from five genera (*Cucumis*, *Citrullus*, *Cucurbita*, *Lagenaria*, and *Luffa*) were assessed for susceptibility to *P. cubensis* in a research field exposed to natural inoculum in Michigan. Eight cultigens from a differential set for pathotype determination were included within the 41 cultigens to detect changes in dominant *P. cubensis* pathotypes present. No pathotype differences were found between 2010 and 2011. *Cucumis melo* cultigen MR-1 was less susceptible to Michigan *P. cubensis* populations than other *C. melo* cultigens. No symptoms or signs of infection were detected on cultigens of *Cucurbita moschata* and *C. pepo*. Disease onset was later in 2011 than 2010; greater than 90% disease severity in pickling cucumber ‘Vlaspi’

was observed in both years. This study confirmed that *Cucumis* is the most susceptible cucurbit genus, while *Citrullus* and *Cucurbita* cultigens were the least susceptible genera to populations of *P. cubensis* in Michigan. Area under the disease progress curve values indicated that disease progress was limited on all *Citrullus* cultigens compared with *Cucumis* cultigens, and pathogen sporulation was not detected under field conditions. Future studies should evaluate the ability of a reduced fungicide program to control downy mildew on less susceptible *Cucumis melo* ‘Edisto 47’, ‘Primo’, ‘Athena’, ‘Strike’, ‘Ananas’, ‘Banana’, and ‘Tam-Dew’. Many of the melon cultivars evaluated were selected on the basis of reported resistance to downy mildew, yet they showed significant disease symptoms. It is important to evaluate candidate cultigens for resistance to local *P. cubensis* populations.

Downy mildew, caused by the oomycete *Pseudoperonospora cubensis* (Berk. & M. A. Curtis) Rostovzev, is one of the most serious foliar diseases of cucurbits (14). Although this pathogen is found in many cucurbit production areas, *P. cubensis* thrives in areas where elevated humidity and warm growing conditions favor its growth, reproduction, and ability to infect (4,12,26). Due to the biotrophic nature of *P. cubensis*, the disease is thought to reestablish annually in temperate regions when sporangia are wind dispersed from year-round cucurbit-growing sites in subtropical regions or greenhouses (17,18). In the eastern United States, inocula likely arrive from fields located in Florida or Mexico (10,17). Michigan is the number one producer of pickling cucumber in the United States and it is possible that primary inocula could also come from cucumber production greenhouses in surrounding areas (21).

Cultivated, semicultivated, and wild Cucurbitaceae genera are affected by *P. cubensis* under field conditions (10,19,22). Species within approximately 20 genera have been reported as hosts of *P. cubensis*; however, *Cucumis*, *Cucurbita*, and *Citrullus* are the most economically important genera affected by cucurbit downy mildew (14). Disease symptoms vary depending on the cucurbit host (Fig. 1). In cucumber (*Cucumis sativus* L.), squash (*Cucurbita pepo* L. or *C. moschata* Duchesne ex Poir.), and loofah (*Luffa* spp.), the symptoms on the upper side (adaxial) of the leaf include irregular, pale-yellow lesions restricted by leaf veins that become necrotic over time; in cantaloupe (*Cucumis melo* L.) and watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai), lesions are not limited by the leaf veins and are more circular (28). Although *P. cubensis* is confined to the leaves, the resulting defoliation results in low productivity and poor fruit quality in each species (20).

During the late 1960s, a completely resistant cucumber cultivar, ‘Poinsett’, was released in the United States, and fungicides were

not required to control downy mildew until 2004, when *P. cubensis* reemerged in North Carolina (7). Subsequent losses were reported in other states in the eastern United States the following year (7). In Michigan, the first report of *P. cubensis* overcoming host resistance in cucumber occurred in 2005; since then, cucurbit downy mildew has been reported annually on cucumber and other economically important cucurbit crops such as squash and melon (6). The resurgence of *P. cubensis* in Europe and in the United States has been attributed to the appearance of a more aggressive pathotype in *P. cubensis* populations (5,7). The initial set of differentials proposed by Thomas et al. (24) in 1987 for pathotype determination was expanded in 2003 by Lebeda and Widrechner (15). This new system includes 12 differentials that belong to six Cucurbitaceae genera (*Cucumis*, *Cucurbita*, *Citrullus*, *Benincasa*, *Luffa*, and *Lagenaria*) to characterize variability in virulence and pathogenicity of *P. cubensis*.

