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REVIEW

# Gaps and perspectives of pathotype and race determination in *Golovinomyces cichoracearum* and *Podosphaera xanthii*

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**Abstract** *Golovinomyces cichoracearum* and *Podosphaera xanthii* (family Erysiphaceae) are the most important species causing cucurbit powdery mildew (CPM), a serious disease of field and greenhouse cucurbits. Both species are highly variable in their pathogenicity and virulence, as indicated by the existence of large number of different pathotypes and races. Various independent systems of CPM pathotype and race determinations and denominations are used worldwide. CPM pathotype identification is based on intergeneric and interspecific differences in host-CPM interactions. The most commonly used set of CPM pathotype differentials includes one genotype from four species representing three agriculturally important cucurbit genera plus two genotypes from a fifth species, melon *Cucumis melo* L. CPM races are characterized by specialization on different cultivars or lines of one host species and have, to date, been differentiated only on melon (*C. melo* L.). The most frequently used set of melon differentials includes 11 genotypes that can differentiate CPM races originating from melon and other cucurbits, e.g., cucumber, *Cucurbita* spp., and watermelon. In this paper, we critically review the current state, gaps, and perspectives in our understanding of pathogenicity variation in these two CPM pathogens at the pathotype and race levels.

**Keywords** Cucurbitaceae · Cucurbit powdery mildews · Denomination · Pathogenicity variation · Screening methodology

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## Introduction

*Golovinomyces cichoracearum* (*Gc*) and *Podosphaera xanthii* (*Px*) (family Erysiphaceae) are considered to be the most important species causing cucurbit powdery mildew (CPM), a serious disease of field and greenhouse cucurbits (McGrath and Thomas 1996; Pérez-García et al. 2009). *Px* is common in subtropical and tropical areas and in greenhouses in temperate areas, while *Gc* occurs more frequently in fields in temperate and cooler areas (Křístková et al. 2007, 2009). Both species may occur singly or together on cucurbits in Central Europe (Křístková et al. 2009).

The two species differ in host range, environmental requirements, and geographic distribution (Křístková et al. 2009; Lebeda et al. 2009b). They are also highly variable in their pathogenicity and virulence, as evidenced by the existence of large number of different pathotypes and races (Bertrand et al. 1992; Lebeda et al. 2004, 2007; Lebeda and Sedláková 2006; McCreight 2006) and by their variability in response to fungicides (McGrath 2001; Sedláková and Lebeda 2008).

Pathogenic specialization in CPM is well known. There is often a very clear expression of compatibility or incompatibility in host plant–powdery mildew interactions that allows for the classification of pathotypes and races based on the reaction patterns of compatible and

incompatible reactions on the differential hosts species or genotypes (Lebeda et al. 2008). A unified, objective system for the determination, denomination, and classification of pathotypes and races on cucurbits remains to be codified (Lebeda and Sedláková 2006; Lebeda et al. 2007, 2008; McCreight 2006).

In a recent paper, we critically reviewed the current state, gaps, and perspectives of our current understanding of pathogenicity variation in these two CPM pathogens at the pathotype and race levels. The need for developing an objective, unified, and internationally standardized differential set of Cucurbitaceae for characterization and for creating uniform system of denomination of pathotypes and races was discussed, including a proposal for broad cooperation in this international endeavor.

## Pathotype determination

Cucurbit powdery mildew pathotypes are based on intergeneric and interspecific differences in host–CPM interactions. Two differential sets for the determination of pathotypes have been proposed (Bertrand 1991; del Pino et al. 2002; Lebeda et al. 2008) (Table 1). Bertrand (1991) assembled the most frequently used differential set for pathotype determination; it included one genotype from each of four species representing three agriculturally important cucurbit genera plus two genotypes from a fifth species, melon *Cucumis melo* L. (Table 1). This set was subsequently expanded by Křístková and Lebeda (1999) and Lebeda et al. (2004, 2007, 2008). Del Pino et al. (2002) created the second pathotype differential set, comprising eight genotypes from four agriculturally important cucurbit species (Table 1). Pathotype denominations differ slightly between the two pathotype sets (Lebeda et al. 2008).

