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Evidence for downy mildew races in cucumber tested in Asia, Europe, and North America

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Abstract

Downy mildew (*Pseudoperonospora cubensis* (Berk. and Curt.) Rostov.) is an important disease in most cucumber (*Cucumis sativus* L.) production areas worldwide. A set of cucumber cultivars and breeding lines (hereafter referred to collectively as cultigens) resistant to downy mildew in particular regions of the world were tested for resistance in geographical regions thought to differ in pathogen virulence or race (US, Poland, China, and India). Cucumber cultigens used in the study were developed in the US, Poland or China, and differed in their resistance to downy mildew. These cultigens were evaluated against local isolates of *P. cubensis* under field conditions (North Carolina and India) or greenhouse conditions (South Carolina and Poland). Significant differences were observed among cultigens for resistance to *P. cubensis* at all locations. Individual cultigens differed in their resistance to the pathogen at different geographic locations, providing evidence that the different local isolates represented different races of the pathogen. Cultigens from PR China that were resistant to downy mildew in that country were also resistant in India. However, those same cultigens were intermediate in resistance in the US and Poland. Cultigens from the US and Poland that were resistant in those countries were intermediate in resistance in India. The most resistant cultigens over all locations were 'Nongchen #4' (PR China) and M 21 (NC State University). © 2002 Elsevier Science B.V. All rights reserved.

Keywords: *Cucumis sativus*; Fruiting; Germplasm evaluation; Vegetable breeding; Fruit number

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1. Introduction

Downy mildew, caused by *Pseudoperonospora cubensis* (Berk. and Curt.) Rostov., is a major foliar disease of cucumber (*Cucumis sativus* L.) in humid production areas of the world (Thomas, 1986). Downy mildew has been reported on species of the genus *Cucumis* from 70 countries worldwide (Cohen, 1981; Palti, 1974; Thomas, 1986). The pathogen has been increasing in occurrence in Central Europe since 1984, reducing yield in many cucumber production areas (Lebeda, 1991). The pathogen can overwinter in areas with mild winter temperatures, such as the extreme southern US in the form of active mycelium in either cultivated or wild species of cucurbits (Bains and Jhooty, 1976). The primary source of inoculum in the field is through airborne sporangia, which also serve as a secondary source of inoculum. Environmental conditions favorable to the pathogen are prolonged periods of high humidity in combination with high day and moderate night temperatures. Dew is also a major factor in the initiation, development, and spread of the disease (Thomas, 1996).

Host range studies with *P. cubensis* were summarized on cucurbits by Palti (1974). The host range of *P. cubensis* is reported to include 40 species in approximately 20 genera of the family Cucurbitaceae, of which 10 host species are reported in the genus *Cucumis* (Thomas, 1986). Recently, nine additional *Cucumis* species were identified as hosts of *P. cubensis* (Lebeda, 1992). Palti (1974) reported that the differences in the species response to the pathogen was likely due to the physiological races in various countries. Five pathotypes of *P. cubensis* have been reported based on their compatibility with specific hosts (Thomas, 1986). Lebeda reported that resistance of cucumber to *P. cubensis* held up against isolates from the US, but not against European isolates. He further reported that only slight differences in field resistance were known among cucumber cultivars against *P. cubensis* (Lebeda, 1992). Wehner and Shetty (1987) evaluated the cucumber germplasm collection in field tests in North Carolina, and reported that the most resistant cultigens originated from the US and were primarily adapted cultigens. The most resistant cultigens in their study were Gy 4, 'Clinton', PI 234517, 'Poinsett 76', Gy 5, 'Addis', M 21, M 27, and Galaxy. Researchers in India, Japan, Israel, and the US have concluded that there is a need to have an unified, international effort to determine the relationships of host specificities for downy mildew in cucurbits (Bains and Jhooty, 1976, 1979; Bains et al., 1977; Cohen, 1981; Thomas et al., 1987). Field and greenhouse evaluations for downy mildew resistance were conducted in the US and Europe in order to identify random amplified polymorphic DNA (RAPD) markers linked to the downy mildew (*dm*) resistance gene. No evidence for race differences in the pathogen were observed between North America and Europe (Horejsi et al., 2000).

