Screening Cucumber for Resistance to Downy Mildew Caused by *Pseudoperonospora cubensis* (Berk. and Curt.) Rostov.

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ABSTRACT

Downy mildew, a foliar disease caused by the oomycete *Pseudoperonospora cubensis* (Berk. and Curt.) Rostov. is one of the most destructive diseases of cucumber (*Cucumis sativus* L.). Moderately resistant cultivars are available, but yield losses are high without the use of fungicides. Higher levels of resistance are needed to reduce the need for fungicides. The objective of this study was to identify new sources of resistance to downy mildew among Plant Introduction accessions from the U.S. National Plant Germplasm System, elite cultivars, and breeding lines of cucumber. A total of 1300 cultigens were tested in Clinton, NC, and Skierniewice, Poland, in 2005 to 2007 under natural field epidemics. The most resistant and susceptible cultigens were further evaluated in replicated experiments in North Carolina and India in 2007 to 2009. Fungicide experiments were run in 2008 and 2009 to identify tolerance, involving weekly applications to one of two sets of material at a location. Results from the retest study confirmed the results of the initial screening. The most resistant cultigens over all environments were PI 605996, PI 330628, and PI 197088. Cultigens have been found that significantly outperform checks in all resistance traits. High yielding and tolerant cultigens have also been identified that could be used in developing improved cultivars.

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Abbreviations: HR, hypersensitive response; RH, relative humidity.

Cucumber (*Cucumis sativus* L.) is the fourth most widely grown vegetable crop in the world after tomato (*Solanum lycopersicum* L. var. *lycopersicum* [syn. *Lycopersicon esculentum* Mill.]), cabbage (*Brassica oleracea* L. var. *capitata* L.), and onion (*Allium cepa* L.) (Tatlioglu, 1993). The People's Republic of China is the world leader in cucumber production, accounting for approximately 62% of the total, followed by Turkey, Iran, the Russian Federation, and the United States (USDA Economic Research Service, 2007). Cucurbit downy mildew, caused by the oomycete pathogen *Pseudoperonospora cubensis* (Berk. and Curt.) Rostov., is a major foliar disease of cucumber (Palti and Cohen, 1980). Most cultivars currently grown in the United States have some resistance. Before a new race of the pathogen appeared in 2004, these cultivars had high resistance. Since then, fungicide spray programs have been

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needed to protect the crop, resulting in increased cost to growers. New sources of resistance could substantially reduce or eliminate fungicide requirements.

Studies on the host range of *P. cubensis* indicate approximately 20 genera, including 50 species in the Cucurbitaceae, are hosts. A total of 19 host species are in the genus *Cucumis* (Palti and Cohen, 1980; Lebeda, 1992a; Lebeda and Widrlechner, 2003). In addition to cucumber, other economically important hosts of *P. cubensis* are melon (*Cucumis melo* L.), watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai], and squash (*Cucurbita* spp.) (Whitaker and Davis, 1962). Epidemics of downy mildew on the genus *Cucumis* have been observed in over 70 countries worldwide (Palti, 1974; Cohen, 1981). Between 1982 and 1988 the estimated incidence of downy mildew on cucumbers in North Carolina was 30% (St. Amand and Wehner, 1991). The average value (US$) loss per year was 2.9% based on yield and quality reduction. Cucumber yield losses from downy mildew remained minimal compared to other diseases until 2004 when a more virulent form of *P. cubensis* caused a 40% loss for cucumber growers (Colucci et al., 2006). The new strains of *P. cubensis* continue to infect cucumber in most production areas in the United States. These losses make it a major threat to cucumber production in the United States.

The cucurbit downy mildew pathogen is an obligate parasite and, with the rare exception of oospore production, can only survive and reproduce on living host tissue (Bains and Jhooty, 1976a). Environmental conditions affect overwintering capacity as well as disease development and intensity (Cohen, 1977). In production regions where conditions are too harsh for *P. cubensis* to survive all year, the pathogen is introduced through the spread of sporangia in wind and storms originating in warm regions where the pathogen can overwinter on wild and cultivated hosts (Bains and Jhooty, 1976a). In 2006 and 2007, *P. cubensis* was reported in greenhouse cucumber operations in Ontario, Canada, and there is concern that this could be another source of inoculum, primarily when the disease is not well controlled (Hausbeck, 2007). Downy mildew has been a serious problem in Poland since 1985 and was considered to be a major limiting factor for cucumber production in that country (Rondomanski, 1988).

Symptoms of cucumber downy mildew generally occur only on the foliage. Infection first appears as small water soaked lesions on the underside of leaves. Lesions are often angular, being bound by leaf veins, and turning chlorotic to varying degrees. Sporulation occurs on the undersides of the leaves. Chlorotic lesions eventually turn necrotic. Eventually the entire leaf will become necrotic and die. Symptoms vary depending on relative susceptibility of the cultigens. The most resistant cultigens exhibit a hypersensitive response (HR) with small necrotic or chlorotic flecks and sparse sporulation, while the most susceptible cultigens are highly chlorotic and necrotic. The HR type resistance was first described by Barnes and Epps (1954) in cucumber PI 197087, from a single resistance gene *dm-1*. Resistance from PI 197087 was used intensively in breeding new cultivars, and most current cultivars are thought to have some resistance derived from PI 197087. This resistance proved effective for many years but has since been overcome. *P. cubensis* has high evolutionary potential and qualitative resistance is generally easily defeated. Bains (1991) described four categories of lesion type: 1. faded green to dull yellow lesions, size restricted, and slow necrosis, 2. yellow spots or flecks, nonangular, slow growing, and slow necrosis, 3. bright yellow, large, angular, fast growing, susceptible type, and high sporulation, and 4. necrotic spots or flecks, nonangular, little chlorosis, and HR type. Most cultivar's lesions are best described as category 3 (A.D. Call, unpublished data, 2009). The determinate pickle 'M 21' resembles category 1 and 'Heidan #1' shows lesion type 2.

Environmental conditions play a fundamental role in disease intensity (Cohen, 1977). Leaf wetness is critical for infection to occur, with sporangia requiring free moisture to germinate, but temperature determines the rate of disease. Sufficient leaf moisture can be supplied by rainfall, dew formation, or irrigation. The ideal temperature for sporulation and subsequent infection is 15°C, but a range between 5 and 30°C will suffice. The pathogen generally thrives in warm humid regions. Variability in the pathogen population may also play a role in cucumber response to downy mildew. Several races of *P. cubensis* have been reported in differential test studies (Palti, 1974; Bains and Jhooty, 1976b; Inaba et al., 1986; Angelov et al., 2000; Shetty et al., 2002). Six pathotypes of *P. cubensis* have been reported based on their compatibility with specific host genera (Thomas et al., 1987; Cohen et al., 2003). Horejsi et al. (2000) stated that no evidence for race differences in the U.S. and European populations of *P. cubensis* exist. Shetty et al. (2002) proposed that at least two races of downy mildew exist, the race in the People's Republic of China and India being distinct from the race present in the United States and Poland. Shetty et al. (2002) also stated that there is no evidence for race differences between the United States and Poland. However, recent studies indicated that European populations of *P. cubensis* are highly variable and may have many pathotypes (Lebeda and Urban, 2004). In the United States, *P. cubensis* does not seem to be as variable. However, historical (Barnes and Epps, 1954) and recent (Holmes et al., 2006) epidemics suggest that the pathogen has the potential to evolve. In the United States, cultivars previously resistant to downy mildew are still resistant to the new strain but at a lower level. Now, resistant cultivars must be used in combination with fungicides for effective control of the disease. Strains of *P. cubensis* resistant to fungicides have been reported (Reuveni et al., 1980), and new sources of genetic host resistance are in high demand.

Wehner and Shetty (1997) examined downy mildew resistance in the U.S. germplasm collection of cucumbers, including cultivars, breeding lines, landraces, and Plant Introduction accessions from around the world, hereafter referred to as cultigens. They reported that in North Carolina, the most resistant cultigens were of U.S. origin and were primarily elite cultivars and breeding lines. Resistance from those cultigens traced back to PI 197087, which was originally identified as resistant by Barnes and Epps (1954). Interestingly, PI 197087 was found to be only intermediate in resistance in their screening studies, indicating a possible change in the Plant Introduction accession since its original use in breeding. Staub et al. (1989) screened the germplasm collection for reaction to *P. cubensis*. Cotyledons were inoculated 3 to 4 d after emergence, incubated at 100% relative humidity (RH) and 20°C for 48 h, and rated 7 to 8 d after inoculation. The source of inoculum was not stated. Plants were rated only as resistant or susceptible, with susceptible being defined as having strong chlorosis. They found that 6.2% of the 753 accessions tested were resistant to downy mildew and 7.2% were susceptible. The remaining accessions were segregating for resistance. Of the resistant accessions, 34% were from the People's Republic of China, 28% from Japan, and 3% from India. Dhillon et al. (1999) tested 217 cultigens for downy mildew resistance in northern India, using natural infestations in the field. They reported that five of the nine most resistant cultigens were of Japanese origin, two were Indian landraces, and two were European. Neykov and Dobrev (1987) also reported that the most resistant cultivars were of Asian origin, mostly from Japan, followed by India and the People's Republic of China. In 1992 (Lebeda, 1992b) and 1994 (Lebeda and Prasil, 1994), 303 and 155 cucumber cultigens, respectively, were tested under controlled conditions for downy mildew resistance. Little resistance was reported in these tests. However, they suggested that some cultivars, despite doing poorly in the greenhouse tests, had a high degree of field resistance.

