Screening the Cucumber Plant Introduction Collection for Young Fruit Resistance to *Phytophthora capsici*

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Abstract. Fruit rot caused by *Phytophthora capsici* is a major constraint in cucumber (*Cucumis sativus*) production. In an effort to identify a source of resistance, we developed a more streamlined detached fruit method for high-throughput screening and tested the U.S. cucumber PI collection for fruit rot resistance. A total of 1076 PI collections, from 54 geographic locations around the world, along with the susceptible commercial cultivar, Vlsapik, were grown in the field and tested for resistance to *P. capsici*. Using the knowledge gained from our prior studies regarding greater susceptibility of young fruits compared with older fruits, very young fruits (≈3 to 4 days post-pollination) were collected and inoculated with zoospore suspensions of *P. capsici* isolate OP97. From the screens performed in 2011 and 2012, 99% of the tested PIs were rated as moderately or highly susceptible based on symptom development and pathogen growth at 5 days post-inoculation. The cv. Vlsapik control showed consistent high susceptibility to *P. capsici* with a mean symptom rating of 8.0 on a 9-point scale. A set of 28 PIs was chosen for further testing in the greenhouse or field in 2013. The disease ratings of PIs rescreened in 2013 were much lower compared with that of the full collection of PIs. Three accessions, PI109483, PI178884, and PI214049, showed consistent low mean disease ratings and may be considered as possible sources of resistance to young cucumber fruit infection by *P. capsici*. Evaluation of the S₁ progeny of PI109483 suggests that the resistance is heritable and should allow for development of useful breeding materials that can be used for developing *P. capsici*-resistant cucumber cultivars.

Cucumber (*Cucumis sativus*) production in the eastern and midwestern United States is subject to severe losses resulting from fruit rot caused by the soilborne oomycete pathogen, *Phytophthora capsici* (Granke et al., 2012; Sonogo and Ji, 2012). The disease causes commercial loads of harvested cucumbers to be rejected for sale and farmland to be removed from cucumber production. *P. capsici* has tremendous reproductive potential, allowing for rapid spread both within and

between fields (Granke et al., 2012). The sporangia, which are continuously produced throughout the growing season, release motile infective zoospores on contact with water and provide a constant source of inoculum for new infections. The pathogen also produces sexual oospores, which serve as long-lived overwintering structures. *P. capsici* is notable for its wide host range including numerous solanaceous, cucurbit, and legume crops (Hausbeck and Lamour, 2004; Tian and Babadoost, 2004). The combined effects of broad host range, spread of the disease through infested irrigation water, and the ability of *P. capsici* oospores to survive in the soil for many years makes control by cultural practices very difficult (Gevens et al., 2007; Granke et al., 2012; Sonogo and Ji, 2012). Furthermore, several strains of *P. capsici* isolated from states in the eastern, southern, and midwestern United States have developed resistance to key fungicides, reducing usefulness of some chemical controls (e.g., Café and Ristaino, 2008; Dunn et al., 2010; Jackson et al., 2012; Lamour and Hausbeck, 2000). Collectively these factors dictate that yield losses resulting from *P. capsici* infection will be a continuing problem in cucumber production unless genetic resistance is developed.

Several recent studies have searched for sources of host plant resistance to crown rot and fruit rot caused by *P. capsici* in cucurbit crops. Screening of *Cucurbita pepo* accessions for crown rot resistance led to identification of eight accessions with low mean disease ratings (Padley et al., 2008). Inheritance studies using a *Cucurbita* breeding line indicated that resistance is conferred by three dominant genes (Padley et al., 2009). Five accessions of *Cucurbita moschata* were identified with resistance to Floridian isolates of *P. capsici* (Chavez et al., 2011); high levels of seedling-stage crown rot resistance were reported in S₁ progeny of three melon (*Cucumis melo*) introductions (Donahoo et al., 2013); and seedling resistance was observed in two accessions of watermelon (*Citrullus lanatus* var. *lanatus*) (Kim et al., 2013). Several bottle gourd (*Lagenaria siceraria*) rootstocks used for grafting with watermelon also were found to confer crown rot resistance (Kousik et al., 2012b). Screening for sources of resistance to *Phytophthora* fruit rot in watermelon identified four *Citrullus lanatus* var. *lanatus* accessions along with a *Citrullus lanatus* var. *citroides* and a *Citrullus colocynthis* accession (Kousik et al., 2012a).