Downy mildew-resistant commercial cultivars are limited, and disease management relies heavily on the use of fungicides. In Michigan alone, cucurbit growers spend about U.S. \$8 million annually on fungicides to manage downy mildew, and fungicide-resistant isolates are becoming common. This value does not take into account related expenses associated with disease management such as labor and equipment costs (6). Hence, genetic resistance is of paramount importance for economically viable disease management. Due to reported differences in the genetic structure of the pathogen populations within and among countries (21), cultigen (cultivars and plant introductions [PIs]) screening on a regional level for downy mildew resistance is imperative. The objectives of this study were to determine the disease response of 41 cultigens to *P. cubensis* populations naturally present in Michigan between 2010 and 2011, and identify changes in pathogen pathotypes between the 2 years.

Materials and Methods

Cucurbit cultigens. Forty-one cultigens (PIs and commercial cultivars) belonging to the genera *Cucumis*, *Citrullus*, *Cucurbita*, *Lagenaria*, and *Luffa* were evaluated for disease response to natural populations of *P. cubensis* in Michigan (Table 1). This set of cultigens included 24 commercial melon and cantaloupe cultivars (Table 1). Of the 24 melon cultivars, 10 were marketed as having

Corresponding author: M. K. Hausbeck; E-mail: hausbec1@msu.edu

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some resistance to downy mildew. ‘Hale’s Best Jumbo’ melon was included as a downy-mildew-susceptible melon check. Pls, watermelon, and different gourds were provided by the U.S. plant germplasm collection at the Plant Genetic Resources Conservation Unit at Griffin, GA (www.ars-grin.gov) (Table 1). These Pls either belonged to the differential set of taxa for *P. cubensis* pathotype determination or had not been screened for downy mildew resistance previously (Table 1). The pickling cucumber ‘Vlaspik’, which is highly susceptible to downy mildew, was included as a susceptible control.

Field trials. Field experiments were conducted at the Plant Pathology Research Farm (Michigan State University, East Lansing at 42° 41’ 32” N, 84° 29’ 13” W). All 41 cultigens were planted in a sandy loam soil (54.2% sand, 35% silt, and 10.8% clay) late in the season (13 July 2010 and 2011), after *P. cubensis* was reported in the area. Additionally, pickling cucumber ‘Vlaspik’ was planted along the edge of the plot as a buffer and susceptible downy mildew host. Rows were sprayed with Roundup Ultra (active ingredient [a.i.] glyphosate; Monsanto Company, St. Louis) at 5.85 liter/ha 2 months prior to planting as weed management; thereafter, the plots were hand weeded. Quintec (a.i. quinoxifen; Dow AgroSciences, Indianapolis, IN) was applied at 438.5 ml/ha three times during the cropping season for powdery mildew control, and Asana XL (a.i. esfenvalerate; Dupont, Wilmington, DE) was applied at 658 ml/ha once for cucumber beetle (*Acalymma vittatum*) control. All applications were made using a backpack air blast sprayer. A 20:20:20 (N-P-K) fertilizer was injected through the drip irrigation system on a weekly basis at 5.6 kg/ha. Plants were drip irrigated twice each week for a total of 6 h per week. To promote infection, overhead irrigation was used 44 days after planting in addition to the standard irrigation schedule during two consecutive weeks in 2010. In 2010, all cultigens were directly sown and thinned to five plants per cultigen per block whereas, in 2011, 3-week-old seedlings of each cultigen were transplanted into the soil at the same plant density as in 2010. All the cultigens were planted into raised beds covered with black polyethylene mulch and spaced 2.4 m apart on center. Spacing between plants was 32 cm. The experiment was set up as a randomized complete block design with four replicates.

Disease assessment. Plants were scouted twice a week to determine the first appearance of symptoms. Data were recorded once per week

for a total of seven measurements, starting at the first date on which symptoms were observed in 2010. One affected leaf per plant per rating day was detached, independently bagged, and brought to the laboratory for *P. cubensis* identification. Symptomatic leaves without obvious pathogen sporulation were placed in a moisture chamber for 3 days to promote sporulation. *P. cubensis* was morphologically identified based on spore dimensions and sporangiophore branching (27). Disease severity (percentage of the total necrotic and chlorotic leaf area of fully expanded leaves) was visually assessed from all plants of each cultivar in each block (20 plants total per cultivar) weekly. Disease severity data were used to calculate the area under the disease progress curve (AUDPC), as described by Campbell and Madden (3).