Cucumber cultivars resistant to downy mildew have been developed (Sitterly, 1973; Wehner and Shetty, 1997) over the past 50 yr. However, cultivars in the United States have been less resistant since 2004. We were interested in identifying higher levels of resistance in the germplasm collection, perhaps from diverse geographic regions, that could be combined to develop cultivars having higher resistance to the new form of the disease. We were also interested in evaluating the 352 accessions added to the germplasm collection since the previous screening studies in 1989. Therefore, the objective of this study was to evaluate the available UDSA Agriculture Research Service (USDA-ARS) cucumber germplasm collection for field resistance to downy mildew in North Carolina and Poland using commercial cultivars and breeding lines as checks.

MATERIALS AND METHODS

Location and Seed Sources

Germplasm Screening

Field studies were conducted at the Horticultural Crops Research Station in Castle Hayne, NC, and at the Research Institute of Horticulture in Skierniewice, Poland, during the summers of 2005 to 2007. All cucumber Plant Introduction accessions were obtained from the North Central Regional Plant Introduction Station in Ames, IA. Countries from which accessions in the collection originated were Afghanistan (16), Albania (one), Australia (three), Belgium (one), Bhutan (four), Brazil (two), Bulgaria (one), Canada (seven), the People's Republic of China (213), Czech Republic (14), Denmark (three), Egypt (22), Ethiopia (two), France (seven), Georgia (three), Germany (five), Greece (one), Hong Kong (four), Hungary (21), India (201), Indonesia (one), Iran (63), Iraq (one), Israel (nine), Japan (63), Kazakhstan (two), Kenya (one), Korea, South (16), Lebanon (four), Macedonia (one), Malaysia (two), Mauritius (one), Moldova (two), Myanmar (two), Nepal (six), Netherlands (40), New Zealand (two), Oman (three), Pakistan (14), Philippines (four), Poland (24), Puerto Rico (five), Russian Federation (60), Spain (70), Sri Lanka (one), Sweden (four), Syria (14), Taiwan (12), Tajikistan (one), Thailand (two), Turkey (171), Ukraine (seven), United States (61), United Kingdom (three), Uzbekistan (six), Yugoslavia (66), Zambia (six), and Zimbabwe (two). Nineteen cucumber cultivars ranging from moderately resistant to highly susceptible were used as reference entries for downy mildew infection. Check cultivars were Calypso (North Carolina State University, Raleigh, NC), Coolgreen (Seminis Vegetable Seeds, Inc., St. Louis, MO), Dasher II (Seminis), Gy 4 (North Carolina State University), Homegreen #2 (USDA-Wisconsin, Madison, WI), H-19 (University of Arkansas, Fayetteville, AR), LJ 90430 (USDA-La Jolla, La Jolla, CA), M 21 (North Carolina State University), M 41 (North Carolina State University), Marketmore 76 (Cornell University, Ithaca, NY), National Pickling (National Seed Storage Laboratory, Fort Collins, CO), Poinsett 76 (Cornell University), Slice (Clemson University, Clemson, SC), Straight 8 (National Seed Storage Laboratory), Sumter (Clemson University), Tablegreen 72 (Cornell University) TMG-1 (the People's Republic of China), WI 2757 (USDA-Wisconsin), and Wisconsin SMR 18 (Wisconsin Applied Ecological Services, Madison, WI).

Germplasm Retest

The 40 most resistant and 10 most susceptible cultigens were tested under field and greenhouse (2007 only) conditions in North Carolina and field conditions in Bangalore, India (2007 only). Twenty additional cultigens of interest were added in 2008 and 2009. Controlled experiments were conducted in greenhouses at the Horticulture Field Laboratory at North Carolina State University in Raleigh, NC. Field experiments were conducted at the Horticultural Crops Research Stations in Clinton, NC, and Castle Hayne, NC, and at the Indian Institute of Horticultural Research, in Bangalore, India. Countries from which plant accessions originated were Czech Republic (one accession), Egypt (two accessions), India (14 accessions), Iran (one accession), Japan (three accessions), Korea, South (one accession), Lebanon (one accession), Pakistan (one accession), Philippines (two accessions), the People's Republic of China (22 accessions), Puerto Rico (one accession), the Soviet Union (two accessions), Syria (one accession), Taiwan (three accessions), Turkey (three accessions), and the United States (12 accessions). Plant Introduction accessions of *Cucumis* were obtained from the North Central Regional Plant Introduction Station in Ames, IA. Twenty-two cucumber cultivars ranging from moderately resistant to highly susceptible were used as checks. These include the 19 cultivars used in the screening, with the exception of M 41 (North Carolina State University) and the addition of 'Ashley' (Clemson University), Gy 57u (North Carolina State University), Heidan #1 (the People's Republic of China), and 'NongChen #4' (the People's Republic of China).

Inoculation Procedure

In the field, plots were exposed to natural epidemics in the course of the growing season. Susceptible cultivars Straight 8 (2008 only) and Coolgreen were used in borders around the field and spreader rows spaced every ninth row to monitor and increase inoculum in the field. Epidemics were encouraged using overhead irrigation. Plots were planted when border rows displayed major symptoms of disease.

For the greenhouse retest, cucumber leaves infected with *P. cubensis* were collected from fields in Clinton, NC, that had not been sprayed with fungicides. Leaves were collected in the morning, placed in plastic bags (Ziploc brand, SC Johnson, Racine, WI) and stored in a cooler with ice, and transported to the laboratory where five heavily infected leaves were soaked in distilled water and rubbed gently with a glass rod to dislodge sporangia. The spore suspension was filtered through four layers of cheesecloth to remove dirt and debris and the concentration was determined with the use of a hemacytometer (Bright-Line model, Reichert Scientific Instruments, Cambridge Scientific, Watertown, MA). The suspension was adjusted to a final concentration of 10,000 sporangia mL^{-1}. Immediately before inoculation, Tween 20 (0.06 g L^{-1}) (Sigma-Aldrich LLC, St. Louis, MO) was added to the inoculum suspension to keep the spores well dispersed in the solution.

In the greenhouse, plants were inoculated at the one- to two-true leaf stage with a hand pump spray bottle (1-L size, Delta Industries, King of Prussia, PA). Inoculum was applied to upper and lower leaf surfaces of cotyledons and true leaves until run-off. Flats were placed in a dark growth chamber with humidifiers (100% RH, 20°C) for 48 h to maximize sporulation. Flats were then moved to a greenhouse (25 to 45°C) and plants were evaluated for disease 8 to 10 d after inoculation.

Field Ratings

Disease was evaluated as chlorotic lesions, necrotic lesions, degree of stunting, lesion size (2008 and 2009 only), and sporulation. Some traits were not evaluated for all years, locations, or ratings. Chlorosis, necrosis, and sporulation were rated on a 0 to 9 scale based on percentage of symptomatic leaf area (0 represents 0%, 1 represents 1–3%, 2 represents 3–6%, 3 represents 6–12%, 4 represents 12–25%, 5 represents 25–50%, 6 represents 50–75%, 7 represents 75–87%, 8 represents 87–99%, and 9 represents 100%) as described by Jenkins and Wehner (1983). The lesion size rating was designed to identify accessions showing HR. Lesion size was rated broadly into three categories: small = small necrotic flecks (possibly HR), medium = medium chlorotic and necrotic lesions, and large = large angular lesions that were mostly chlorotic. In the field, lesion size was rated numerically as 1, 5, and 9 for small, medium and large, respectively. Therefore the means of lesion size data are not very useful, except in identifying cultigens with means at low and high extremes. In this case, nonparametric analysis should be used, because for means in the middle of the range it cannot be determined if they were a mix or consistently rated in the middle without looking at the data. We will likely incorporate this technique in the future, but for this study, our main focus was identifying cultigens that showed smallest lesion size, indicated by the smallest overall mean.

Disease ratings were started when most test plots showed disease. Chlorosis and necrosis were rated visually as the percentage of leaves displaying each symptom. Plots were rated using all diseased leaves on all plants. Stunting was rated as reduction in plant size relative to the larger cultivars used as checks. It is a rating indicating the ability to grow large and branched. Therefore, even without disease, different genotypes would have different stunting ratings. Nevertheless, it allows us to identify those cultigens that remain large and highly branched under a disease epidemic. Stunting was rated on the last three dates only in 2008, due to the difficulty of rating that trait when plants were small. Lesion size was added as a disease component in 2008, with data taken on the second and third ratings (out of six total) only.

It is difficult to separate cultigens into resistant and susceptible classes since there were no obvious gaps in their distribution over the 0 to 9 scale. However, plant breeders often use those terms for quantitative traits. In keeping with that practice and to remain consistent with previous studies, cultigens having ratings less than 3.0 were classified highly resistant, from 3.1 to 4.0 moderately resistant, from 4.1 to 6.0 intermediate, from 6.1 to 7.0 moderately susceptible, and from 7.1 to 9.0 highly susceptible.

Experiment Design

Germplasm Screening

The experiment was an augmented design with two locations (Poland and North Carolina) and 3 yr (2005 to 2007). Year was treated as a random effect and location as fixed. Data were analyzed using the General Linear Model, Means and Correlation procedures of the Statistical Analysis System (SAS Institute, 2008).