Some of the economically important hosts of *P. cubensis* are cucumber, melon (*Cucumis melo* L.), watermelon (*Citrullus lanatus* (Thunb.) Matsum. and Nakai), and squash (*Cucurbita* spp.) (Whitaker and Davis, 1962). Early research on resistance of cucumbers to downy mildew showed that at least one single recessive gene, *dm*, controlled resistance in 'Poinsett' (Van Vliet and Meysing, 1977). However, more recent work indicated that several genes control the trait (see review by Pierce and Wehner, 1990). Doruchowski and Lakowska-Ryk (1992) reported that inheritance of resistance to downy mildew in an inbred cucumber line derived from WI 4783 was controlled by three recessive genes (*dm-1*, *dm-2*,

and *dm-3*). Based on the information available, the number of genes controlling resistance in cucumber to downy mildew ranges from 1 to 3 (Doruchowski and Lakowska-Ryk, 1992; Pierce and Wehner, 1990; Van Vliet and Meysing, 1977). Therefore, the number of possible races of downy mildew on cucumber could range up to eight if there were a gene-for-gene system for the disease. RAPD markers G14₈₀₀ and BC519₁₁₀₀ were found to be linked in the repulsion phase to the *dm* allele, and X15₁₁₀₀, AS5₈₀₀, and BC526₁₀₀₀ were found linked in the coupling phase in a study to identify RAPD markers which could be suitable for marker assisted selection (MAS) (Horejsi et al., 2000).

The objectives of this experiment were to test a set of cultigens which differed in their resistance to downy mildew to local isolates of *P. cubensis* in different geographical regions of the world, and determine whether they differed in resistance to the pathogen at those locations. We were specifically interested in the performance of cultigens bred in the east (Asia) when tested in the west (North America) and vice versa.

2. Materials and methods

The cucumber cultigens used in this study were developed in Poland, PR China, and the US, and were chosen because they differed in their resistance to downy mildew (Hongwen Cui, personal communication, Northwestern Agricultural University, PR China, 1994, and unpublished data Poland and US). Cultigens reported to be highly resistant to downy mildew were 'Chipper', M 21, 'Poinsett 76', WI 1983, WI 2238, WI 2757, WI 4783, and WI 5207 from the US, G 367 and SKW 793 from Poland, and 'Jinza #2' and 'Nongchen #4' from PR China. Cultigens reported moderately resistant (also called intermediate) to downy mildew were 'Aladyn' and G 400 from Poland, and 'Heidan #1' and 'Longli Zao' from PR China. Cultigens reported to be susceptible to downy mildew were 'Straight 8' and 'Wisconsin SMR 18' from the US, 'Mieszko' and 'Sremski' from Poland, and 'Changchi Mici' and 'Zhong Nong' from PR China.

2.1. Greenhouse experiment, South Carolina

Seeds of each cultigen were sown into Jiffy 7 peat pellets and grown in the greenhouse at Charleston, SC. At the second true-leaf stage, seedlings were inoculated with a South Carolina isolate of *P. cubensis* isolated from cucumber. The adaxial surfaces of leaves one and two on each plant were sprayed to incipient run-off with an inoculum suspension (5×10^3 sporangia ml⁻¹). Following inoculation, seedlings were placed in a dark, 20 °C, dew chamber (100% relative humidity) for 18 h, then placed on a greenhouse bench for 16 h. Finally, seedlings were returned to the 20 °C dew chamber for 18 h to facilitate sporulation. Eight days after inoculation, plants were removed from the dew chamber and rated for severity of downy mildew infection.