The primary losses caused by *P. capsici* infection of cucumber result from fruit rot (Hausbeck and Lamour, 2004). *P. capsici* preferentially infects cucumber fruits, whereas leaves and vines remain healthy (Ando and Grumet, 2006; Grumet et al., 2013). Thus, it is essential that screening for resistance is performed directly on fruit. A prior study (Gevens et al., 2006) tested more than 300 cucumber varieties and PIs, including 100 genotypes selected to provide a representative sample of genetic variance in the cucumber germplasm as determined by Knerr et al. (1989). That study did not identify a suitable source of genetic resistance.

In the process of that screening, which was performed on harvest-stage fruit, we observed that larger fruit appeared to be less susceptible than smaller fruit. Analysis of hand-pollinated fruit of known ages ranging from 0 to 16 d post-pollination (dpp) showed that very young fruit (e.g., 0 to 4 dpp) were most highly susceptible (Gevens et al., 2006). As fruits completed the period of rapid fruit elongation, at ≈10 to 12 dpp, they became less susceptible and were essentially resistant by 16 dpp. Developmentally regulated or age-related resistance wherein resistance increases with plant or tissue age, has been observed in other host plant–pathogen interactions, including *P. capsici* infection of pepper, and subsequent studies with *P. capsici* infection of other cucurbit fruits (Ando et al., 2009; Develey-Rivière and Galian, 2007; Hwang et al., 1996; Meyer and Hausbeck, 2013). These results have implications for disease control strategies including appropriate location and timing of fungicide applications. They also indicate that it is critical to screen the highly susceptible, young cucumber fruit when testing for resistance to *P. capsici*.

Fruit testing is time-, labor-, and space-intensive. The objectives of this study were to

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develop a modified testing method to allow for a more efficient inoculation for high-throughput screening using young cucumber fruit and to screen the full U.S. cucumber PI collection for resistance to *P. capsici*. We used knowledge gained in our prior studies regarding greater susceptibility of floral ovaries and very young fruit and lack of difference in susceptibility between pollinated and parthenocarpic fruit (Ando, 2009; Ando et al., 2009; Gevens et al., 2006), to develop a more streamlined fruit screening method and prevent misassessment of potential resistance that can occur as the fruits become older. Screening of the cucumber PI collection identified three accessions as potential sources for young fruit resistance to *P. capsici*.

Materials and Methods

Seed of 1297 cucumber PI accessions was provided by the North Central Regional Plant Introduction Station, Ames, IA (<<http://www.ars-grin.gov/cgi-bin/npgs/html/taxon.pl?12580#image>>). Of those, 1076 PIs were not previously screened for resistance to *P. capsici*. The 1076 accessions were planted in small-plot, unreplicated trials of three plants/plot at the Michigan State University Horticulture Teaching and Research Center, East Lansing, MI, in the summers of 2011 and 2012. Seeds were planted into 0.8-m wide plastic mulch with 2 m between rows and 1-m spacing within rows. Local standard commercial production guidelines were followed for fertilization and insect and weed control (Bird et al., 2005). Water was supplied by rain or by trickle irrigation to provide 25 mm per week. Pollination was facilitated by bees. Once the period of fruit setting

began, fruit were harvested two or three times a week until 10 fruit had been collected from each PI. Fruit were collected on 15 dates in 2011 and 20 dates in 2012. Very young fruits, estimated to be ≈ 3 to 4 dpp based on fruit size and blossom appearance, were harvested and brought to the laboratory for inoculation.

The harvested fruit were washed, surface-sterilized by brief immersion in a 5% sodium hypochlorite solution, rinsed with water several times, and allowed to air-dry. A modified inoculation procedure based on the methods of Gevens et al. (2006) was developed to streamline the screening process. *Phytophthora* zoospore suspensions were prepared from *P. capsici* isolate OP97 mycelia cultured on diluted V8 agar media as per Gevens et al. (2006). After 7 d of culture, the plates were flooded with 6 mL sterile distilled water to release zoospores. A 20- μ L aliquot was removed for quantitation by a hemocytometer. The remainder was diluted to a concentration of 1×10^5 zoospores/mL; 30 μ L of the zoospore suspension was applied to the center of each fruit. Incubation was performed under constant light at 23 to 25 °C in covered trays lined with wet paper towels to maintain high humidity as described by Gevens et al. (2006). Fruit from the susceptible control ‘Vlaspik’ were included at each harvest to ensure effectiveness of the inoculation procedure. On rare occasions (less than 1% of fruit tested), the droplet did not remain on the surface of the fruit. In those cases, an additional one or two droplets were applied; in most cases, the droplet stayed on the surface after the repeat application. In those cases in which the droplet still fell off the surface, the combined droplets created a “pool.” The fruits were then placed on top of the pool for