Field tests were performed in 2005, 2006, and 2007 in Poland and North Carolina. Fertilizer was incorporated before planting at a rate of 90–39–74 kg ha^{-1} (N–P–K) with an additional 34 kg N ha^{-1} applied at the vine-tip-over stage (four to six true leaves). Seeds were planted by hand on raised, shaped beds with centers 1.5 m apart and plots 1.5 m long. Plots were later thinned to six plants at the first true leaf stage. Irrigation was applied when needed to provide a total of 25 to 40 mm per week and a tank mix of Curbit (Ethalfluralin) (Loveland Products, Inc., Loveland, CO) and Command (Clomazone) (FMC Corporation, Philadelphia, PA) was applied preplant for weed control using the manufacturer's specified rates. Plots were separated at each end by 1.5 m alleys. Field plots were evaluated three times (on a weekly basis) after symptoms of downy mildew developed.

Germplasm Retest

Selections were based on mean data over locations from the germplasm screening in 2005 and 2006. The 40 most resistant and 10 most susceptible cultigens were tested under field and greenhouse (2007 only) conditions in North Carolina and field conditions in Bangalore, India (2007 only). There were 20 cultigens of interest added in 2008 and 2009. Seeds for some cultigens were in limited supply and not grown in all years and cultigens were added as they became available in subsequent years. All cucumbers were grown using recommended horticultural practices as summarized by Schultheis (1990). Fertilizer was incorporated before planting at a rate of 90.6–90.6–90.6 kg ha^{-1} (N–P–K) with an additional 33.6 kg N ha^{-1} applied at the vine-tip-over stage (four to six true leaves). Weeds were controlled as in the screening (see above). Field layout was also the same as in the screening. Ten seeds were hand planted into each plot.

In greenhouse tests, seeds were pregerminated for 36 to 48 h to ensure maximum plant stand. Seeds were planted in 9 by 4 flats filled with a mix of peat, vermiculite, and perlite (Sun Gro Horticulture, Metromix 200, Bellevue, WA). Greenhouse temperature was 45/25°C day/night. Greenhouse ratings were taken once, 8 to 10 d after inoculation, on four plants per cultigen.

In 2008 and 2009, the retest experiment at the Horticultural Crops Research Station in Clinton, NC, was modified to a split block with the addition of a fungicide treatment for control of downy mildew to allow the measurement of tolerance (the ability to produce yield under epidemic disease). Fungicides were whole plot with replications within fungicides. A fungicide treatment was applied weekly to one field as a mixture of Bravo (Syngenta Crop Protection, LLC, Greensboro, NC) and Previcure Flex (Bayer CropScience, Research Triangle Park, NC) alternating with Mancozeb (DuPont Agricultural Products, Wilmington, DE) and Tanos (DuPont Agricultural Products), beginning at true leaf stage. In 2009, an additional no-fungicide planting was done at the Horticultural Crops Research Stations in Castle Hayne, NC.

The 92 cultigens that were the most resistant or most susceptible for downy mildew resistance were grown under heavy downy mildew incidence in the field. Some cultigens were not planted in all years because of seed limitations, and some cultigens were added to fill missing spots. Cultigens not grown in all environments, years, or locations, were not included in the analysis over environment, years, or locations. They were only included if represented fully. Plots were rated weekly for disease (4, 5, and 6 ratings in 2007, 2008, and 2009, respectively), with yield data (two harvests) taken in 2008 and 2009 only. The experiment was a randomized complete block design with four replications in each environment. Data were analyzed using the General Linear Model, Means, and Correlation procedures of SAS (SAS Institute, 2008). Data were analyzed over eight environments from 2007 to 2009 (2007: Castle Hayne, NC; Horticulture Field Lab; North Carolina State University, Raleigh, NC; and Bangalore, India; 2008: Clinton, NC; and Clinton, NC, with fungicide; 2009: Castle Hayne, NC; Clinton, NC; and Clinton, NC, with fungicide).

RESULTS

Germplasm Screening

A significant cultigen effect for North Carolina, Poland, and the two locations combined was found by ANOVA (data not shown). There was also a significant cultigen × location interaction. The use of multiple years and locations is important for identification of a high level of resistance due to environmental influence of overall disease and disease progress. The mean downy mildew rating at 5 wk after planting in North Carolina was 4.8, 5.2, and 5.4 for each test in 2005, 2006, and 2007, respectively. The downy mildew rating at 5 wk after planting in Poland was 6.2, 7.7, and 5.3 for each test in 2005, 2006, and 2007, respectively.

The *F* ratio for cultigen at each location over all years was highest for the rating taken 5 wk after planting, the last ratings of the season. That rating had a higher *F* ratio and a lower CV than the ratings at 3 or 4 wk after planting, so we considered that the most useful for distinguishing among cultigens. Ratings taken at 5 wk after planting are also useful indicators of how well cucumber plants are responding to downy mildew before fruit set. Cucumber cultigens, including resistant ones, appear to become more susceptible after fruit set (Barnes and Epps, 1954).

Data were summarized as the mean of all ratings taken at 5 wk after planting for each location and combined over locations as well as standard deviations and number of missing observations (Table 1). Cultigens were ranked from most to least resistant based on ratings taken 5 wk after planting. The LSD (5%) for downy mildew resistance rating was 1.79 in North Carolina, 3.14 in Poland, and 1.60 for locations combined. The LSD was higher in Poland than in North Carolina. The extra variation may have been due to Fusarium wilt (caused by *Fusarium oxysporum* f. sp. *cucumerinum*) and angular leaf spot (caused by *Pseudomonas syringae* pv. *lachrymans*) present in addition to downy mildew. Differences in disease severity between locations and among replications may have resulted in higher variability.

Cultigens resistant over multiple environments are preferred over those that are resistant in only one environment, so all cultigens were ranked using the combined results from Poland and North Carolina (Table 1). There were 81 highly resistant, 130 moderately resistant, 406 intermediate, 408 moderately susceptible, and 271 highly susceptible cultigens. Data from Poland showed a greater range of mean downy mildew ratings compared with data from North Carolina (0.3 to 9.0 compared with 1.0 to 7.3, respectively). The most resistant Plant Introduction accessions were not significantly more resistant than the most resistant commercial cultivars used in Poland or North Carolina.

Germplasm Retest

Over the six environments not receiving a fungicide treatment, a significant cultigen and location effect was found for chlorosis, necrosis, and stunting (data not shown). Significance was also found in chlorosis for year, cultigen × year, cultigen × location, and cultigen × year × location. For necrosis and stunting, significance was found for cultigen × year, year × location, and cultigen × location. The mean squares for these

Table 1. Cucumber germplasm screening ranked from most to least downy mildew resistant by rating three (taken 5 wk after planting) with standard deviation, means of rating three in North Carolina and Poland, and number of missing replications.

Rank	Cultigen	Seed source	Rating 3 combined†	SD	Rating 3 North Carolina‡	Rating 3 Poland§	Missing replications¶
			Twenty most resistant				
1	PI 197088	India	1.0	1.1	1.7	0.3	0
2	Ames 2354	United States	1.0	0.9	1.7	0.3	0
3	PI 267942	Japan	1.0	–	–	1.0	5
4	Ames 2353	United States	1.0	0.9	1.7	0.3	0
5	PI 197085	India	1.2	1.2	1.3	1.0	0
6	PI 330628	Pakistan	1.2	1.2	2.0	0.3	0
7	PI 432878	PRC#	1.3	1.2	1.7	1.0	0
8	PI 618931	PRC	1.3	1.2	2.0	0.0	3
9	SC 50	United States	1.3	1.2	2.3	0.3	0
10	PI 605996	India	1.3	1.0	1.0	1.7	0
11	PI 321008	Taiwan	1.5	1.4	2.7	0.3	0
12	PI 432875	PRC	1.5	1.2	2.0	1.0	0
13	Poinsett 76	Cornell Univ.	1.6	1.3	3.0	0.7	1
14	PI 432882	PRC	1.7	1.4	2.3	1.0	0
15	PI 618937	PRC	1.7	1.4	2.3	1.0	0
16	PI 605924	India	1.7	1.5	2.7	0.7	0
17	Ames 7752	United States	1.7	1.5	2.5	0.0	3
18	PI 197086	India	1.8	1.3	1.7	2.0	0
19	PI 321009	Taiwan	1.8	2.6	3.3	0.3	0
20	PI 432886	PRC	1.8	1.7	2.7	1.0	0
			Ten least resistant				
1287	PI 344350	Turkey	7.8	1.3	6.7	9.0	0
1288	Ames 19225	Russian Fed.	7.8	1.0	7.3	8.3	0
1289	PI 226509	Iran	8.0	1.4	6.5	9.0	1
1290	PI 169385	Turkey	8.0	2.0	5.0	9.0	2
1291	PI 212599	Afghanistan	8.0	1.3	7.0	9.0	0
1292	PI 169328	Turkey	8.0	1.7	6.0	9.0	3
1293	PI 172846	Turkey	8.0	1.1	7.0	9.0	0
1294	PI 137848	Iran	8.2	1.1	7.0	9.0	1
1295	PI 172852	Turkey	8.3	1.2	–	8.3	3
1296	PI 284699	Sweden	9.0	–	–	9.0	5
LSD (5%)			1.60		1.79	3.14	

†Mean of all ratings taken at week 5 after planting for North Carolina and Poland during 2005, 2006, and 2007.

‡Mean of ratings taken at week 5 after planting for North Carolina during 2005, 2006, and 2007.

§Mean of ratings taken at week 5 after planting for Poland during 2005, 2006, and 2007.

¶Each year and each location is considered a replication for a total of six replications.

#PRC, the People's Republic of China.

effects, although significant, were generally far less than the significant cultigen, location, and year mean squares.