The level of sporulation was rated for each leaf as 0 or 1, where 0 = no sporulation and 1 = sporulation present. Sporulation ratings were included as an indicator of pathogenicity and disease, consistent with Lebeda et al. (15). Final disease ratings for the selected cultigens in host range determination were considered as compatible interactions if chlorosis, necrosis, or sporulation was observed. Final percentage disease ratings were transformed into a 0-to-9 ordinal scale, where 0 = no symptoms; 1 = 1 to 8, 2 = 9 to 14, 3 = 15 to 25, 4 = 26 to 40, 5 = 41 to 60, 6 = 61 to 75, 7 = 76 to 88, and 8 = 89 to 99% symptomatic; and 9 = dead plant for comparisons with disease data on the same cultigens collected independently in South Carolina. Ordinal data were analyzed as repeated measures data with nonparametric analysis, as described by Shah and Madden (23) and Brunner et al. (2). Analyses of ordinal data were performed in SAS (v. 9.2; SAS Institute, Cary, NC) using the F1_LD_F1 macro to determine the effect cultigen, time, and their interaction on disease severity, and testing pairwise comparisons of the relative treatment effects (RTEs) within factors (1). Rank means, RTEs, and confidence intervals were estimated using the LD_CI macro implemented in SAS. Data were analyzed independently for each year because significant differences were detected between the 2 years. The means procedure (PROC MEANS) of SAS was used to calculate final rating means per cultivar and genus for each year. Severity was calculated within and between years using analysis of variance on final percentage or AUDPC values using PROC MIXED of SAS. In the final model, genus or line

Fig. 1. Symptoms and signs of cucurbit downy mildew on **A–C**, cucumber and **D–F**, cantaloupe hosts with close-ups of lesions on the abaxial (**B** and **E**) and adaxial (**C** and **F**) sides of the leaf.

was included as a main effect. Unequal variances were assessed using Levene's Test and, when necessary, grouped using the repeated group statement of SAS. Denominator degrees of freedom were calculated using the Kenward-Rogers approximation. Mean separation was conducted for species level using the Fisher's protected least significant difference test and at the genus level was adjusted using Tukey's honestly significant difference ($P \leq 0.05$).

Results

Disease response. In 2010 and 2011, *P. cubensis* was first detected and confirmed on pickling cucumber 'Vlaspik'. 'Vlaspik' exhibited small, pale yellow (Fig. 1A), water-soaked lesions on the

abaxial leaf surface 28 and 42 days after planting in 2010 and 2011, respectively. Significant differences in disease severity between years were found. Disease pressure was high (final ratings >90% on the susceptible control 'Vlaspik') in both years (Table 2). 'Vlaspik' had the highest AUDPC values (3,207 and 2,173 in 2010 and 2011, respectively; Table 2). Final disease severity values were higher in 2011 than 2010 for most *Cucumis melo* cultigens; lower values were observed in 2011 for select *Citrullus lanatus* cultigens compared with 2010 (Table 2). In 2010 and 2011, *Cucumis* accessions were significantly more susceptible than *Lagenaria*, *Citrullus*, *Luffa*, or *Cucurbit* accessions (Table 3). *Cucurbit* spp. had the lowest disease severity of cucurbit downy mildew in 2010 and 2011.

Table 1. Cucurbit cultigens assessed for field resistance to natural populations of *Pseudoperonospora cubensis*

Cultigen	Origin	Seed source ^w	Resistance ^x	Alternate ID	Maturity ^y
<i>Cucumis sativus</i>					
Vlaspik ^z	United States	Seminis	Susceptible	...	50
<i>C. melo</i>					
Hale's Best Jumbo	United States	Willhite	Susceptible	...	85
Crete	United States	Stokes Seed	Resistant	...	88
Atlantis	United States	Siegers Seed	Unknown	...	80–85
Ambrosia Hybrid	United States	Siegers Seed	Unknown	...	86
Planters Jumbo	United States	Willhite	Resistant	...	89
Topmark ^z	United States	Everwilde	...	...	80–90
Grand Slam	United States	Siegers Seed	Unknown	...	85
Python	United States	NE Seed	Resistant	...	80–85
Toscana	United States	NE Seed	Resistant	...	77–82
Mainstream	United States	Willhite	Resistant	-	90
Aphrodite	United States	Siegers Seed	Unknown	...	72
Tekos	United States	Willhite	Resistant	...	75–80
Minerva	United States	Siegers Seed	Unknown	...	78
Sun Jewel	United States	Johnny's	Resistant	...	68
Odyssey	United States	Siegers Seed	Unknown	...	80
Melon Gold Bar	United States	Park Seed	Tolerant	...	68
Tam-Dew	United States	Willhite	Resistant	...	100
Banana	United States	Willhite	Unknown	...	90
Ananas	United States	Willhite	Unknown	...	110
Strike	United States	Siegers Seed	Unknown	...	85
Athena	United States	Siegers Seed	Unknown	...	75
Primo	United States	Stokes Seed	Tolerant	...	79
Edisto 47	United States	USDA ARS	Resistant	...	86
MR-1	India	USDA ARS	Resistant	...	...
<i>Lagenaria siceraria</i>					
PI 642042 ^z	United States	USDA GRIN	...	Snake	...
<i>Citrullus lanatus</i> var. <i>lanatus</i>					
PI 169290	Turkey	USDA GRIN	Unknown	Kurbagi Alacasi	...
PI 490378	Mali	USDA GRIN	Unknown	Egusi	...
PI 629106	United States	USDA GRIN	Unknown	Florida Favorite	...
PI 438676	Mexico	USDA GRIN	Unknown	Charleston Gray	87
PI 171584 ^z	Turkey	USDA GRIN	...	...	...
PI 612145	United States	USDA GRIN	Unknown	Dixie Queen	80
PI 595218	United States	USDA GRIN	Unknown	Charleston 76	...
PI 171392	Africa	USDA GRIN	Unknown	Tsamma	...
<i>Luffa aegyptiaca</i>					
PI 527331 ^z	China	USDA GRIN	...	Rou Si Gua	...
<i>Cucurbita moschata</i>					
PI 169410	Turkey	USDA GRIN	Unknown	...	...
PI 358507	United States	USDA GRIN	Unknown	Golden Cushaw	...
<i>C. pepo</i>					
PI 171622 ^z	Turkey	USDA GRIN	...	Dolmalik	...
PI 508468	S. Korea	USDA GRIN	Unknown	Golden Zucchini	...
<i>C. pepo</i> subsp. <i>fraterna</i>					
PI 532355 ^z	Mexico	USDA GRIN	...	...	...
<i>C. pepo</i> var. <i>texana</i>					
PI 614687 ^z	United States	USDA GRIN	...	...	...