24 h, a time that our prior methods development tests had shown was sufficient to establish infection. The fruits were then rotated so that the surface that was in contact with the inoculum was visible for scoring. In no case was potential resistance associated with failure of the droplet to remain on the fruit surface. In any case where it was not clear if the droplet ran off the fruit, the fruit was discarded from analysis.

The fruit were monitored daily for symptom development and obvious pathogen growth for a period of at least 5 d. All disease ratings used for analysis were taken at 5 d post-inoculation. In 2011 the fruit responses were scored using a disease rating scale of 1 to 5 defined as: 1 = no symptoms; 2 = mild water-soaking; 3 = water-soaking with necrosis; 4 = extensive water-soaking (may also include necrosis and/or obvious mycelium growth); 5 = tissue collapse (with or without obvious mycelium growth). In 2012 the rating system was modified to a 1 to 9 scale (illustrated in Fig. 1) to better capture the range of symptoms observed among the diverse genotypes. Responses with scores of 1 to 3 (i.e., no symptoms or minor symptoms limited to the point of inoculation) were considered resistant; 4 to 6 (i.e., moderate to extensive water-soaking and/or limited necrosis or mycelial growth), moderately susceptible; and 7 to 9 (i.e., moderate to extensive mycelium growth, sporulation, necrosis, and tissue collapse), highly susceptible.

Based on the initial screen of the full PI collection, 28 accessions were selected for further testing for reproducibility of observed potential resistance. The selected PIs had mean disease scores less than 2 in 2011 or less than 4 in 2012. An additional 16 accessions

Fig. 1. Symptom rating scale for young cucumber fruit response to inoculation with *P. capsici*. R = resistant; S = susceptible; HS = highly susceptible.

from the moderate disease rating group that appeared to be segregating for resistance were also included for further testing.

To account for the possibility of segregation within the PI sample, subsequent testing of the putatively resistant PIs in 2013 was performed in the greenhouse and/or field using individual plants. To increase the number of samples that could be tested per plant in the greenhouse, a preliminary study was performed to verify correspondence between the response of unpollinated ovaries from female flowers at anthesis with that of young fruit (data not shown). For the greenhouse trials, five to 10 unpollinated female flowers were collected from each plant at anthesis and ovaries inoculated with zoospore suspensions as described previously. Progeny were produced on three accessions in the greenhouse for which individual plants had been verified to produce resistant fruit: PI109483, PI175693, and Ames 26084. One or two female flowers from those individual plants were hand-pollinated using male flowers from the same plant. Mature fruits were collected at 30 to 35 dpp and seed extracted for field planting in 2013.

Conditions for the 2013 field test were as described previously with the exception that 10 individuals of each potentially resistant PI were planted 2 m apart within a row, 3 m between rows, to allow testing of fruit from

each plant separately. Harvesting of very young fruits and inoculation with *P. capsici* was performed as described previously. Fruit were harvested on 13 dates. In most cases 10 to 15 fruit were tested per plant with 100 to 200 fruit tested per PI or family sampled over multiple harvest dates.

Data were analyzed by Kruskal-Wallis test in SAS (SAS Institute, Cary, NC) followed by multiple comparisons using the Dunn method.

Results and Discussion

Sampling of very young fruits from the field, or ovaries from unpollinated flowers at anthesis in the greenhouse, combined with a revised zoospore inoculation procedure allowed us to more quickly prepare and apply inoculum, reduce space needed to perform the inoculation experiments, and prevent misassessment of potential resistance that can occur as the fruits increase in age. The vast majority of the tested PIs were susceptible or highly susceptible to *P. capsici* (Table 1; Fig. 2A–B). By 5 d post-inoculation, nearly 99% (1064 of 1076) of the accessions had mean symptom ratings 2.0 or greater/5.0 scale in 2011 or 4.0 or greater/9.0 scale in 2012 indicating effectiveness of the screening method in causing infection. The mean disease rating for the population was 4.5/5.0

in 2011 and 7.3/9.0 in 2012. The control cultivar Vlaspek had ratings of 5.0 and 8.0 in 2011 and 2012, respectively. The very small number of potentially resistant PIs is consistent with the previous screening study in which all of the tested accessions were susceptible to fruit infection by *P. capsici* (Gevens et al., 2006).