A subset of the data having four environments (Clinton, NC, with and without fungicides in 2008 and 2009) was analyzed to determine the effect of fungicide on disease and yield traits and to identify tolerance (the ability to produce yield under a disease epidemic). A significant cultigen and fungicide effect was found for chlorosis, necrosis, and stunting. Significance was also found for all traits for cultigen by year, cultigen by fungicide, and cultigen by year by fungicide.

In this subset of the data, all effects for total yield (year, fungicide, fungicide by year, replication within fungicide by year, cultigen, cultigen by year, cultigen by fungicide, and cultigen by fungicide by year) were significant at $p < 0.001$. Significance in higher order interactions may have been due to the large number of degrees of freedom available for testing the effects (data not shown). The largest effects on yield traits were year, fungicide, and fungicide by year. Because this was a disease study, it was designed to encourage disease, so yield from the checks was generally low and variable compared to a grower field where the system is optimized for high yield. A significant fungicide effect was found for total and marketable yield and fruit size but not for percent early fruit. The cultigen effect on yield was significant for all yield traits, but the mean squares were far less than the year and fungicide effects. This is also likely due to the encouragement of disease versus optimizing for yield.

The F ratio and CV were examined for the means of all component ratings and the means of each weekly rating taken for each environment (data not shown). For chlorosis and necrosis, results indicated that the means of all ratings for each trait in each environment were most useful for determining differences among cultigens. These ratings had a higher F ratio and lower CV than the means of any of the weekly ratings. The F ratio and CV for stunting means over all ratings were not as consistent. For Bangalore, India, in 2007 and all environments in 2008 and 2009, stunting ratings taken on the final date had the highest F ratio and lowest CV. This is likely because differences among plots become progressively more apparent as the plants grew larger. Stunting data were taken on only two early ratings in Castle Hayne, NC, in 2007 and not at all in the greenhouse tests. These results are important for future studies, as they indicate that stunting ratings need only be taken on the final one or two rating dates, saving time and labor.

All correlations were calculated using the Pearson product-moment correlation and Spearman rank correlation. Correlations of environments for disease were calculated using the mean chlorosis rating for each environment (data not shown). All combinations were significant at $p = 0.001$ with the exception of the Spearman correlation of Bangalore, India, in 2007 with the greenhouse tests at the Horticulture Field Laboratory in 2007. This combination had a correlation of 0.44, which was significant at $p = 0.01$. Despite some unusual results in the greenhouse, correlation between the field and greenhouse germplasm retests was moderate to high, with Pearson correlations ranging from $R^2 = 0.60$ to 0.78 ($p < 0.001$) for all other environments.

Correlation of environments for yield was analyzed using the total yield (Mg ha^{-1}), marketable yield (Mg ha^{-1}), and percent early fruit for fungicide and no-fungicide environments in Clinton, NC, in 2008 and 2009 (data not shown). Total yield at Clinton, NC, with fungicide in 2008 was not correlated with either environment in 2009. For marketable yield, the Spearman rank correlation was significant ($p = 0.001$) between Clinton, NC, with fungicide in 2008 and both fungicide and no-fungicide 2009 environments. The Pearson correlation was not significant. All environments were significantly correlated (at least $p = .05$) for percent early fruit using the Pearson correlation. The Spearman correlation did not find significant correlation between data from Clinton, NC, with fungicide in 2008 and both environments in 2009.

Correlation of disease traits was measured using the mean of all ratings over environments (data not shown) for chlorosis, necrosis, and stunting. All correlations were significant at $p < 0.001$. Chlorosis and necrosis were highly correlated for the Pearson and Spearman tests (0.87 and 0.81, respectively), indicating they are likely the same trait. Both were also significantly correlated with stunting but to a lesser extent at 0.35 and 0.34 for chlorosis and 0.42 and 0.36 for necrosis, respectively. Correlation of disease traits was also measured using the mean of all ratings over the subset of environments containing fungicide and no-fungicide treated Clinton, NC, data from 2008 and 2009 (Table 2). Chlorosis and necrosis were highly correlated for the Pearson and Spearman tests (0.90 and 0.83, respectively). It is likely these are the same trait with the environmental conditions affecting the phenotype. Stunting was significantly correlated with chlorosis (0.37 and 0.34), necrosis (0.34 and 0.30), and lesion size (0.53 and 0.56). This indicates stunting ratings are related to tissue lesions, but other factors influence stunting as well, namely differences in genotypes. Lesion size was significantly correlated with chlorosis (0.65 and 0.69), necrosis (0.61 and 0.62), and stunting (0.53 and 0.56). In the field it was observed that most susceptible cultigens, those showing a high incidence of chlorosis and necrosis (7 to 9 ratings), also generally had large lesions. Most cultigens with small lesions were moderately to highly resistant (1 to 5 ratings for chlorosis and necrosis).

To compare environments, data were standardized to a mean of 4.5 and standard deviation of 1.5. A combined best rating was devised that consisted of the means of the best weekly ratings for chlorosis, necrosis, and stunting in each environment. No stunting data were taken in greenhouse tests. Greenhouse data are presented separately. The *F* ratio and CV were examined for the means of each weekly rating taken for each environment do determine the combined best rating. The best rating is defined as the rating with the highest *F* ratio and lowest CV, which we consider most useful for distinguishing among cultigens. For example, in 2008, for both environments, the combined best rating was the mean of the chlorosis, necrosis, and stunting data taken on the fifth weekly rating. In 2009, for all environments, the combined best rating was the mean of the fourth weekly rating for chlorosis and necrosis and the fifth weekly rating for stunting. The combined best rating was determined each year for all North Carolina locations combined, so the same ratings at each location were used.

Table 2. Pearson product-moment correlation coefficients (above diagonal) and Spearman rank correlation coefficients (below diagonal) of disease traits in Clinton, NC, with and without fungicide in 2008 and 2009.†

Trait	Chlorosis‡	Necrosis§	Stunting¶	Lesion size#
Chlorosis		0.90***	0.37***	0.65***
Necrosis	0.83***		0.34***	0.61***
Stunting	0.34**	0.30***		0.53***
Lesion size	0.69***	0.62***	0.56***	

**Significant at the 0.01 probability level.

***Significant at the 0.001 probability level.

†Data are from four replications.

‡Data are mean of all chlorosis ratings.

§Data are mean of all necrosis ratings.

¶Data are mean of all stunting ratings.

#Data are mean of all lesion size ratings.

Cultigens showing high resistance for all traits in all environments would be most useful, so the combined best standardized ratings for chlorosis, necrosis, and stunting were used to compare performance in the seven field environments (Table 3). Among the accessions that were tested in every environment, the top performing cultigens were PI 605996, PI 330628, PI 197088, PI 197086, and PI 605924. The mean combined ratings for these cultigens ranged from 2.8 to 3.0. The highest performing checks were Slice and M 21, with standardized mean best combined ratings over all environments of 4.0 and 4.1, respectively. Some cultigens were not tested in all environments. The greenhouse results were variable and some cultigens did not exhibit typical responses (data not shown). For example, Straight 8, a susceptible check cultivar, was rated highly resistant. Some of the results may be explained by high greenhouse temperature (45°C) during the test. The mean ratings for the greenhouse test ranged from 0.6 to 6.3 with an LSD (5%) of 1.70. Field ratings at Castle Hayne, NC, in 2007 ranged from 0.5 to 7.2 with an LSD (5%) of 1.31.

Table 3. Combined best downy mildew disease ratings in environments.[†]

