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RESPONSE OF WILD AND WEEDY *CUCURBITA* L. TO PATHOTYPES OF *PSEUDOPERONOSPORA CUBENSIS* (BERK. & CURT.) ROSTOV. (CUCURBIT DOWNY MILDEW)

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1. INTRODUCTION

The genus *Cucurbita* includes ca 14 species native to the New World from the United States south to Argentina. It includes at least five different species domesticated before European contact (Sanjur *et al.*, 2002). In many parts of the world, these domesticated species are widely cultivated as vegetables and, to a lesser extent, as oilseeds, animal forages, and ornamentals. Wild populations of *Cucurbita* often possess disease-resistance genes that are unknown or extremely rare in domesticated populations. This has been demonstrated for resistance to many viruses and fungal pathogens that infect *Cucurbita* (Rhodes, 1964; Provvidenti, 1990; McCreight and Kishaba, 1991; Munger, 1993; Provvidenti, 1993). Extensive research has also been conducted to transfer disease-resistance genes from wild species into modern *Cucurbita* cultivars (Contin and Munger, 1977; de Vault and Pitrat, 1979; Washek and Munger, 1983; Whitaker and Robinson, 1986; Herrington *et al.*, 1988a, 1988b, 1989; Robinson *et al.*, 1988; Tasaki and Dusi, 1990).

Pseudoperonospora cubensis (cucurbit downy mildew) is one of the most important foliar pathogens infecting cucurbits (Palti and Cohen, 1980; Thomas, 1996; Lebeda and Widrlechner, 2003). It is widely distributed throughout the world and can inflict major production losses in both open field and protected culture. *P. cubensis* is characterized by large variation in

pathogenicity, which was recently reviewed by Lebeda and Widrlechner (2003). There is limited information on interactions between various *Cucurbita* species and *P. cubensis*; only three species (*C. maxima*, *C. moschata*, *C. pepo*) have been reported as natural hosts of the pathogen (Palti and Cohen, 1980). Limited research and breeding of *Cucurbita* species for resistance to *P. cubensis* have been conducted (Lebeda, 1992). It was suggested that host-parasite specificity between *Cucurbita pepo* and *P. cubensis* is controlled by race-specific factors (Lebeda and Křístková, 1993). Host-parasite specificity among *Cucurbita* species and various *P. cubensis* isolates is a complex phenomenon deserving closer analysis (Lebeda and Křístková, 1993; Lebeda and Widrlechner, 2003).

Considering the past success of efforts to identify disease-resistance genes in wild *Cucurbita* species and our general desire to clarify these host-parasite relationships, we designed the present study to evaluate a set of wild and weedy *Cucurbita* populations, representing a wide phylogenetic cross-section of the genus with relationships to all five domesticated species, for their responses to diverse *P. cubensis* pathotypes.

2. MATERIALS AND METHODS

The first step of this work was to survey the holdings of the National Plant Germplasm System (NPGS) of the United States to develop a representative set of *Cucurbita* species for evaluation. This set focused on wild and weedy taxa, given that many domesticated *Cucurbita* populations have already been evaluated (Chauhan, 1984; Bains and Sharma, 1986; Lebeda and Křístková, 1993; Wessel-Beaver, 1993; Ríos-Labrada *et al.*, 1997; Lebeda and Křístková, 2000; Keinath and Du Bose, 2000). Seed samples of this initial set were provided by five NPGS units and included 97 accessions representing 14 taxa and 10 *Cucurbita* species (Table 1).

These 97 accessions (Table 1) were grown in a growth chamber and/or a glasshouse in plastic pots filled with garden soil under day/night temperatures of 25°C/15°C. Five plants were grown from each accession. The plants were regularly irrigated and once per week the nutritional solution Kristalon, version "Fruit and Flower" (Hydro Agri Rotterdam, The Netherlands; N 15%, P₂O₅ 5%, K₂O 30%, MgO 3%) was added. No other chemical treatments were applied to the plants during cultivation. Well developed leaves (3 or 4 true leaves) of 6 to 8-week old plants were used for the screening. Tests were carried out on five leaf discs (20 mm in diameter) per plant (Lebeda, 1991).

Altogether, 11 isolates of *P. cubensis* originating from the Czech Republic (8 isolates) and from France, Spain and the Netherlands (one isolate from each country) were used (Table 2). These isolates represent 9

Table 1. Set of *Cucurbita* spp. accessions used for screening.