Each plant was rated on a 0–9 scale of increasing disease severity with the use of a set of disease assessment keys prepared for foliar diseases (such as downy mildew) on cucumber (Jenkins and Wehner, 1983). These assessment keys used percentage infected leaf area diagrams based on the Horsfall–Barrett scale and represented a range of 0–97% infected leaf area as follows: 1 = 3%, 2 = 6%, 3 = 12%, 4 = 25%, 5 = 50%, 6 = 75%, 7 = 87%,

8 = 94%, and 9 = 97%. Portions of leaves which were chlorotic or necrotic were considered to be infected.

The experiment was performed twice (10 October and 6 November 1996). The first test had four replications of five plants in each treatment, and the second test had three replications of eight plants in each treatment. The experiment was a randomized complete block design.

2.2. Greenhouse experiment, Poland

The greenhouse experiments were run at the Research Institute of Vegetable Crops, Skierniewice, Poland during 1995 and 1997 under controlled conditions in a growth chamber using a local race of *P. cubensis*. Plants to be inoculated were grown in flats with sterilized soil at 26 °C during the day and 21 °C at night with a 14 h photoperiod in the greenhouse.

Plants were inoculated with a suspension of *P. cubensis* (5×10^3 sporangia ml⁻¹) at the two true-leaf stage. The plants were sprayed on the adaxial surface of the leaves with the inoculum suspension until incipient run-off. Inoculated plants were placed in the dark in a dew chamber at 20 °C and 100% RH for 48 h. Plants were then transferred to the greenhouse having a temperature of 24–28 °C for 5 days. After 7–8 days, the plants were evaluated according to the reaction of the plants to the disease on a scale of 0–9 as described above. The first (1995) and second (1997) tests had six replications of eight plants in each treatment. The experiment was a randomized complete block design.

2.3. Field experiments, North Carolina and India

All experiments were conducted using recommended horticultural practices as summarized by Schultheis (Schultheis, 1990), with specific methods as follows. Field experiments were conducted at the Horticultural Crops Research Station at Castle Hayne, NC, during 1995 and 1997, and at Bangalore, India during 1997. Fertilizer was incorporated before planting at a rate of 90–39–74 kg ha⁻¹ (N–P–K) with an additional 34 kg ha⁻¹ N applied at the vine-tip-over stage (4–6 true leaves). Seeds were planted on raised, shaped beds with centers 1.5 m apart. Plots 1.5 m long were seeded, and later thinned to five plants at the first true-leaf stage. Irrigation was applied when needed to provide a total of 25–40 mm per week. A tank mix of 2.2 kg ha⁻¹ of naptalam (2-[(1-naphthalenylamino) carbonyl] benzoic acid) and 4.4 kg ha⁻¹ of bensulide (*O,O*-bis(1-methylethyl) S-[2-[(phenylsulfonyl) amino] ethyl] phosphorodithioate) was applied preplant for weed control in North Carolina field tests.

The field experiments in India were conducted on 10 July 1997–18 September 1997 and 8 September 1997–13 November 1997 at the Indo-American Hybrid Seeds farm in Bangalore, India. Climatic conditions during July–November in Bangalore are ideal for screening downy mildew because it is the most prevalent disease in cucumber production fields. The fields were kept free of weeds by hand weeding the plots weekly.

No artificial inoculum was used in the field experiments. Fields were exposed to natural inoculum during the growing season. Disease development was encouraged by planting susceptible 'Wisconsin SMR 18' every fourth row in each field as spreader rows, and by

applying overhead irrigation (twice each week). Plants usually showed significant symptoms of downy mildew by the vine-tip-over stage (approximately 3 weeks after planting).

Field plots were rated for foliar downy mildew at weekly intervals after infection lesions using a 0–9 visual rating scale (0: no foliar symptoms, 1–2: trace, 3–4: slight, 5–6: moderate, 7–8: advanced, 9: plant dead) (Jenkins and Wehner, 1983). The amount of leaf damage in ratings were standardized from the eight levels described pictorially for anthracnose (*Colletotrichum orbiculare* (Pass.) Ellis and Halst.) leaf damage by Thompson and Jenkins (1985), which corresponded to rating units 1 through 8, with 0 and 9 (the obvious end points) not shown.