^w USDA = United States Department of Agriculture, ARS = Agricultural Research Service, and GRIN = Germplasm Resources Information Network.

^x Resistance to downy mildew caused by the pathogen *Pseudoperonospora cubensis* as reported by seed company.

^y Days to maturity as reported by the seed company.

^z Subset of cultigens used for the determination of host range and pathogenic variability between 2010 and 2011.

Pathotype assessment. The eight cultigens representing the six genera used for pathotype differentiation were evaluated for signs and symptoms of downy mildew. Cultigens from the genera *Cucumis*, *Citrullus*, *Luffa*, and *Lagenaria* all showed symptoms of

Table 2. Final disease rating (FDR) and area under the disease progress curve (AUDPC) of the 41 cultigens assessed for field resistance to natural populations of *Pseudoperonospora cubensis* in Michigan

Species, cultigen	AUDPC ^w		FDR ^x	
	2010	2011	2010	2011
<i>Cucumis sativus</i>				
Vlaspik ^y	3,207 a	2,173 a	95 a	99 a
<i>C. melo</i>				
Hale's Best Jumbo	1,380 d–g	1,931 b	52 c–e	89 d
Crete ^z	1,594 bc	1,815 d	54 bc	97 ab
Atlantis	1,374 d–g	1,096 lm	47 d–f	54 n
Ambrosia Hybrid	1,721 b	1,906 bc	59 b	92 c
Planters Jumbo ^z	1,362 d–h	1,813 d	43 f–h	96 b
Topmark ^y	1,442 c–e	1,806 d	55 bc	91 cd
Grand Slam	1,436 cd	1,682 e	52 cd	85 e
Python ^z	1,322 d–h	1,565 f	47 d–f	83 gh
Toscana ^z	1,267 e–i	1,553 f	38 h–j	83 f–h
Mainstream ^z	1,287 d–i	1,547 de	46 ef	90 d
Aphrodite	1,368 d–h	1,497 gh	45 f	85 ef
Tekos ^z	1,265 e–i	1,492 h	48 d–f	85 e–g
Minerva	1,241 f–j	1,469 h	37 ij	77 i
Sun Jewel ^z	1,036 k	1,397 i	33 j	82 h
Odyssey	1,335 d–h	1,369 ij	37 ij	70 jk
Melon Gold Bar	1,080 jk	1,325 j	44 fg	75 i
Tam-Dew ^z	1,130 i–k	1,159 k	38 ij	69 k
Banana	827 l	1,131 kl	34 ij	57 m
Ananas	1,140 i–k	1,872 c	35 ij	90 cd
Strike	1,205 h–j	1,077 m	39 g–i	55 n
Athena	1,212 g–j	1,070 m	44 fg	64 l
Primo ^z	1,397 ef	1,062 m	48 d–f	71 j
Edisto 47 ^z	985 kl	794 n	33 j	41 o
MR-1 ^z	323 mn	326 o	15 k	19 p
<i>Lagenaria siceraria</i>				
PI 642042 ^y	418 m	410 o	14 kl	20 p
<i>Citrullus lanatus</i> var. <i>lanatus</i>				
PI 169290	258 m–o	140 p	9 lm	9 q
PI 490378	193 no	107 p–r	5 mn	7 rs
PI 629106	150 op	105 p–r	5 mn	7 qr
PI 438676	170 no	67 q–s	5 mn	5 st
PI 171584 ^y	186 no	55 rs	5 mn	3 u
PI 612145	183 no	46 st	5 mn	3 tu
PI 595218	214 m–o	42 st	5 mn	3 tu
PI 171392	122 op	36 st	5 mn	3 u
<i>Luffa aegyptiaca</i>				
PI 527331 ^y	138 op	118 pq	5 mn	9 qr
<i>Cucurbita moschata</i>				
PI 169410	0 p	0 t	0 n	0 v
PI 358507	0 p	0 t	0 n	0 v
<i>C. pepo</i>				
PI 171622 ^y	0 p	0 t	0 n	0 v
PI 508468	0 p	0 t	0 n	0 v
<i>C. pepo</i> subsp. <i>fraterna</i>				
PI 532355 ^y	0 p	0 t	0 n	0 v
<i>C. pepo</i> var. <i>texana</i>				
PI 614687 ^y	0 p	0 t	0 n	0 v