Taxon	No. of accessions	Supplier ¹
<i>C. argyrosperma</i> C. Huber var. <i>palmeri</i> (L.H. Bailey) L. Merrick & D.M. Bate	18	PGRCU
<i>C. argyrosperma</i> C. Huber subsp. <i>sororia</i> (L.H. Bailey) L. Merrick & D.M. Bates	25	PGRCU
<i>C. cylindrata</i> L.H. Bailey	1	PGRCU
<i>C. digitata</i> A. Gray	1	PGRCU
<i>C. ecuadorensis</i> H.C. Cutler & Whitaker	3	PGRCU
<i>C. ficifolia</i> Bouche	4	PGRCU
<i>C. foetidissima</i> Kunth	5	WRPIS
<i>C. maxima</i> Duchesne subsp. <i>andreana</i> (Naudin) Filov	3	PGRU
<i>C. okeechobeensis</i> (Small) L.H. Bailey subsp. <i>martinezii</i> (L.H. Bailey) T.W. Walters & D.S. Decke	7	PGRCU
<i>C. pedatifolia</i> L.H. Bailey	1	PGRCU
<i>C. pepo</i> L.	6	NCRPIS
<i>C. pepo</i> L. var. <i>fraterna</i> (L.H. Bailey) Filov	4	NCRPIS
<i>C. pepo</i> L. var. <i>ovifera</i> (L.) Harz	1	NCGRP
<i>C. pepo</i> L. var. <i>texana</i> (Scheele) Filov	18	NCRPIS

¹ NCGRP = National Center for Genetic Resources Preservation, Fort Collins, Colorado;
 NCRPIS = North Central Regional Plant Introduction Station, Ames, Iowa;
 PGRCU = Plant Genetic Resources Conservation Unit, Griffin, Georgia;
 PGRU = Plant Genetic Resources Unit, Geneva, New York;
 WRPIS = Western Regional Plant Introduction Station, Pullman, Washington.

P. cubensis pathotypes (Lebeda and Gadasova, 2002; Lebeda and Widrlechner, 2003) differing substantially in their pathogenicity. For the purpose of this study, no pathogen isolates were available from the New World centers of origin or diversity for *Cucurbita*. The isolates were maintained and multiplied on leaf segments or leaf discs of *Cucumis sativus* cv. Marketer 430, which also served as a susceptible control. Long-term maintenance of pathogen isolates was achieved through storage of cultures (leaves bearing conidiophores) in a low-temperature freezer (-80 C).

Table 2. Set of *Pseudoperonospora cubensis* isolates used for screening of *Cucurbita* spp. accessions (modified from Lebeda and Gadasová, 2002; Lebeda unpublished results).

Differential genotype	<i>P. cubensis</i> isolate (PC)/reaction pattern										
	3/00 ¹	6/97	1/88	11/00	2/95	6/96	1/00 ²	14/00	12/00	2/00	1/97
<i>Cucumis sativus</i>	+	+	+	+	+	+	+	+	+	+	+
<i>C. melo</i> subsp. <i>melo</i>	+	-	+	-	-	-	+	+	+	+	+
<i>C. melo</i> var. <i>conomon</i>	-	-	-	-	-	-	-	-	-	-	+
<i>C. melo</i> var. <i>acidulous</i>	-	-	-	-	-	-	+	-	+	+	+
<i>Cucurbita pepo</i> var. <i>pepo</i>	-	-	-	-	-	-	-	-	-	-	-
<i>C. pepo</i> var. <i>texana</i>	-	+	+	+	+	+	-	+	+	+	+
<i>C. pepo</i> var. <i>fraterna</i>	-	-	-	-	-	-	-	-	-	-	-
<i>C. maxima</i>	-	-	-	+	+	+	-	+	+	+	+
<i>Citrullus lanatus</i>	-	-	-	-	-	-	-	-	-	+	+
<i>Benincasa hispida</i>	-	+	+	+	+	+	+	+	+	+	+
<i>Luffa cylindrica</i>	-	-	-	-	-	-	-	-	+	-	-
<i>Lagenaria siceraria</i>	-	+	+	+	+	+	+	+	+	+	+

PC = general designation of *P. cubensis* isolates, coding = isolate number/year of collecting, with origin of isolate, ¹ = France, ² = The Netherlands, others = Czech Republic; - = resistant reaction, no visible symptoms of sporulation or very sparse sporulation; + = susceptible reaction (moderate or abundant sporulation).

Inoculation, incubation and disease assessment was carried out following methods described elsewhere (Lebeda, 1986; Lebeda, 1991; Lebeda and Křístková, 1993; Lebeda and Widrlechner, 2003). Final evaluation of phenotypic expression of host-parasite interaction was made 14 days after inoculation according to a 0-4 scale (Lebeda, 1991).