Both the field experiments were randomized complete block designs with six replications of 22 cultigens. Prior to analysis, data were checked for normality and error variance homogeneity. Residual plots had a random distribution, indicating that the statistical model was valid and its assumptions were met (Fernandez, 1992). Rating scale data were not transformed because assumptions for the analysis of variance were met (Little, 1985). Data were analyzed using the GLM and CORR procedures of SAS (SAS Institute, 1988).

3. Results and discussion

Highly significant differences were observed among cultigens for resistance to downy mildew at all locations. Ratings with the lowest coefficient of variance (CV) and the highest range/LSD were chosen as the rating for a particular location (Table 1). The mean rating was computed based on the mean of all ratings across all locations for the particular cultigen. The means for downy mildew ratings in the different environments ranged from 2.8 to 7.0 (Table 1). The ratings were standardized to a mean of 4.5 and a standard deviation of 1.0 for comparison of resistance across locations (Table 2). Standardization permitted comparison of cultigens across locations uniformly. The value of 4.5 was chosen as the midpoint of the 0–9 rating scale, and 1.5 was chosen as a standard deviation because a range of ± 3 standard deviations would include 99% of the population and range from 0 to 9, corresponding to the original, unstandardized rating.

The multiple comparison procedures for mean separation of unstructured qualitative treatments for cultigens and germplasm screening is valid statistically and makes mean comparisons easy (Petersen, 1977; Steel and Torrie, 1980). Single degree of freedom contrasts are not appropriate if no logical a priori structure exists among the treatments of a test. The LSD method was used for mean separations because it controls the comparison-wise error rate better than other methods (Steel and Torrie, 1980).

Correlations for downy mildew ratings for the different environments were computed. The ratings for downy mildew at locations in Poland and India during the 2 years tested were highly correlated (Poland (1995 vs. 1997, $r^2 = 0.77$) and India (1997 spring vs. 1997 summer, $r^2 = 0.70$)). However, the ratings for downy mildew in North Carolina between the 2 years tested were not highly correlated (1995 vs. 1997, $r^2 = 0.44$). The ratings for the spring season of India in 1997 were poorly correlated to the ratings at other locations (Table 3). This evidence suggests that there may be a different race of *P. cubensis* in India when compared to the other locations. This is of interest because the spring season in India is the season where the disease is most severe due to ideal environmental conditions for the

Table 1

Mean ratings^a for resistance of cucumber cultivars to local races of *P. cubensis* in different geographical locations of the world in field and greenhouse tests

Cultigen name	Location of seed origin	Field				Greenhouse		
		NC ^b		India		SC ^c , 1995	Poland	
		FL ^d 95	FL ^d 97	SP ^e 97	SM ^f 97		1995	1997
Aladyn	Europe (Poland)	3.0	3.5	7.3	0.5	1.8	4.0	3.7
Changchi Mici	Asia (PR China)	6.0	5.0	5.5	0.0	2.7	5.1	4.5
Chipper	US (SC)	5.2	3.3	7.6	1.0	1.8	1.1	2.6
G 367	Europe (Poland)	3.3	3.0	7.7	1.3	1.9	3.1	2.2
G 400	Europe (Poland)	3.6	3.8	7.4	1.0	1.8	3.0	4.4
Heidan #1	Asia (PR China)	5.4	4.8	0.8	0.0	3.7	7.4	6.8
Jinza #2	Asia (PR China)	3.8	6.3	8.1	–	2.2	2.6	6.7
Longli Zao	Asia (PR China)	4.0	4.3	7.6	1.0	2.2	3.5	4.4
Mieszko	Europe (Poland)	4.8	5.2	8.3	2.0	3.2	6.2	5.4
M 21	US (NC)	3.8	4.2	7.1	0.2	1.7	1.6	3.0
Nongchen #4	Asia (PR China)	5.0	4.2	0.0	0.0	2.4	3.2	4.2
Poinsett 76	US (SC)	6.2	4.0	7.6	1.2	2.2	2.5	2.8
SKW 793	Europe (Poland)	5.5	3.5	7.6	1.7	1.5	3.7	3.7
Sremski	Europe (Poland)	5.0	5.7	7.9	6.7	5.1	5.9	4.7
Straight 8	US (Wisconsin)	7.5	6.5	8.7	7.0	5.7	5.3	7.2
WI 1983	US (Wisconsin)	–	–	7.6	–	1.8	–	2.8
WI 2238	US (Wisconsin)	4.7	3.0	7.4	–	1.5	1.1	0.2
WI 2757	US (Wisconsin)	5.2	4.3	7.4	0.8	2.1	2.9	2.7
WI 4783	US (Wisconsin)	3.8	3.8	7.2	1.3	1.1	1.3	1.8
WI 5207	US (Wisconsin)	7.0	4.5	–	–	–	–	1.6
Wis. SMR 18	US (Wisconsin)	6.0	5.3	8.6	7.7	5.6	6.8	6.1
Zhong Nong	Asia (PR China)	6.7	4.8	8.9	6.7	5.3	7.0	6.0
Mean		4.9	4.4	7.0	3.8	2.8	3.9	3.9
CV (%)		22	17	11	34	26	22	24
LSD (5%)		1.1	0.9	0.9	1.5	1.0	1.0	1.1
Range/LSD		5.7	4.0	10.4	5.9	4.2	6.9	7.7