^w Mean AUDPC calculated from percentage of the total chlorotic and necrotic leaf for each year. Mean separation performed by year using least significant difference (LSD; $\alpha = 0.05$). Numbers followed by the same letter are not significantly different from each other. High values represent high levels of susceptibility.

^x Mean disease severity (%) at the final rating; mean separation performed by year using LSD ($\alpha = 0.05$).

^y Subset of cultigens for the determination of host range and variability between 2010 and 2011.

^z Lines had previously been reported as downy mildew resistant or tolerant.

infection. Abundant sporulation was observed on the *Cucumis sativus* cultivar and several of the melon (*Cucumis*) cultivars (data not shown). Sporulation was observed on *Citrullus lanatus* var. *lanatus* cultigens but *Cucurbita pepo*, including the subspecies *fraterna* and *texana*, and *C. moschata* showed no symptoms or signs of infection. No differences between 2010 and 2011 regarding the predominant pathotype in Michigan *P. cubensis* populations were found (Table 4).

Cultigen disease ratings in Michigan were variable compared with the cultigens' performance in South Carolina (Table 5). Significant differences were detected among the cultivars ($P < 0.0001$), and time ($P < 0.0001$) had a significant effect on disease progression. *Cucumis melo* cultigens 'Sun Jewel', 'Melon Gold Bar', 'Tam-Dew', 'Ananas', and 'Edisto 47' had higher disease ratings in South Carolina compared with Michigan; only *C. melo* 'Atlantis' had less disease.

Differences in susceptibility between cucurbit cultigens. Significant differences were found among AUDPC, rank means, and disease severity values for cultigens evaluated ($P < 0.0001$) for both years. For AUDPC and disease severity, year, and the interaction between species or genera and year were significant ($P < 0.0001$). Overall disease severity was less in 2010 (up to 59%) than in 2011 (up to 97%) on the evaluated cultigens, with the exception of 'Vlaspik' (Table 2). In 2010, 35 cultigens had less than 50% disease whereas in 2011, 23 cultigens had disease severity greater than 50% (Table 2). Final disease ratings were within 5% for 16 accessions between the 2 years. Final disease severity and AUDPC values were higher in 2011 than in 2010 for most *C. melo* cultigens (Table 2).

Among *C. melo* cultigens, 'Ambrosia Hybrid' ($58.65 \pm 1.98\%$) and 'Crete' ($97.4 \pm 0.73\%$) had the highest disease severity in 2010 and 2011, respectively. 'Ambrosia Hybrid' was significantly more susceptible than the susceptible *C. melo* check, 'Hale's Best

Table 3. Final disease severity (FDS) and area under the disease progress curve (AUDPC) of the genera assessed for field resistance to natural populations of *Pseudoperonospora cubensis* in Michigan

Genus	FDS ^y		AUDPC ^z	
	2010	2011	2010	2011
<i>Cucumis</i>	44.73 a	76.07 a	1320 a	1440 a
<i>Citrullus</i>	5.54 c	5.01 d	184 c	75 d
<i>Lagenaria</i>	14.11 b	20 b	417 b	410 b
<i>Luffa</i>	4.89 c	8.75 c	137 c	118 c
<i>Cucurbita</i>	0 d	0 e	0 d	0 d

^y Mean FDS rating. Mean separation performed by year using honestly significant difference (HSD) ($\alpha = 0.05$), and variances grouped by genus. Numbers followed by the same letter are not significantly different from each other. High values represent high levels of susceptibility.