Prior studies by Enzenbacher and Hausbeck (2012) and Gevens et al. (2006) tested several *P. capsici* isolates for virulence on cucurbits. With the exception of one that was less severe than the OP97 isolate used in this study, all were comparable to OP97 for infectivity on cucumber fruit. The virulence of OP97 was further demonstrated by the highly susceptible responses of the great majority of tested accessions (Table 1). These results also indicate effectiveness of the zoospore inoculation procedure, which, in addition to greater ease of application for very large numbers of samples, more closely resembles the primary mode of inoculation in the field.

Of the PIs with very low symptom ratings at 5 d post-inoculation, there appeared to be two types of responses. Some exhibited delayed and much reduced symptom development (i.e., only some water-soaking without sporulation). Others did not produce symptoms or only showed small, localized necrosis limited to the site of inoculation (e.g., score of 2 or 3 on a 9-point scale; Fig. 1A),

Table 1. Disease scores of the cucumber PI collection for fruit response to inoculation by *P. capsici*.^z

Resistant mean disease rating less than 2.0 (2011) or less than 4.0 (2012) (N = 12; 1.1%)	Susceptible mean disease rating 2.0 to 2.99 (2011) or 4.0 to 6.99 (2012) (N = 181; 16.8%)						Highly susceptible mean disease rating greater than 3 (2011) or greater than 7 (2012) (N = 883; 82.1%)
Ames: 26084	Ames: 7753	176520	357831	432896	605961	618874	The list of the 883 highly susceptible PIs is provided in Supplemental File 1.
PI: 174166	7785	176521	357832	436609	605963	618875	
175693	12782	176523	357838	436648	605964	618881	
206425	13257	176525	357847	436649	605967	618899	
214049	13353	176526	357851	436672	605968	618911	
285608	13357	178884	357852	458848	605972	618915	
357830	19222	178887	357858	458849	605973	618923	
432865	19227	179678	357861	458850	605981	618930	
605945	19229	181752	357862	478366	605982	618933	
605947	22384	188807	357866	481616	605984	618944	
605979	22385	197087	368549	481617	605987		
606013	23612	205996	368552	483339	605988		
	25936	206953	368553	483343	605989		
	PI: 92806	206954	368554	508459	605992		
	109483	209066	368560	511818	605993		
	163214	224668	370022	511821	605997		
	163216	227664	370447	512595	605998		
	163223	255934	370448	512597	606000		
	164734	255935	372900	512598	606001		
	164951	263079	372905	512599	606007		
	165506	264231	378066	512609	606008		
	169351	267742	379279	512616	606009		
	169380	279464	379282	512618	606010		
	169389	281448	379283	532520	606011		
	169390	283901	379286	532521	606012		
	169395	321010	385967	532522	606014		
	169401	338235	390250	532523	606020		
	171604	339248	390256	605934	606023		
	173889	344347	414159	605936	606037		
	173893	344348	419078	605948	606042		
	175111	344432	422177	605949	606045		
	175679	344433	432854	605952	606048		
	175681	344434	432859	605953	606050		
	175691	355052	432860	605954	618866		
	175692	356832	432894	605959	618871		

^zA total of 1076 were screened. Disease ratings are the mean of five to 10 young fruit/PI inoculated as described in “Methods.” Bold type indicates PIs selected for further testing.

Fig. 2. Distribution of disease scores for cucumber PIs screened for young fruit resistance to *P. capsici*. (A–B) Distribution of disease scores of PIs from *P. capsici* inoculation of field-grown fruit in 2011 and 2012. Value for each PI is the mean of five to 0 fruit at 5 d post-inoculation (dpi). (C) Distribution of disease scores of PIs selected for potential fruit resistance based on screens in 2011 and 2012 and tested as individual plants in 2013. With the exception of three PIs, the value for each PI or S₁ family is the mean of 80 to 200 fruit from eight to 10 plants. The disease rating for the susceptible control ‘Vlaspik’ is indicated by the solid arrows; the mean disease rating for the set of tested PIs is indicated by the dashed arrows.

possibly indicative of a hypersensitive response. In some cases, we observed a mixture of fruit within the same PI sample that exhibited resistant and susceptible responses. Because the close spacing of plants within the initial trials did not allow for differentiation among fruit produced by individual plants, it is possible that a mixed disease response could result from variability within the PI sample. Variability within cucurbit PI accessions for disease resistance responses has been

observed frequently (e.g., Davis et al., 2007; Donahoo et al., 2013; Wechter et al., 2011), possibly as a result of a mixed initial sample, or cross-pollination before or after initial collection.