## Race determination

Cucurbit powdery mildew races are characterized by the interactions of different isolates of a pathogen with different cultivars of a given host species (Bardin et al. 1999; Bertrand 1991; Lebeda and Sedláková 2010; Pitrat et al. 1998). Races of *Gc* and *Px* have, to date, been differentiated only on melon (Table 2). McCreight (2006) and Lebeda et al. (2008) summarized the different genotypes and systems used for CPM race identification and denomination (Tables 2, 3). An overview of the various sets of CPM race differentials is shown in chronological order in Table 2, starting from the appearance of the second race of *P. xanthii* (in 1938). The most frequently used sets of melon differentials include 11 genotypes of *C. melo* (Table 2) that can differentiate CPM races originating from melon (McCreight 2006) and other cucurbits, such as cucumber, *Cucurbita* spp., and watermelon (Lebeda and Sedláková 2006, 2010; Lebeda et al. 2004, 2007, 2008). CPM race designations are not uniform, methodical, objective, or meaningful (Table 3), and three methods of race denominations are in use: numbers (e.g., 1, 2, 3), letters (e.g., A, B, C), and combinations of numbers and letters (e.g., 1J, 2F, 2US) (Lebeda et al. 2008).

**Table 1** Differential sets used for the determination of pathotypes

| Differential species | Genotype | Code[a] | References |
|---|---|---|---|
| The most frequently used differential set[b] | | | Bertrand (1991) |
| *Cucumis sativus* | Marketer 430 | A | |
| *Cucumis melo* | Védrantais | B1 | |
| *Cucumis melo* | PMR 45 | B2 | |
| *Cucurbita pepo* | Diamant F1 | C | |
| *Citrullus lanatus* | Sugar Baby | D | |
| *Cucurbita maxima* | Goliáš | Cm | Křístková and Lebeda (1999) |
| Differential set used only in Spain[c] | | | del Pino et al. (2002) |
| *Cucumis sativus* | Bellpuig | A | |
| | Negrito | | |
| *Cucumis melo* | Piel de Sapo | B | |
| | Rochet | | |
| *Cucurbita pepo* | Negro Belleza | C | |
| | Virginia Blanco | | |
| *Citrullus lanatus* | Klondike | D | |
| | Sugar Baby | | |

[a] Code for each species

[b] Assembled by Bertrand (1991), comprising one genotype from each of four species representing three agriculturally important cucurbit genera plus two genotypes from a fifth species, and expanded by Křístková and Lebeda (1999) with a genotype from one species

[c] Pathotype differential set, comprising eight genotypes from four agriculturally important cucurbit species

**Table 2** Race differential sets (in chronological order) used for cucurbit powdery mildew incited by *Podosphaera xanthii* (*Px*) and *Golovinomyces cichoracearum* (*Gc*) on melon

| *Px* and *Gc* races | Number of genotypes | *C. melo* genotype(s) | References |
|---|---|---|---|
| *Px* races 1 and 2 | 1 | PMR 45 | Jagger et al. (1938) |
| *Px* races 1, 2, and 3 | 5 | Hale's Best Jumbo, PMR 45, PMR 5, PMR 6, Edisto 47 | Thomas (1978) |
| *Px* races 1, 2, and 3 | 10 | Delicious 51, Top Mark, Védrantais, PMR 45, PMR 450, PMR 6, Perlita, PI 124111, PI 124112, Seminole | McCreight et al. (1987) |
| *Px* races 1 and 2 | 4 | Piel de Sapo, PMR-45, PMR-5, PI 124112 | Vakalounakis and Klironomou (1995) |
| *Px* races 0, 1, 2U.S., 2F, 3, 4, 5 | 11 | Iran H, Védrantais, Top Mark, Ananas, PMR 45, PMR 5, WMR 29, Edisto 47, PI 414723, MR-1, PI 124112 | Bardin et al. (1999); Jahn et al. (2002); Lebeda and Sedláková (2010); Pitrat et al. (1998) |
| Survey of *Gc* and *Px* races in Czech Republic | 11 | Iran H, Védrantais, Solartur, PMR 45, PMR 5, WMR 29, Edisto 47, PI 414723, MR-1, PI 124112, Nantais Oblong | Křístková and Lebeda (1999); Lebeda and Sedláková (2004, 2006); Lebeda et al. (2004, 2007) |
| *Px* races 2F, 2Z | 11 | Doublon, Rochet, PMR 45, PMR 5, Edisto 47, WMR 29, PI 124112, PI 414723, Negro, BG 6011, BG 6016 | Alvarez et al. (2000) |
| *Px* races 1, 2F, 2U.S., 3, 4, 5, N1, N2, N3, N2 | 10 | Fuyu 3, PMR 45, PMR 5, WMR 29, Edisto 47, PI 414723, Hainan 21, Quincy, Earl's Knight Natsu 2, Earl's Miyabi Natsu 2 | Hosoya et al. (2000) |
| *Px* races 1 and 2 | 8 | PMR 45, PMR 5, WMR 29, Edisto 47, PI 313970, PI 124111, PI 124112, PI 414723 | McCreight (2003) |
| *Px* races 1, 2 and 5 | 8 | Fuyu 3, PMR 45, PMR 5, WMR 29, Edisto 47, MR-1, PI 124112, PI 414723 | Kuzuya et al. (2006) |
| *Px* races 1 and 2 | 11 | Iran H, Védrantais, Top Mark, PMR 45, PMR 5, WMR 29, Edisto 47, PI 414723, MR-1, PI 124111, PI 124112 | McCreight (2006) |