^z Mean AUDPC calculated from percentage of the total chlorotic and necrotic leaf for each year. Mean separation performed by year using HSD ($\alpha = 0.05$), and variance grouped by genus. Numbers followed by the same letter are not significantly different from each other. High values represent high levels of susceptibility.

Table 4. Interaction of *Pseudoperonospora cubensis* and selected cultigens for the determination of host range variability in 2010 and 2011

Taxa	Common name	<i>P. cubensis</i> reaction ^z	
		2010	2011
<i>Cucumis sativus</i>	Cucumber	+	+
<i>C. melo</i> subsp. <i>melo</i>	Cantaloupe	+	+
<i>Cucurbita pepo</i> var. <i>pepo</i>	Zucchini	–	–
<i>C. pepo</i> var. <i>texana</i>	Texas gourd	–	–
<i>C. pepo</i> var. <i>fraterna</i>	Gourd	–	–
<i>Citrullus lanatus</i>	Watermelon	+	+
<i>Luffa aegyptiaca</i>	Loofah	+	+
<i>Lagenaria siceraria</i>	Bottle gourd	+	+

^z Symbols: – = incompatible host reaction, no visible symptoms; + = compatible reaction based on final ratings > 0 , evident downy mildew symptoms, and *P. cubensis* morphological identification.

Jumbo', in 2010. 'Crete' was significantly more susceptible than 'Hale's Best Jumbo' in 2011. 'Banana' ($33.7 \pm 1.98\%$ in 2010 and $57.4 \pm 0.73\%$ in 2011) was significantly more resistant than the highly susceptible 'Ambrosia Hybrid' and 'Hale's Best Jumbo' in 2010 and 2011 but significantly less resistant than the cultigen 'MR-1' ($18.75 \pm 0.73\%$) in 2011. *C. melo* cultigens 'Ambrosia Hybrid' and 'Hale's Best Jumbo' had the highest AUDPC values for 2010 and 2011, respectively, but were significantly less susceptible than 'Vlaspik'. In 2010

and 2011, 'Hale's Best Jumbo' had a significantly higher AUPDC than moderately resistant 'Primo' and 'Edisto 47' and the partially resistant control 'MR-1'.

According to the final disease severity and AUDPC values in 2010 and 2011, the cultigens 'Primo' and 'Melon Gold Bar' were significantly more susceptible than the resistant melon lines 'MR-1' and 'Edisto 47' but had significantly lower AUDPC values than the susceptible cucumber control 'Vlaspik' (Table 2). Seed companies had previously

Table 5. Rank mean comparisons between Michigan and South Carolina for 41 cultigens^y

Species/cultigen	RTE ^w			Final ratings ^x		
	2010	2011	SC	2010	2011	SC
<i>Cucumis sativus</i>						
Vlaspik ^y	0.82 a	0.68 a	–	8	8	–
<i>C. melo</i>						
Hale's Best Jumbo	0.65 bc	0.62 c–e	0.51 b–d	5	8	5.67
Crete ^z	0.69 bc	0.63 bc	0.52 b–d	5	8	6.00
Atlantis	0.65 bc	0.57 h–k	0.31 bc	5	8	4.00
Ambrosia Hybrid	0.70 b	0.62 cd	0.59 fg	5	8	7.00
Planters Jumbo ^z	0.65 bc	0.61 d–f	0.52 b–d	5	8	5.67
Topmark ^y	0.64 bc	0.64 b	0.55 b–d	5	8	6.00
Grand Slam	0.65 bc	0.61 c–f	0.41 fg	5	7	4.67
Python ^z	0.66 bc	0.59 gh	0.45 de	5	7	4.67
Toscana ^z	0.63 bc	0.59 gh	0.54 b–d	4	7	6.00
Mainstream ^z	0.63 c	0.59 gh	0.55 bc	5	8	7.00
Aphrodite	0.64 bc	0.58 gh	0.42 fg	5	7	4.67
Tekos ^z	0.62 c–e	0.59 gh	0.51 b–d	5	7	7.33
Minerva	0.63 c	0.59 fg	0.41 fg	4	7	5.00
Sun Jewel ^z	0.58 de	0.58 g–i	0.63 b	4	7	8.33
Odyssey	0.67 bc	0.58 hi	0.42 f	4	6	4.67
Melon Gold Bar	0.60 c–e	0.56 i–k	0.45 e	5	6	7.00
Tam-Dew ^z	0.62 cd	0.56 k	0.60 bc	4	6	8.00
Banana	0.56 e	0.56 jk	0.42 f	4	5	4.67
Ananas	0.60 c–e	0.61 c–e	0.65 ab	4	5	9.00
Strike	0.63 cd	0.60 e–g	0.46 c–e	4	5	4.66
Athena	0.61 c–e	0.59 f–h	0.48 b–d	5	6	5.33
Primo ^z	0.65 bc	0.57 h–k	0.46 c–e	5	6	5.33
Edisto 47 ^z	0.58 de	0.53 l	0.50 b–d	4	5	6.00
MR-1 ^z	0.44 fg	0.50 m	0.24 h	3	3	2.67
<i>Lagenaria siceraria</i>						
PI 642042 ^y	0.45 f	0.50 m	–	2	3	–
<i>Citrullus lanatus</i> var. <i>lanatus</i>						
PI 169290	0.42 f–h	0.46 n	–	2	2	–
PI 490378	0.38 i	0.44 o	–	1	1	–
PI 629106	0.38 hi	0.45 no	–	1	1	–
PI 438676	0.39 g–i	0.43 o	–	1	1	–
PI 171584 ^y	0.40 g–i	0.44 o	–	1	1	–
PI 612145	0.37 ij	0.43 o	–	1	1	–
PI 595218	0.41 f–i	0.3828 p	–	1	1	–
PI 171392	0.33 j	0.39 p	–	1	1	–
<i>Luffa aegyptiaca</i>						
PI 527331 ^y	0.32 j	0.45 no	–	2	2	–
<i>Cucurbita moschata</i>						
PI 169410	0.15 k	0.23 q	–	0	0	–
PI 358507	0.15 k	0.23 q	–	0	0	–
<i>Cucurbita pepo</i>						
PI 171622 ^y	0.15 k	0.23 q	–	0	0	–
PI 508468	0.15 k	0.23 q	–	0	0	–
<i>C. pepo</i> subsp. <i>fraterna</i>						
PI 532355 ^y	0.15 k	0.23 q	–	0	0	–
<i>C. pepo</i> var. <i>texana</i>						
PI 614687 ^y	0.15 k	0.23 q	–	0	0	–