^a Mean of the six disease ratings with the best CV and range/LSD for each of the locations in the study. Ratings were 0–9 (0: no foliar symptoms, 1–2: trace, 3–4: slight, 5–6: moderate, 7–8: advanced, 9: plant dead).

^b North Carolina.

^c South Carolina.

^d Fall.

^e Spring.

^f Summer.

pathogen. Based on the results from our study, the race of *P. cubensis* in Poland (Europe) may be similar to the race in the US. This is similar to the findings of Horejsi et al. (2000) who report that there was no evidence for race differences in *P. cubensis* between North America and Europe based on their study in five locations in Europe and North America. They also observed that the European test locations tended to have higher downy mildew scores compared to the North American locations (Horejsi et al., 2000).

Cultigens differed in their resistance level at different locations, suggesting that different races of *P. cubensis* were present in the various locations where the tests were conducted

Table 2

Ratings^a for resistance of cucumber cultivars to local races of *P. cubensis* in different geographical locations of the world in field and greenhouse tests

Cultigen	Location of seed origin	Reported	US		Europe (Poland) ^a	Asia (India) ^a
			NC ^a	SC		
Chipper	US (SC)	R	R	R	R	I
M 21	US (NC)	R	R	R	R	I
WI 1983	US (Wisconsin)	R	–	R	R ^b	I ^b
WI 2757	US (Wisconsin)	R	R	R	R	I
WI 4783	US (Wisconsin)	R	R	R	R	I
WI 2238	US (Wisconsin)	R	R	R	R	S ^b
Poinsett 76	US (SC)	R	I	R	R	I
WI 5207	US (Wisconsin)	R	I	–	R ^b	–
G 367	Europe (Poland)	R	R	R	R	I
SKW 793	Europe (Poland)	R	R	R	I	I
Jinza #2	Asia (PR China)	R	S	R	I	S ^b
Nongchen #4	Asia (PR China)	R	I	R	I	R
Aladyn	Europe (Poland)	I	R	R	I	I
G 400	Europe (Poland)	I	R	R	I	I
Heidan #1	Asia (PR China)	I	I	I	S	R
Longli Zao	Asia (PR China)	I	I	R	I	I
Mieszko	Europe (Poland)	S	I	I	S	I
Sremski	Europe (Poland)	S	S	S	S	S
Straight 8	US (Wisconsin)	S	S	S	S	S
Wis. SMR 18	US (Wisconsin)	S	S	S	S	S
Changchi Mici	Asia (PR China)	S	I	R	I	R
Zhong Nong	Asia (PR China)	S	S	S	S	S

^a Rating classifications were based on the average of the two mean ratings per season at each location. Classifications were resistant, intermediate, or susceptible (R = 1–3, I = 4–6 and S = 7–9) based on the ratings over replications at each location. The intermediate ratings for India indicated that the cultivars were resistant in the summer and susceptible in the spring season.