Location	All	2007			2008		2009	
		C.Hayne[‡]	Bang.[§]	Clint.[¶]	Clint.[#]	C.Hayne[†]	Clint.[††]	Clint.[‡‡]
Fungicide[§§]:	–	N	N	N	F	N	N	F
Cultigen								
PI 605996[¶¶]	2.8	3.1	2.9	3.2	3.4	3.6	2.4	2.7
PI 330628	2.9	2.1	3.6	2.9	3.4	2.4	1.7	2.2
PI 197088	2.9	2.5	3.5	3.2	3.3	1.9	1.6	2.3
PI 605928	3.0	–	–	3.3	3.7	4.0	3.6	4.0
PI 197086	3.0	2.3	3.4	3.4	3.8	2.5	1.9	3.3
PI 605924	3.0	3.4	3.3	3.9	4.0	3.7	3.5	3.5
PI 197085	3.1	2.1	3.2	3.3	4.0	3.2	2.6	2.7
Ames 20089	3.3	–	–	–	–	3.7	3.1	2.9
PI 618893	3.3	4.2	2.8	3.8	3.8	–	–	–
PI 618907	3.4	–	–	3.6	4.0	4.1	3.9	3.3
PI 618861	3.5	–	–	3.7	4.2	3.6	3.7	3.7
PI 432886	3.5	4.1	2.8	4.3	3.7	3.7	2.8	3.0
PI 432878	3.7	4.9	–	3.7	3.2	3.1	3.1	2.7
Gy 57u	3.7	–	–	–	–	3.2	2.9	3.2
PI 390267	3.7	3.8	3.5	4.1	4.0	3.8	2.9	3.3
PI 432875	3.7	4.8	2.9	4.3	3.9	2.9	3.3	2.8
Ames 418962	3.7	–	–	–	–	3.7	3.7	3.8
PI 432885	3.7	–	–	–	–	3.6	3.2	2.8
PI 432874	3.8	–	3.0	3.8	3.5	3.4	3.0	2.7
PI 618937	3.8	4.4	3.2	4.7	3.7	4.5	4.5	3.7
PI 432876	3.8	–	–	–	–	3.8	2.8	3.3
PI 432884	3.8	4.2	2.8	4.2	3.8	3.5	3.3	3.4
PI 605995	3.8	4.8	5.1	5.1	4.2	3.9	4.4	4.4
PI 606051	3.8	4.9	5.8	4.0	4.2	5.4	4.8	4.4
PI 605932	3.9	3.1	3.7	3.0	3.3	2.9	3.2	3.7
PI 532523	3.9	–	–	6.5	5.0	4.6	5.1	4.4
PI 606017	3.9	4.9	5.0	4.3	4.3	4.7	4.6	4.9
TW-3	3.9	3.5	3.3	3.3	3.5	–	–	–
PI 606019	4.0	6.3	4.6	5.2	4.3	5.5	5.1	5.1
PI 432859	4.0	5.0	3.0	5.2	5.0	4.2	4.5	4.7
PI 606015	4.0	5.1	5.5	4.7	4.0	4.6	4.9	4.6
Ames 2353	4.0	2.2	2.8	3.4	2.9	3.3	3.7	3.6
PI 426170	4.0	3.9	4.4	3.2	3.0	3.8	4.0	3.5
TW-2	4.0	3.3	3.0	3.4	3.5	–	–	–
PI 518849	4.0	5.0	–	4.7	3.3	3.4	4.3	3.1
Slice	4.0	4.3	4.1	2.8	3.8	3.0	3.1	4.3
M 21	4.1	2.2	3.4	3.4	3.0	3.4	3.1	3.4
NongChen #4	4.1	4.3	3.0	5.2	4.8	5.3	4.9	4.4
Ames 2354	4.1	2.8	2.8	3.4	3.5	2.8	3.5	3.8
PI 321008	4.1	4.4	3.9	3.2	4.2	4.5	4.4	3.9
PI 618922	4.2	–	–	2.7	4.1	4.9	4.5	3.4
PI 432877	4.2	–	–	–	–	3.5	3.1	2.9
PI 432882	4.2	–	–	–	–	3.0	3.6	3.5
SC 10	4.2	2.7	4.5	3.6	3.2	3.5	4.3	3.8
PI 605929	4.2	3.7	4.0	3.3	3.5	3.1	4.0	4.0
Model	4.2	–	–	3.3	3.1	4.1	4.0	4.4
Gy 4	4.3	3.4	4.4	3.3	3.2	3.6	4.3	4.8
PI 321009	4.3	4.1	4.0	2.9	4.0	4.1	4.1	4.3
Heidan #1	4.3	4.4	3.4	4.5	4.2	4.5	5.5	4.0
SC 50	4.3	3.6	3.5	3.2	3.2	2.7	3.7	3.8
PI 418963	4.4	4.8	3.4	4.6	3.7	4.9	4.2	5.4
Mariner H-423	4.4	4.3	4.0	5.0	3.5	4.2	4.7	4.1
Poinsett 76	4.5	3.5	3.7	3.6	3.1	3.2	3.6	4.1

Table 3. Continued.

Location	All	2007 C.Hayne‡	2007 Bang.§	2007 Clint.¶	2008 Clint.#	2008 C.Hayne†	2009 Clint.††	2009 Clint.‡‡
Homegreen #2	4.5	4.8	5.5	3.4	3.7	3.8	4.0	4.0
PI 508455	4.5	5.2	3.5	4.8	4.2	5.1	5.7	4.6
TW-1	4.6	5.1	3.4	5.2	5.1	–	–	–
WI 2238	4.6	–	–	–	–	2.9	3.5	3.9
Polaris	4.7	–	–	2.5	3.3	3.5	3.3	3.7
Calypso	4.7	3.4	5.2	3.1	3.4	4.9	4.8	5.2
Marketmore 76	4.7	5.3	5.7	5.3	5.3	4.9	4.4	4.0
PI 618944	4.7	–	–	7.0	4.2	6.0	5.9	5.5
Sumter	4.8	4.4	–	4.3	3.9	4.1	4.8	5.2
TW-4	4.8	4.9	3.0	4.7	5.0	–	–	–
PI 618931	4.8	–	–	1.7	3.1	5.7	5.2	5.2
PI 618955	4.8	–	–	6.1	4.5	4.7	5.4	5.2
Dasher II	4.8	4.7	6.0	4.8	4.5	5.7	5.5	5.2
PI 511819	4.9	–	–	5.9	7.3	6.2	5.2	5.0
Ashley	4.9	5.6	5.3	4.7	4.6	4.6	5.6	4.6
Ames 426169	4.9	–	–	–	.	4.1	3.9	4.6
WI 2757	5.0	–	–	–	.	2.7	3.2	3.5
PI 179676	5.0	–	–	5.7	5.7	5.5	6.0	6.1
PI 267741	5.1	–	5.1	3.7	4.7	4.9	4.7	4.6
H-19	5.3	–	–	–	–	4.3	4.5	4.4
National Pickling	5.3	5.6	6.2	–	–	–	–	–
PR 39	5.4	–	–	–	–	5.6	5.8	5.1
LJ 90430	5.5	–	6.3	–	–	–	–	–
Ashe	5.9	–	–	–	–	5.7	5.9	5.3
Wisconsin SMR 18	6.0	6.6	6.7	7.0	6.9	6.5	6.9	8.2
PI 176523	6.1	5.9	6.5	6.9	7.4	7.0	6.9	7.1
PI 218199	6.2	6.7	6.4	6.1	7.1	6.1	7.1	7.8
PI 211983	6.2	5.4	6.7	6.8	7.6	6.7	7.0	7.0
Straight 8	6.3	5.4	6.5	6.2	7.1	7.0	6.7	6.5
PI 458851	6.3	6.2	7.0	6.7	6.9	6.2	7.1	7.2
PI 525151	6.4	6.4	6.6	6.6	7.4	7.2	6.8	7.0
Ames 23009	6.4	6.2	6.8	6.8	7.3	7.2	7.2	6.7
PI 171601	6.5	5.8	6.8	7.1	7.6	7.5	7.0	7.3
Poinsett	6.5	–	–	–	–	5.6	5.7	4.8
Ames 19225	6.5	6.5	6.0	6.1	4.5	6.4	6.8	6.9
PI 344350	6.7	6.9	6.8	7.4	6.8	7.2	6.9	7.6
Coolgreen	6.7	–	–	6.1	7.2	7.6	7.0	7.2
Ames 25699	6.8	6.9	6.9	6.9	8.3	7.5	7.3	7.6
LSD (5%)	0.7	0.7	0.6	0.7	0.5	0.7	0.6	0.6

†Data are from four replications per location using combined best ratings (chlorosis, necrosis, and stunting) based on *F*-value. Data are standardized to mean of 4.5 and standard deviation of 1.5.

‡Data are from Castle Hayne, NC, in 2007.

§Data are from Bangalore, India, in 2007.

¶Data are from Clinton, NC, in 2008.

#Data are from Clinton, NC, in 2008 with fungicide.

††Data are from Clinton, NC, in 2009.

‡‡Data are from Clinton, NC, in 2009 with fungicide.

§§Weekly application of Previcure Flex (Bayer CropScience, Research Triangle Park, NC) and Mancozeb (DuPont Agricultural Products, Wilmington, DE) alternating with Tanos (DuPont Agricultural Products) and Bravo (Syngenta Crop Protection, LLC, Greensboro, NC). N, no fungicide environment; F, fungicide environment.

¶¶Underlined cultigens are top group from Table 1.

Cultigens tested in Clinton, NC, in 2008 and 2009 with and without fungicide were ranked by their combined best rating (see above) of chlorosis, necrosis, and stunting (Table 4). The most resistant accessions were PI 605996, PI 618893, PI 330628, PI 605924, PI 605928, PI 197086, and PI 197088. These also performed well in the screening and retest experiments run in other environments. Disease incidence data from environments with weekly fungicide treatments of Tanos and Previcur Flex alternating with Bravo and Mancozeb, in Clinton, NC, in 2008 and 2009 showed reduced means over all ratings for chlorosis (3.3 vs. 4.5), necrosis (4.3 vs. 5.5), and stunting (3.6 vs. 4.3) and combined best ratings (3.7 vs. 4.6) compared to the no-fungicide controls. Lesion size showed a slight increase in overall mean in the fungicide environment versus the no-fungicide environments (6.9 vs. 6.7). This difference is very small and likely due to sampling error. In the field, some plots showed different lesion sizes, making them difficult to rate. These differences were generally observed on different parts of the plant, not on the same leaf. The weekly application of fungicide lowered the mean disease rating in the field by approximately 1 point on the 0 to 9 rating scale for Clinton, NC, in 2008 and 2009. The effect on yield was larger (Table 5) with mean total yield increasing from 7.2 to 15.9 Mg ha^{-1}, a 121% increase. Marketable yield increased from 5.1 to 13.4 Mg ha^{-1}, a 163% increase.