^y Values in SC columns are for select melon cultivars in a separate study conducted in South Carolina; the numbers are reprinted from Kousik et. al (11); – indicates cultigens not evaluated in the South Carolina study.

^w Relative treatment effect (RTE) values for cucumber downy mildew disease ratings.

^x Final rating based on a 1-to-9 scale, where 0 = no symptoms; 1 = 1 to 8, 2 = 9 to 14, 3 = 15 to 25, 4 = 26 to 40, 5 = 41 to 60, 6 = 61 to 75, 7 = 76 to 88, and 8 = 89 to 99% symptomatic; and 9 = dead plant.

^y Subset of cultigens for the determination of host range and variability between 2010 and 2011.

^z Lines had previously been reported as downy mildew resistant or tolerant.

marketed both 'Primo' and 'Melon Gold Bar' as "tolerant" to downy mildew. All eight *Citrullus lanatus* var. *lanatus* cultigens were significantly more resistant than the partially resistant *Cucumis melo* cultigen 'MR-1' and the susceptible control 'Vlaspik' according to AUDPC and final rating values in 2011 but not 2010.

There were no significant differences between *Citrullus lanatus* var. *lanatus* cultigens, and between the *Lagenaria siceraria* or *Luffa aegyptiaca* cultigen evaluated. Overall, *Cucumis* cultigens were significantly more susceptible to cucurbit downy mildew compared with *Citrullus*, *Cucurbita*, *Lagenaria*, and *Luffa* spp. (Table 3). *Cucurbita* spp. were the least susceptible and *Citrullus* and *Luffa* were more susceptible than *Cucurbita* but less susceptible than *Lagenaria*.

Pathogen sporulation was observed on all *Cucumis* cultigens in the field (data not shown). Conversely, no sporulation was detected under field conditions on *C. lanatus* var. *lanatus* cultigens. However, under elevated humid conditions in incubation chambers in the laboratory, *P. cubensis* sporulation was observed after 3 days of incubation. No sporulation was detected on *Cucurbita* spp. in field or lab conditions.

Discussion

Different levels of resistance to *P. cubensis* were detected among cucurbit cultigens grown in the field. More precipitation events and a greater total rainfall amount occurred during the field season in 2011 (30 events and 280.6 mm) than in 2010 (23 events and 172.3 mm). Prolonged leaf wetness periods favor *P. cubensis* infection and disease severity (16). Thus, the lower number of cultigens significantly different from each other observed in 2010 for AUDPC values could have resulted from less favorable environmental conditions for pathogen infection and disease progression compared with the conditions in 2011.