Based on the screens in 2011 and 2012, 28 PIs were chosen for further testing in the greenhouse or field in 2013. In addition to PIs showing resistant phenotypes (mean disease scores less than 2 in 2011 or less than 4 in 2012), 16 accessions from the moderate disease

rating group that appeared to be segregating for resistance were included for further testing (Table 1). The majority (61%) of the selected PIs were collected from Turkey or India (Table 2). Although there were a greater number of accessions from China in the PI collection, only one showed potential resistance in the 2011–12 screens. This distinction among different geographical regions is consistent with population structure analysis indicating that cucumber germplasm comes from three distinct populations: China; India and Xishuangbanna; and Europe, America, and Central and West Asia (Lv et al., 2012). It appears likely that the resistance arose in Indian and/or West Asian germplasm.

To account for possible variability within the seed sample, subsequent testing of the putatively resistant PIs in 2013 was performed on individual plants. A small number was tested in the greenhouse in the spring of 2013; the majority were tested in the field. S₁ progeny were produced on three PIs in the greenhouse. In most cases 10 to 15 fruit were tested per plant with a total of 100 to 200 fruit tested for each PI or S₁ family. The PIs retested in the field in 2013 had much lower disease ratings than the full collection of PIs (*t* test, $P < 0.00001$), as evidenced by a shift in the population distribution and a mean disease rating of 4.7, indicating general reproducibility of resistance for the selected PIs (Fig. 2C; Table 2). The susceptible control, ‘Vlaspik’, had a rating of 7.7, consistent with results in 2012. In some cases there was a range in mean disease scores for fruit from individual plants within a given accession or family, e.g., PI605979, for which single plant means ranged from 2.1 to 6.5, suggesting genetic variability or segregation for resistance within the accession (Table 2).

Three accessions (PI 109483 and PI 178884 collected from Turkey and PI 214049 from India) had low PI or family means; multiple plants with mean fruit scores less than 3.5; and 70% to 90% of total fruit with disease scores less than 4 (Table 2). In the case of PI 109483, scores from individual fruit in 2012 suggested segregation within the PI seed sample (Table 1). Self-pollinated progeny from greenhouse-grown individual plants with resistant fruit provided several S₁ families that showed resistance. Disease progression lines for PIs 109483, 178884, and 214049 showed slow development of necrosis limited to the region of inoculation (Fig. 3). Observation of the fruit for an additional 2 to 3 d did not show further disease development. Although promising for resistance, PI 214049 was slow to produce female flowers and fruit in Michigan growth conditions (Table 2).

Based on these studies, PI109483, PI178884, and PI214049 may be considered as possible sources of resistance to young cucumber fruit infection by *P. capsici*. Evaluation of the S₁ progeny of PI109483 indicates that the resistance is heritable and should allow for development of useful breeding materials that can be used for developing *P. capsici*-resistant cucumber cultivars. As a result of the possible variation or segregation within

Table 2. Retest of cucumber PIs selected for potential fruit resistance to *P. capsici*, 2013.^z