Table 4. Downy mildew resistance components for plants tested with and without fungicide at Clinton, NC, from 2008 and 2009.†

Component	Combined‡		Chlorosis§		Necrosis¶		Stunting#		Lesion size††	
Fungicide	None	Fungicide‡‡	None	Fungicide	None	Fungicide	None	Fungicide	None	Fungicide
Mean	**4.6**	**3.7**	**4.5**	**3.3**	**5.5**	**4.3**	**4.3**	**3.6**	**6.7**	**6.9**
Cultigen										
PI 605996	1.8	1.4	2.8	2.0	3.8	3.0	2.0	2.1	4.6	5.7
PI 618893	1.9	1.8	3.8	2.5	5.5	4.2	2.4	2.1	3.5	6.5
PI 330628	2.2	1.4	2.2	1.8	4.3	2.6	2.6	2.1	2.6	3.7
PI 605924	2.3	1.9	3.7	2.7	4.5	4.0	1.9	1.7	4.9	5.8
PI 605928	2.3	2.0	3.5	2.8	4.1	3.6	2.7	2.7	5.5	6.2
PI 197086	2.5	2.4	2.6	2.5	4.4	3.5	2.3	2.5	4.2	4.9
PI 197088	2.5	1.6	2.4	1.8	3.7	3.3	2.9	2.0	4.7	4.3
PI 432875	2.9	2.7	3.8	2.3	5.2	3.5	3.6	4.2	4.3	5.7
PI 618861	2.9	2.9	3.7	2.8	4.3	3.8	3.5	3.6	6.2	5.9
PI 606015	3.0	2.7	4.8	3.2	5.3	4.2	2.7	2.8	5.9	7.4
PI 606019	3.0	2.8	5.1	3.5	5.8	4.3	2.7	2.5	5.5	7.0
PI 606051	3.0	2.3	4.5	3.1	5.0	4.2	3.5	2.4	5.2	7.5
PI 432878	3.1	2.1	3.4	1.9	5.0	3.2	3.6	3.2	3.9	5.6
PI 605995	3.1	2.7	4.7	3.1	5.5	4.4	2.4	2.8	6.8	7.6
PI 606017	3.1	2.5	4.5	3.5	5.3	4.3	2.7	2.1	6.6	7.0
PI 618907	3.1	2.7	3.8	2.5	4.8	3.5	2.3	3.0	4.8	5.1
PI 432874	3.2	2.1	3.4	2.0	4.9	3.3	3.5	3.0	4.6	5.6
PI 432884	3.2	3.1	3.7	2.5	5.1	3.4	4.0	4.0	4.3	6.5
Ames 20089	3.3	1.9	3.1	2.1	4.0	2.8	2.9	2.5	3.8	4.6
PI 390267	3.3	2.5	3.5	2.5	4.9	3.9	4.3	2.8	4.1	5.1
PI 432876	3.3	3.2	2.9	2.5	4.0	3.4	5.6	5.4	4.6	5.6
PI 432882	3.3	4.0	3.6	2.7	4.4	4.1	4.2	3.5	5.3	6.2
PI 432885	3.3	2.8	3.2	2.0	4.2	3.4	4.3	3.1	5.4	5.0
PI 432886	3.3	2.3	3.5	2.3	5.1	3.9	4.4	3.4	4.1	5.7
PI 197085	3.5	2.4	2.9	2.3	5.0	3.6	3.0	2.8	4.4	4.8
PI 518849	3.7	2.6	4.4	2.1	5.6	3.9	3.6	3.1	4.7	6.2
PI 432877	3.8	2.8	3.2	2.1	3.8	3.1	5.7	4.2	6.2	4.4
PI 605932	3.8	3.3	3.1	2.4	4.9	4.0	5.0	3.9	7.5	7.1
PI 618937	3.8	2.3	4.6	2.6	5.7	3.8	3.1	2.8	5.4	7.9
Slice	3.8	3.5	3.0	2.9	5.5	4.6	4.3	3.2	7.8	8.1
PI 532523	3.9	3.4	5.8	3.5	5.6	4.7	2.7	2.2	4.8	5.7
PI 321008	4.0	3.2	3.8	2.9	4.5	3.3	4.5	3.8	7.6	8.0
PI 321009	4.0	3.7	3.6	3.0	4.1	3.7	4.7	5.1	7.7	8.1
PI 418963	4.0	3.8	4.4	3.4	5.1	4.4	4.4	4.1	6.4	8.1
PI 618922	4.0	3.5	3.7	2.6	4.7	3.9	4.3	3.6	4.6	5.9
PI 426170	4.1	3.0	3.6	2.2	5.8	3.9	3.1	2.9	8.3	7.7
PI 489753	4.1	4.0	4.2	3.6	4.7	4.3	3.9	4.3	8.1	7.7
TW-2	4.2	2.9	3.4	2.2	6.1	4.6	4.3	4.3	5.5	5.0
Model	4.3	3.5	3.7	2.7	5.2	3.7	4.2	3.7	8.0	7.2

Table 4. Continued.

Component	Combined‡		Chlorosis§		Necrosis¶		Stunting#		Lesion size††	
Fungicide	None	Fungicide‡‡	None	Fungicide	None	Fungicide	None	Fungicide	None	Fungicide
Mean	**4.6**	**3.7**	**4.5**	**3.3**	**5.5**	**4.3**	**4.3**	**3.6**	**6.7**	**6.9**
Poinsett 76	4.3	3.7	3.6	2.5	5.6	4.2	4.3	3.7	7.6	7.1
TW-3	4.3	2.5	3.3	2.2	6.0	4.5	5.0	3.9	5.0	6.5
M 21	4.4	3.3	3.2	2.1	4.9	3.2	5.6	5.1	5.9	6.1
PI 432859	4.4	3.0	4.8	3.7	5.9	5.0	3.9	2.8	5.6	6.2
NongChen #4	4.5	3.3	5.0	3.4	5.6	4.1	4.0	2.7	7.2	7.5
PI 511819	4.5	4.6	5.5	4.9	5.4	4.7	3.5	3.8	8.4	8.1
PI 618931	4.5	4.4	3.6	3.0	4.7	3.8	4.1	4.2	7.9	7.8
Ames 2354	4.6	3.0	3.5	2.5	4.9	3.2	5.1	3.6	6.4	7.2
SC 50	4.6	2.8	3.5	2.4	5.4	4.0	3.8	2.8	7.8	7.4
Heidan #1	4.7	2.6	5.0	3.0	5.2	3.7	4.8	2.9	5.4	6.7
PI 605929	4.7	3.2	3.7	2.6	5.4	3.7	5.0	4.0	8.1	7.2
Ames 2353	4.8	2.9	3.6	2.2	5.1	3.1	4.2	3.8	7.4	6.9
Homegreen #2	4.8	3.4	3.8	2.7	5.1	3.5	5.8	5.2	6.9	8.6
WI 2757	4.9	4.6	3.2	2.6	3.6	3.0	6.7	7.3	8.6	8.0
Gy 4	5.0	3.9	3.8	2.9	5.6	4.4	4.1	3.5	7.3	7.3
PI 267741	5.0	3.8	4.3	3.5	4.9	4.0	5.2	5.2	7.6	7.6
PI 618955	5.0	4.1	5.7	3.7	5.8	4.6	4.2	3.6	8.3	7.8
Polaris	5.1	3.3	2.9	2.4	4.4	3.9	6.4	4.8	8.7	8.4
Calypso	5.2	4.2	4.0	3.2	5.4	4.6	4.9	2.9	7.5	8.0
Marketmore 76	5.2	3.5	4.8	3.5	5.7	4.3	5.1	4.1	8.3	7.5
PI 618944	5.2	3.8	6.4	3.7	6.5	4.3	3.2	3.0	8.3	6.2
PI 179676	5.3	4.2	5.8	4.7	6.2	5.2	4.2	2.7	8.6	8.4
SC 10	5.3	3.5	4.0	2.4	5.4	3.7	4.9	3.8	6.7	6.3
TW-1	5.3	3.5	5.0	3.6	6.6	4.5	5.9	4.8	5.5	7.0
WI 2238	5.3	3.3	3.5	3.1	5.1	4.1	4.6	3.3	7.6	7.4
Ashley	5.4	4.0	5.2	3.4	5.8	4.1	4.9	4.5	7.9	8.3
Sumter	5.4	4.3	4.6	3.4	6.5	4.9	4.4	3.7	7.7	7.4
Dasher II	5.5	4.0	5.2	3.7	5.8	5.1	3.9	2.8	8.4	8.1
PI 508455	5.5	3.8	5.3	3.2	6.4	4.5	4.5	3.5	5.3	6.3
TW-4	5.7	3.6	4.5	3.6	6.4	5.1	6.3	5.1	7.0	6.0
Mariner H-423	5.8	3.8	4.8	2.7	6.1	4.3	4.9	3.0	7.5	7.1
Straight 8	6.6	6.2	6.5	5.5	7.1	6.1	4.9	4.1	9.0	8.7
PI 525151	6.8	6.2	6.6	5.9	7.3	6.0	4.9	4.0	8.7	7.3
Wisconsin SMR 18	6.8	6.2	6.9	6.2	7.1	6.4	5.1	3.2	8.5	7.7
Coolgreen	7.1	6.5	6.6	5.9	7.2	5.6	6.1	4.0	8.3	7.9
PI 218199	7.1	6.5	6.6	6.1	7.1	6.2	5.5	4.2	9.0	8.0
PI 171601	7.3	6.8	7.0	6.1	7.4	6.5	5.4	4.2	9.0	8.0
PI 458851	7.3	5.8	6.9	5.7	7.0	6.0	5.5	3.3	9.0	8.0
PI 211983	7.4	6.2	6.9	6.0	7.3	5.9	6.1	4.1	8.8	8.3
PI 176523	7.5	6.6	6.9	5.9	7.0	5.9	6.1	4.8	8.5	8.8
PI 344350	7.5	6.5	7.1	5.9	7.3	5.8	5.7	4.5	8.9	8.3
Ames 25699	7.6	6.9	7.1	6.5	7.5	6.4	5.9	4.0	8.8	8.0
Ames 23009	7.8	6.5	7.0	5.7	7.4	6.2	5.6	4.0	7.8	8.0
Ames 19225	7.9	6.4	6.4	4.5	7.5	6.0	7.3	6.5	8.4	7.6
LSD (5%)	0.3	0.3	0.5	0.4	0.5	0.4	0.8	0.7	1.0	1.0

†Data are from 2 yr and four replications.