3. RESULTS AND DISCUSSION

From the perspective of phenotypic expression, we observed extensive variation in the response of the studied set of *Cucurbita* spp. and accessions to 11 isolates of *P. cubensis*. Here we will summarize and interpret only a portion of those results. In total, 57 different reaction patterns were recorded with 13 accessions completely resistant, 12 accessions completely susceptible, and 32 accessions expressing pathotype (race) specific patterns.

Table 3. List of taxa and accessions of *Cucurbita* spp. with completely resistant reaction.

Taxon	Accession
<i>C. argyrosperma</i> var. <i>palmeri</i>	PI 512201
<i>C. argyrosperma</i> subsp. <i>sororia</i>	PI 438832, PI 442345, PI 442348, PI 442358, PI 489696, PI 512209, PI 512218, PI 512219, PI 512221, PI 512222, PI 512223,
<i>C. foetidissima</i>	PI 442200

Table 4. List of taxa and accessions of *Cucurbita* spp. with completely susceptible reaction.

Taxon	Accession
<i>C. maxima</i> subsp. <i>andreaana</i>	G 5285, G 29253
<i>C. pepo</i>	PI 173681
<i>C. pepo</i> var. <i>fraterna</i>	PI 614683
<i>C. pepo</i> var. <i>ovifera</i>	NSL 91999
<i>C. pepo</i> var. <i>texana</i>	PI 614694, PI 614696, PI 614697, PI 614698, PI 614699, PI 614700, PI 614701

Few *Cucurbita* species (*C. argyrosperma*, *C. foetidissima*) and accessions exhibited a completely resistant reaction (Table 3) to the 11 isolates. Similarly, relatively few species (*C. maxima*, *C. pepo*) and accessions expressed a completely susceptible reaction (Table 4). These results showed that in most host-parasite interactions there are various

levels of resistance based on clear expression of pathotype and/or race-specificity. However, this was complicated by frequent observation of incomplete resistance characterized by limited sporulation of the pathogen (data not presented here).

Occurrence of pathotype-specific patterns in wild and weedy *Cucurbita* species is summarized in Table 5, which shows that most of the studied taxa displayed pathotype and/or race-specificity. The most variable taxa include *C. argyrosperma*, *C. foetidissima*, *C. okeechobensis* and *C. pepo* (Table 5). Specific reaction patterns are not presented in this paper.

Table 5. Occurrence of pathotype (race)-specific patterns in wild and weedy *Cucurbita* spp.

Taxon	No. of tested accessions	No. of reaction patterns	Ratio patterns/accession
<i>C. argyrosperma</i> var. <i>palmeri</i>	18	16	0.89
<i>C. argyrosperma</i> subsp. <i>sororia</i>	25	12	0.48
<i>C. cylindrata</i>	1	1	1.00
<i>C. digitata</i>	1	1	1.00
<i>C. ecuadorensis</i>	3	2	0.67
<i>C. ficifolia</i>	4	4	1.00
<i>C. foetidissima</i>	5	4	0.80
<i>C. maxima</i> subsp. <i>andreana</i>	3	2	0.67
<i>C. okeechobensis</i> subsp. <i>martinezii</i>	7	6	0.86
<i>C. pedatifolia</i>	1	1	1.00
<i>C. pepo</i>	6	5	0.83
<i>C. pepo</i> var. <i>fraterna</i>	4	4	1.00
<i>C. pepo</i> var. <i>texana</i>	18	9	0.50
<i>C. pepo</i> var. <i>ovifera</i>	1	1	1.00

For the first time, pathotype specificity has been described for *C. maxima* and *C. moschata* (Bains and Sharma, 1986; Thomas *et al.*, 1987), which expands our knowledge of pathotype specificity based only on *C. pepo* cultivars (Lebeda and Křístková, 1993). Notably, *C. pepo* cultivars with the fruit types acorn, straightneck and ornamental gourd are more susceptible to *P. cubensis* when compared with zucchini, cocozelle and vegetable marrow (Lebeda and Křístková, 2000). Our recent results support those findings, and demonstrate broad genetic variation in resistance to *P. cubensis* among in wild and weedy *Cucurbita* spp., including *C. pepo*. This at least partially contradicts the conclusions of Paris (2001), who considered *C. pepo* deficient in genes for disease resistance. Data reported in this paper

should be valuable for future research and exploitation in breeding cucurbits for disease resistance.

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