PI #	Origin	No. of plants tested	No. of fruit tested	Date of first fruit harvested	Range of plant mean disease scores	PI/family mean $\pm$ SE	P value (Dunn)	Percent fruit score less than 4
PI 214049	India	3	24 ^x	13 Aug.	2.0–3.0	2.59 $\pm$ 0.52	0.0014 ^w	90%
PI 109483-2 ^y	Turkey	8	83	26 July	2.5–4.7	3.45 $\pm$ 0.30	<0.0001	80%
PI 178884	Turkey	10	165	17 July	2.8–4.4	3.53 $\pm$ 0.19	<0.0001	80%
PI 109483-5 ^y	Turkey	10	141	26 July	2.0–6.1	3.70 $\pm$ 0.47	<0.0001	72%
Ames 22385	Nepal	10	120	17 July	2.8–5.1	4.10 $\pm$ 0.22	<0.0001	59%
PI 605981	India	9	186	29 July	3.3–5.7	4.12 $\pm$ 0.22	0.0001	64%
PI 175679	Turkey	10	141	18 July	3.4–5.3	4.18 $\pm$ 0.19	<0.0001	62%
PI 109483-3 ^y	Turkey	10	153	26 July	2.5–6.2	4.21 $\pm$ 0.38	0.0002	58%
PI 285608	Poland	5	86	17 July	2.8–5.3	4.30 $\pm$ 0.44	0.0096	63%
PI 368552	F. Serbia/Mont	10	133	17 July	3.3–7.3	4.40 $\pm$ 0.40	0.0002	55%
PI 606103	India	10	149	17 July	3.6–5.3	4.44 $\pm$ 0.23	0.0009	58%
PI 605979	India	9	101	6 Aug.	2.1–6.5	4.46 $\pm$ 0.42	0.0022	55%
Ames 26084-2 ^y	U.S.	10	197	26 July	3.4–6.2	4.53 $\pm$ 0.31	0.0010	55%
PI 605998	India	10	145	17 July	3.5–4.6	4.71 $\pm$ 0.20	0.0088	54%
PI 169387	Turkey	10	125	17 July	3.5–6.1	4.82 $\pm$ 0.28	0.0160	44%
PI 357830	F. Serbia/Mont	9	110	17 July	3.7–6.0	4.87 $\pm$ 0.28	0.0289	44%
PI 432896	China	10	120	17 July	3.9–6.9	4.98 $\pm$ 0.28	0.0394	47%
PI 435946	Former Soviet Union	10	157	17 July	3.3–7.2	5.00 $\pm$ 0.43	0.0228	47%
PI 532522	Japan	9	138	29 July	3.0–6.5	5.06 $\pm$ 0.37	0.1090	49%
PI 169389	Turkey	10	126	29 July	4.2–6.9	5.13 $\pm$ 0.34	0.0567	42%
PI 605948	India	9	91	29 July	3.0–7.9	5.39 $\pm$ 0.47	0.3912	41%
PI 206425	Turkey	8	178	17 July	3.2–7.5	5.41 $\pm$ 0.44	0.6568	41%
PI 175693-5 ^y	Turkey	9	122	17 July	2.8–6.8	5.41 $\pm$ 0.36	1	35%
PI 605945	India	5	33 ^x	15 Aug.	4.2–6.3	5.54 $\pm$ 0.46	1	32%
PI 605947	India	9	133	8 Aug.	5.3–7.2	5.66 $\pm$ 0.25	1	29%
PI 175693-3 ^y	Turkey	10	199	17 July	4.3–7.9	5.91 $\pm$ 0.37	1	31%
PI 344434	Iran	9	130	17 July	4.3–9.0	6.35 $\pm$ 0.51	1	22%
Vlaspik		5	64	17 July	7.4–8.0	7.70 $\pm$ 0.19	—	0%

^zField-grown young fruits were harvested for each plant separately and inoculated in the laboratory as described in “Methods.”

^yDenotes S₁ progeny family.

^xA limited number of fruit was tested as a result of late production of female flowers and fruit.

^wData were analyzed by Kruskal-Wallis test; $P < 0.0001$. P values listed in the table are for Dunn’s comparison with control ‘Vlaspik’.

Fig. 3. Response of young fruit of PIs or S₁ progeny of 109483, 178884, and 214049 to inoculation by *Phytophthora capsici*. (A) Disease development curves after inoculation. Disease rating scale is as described in Figure 1; numbers of plants and fruits sampled are indicated in Table 2. (B) Example of disease response of ‘Vlaspik’ (top) and PI109483-5 S₁ (158-5, Plant #9). The photograph was taken 5 d post-inoculation. The disease responses of PI 109483 fruit are limited to the site of inoculation (i.e., disease scores of 2 and 3).

accessions, it will be important to develop true breeding-resistant stock lines to facilitate future breeding efforts.

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Supplemental Table 1. Cucumber PIs that were rated as highly susceptible (mean disease rating >3 in 2011 or >7 in 2012). Disease ratings are the mean of 5-10 young fruit/PI inoculated as described in methods.