‡Combined is mean of best ratings for each year based on *F*-value.

§Data are means of chlorosis ratings for 2008 and 2009.

¶Data are means of necrosis ratings for in 2008 and 2009.

#Data are means of stunting ratings for in 2008 and 2009.

††Data are means of lesion size ratings for 2008 and 2009.

‡‡Weekly application of Previcure Flex (Bayer CropScience, Research Triangle Park, NC) and Mancozeb (DuPont Agricultural Products, Wilmington, DE) alternating with Tanos (DuPont Agricultural Products) and Bravo (Syngenta Crop Protection, LLC, Greensboro, NC).

Fungicide also had a significant effect ($p = 0.001$) on percent marketable yield, or total yield minus culls (data not shown). We used the original definition of tolerance, the ability to produce yield under a disease epidemic. Mean total marketable yield ranged from 0.0 to 25.8 Mg ha^{-1} in no-fungicide environments and from 0.9 to 43.6 Mg ha^{-1} in the fungicide environments. High yielding cultigens in no-fungicide fields over both years (2008 and 2009) include PI 618907, PI 432885, PI 197086, Ames 20089, and PI 330628. Some high yielding cultigens yielded similarly in both fungicide and no-fungicide treated locations (PI 618907 and PI 197086). The mean percent early yield (harvest 1 of 2) decreased slightly from 27.8 to 23.8 in untreated and fungicide-treated environments, respectively. This was likely due to a drop in yield for the second harvest of no-fungicide treated environments. Increased disease between harvests causes reduction in photosynthesis and therefore yield was reduced as well.

Some cultigens were tested in 2009 only (data not shown). The highest yielding cultigens without fungicide were PI 618907, PI 197086, and PI 330628 with 47.0, 36.7, and 35.4 Mg ha^{-1}, respectively. High yielding cultigens at Clinton, NC, without fungicide were also high yielding without fungicide at Castle Hayne, NC (data not shown),

Table 5. Yield traits for plants tested with and without fungicide at Clinton, NC, from 2008–2009†.

Component:	Total Mg ha^{-1}‡		Marketable Mg ha^{-1}§		Percent early fruit¶		Mean kg per fruit#	
Fungicide:	None	Fungicide††	None	Fungicide	None	Fungicide	None	Fungicide
Mean:	**7.2**	**15.9**	**5.1**	**13.4**	**27.8**	**23.8**	**0.31**	**0.36**
Cultigen								
PI 618907	25.8	24.9	18.1	19.1	32.0	28.0	0.53	0.51
PI 432885	25.8	36.3	20.1	28.4	5.0	20.0	0.53	0.41
PI 197086	21.2	18.3	20.9	18.3	21.0	8.0	0.22	0.26
Ames 20089	20.9	43.6	16.2	40.9	9.0	15.0	0.45	0.61
PI 330628	20.4	33.1	20.1	31.7	6.0	4.0	0.28	0.31
PI 432882	18.8	30.6	15.5	29.3	4.0	17.0	0.37	0.44
PI 618937	17.6	33.9	9.9	28.3	50.0	22.0	0.31	0.51
PI 432874	14.7	21.1	11.8	18.5	13.0	5.0	0.31	0.52
PI 432878	14.6	16.7	10.6	14.3	15.0	15.0	0.34	0.28
PI 532523	14.3	31.8	8.3	26.6	45.0	27.0	0.28	0.28
PI 605924	13.8	22.5	12.3	18.8	8.0	8.0	0.40	0.41
PI 606015	13.6	26.6	12.7	21.7	2.0	2.0	0.72	0.96
PI 432875	12.8	16.6	7.3	14.8	20.0	8.0	0.25	0.33
PI 518849	12.7	18.9	9.0	16.1	31.0	8.0	0.32	0.47
PI 197088	12.7	23.8	12.2	23.5	15.0	1.0	0.27	0.36
PI 432877	12.4	32.3	10.3	28.7	0.0	10.0	0.40	0.43
PI 605995	12.3	21.2	11.0	19.1	9.0	1.0	0.55	0.96
PI 197085	11.8	15.3	11.7	13.6	22.0	7.0	0.27	0.33
PI 606019	11.6	30.4	10.6	26.4	1.0	8.0	0.45	0.59
PI 418963	11.3	15.0	5.6	13.1	17.0	25.0	0.46	0.55
PI 508455	10.3	25.6	7.3	20.9	59.0	48.0	0.21	0.31
PI 511819	10.1	13.7	7.5	12.1	38.0	41.0	0.33	0.47
PI 390267	10.1	17.3	7.4	16.0	20.0	9.0	0.37	0.49
PI 432859	9.7	24.8	5.1	19.1	32.0	28.0	0.34	0.60
PI 605928	9.6	16.6	9.1	14.6	5.0	6.0	0.56	0.58
PI 618861	9.5	16.0	5.7	14.0	7.0	16.0	0.39	0.46
PI 432884	9.5	11.1	5.0	10.4	2.0	6.0	0.28	0.30
PI 426170	9.5	21.1	3.1	16.3	25.0	23.0	0.26	0.30
TW-2	9.4	7.8	6.2	6.3	88.0	67.0	0.17	0.13
PI 618922	8.5	24.4	7.1	22.3	50.0	22.0	0.37	0.67
PI 432886	7.5	20.3	6.1	17.9	0.0	7.0	0.33	0.45
PI 606017	7.2	27.9	6.6	23.5	0.0	8.0	0.54	0.50
Mariner H-423	6.9	20.3	5.5	17.4	76.0	42.0	0.22	0.26
Ames 2353	6.9	10.3	4.5	8.9	30.0	19.0	0.22	0.25
PI 432876	6.6	14.0	6.1	13.9	4.0	1.0	0.41	0.46
Model	6.6	15.0	3.6	13.1	29.0	32.0	0.18	0.27
Heidan #1	6.5	19.6	4.2	16.3	7.0	4.0	0.27	0.40

Table 5. Continued.

Component:	Total Mg ha^{-1}‡		Marketable Mg ha^{-1}§		Percent early fruit¶		Mean kg per fruit#	
Fungicide:	None	Fungicide††	None	Fungicide	None	Fungicide	None	Fungicide
Mean:	**7.2**	**15.9**	**5.1**	**13.4**	**27.8**	**23.8**	**0.31**	**0.36**
NongChen #4	6.4	30.1	5.0	23.6	6.0	15.0	0.23	0.30
TW-3	6.1	8.8	2.3	6.6	92.0	66.0	0.16	0.17
SC 50	6.0	16.4	2.5	14.2	21.0	28.0	0.13	0.25
PI 489753	5.9	10.4	5.0	10.3	1.0	1.0	0.55	0.66
Gy 4	5.6	20.3	2.6	15.6	73.0	51.0	0.14	0.30
PI 618893	5.3	5.1	1.8	1.2	19.0	17.0	0.26	0.26
PI 605996	5.3	8.4	5.2	8.3	0.0	0.0	0.31	0.45
TW-1	4.9	5.4	3.8	3.5	89.0	64.0	0.21	0.16
Ames 2354	4.8	13.1	2.6	11.0	24.0	20.0	0.39	0.28
PI 605929	4.7	10.2	2.9	9.1	22.0	13.0	0.18	0.20
M 21	4.2	6.6	3.1	5.7	32.0	28.0	0.15	0.18
PI 618944	4.1	16.3	2.2	14.2	29.0	19.0	0.23	0.46
SC 10	4.0	13.2	1.7	11.1	42.0	31.0	0.11	0.25
WI 2238	3.7	27.2	3.3	26.2	17.0	10.0	0.17	0.32
TW-4	3.7	5.3	1.8	4.2	86.0	73.0	0.17	0.14
Poinsett 76	3.7	12.0	1.1	10.2	32.0	25.0	0.16	0.27
PI 606051	3.7	26.1	2.7	23.8	0.0	9.0	0.27	0.46
Calypso	3.5	21.2	2.0	17.2	35.0	41.0	0.24	0.26
Dasher II	2.9	23.1	1.7	19.6	16.0	39.0	0.21	0.27
PI 321008	2.6	1.1	1.5	1.0	0.0	0.0	0.70	0.60
Slice	2.5	16.6	1.0	12.7	8.0	22.0	0.15	0.28
Sumter	2.2	14.3	0.9	11.9	20.0	37.0	0.15	0.26
PI 605932	2.1	10.8	1.1	8.7	20.0	17.0	0.18	0.20
PI 618931	1.9	12.1	0.5	9.6	39.0	74.0	0.17	0.32
PI 179676	1.7	12.4	0.5	9.6	0.0	6.0	0.36	0.35
PI 618955	1.6	9.5	1.2	8.4	50.0	22.0	0.26	0.37
Ashley	1.5	6.5	0.6	5.8	7.0	8.0	0.20	0.22
WI 2757	0.7	2.8	0.4	2.1	19.0	2.0	0.20	0.24
Polaris	0.7	2.6	0.2	2.0	0.0	2.0	0.41	0.23
PI 267741	0.7	3.1	0.3	3.1	0.0	35.0	0.54	0.34
PI 525151	0.6	7.9	0.1	5.4	34.0	50.0	0.14	0.26
PI 218199	0.5	6.1	0.3	4.8	48.0	71.0	0.18	0.32
Wisconsin SMR 18	0.4	11.2	0.1	7.7	40.0	37.0	0.14	0.22
Marketmore 76	0.4	3.0	0.3	2.9	0.0	2.0	0.29	0.24
Ames 23009	0.3	2.1	0.1	1.4	55.0	62.0	0.27	0.21
Ames 19225	0.3	4.2	0.0	2.9	90.0	51.0	0.02	0.20
PI 344350	0.2	2.1	0.1	1.9	100.0	69.0	0.14	0.24
Coolgreen	0.2	5.9	0.0	4.7	0.0	53.0	.	0.26
PI 321009	0.1	4.9	0.0	2.9	0.0	0.0	.	0.48
PI 176523	0.1	1.3	0.0	0.9	100.0	33.0	.	0.34
PI 171601	0.1	7.3	0.0	6.3	100.0	57.0	.	0.26
Homegreen #2	0.1	3.0	0.0	2.5	0.0	0.0	.	0.40
Straight 8	0.0	8.0	0.0	5.0	100.0	38.0	0.05	0.25
PI 458851	0.0	5.1	0.0	2.8	0.0	19.0	.	0.25
PI 211983	0.0	0.9	0.0	0.5	.	11.0	.	0.32
Ames 25699	0.0	6.1	0.0	4.3	100.0	87.0	.	0.20
LSD (5%)	5.1	7.0	4.1	6.6	19	15	0.12	0.10