^b Indicates classification based on one rating at location.

(Tables 1 and 2). Based on the mean response ratings, the most resistant cultivar across all locations was ‘Nongchen #4’ (China); ‘Wisconsin SMR 18’ was the most susceptible.

Cultivars that were reported resistant to *P. cubensis* usually were resistant to the pathogen in one or more locations, with the exception of ‘Jinza #2’ which was intermediate in resistance or susceptible in most locations. Cultivars from the US which were reported to be resistant were mostly resistant in the US and Europe. The exceptions were ‘Poinsett 76’ and ‘WI 5207’ which were intermediate in North Carolina, and intermediate or susceptible in India. Cultivars reported to be resistant in Poland (G 367 and SKW 793) were also found to have intermediate resistance in India. The resistant cultivar ‘Nongchen #4’ was found to be resistant to the pathogen in India and South Carolina but was found to have only intermediate resistance in North Carolina and Poland. Cultivars reported to be susceptible to the pathogen were also susceptible in one or more of the test locations, except ‘Changchi Mici’ which was either resistant or intermediate in its reaction at all locations and ‘Mieszko’ which was intermediate at all locations except Poland.

Table 3

Phenotypic correlations for resistance of cucumber cultivars to local isolates of *P. cubensis* at different locations

Cultigen name	Year	Field				Greenhouse (Poland)	
		NC ^a		India		1995	1997
		FL ^b 95	FL ^b 97	SP ^c 97	SM ^d 97		
<i>Field</i>							
North Carolina	1997	0.44*					
India (Spring)	1997	0.02 ns ^c	0.10 ns ^c				
India (Summer)	1997	0.55*	0.67**	0.70**			
<i>Greenhouse</i>							
Poland	1995	0.48*	0.58**	−0.10 ns ^c	0.56**		
Poland	1997	0.26 ns ^c	0.79**	−0.09 ns ^c	0.56**	0.77**	
South Carolina	1995	0.67**	0.72**	0.12 ns ^c	0.87**	0.82**	0.73**

^a North Carolina.^b Fall.^c Spring.^d Summer.^e Indicates correlation not significant.

* Indicates correlation significant at the 5% level.

** Indicates correlation significant at the 1% level.

Cultigens from PR China which were reported to be resistant were resistant in India. However, those same cultigens were intermediate or susceptible in Poland and the United States. Similarly, cultigens that were resistant or intermediate in Poland and the United States were intermediate or susceptible in India. This indicates that at least two races of *P. cubensis* were present among the test locations. Reports indicated that the number of genes controlling resistance to downy mildew ranged from 1 to 3 (Doruchowski and Lakowska-Ryk, 1992; Pierce and Wehner, 1990; Van Vliet and Meysing, 1977). Therefore there may be 2–8 races of *P. cubensis* if the inheritance follows the gene-for-gene theory. Horejsi et al. (2000) report that the growing conditions in Europe may be so favorable for disease development that the *dm* allele may not provide adequate control. It appears that breeders should screen new germplasm for additional genes for resistance (Horejsi et al., 2000).

4. Summary

There appear to be distinct races of *P. cubensis* in Asia, Poland, and the US. The race of *P. cubensis* in Poland is similar to the race in the US, but is distinct from the race in Asia based on the response of the cultigens to *P. cubensis* at these locations. The existence of different races could be further investigated using isolates from the different locations in a single test location having the differential cultivars. Cultivars that were developed in the United States and Poland with resistance to local downy mildew races will not necessarily be resistant to *P. cubensis* race(s) in Asia, and vice versa. ‘Nongchen #4’ is a good source for use in breeding for resistance to downy mildew, because it is highly resistant to the Asian and American races. We recommend that cucumber cultivars developed in the US

and Europe be tested for resistance to *P. cubensis* using the Asian race of the pathogen before releasing them for production there.

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