Ames:	19218	118279	169399	176952	211983	264230	339245	379284	427089	458852	500366	512625	535881	605976	606068	618926
1760	19219	135122	169402	176953	211984	265887	339246	379285	427090	458853	500370	512626	540414	605977	606539	618927
2353	19220	135345	169403	176954	211985	267086	339247	379286	427130	458854	502331	512627	540415	605978	618860	618928
2354	19221	137835	171600	176956	211986	267087	339250	379287	430585	458855	504561	512628	540416	605980	618863	618929
3941	19223	137839	171601	176957	212599	267088	342951	390239	432848	458856	504562	512631	561144	605983	618864	618934
3942	19224	137844	171602	177359	212985	267197	343451	390242	432849	462369	504563	512632	561145	605986	618865	618936
3947	19225	137847	171603	177360	214155	267741	343452	390243	432850	464873	504564	512633	561146	605990	618867	618937
3949	19226	137848	171605	177361	217946	267942	344349	390244	432852	466922	504565	512634	561147	605991	618868	618938
3951	19228	137856	171606	178885	218036	269482	344353	390245	432853	466923	504566	512635	601338	605995	618869	618939
4421	19230	163221	171607	178886	218199	271331	344437	390246	432855	478364	504567	512636	605911	605996	618870	618940
4832	19231	163222	171608	178887	220169	271334	344438	390247	432856	478365	504568	512637	605912	605999	618872	618941
5732	20149	164284	171609	179260	220171	271337	344439	390248	432857	478367	504569	512638	605913	606003	618873	618942
5739	20151	164465	171610	179263	220338	271753	344440	390251	432858	481612	504570	512639	605914	606004	618876	618943
5740	20206	164670	171611	179259	220789	275410	344441	390252	432861	481614	504571	512640	605915	606005	618877	618945
5754	21694	164679	171612	179921	220790	275411	344442	390253	432862	482412	504572	512641	605916	606006	618878	618946
7730	21695	164743	171613	181753	220791	277741	344443	390257	432864	482463	504573	512644	605917	606015	618879	618947
7731	21696	164819	172839	181756	221440	279463	344444	390258	432866	483341	504813	518848	605918	606016	618880	618948
7735	21698	164950	172840	181910	222243	279465	351139	390259	432868	483342	504814	518849	605919	606017	618882	618949
7736	21761	164952	172841	181940	222244	279469	355053	390260	432870	483344	504815	518850	605920	606018	618883	618950
7737	22250	165029	172842	182188	222782	279807	357835	390261	432871	487424	504816	518851	605921	606019	618884	618951
7739	22386	165046	172843	182189	222783	283899	357837	390263	432872	489752	506461	518852	605922	606021	618885	618952
7740	23007	165499	172844	182190	222985	283902	357840	390265	432873	489753	506462	518853	605923	606022	618886	618953
7741	23008	167043	172845	182192	222986	285603	357841	390266	432874	489754	506463	518854	605924	606024	618888	618954
7742	25154	167050	172846	183056	223437	285606	357842	390267	432875	490996	506464	525075	605925	606026	618889	618955
7745	25155	167052	172847	183127	226509	285607	357843	390268	432876	500359	506465	525150	605926	606027	618891	618956
7749	25156	167079	172848	183231	227013	285609	357844	390269	432878	500360	507874	525151	605927	606028	618892	618957
7750	25699	167134	172849	183677	227208	285610	357845	390951	432879	500361	507875	525152	605928	606029	618893	618958
7751	25929	167198	172851	183967	227210	288237	357846	390952	432880	500365	507876	525153	605929	606030	618894	618959
7752	25930	167358	172852	188749	227235	288991	357848	390953	432881	500366	508454	525154	605930	606031	618895	618961
7755	25931	167389	173674	193497	228344	288992	357850	391568	432882	500370	508455	525155	605932	606033	618896	
7758	25932	169315	173892	197086	229309	288993	357853	391569	432883	502331	508457	525156	605933	606034	618897	
7760	25933	169319	174160	200818	233932	288994	357854	391571	432884	504561	508458	525157	605935	606035	618898	
12781	25934	169328	174167	202801	234517	288995	357855	391572	432885	504562	511817	525158	605937	606036	618900	
13334	25935	169334	174172	204567	248778	288996	357856	391573	432886	504563	512336	525159	605938	606038	618901	
13335	25937	169350	174173	204568	249550	289698	357860	392292	432887	504564	512594	525161	605939	606039	618902	
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13358	105340	169394	176924	211977	263085	326598	376064	419136	458846	500359	512619	534541	605970	606060	618920	
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19039	113334	169397	176951	211980	264229	339241	379281	419183	458851	500361	512623	534545	605974	606065	618922	
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