†Data are from 2 yr and four replications with two harvests each.

‡Total yield measured as Mg ha^{-1}.

§Marketable (non-cull) yield measured as Mg ha^{-1}.

¶Percent early fruit is data from harvest number 1 only.

#Mean weight per fruit in kg per fruit.

††Weekly application of Previcure Flex (Bayer CropScience, Research Triangle Park, NC) and Mancozeb (DuPont Agricultural Products, Wilmington, DE) alternating with Tanos (DuPont Agricultural Products) and Bravo (Syngenta Crop Protection, LLC, Greensboro, NC).

although overall yield was much greater at the Clinton, NC, location compared to the Castle Hayne, NC, location. In 2009, the highest yielding cultigens with fungicide were PI 618937, PI 330628, and PI 532523 with 64.6, 62.7, and 62.5 Mg ha^{-1}, respectively. Interestingly, the top cultigen for total yield, PI 618907, yielded similarly in both the fungicide and no-fungicide environments (49.0 and 47.0 Mg ha^{-1}, respectively). This cultigen stands out as tolerant, since it did not have a reduction in yield in no-fungicide environments, that is, under heavy disease pressure. Other cultigens showing tolerance were PI 197086 and PI 432878. The top performing check in 2009 was Gy 57u with 24.8 and 43.3 Mg ha^{-1} in no-fungicide and fungicide environment, respectively. Fungicide response for yield tended to be greater in susceptible cultivars. This result was also seen in a separate study on fungicide efficacy levels and levels of host plant resistance (A.D. Call, unpublished data, 2009).

Cultigens that were resistant in the retest were also resistant in the germplasm screening experiment. Cultigens with the lowest ratings in the retest also had the lowest ratings in the germplasm screening. Cultigens showed reduced disease means in environments with fungicide compared to no-fungicide environments. Mean total and marketable yield was also much higher in fungicide treated fields. Cultigens were identified that are both resistant and high yielding. Tolerance has also been found in some high yielding cultigens.

DISCUSSION

Cultigens have been found that significantly outperform checks in all resistance traits. More studies need to be done to determine the inheritance of this resistance. Resistant cultigens were resistant in all environments. High yielding and tolerant cultigens have also been identified, which could be used in developing improved cultivars. Environments with weekly fungicide applications outperformed no-fungicide environments in mean disease and yield ratings, with the greatest affect seen on total yield. Similar results were found in another study on resistance and fungicide levels (A.D. Call, unpublished data, 2009).

Some cultigens that were resistant in other studies were also resistant in this study. Wehner and Shetty (1997) summarized the downy mildew resistance in the U.S. germplasm collection of cucumbers from around the world that had been tested in North Carolina by Wehner in 1988 and 1989 during an unusually severe epidemic of downy mildew. They reported that the most resistant cultigens were of U.S. origin and were primarily elite cultivars and breeding lines. The most resistant cultigens, for which multiple-year data were available, were Gy 4, 'Clinton', PI 234517 (SC 50), Poinsett 76, Gy 5, 'Addis', M 21, M 27, and 'Galaxy'. All of these sources have PI 197087 in their pedigree as the source of downy mildew resistance. Plant Introduction 234517 (SC 50) also has Ashley as a source of resistance. The resistance in Ashley is from 'PR 40' (Puerto Rico 40) and was reported by Barnes (1955). The combination of two resistance sources in PI 234517 did not give a significant increase in resistance compared with the resistance from PI 197087 alone. Plant Introduction 401734, which is PR 39 from the Puerto Rico Agricultural Experiment Station (San Juan, PR), rated as moderately susceptible in the screening by Wehner and Shetty (1997), also indicating the resistance gene shared by PR 39 and PR 40 was still not effective. Plant Introduction 197087 was found to be only intermediate in resistance in 1988 and 1989, indicating a change in the Plant Introduction accession since its use in breeding in 1952. Plant Introduction 197087 showed intermediate resistance in our germplasm screening study. Wehner and Shetty (1997) also suggested that PI 197087 may have lost resistance as it went through seed increase and maintenance. It now seems more likely that this resistance has been overcome by the pathogen, since cultivars that owe their resistance to PI 197087 (Gy 4, M 21, and Poinsett 76) now also show only a moderate level of resistance.

Staub et al. (1989) reported 47 Plant Introduction accessions as having high resistance. Twenty-three of these accessions were reported as resistant to downy mildew and one or more other cucumber diseases. Wehner and Shetty (1997) reported that 19 of the 23 accessions reported as resistant by Staub et al. (1989) were highly resistant in their study conducted in North Carolina in 1988 and 1989. The most resistant cultigens from their screening, such as Gy 4, PI 234517, M 21, and Poinsett 76, were generally intermediate in our study. Interestingly, the most resistant cultigens from our study, PI 330628, PI 197088, PI 197086, and PI 197085, were only moderately resistant in the screening by Wehner and Shetty (1997). This indicates that a shift in the pathogen population has changed the resistance ranking of the cultigens, although susceptible cultigens were susceptible in both screening studies. This also may indicate allelism of the resistance gene in these cultigens. If PI 197088 has a different allele of the same gene found in Poinsett 76, it is possible that a single mutation could have caused the ability to overcome the more common allele (found in Poinsett 76 and tracing to PI 197087) and also the loss of the ability to overcome the allele in PI 197088 and other cultigens identified as highly resistant in this study. This would explain the change in rank from before and after the outbreak in 2004. Studies are being conducted to determine the inheritance of high resistance in the cultigens identified in this study.

There are at least three resistance genes to downy mildew in cucumber. One of the earliest sources of resistance came from a Chinese cultivar used in 1933 at the Puerto Rico Agricultural Experiment Station to develop PR 40. No inheritance data are available for PR 40. Resistance in many current cultivars traces back to PI 197087 (Wehner and Shetty, 1997). Barnes and Epps (1954) reported high resistance in cucumber PI 197087, which was used in developing cultivars such as 'Poinsett'. Resistance in Poinsett was reported by Van Vliet and Meysing (1977) to be from at least one single recessive gene, *dm* (*dm-1*). If both of these genes have been overcome, which is suspected, the highly resistant cultigens in these studies likely have one or more resistance genes that have not been overcome. One of the most resistant accessions in the screening and retest was PI 197088. Angelov (1994) reported that resistance in PI 197088 was due to two recessive genes and that Poinsett resistance was due to one recessive gene. Plant Introduction 197088 was collected from the same region and at the same time as PI 197087. It appears that there are at least three genes for resistance to downy mildew in cucumber: one from the Chinese cultivar used in developing the PR lines, one from PI 197087, and one from PI 197088 (assuming that PI 197087 and PI 197088 share one resistance gene, *dm-1*). It is likely that the resistance gene in Poinsett is from PI 197087 and possibly shared as one of the two resistance genes in PI 197088. Plant Introduction 197088 is currently highly resistant while cultigens tracing resistance back to PI 197087 are no longer highly resistant.

Although they trace to the same source of resistance, some variability exists in the resistance of check cultivars. In the absence of a major resistance gene, resistance appears to be more quantitative. There may be minor genes that affect overall resistance when not masked by a major gene. Other factors such as overall vigor or plant architecture may play a role in resistance. In the field, highly vigorous plants did not appear to succumb to downy mildew as quickly as less vigorous plants. Faster growth may allow the plant to outgrow the disease.

CONCLUSIONS

Cultigens with high resistance, high yield, and high tolerance have been identified. Breeders should utilize these cultigens in their programs to provide growers with cultigens that perform well in the face of the "new" downy mildew. Cultigens that were previously highly resistant no longer are and should therefore only be used in breeding for improvement of traits separate from downy mildew resistance. Utilization of the top performing cultigens identified in this study should allow breeders to develop cultivars with high resistance. Although the fruit are not of marketable type, high yielding cultigens identified in the study may allow improvement of overall yield. The incorporation of cultigens showing tolerance to downy mildew for cultivar development may also have a major impact for growers, allowing the grower to achieve better yields even when pathogen pressure is high. Combining high resistance, high yield, and high tolerance with desired agronomic traits already available should lead to cultivars that are much improved over those available today.

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