The most susceptible cultigens were observed in the *Cucumis* genus; Vlaspik, a pickling cucumber cultivar, was the most severely infected by *P. cubensis* (highest AUDPC value and final severity value). Overall, downy mildew was less severe on *Citrullus*, *Lagenaria*, and *Luffa* spp. and symptoms were absent on *Cucurbita* spp. compared with *Cucumis* spp. These results agree with other empirical studies that indicated that *Cucumis sativus* cultivars are more susceptible compared with other Cucurbitaceae spp. (16). Among *C. melo* cultigens, the breeding line 'MR-1' was the least susceptible to *P. cubensis*, followed by 'Edisto 47'. Low levels of susceptibility to downy mildew in 'MR-1' and 'Edisto 47' are attributed to the inclusion of PI 124111 and PI 124112, respectively, into their pedigrees (8,9,25).

In Michigan, final disease ratings varied compared with those from South Carolina. Of the 24 cultigens evaluated in South Carolina, 13 had final disease ratings within the value range of the 2010 and 2011 Michigan ratings. The remaining 11 cultigens were more susceptible to South Carolina populations of *P. cubensis* with the exception of 'MR-1', 'Tekos', and 'Sun Jewel'. *C. melo* cultigens 'Tam-Dew' and 'Ananas' were more susceptible to *P. cubensis* infection in South Carolina than in Michigan. 'MR-1' was among the most resistant melon cultivars in this study and in a study in South Carolina (11). Differences found in this study in disease response among melon cultigens in Michigan compared with South Carolina could be due to differences in pathogen populations or environmental conditions (21). Our data suggest that there are differences in virulence and pathogenicity between Michigan and South Carolina, consistent with hypotheses that these populations are not from the southern United States. Annual changes in virulence and pathogenicity can occur in field populations but, in this study, no changes were evident in pathotype between the 2 years (13).

In our study, downy mildew symptoms differed based on the host. Chlorotic and necrotic leaf lesions were angular and restricted by the leaf veins in cucumber and loofah, whereas lesions were more circular and not restricted by the leaf veins in cantaloupe, watermelon, and bottle gourd. We measured disease development both over time and as final disease severity to calculate the AUDPC to determine the susceptibility of each cultigen to *P. cubensis*. For instance, *C. melo* 'Primo' had a final disease rating of 48 and 71% in 2010 and 2011, respectively, with significantly lower AUDPC values compared with the

control ('Vlaspik'), suggesting a delay in disease development. This delay in downy mildew onset might also be the result of new pathotypes entering the field throughout the growing season.

Differences in virulence or pathotype were not evident within Michigan's predominant *P. cubensis* populations during the 2010 and 2011 field seasons using the subset of differential taxa for pathotype determination. A previous study found similarities in the genetic cluster composition year to year (2007 to 2009) of *P. cubensis* populations in the United States and in Michigan, which supports these results (21). It has been proposed that Michigan downy mildew primary populations originate either from the Georgia, South Carolina, and North Carolina areas or from greenhouses located along the border with Canada (18,21). Differences in the susceptibility of *C. melo* and *Citrullus lanatus* cultigens to Michigan and South Carolina populations of cucurbit downy mildew may be the result of significant genotype-environment interactions, or could suggest that Michigan's primary inocula was not the same as that of South Carolina in this study.

'Melon Gold Bar', a *Cucumis* hybrid resulting from the interspecific hybridization of *Cucumis sativus* (cucumber) × *C. hystris* Chakr. (wild melon), was significantly less susceptible than 'Vlaspik' and significantly more susceptible than 'Edisto 47' or 'MR-1'. However, this cultivar yielded high numbers of fruit compared with other *Cucumis* cultivars (data not shown). The relatively short maturity time of the 'Melon Gold Bar' cultivar (68 days) compared with the *C. melo* cultivars (78 to 100 days) may allow the plant to produce fruit before disease pressure limits production.

'Crete' and 'Planters Jumbo' were selected for the study because of their stated resistance to downy mildew. However, they were highly susceptible in 2011 and had intermediate resistance in 2010. 'Edisto 47', released in 1964 (Clemson University), and 'MR-1', released in 1986 (25), had significantly better resistance to the currently prevailing downy mildew pathogen in Michigan compared with the other *C. melo* cultigens. 'MR-1' may still be useful as a source of resistance to the prevailing downy mildew pathotypes in Michigan.

Growers may benefit from cultivars with vigorous growth habits that could better withstand downy mildew. Also, early-season plantings may not be exposed to the influxes of sporangia that are more common as the season progresses. Cucurbits with resistance may require fewer fungicide applications than susceptible cultigens. Future studies will need to evaluate 'Edisto 47', 'Strike', 'Banana', 'Primo', 'Athena', 'Tam-Dew', and 'Ananas' cantaloupe for their performance in reduced fungicide programs in Michigan.

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