**Table 3** Three methods for denomination of *Px* and *Gc* races

| Method | Example | References |
|---|---|---|
| Numbers | 1, 2, 3 | Jagger et al. (1938); Thomas (1978, 1988) |
| Letters | A, B, C | Křístková and Lebeda (1999); Lebeda and Sedláková (2004, 2006); Lebeda et al. (2007) |
| Numbers and letters | 1J, 2F, 2US | Alvarez et al. (2000); Bertrand (2002); Cohen et al. (2004); Floris and Alvarez (1995); Hosoya et al. (2000); Křístková and Lebeda (1999); Lebeda and Sedláková (2004, 2006, 2010); Lebeda et al. (2004, 2007, unpublished); McCreight et al. (1987); Pitrat et al. (1998) |

## Pathogenicity variation in CPM populations: the current situation

Both CPM species are characterized by very broad pathogenic variation represented by the existence of a large number of pathotypes and races (Table 4). The most comprehensive population survey of CPM (a virulence analysis of more than 400 isolates of both species), which was done from 2000 through to 2007 in the Czech Republic, revealed: (1) the species spectrum in Czech Republic differs from that in other European countries (Křístková et al. 2009); (2) the pathogenicity structure of Czech CPM populations is different from that in France and Spain (comparable data from other European countries are not available) and from that in other non-European countries; (3) a large number of new pathotypes and races occur in Czech Republic; (4) Czech CPM populations vary temporally and spatially (Lebeda and Sedláková 2004, 2006, 2010; Lebeda et al. 2004, 2007, unpublished).

No information on the genetic bases for the pathogenicity of CPM pathotypes or races is currently available at either the molecular or Mendelian level. Moreover, breeding of cucurbits for resistance to CPM is hindered by: (1) the lack of clear and uniform, objective descriptions of CPM pathotypes and races, and (2) an incomplete knowledge of the genetics of host plant resistance. There are, instead, various independent systems of CPM pathotype and race determinations and denominations in use worldwide, and

**Table 4** Summary of *Px* and *Gc* pathotypes and races identified worldwide[a]

| Category of pathogenicity | No. of detected pathotypes or races | | References |
|---|---|---|---|
| | *Gc* | *Px* | |
| Pathotypes | | | |
| France | 4 | 3 | Bertrand (1991); Bertrand et al. (1992) |
| Spain | – | 4 | del Pino et al. (2002) |
| Czech Republic | 13 (12/1)[b] | 8 (7/1)[b] | Lebeda and Sedláková (2004); Lebeda et al. (2004, 2007, unpublished) |
| Races | | | |
| Worldwide | 2 | 25[c] | Bardin et al. (1999); Bertrand (2002); Hosoya et al. (2000); Pitrat et al. (1998); summarized by McCreight (2006) |
| Czech Republic 2000–2007 | 86 (86/0)[b] | 48 (44/4)[b] | Lebeda and Sedláková (2004, 2006, 2010); Lebeda et al. (2004, 2007, unpublished) |

[a] Lebeda et al. 2007; Lebeda et al. unpublished data; McCreight 2006, modified

[b] Number of pathotypes or races detected only in the Czech Republic/no. of pathotypes or races also known from other countries

[c] Number of detected *Px* races includes: eight variants of race 1, six variants of race 2, three variants of race 3, and eight other *Px* races

although there is no international cooperation or agreement in these areas, the utility of a unified and uniform system of CPM pathotype and race determination and denomination is generally acknowledged (Lebeda et al. 2008).

A unified and uniform system of CPM pathotype and race determination and denomination should be characterized by three criteria: (1) standard sets of pathotype and race differentials; (2) uniform codes for the host–CPM interactions/scores; (3) a uniform screening methodology (Lebeda and Sedláková 2010). Agreement on the first two criteria should be achievable relatively easily within an acceptably short period of time—with discussion among all interested parties. The third criterion is potentially contentious as some researchers support of a leaf disc-based protocol, whereas others prefer whole plants for pathotype and race determinations. The two methodologies do not have to be mutually exclusive. An important feature of the leaf disc-based protocol is the uniformity of the test conditions and, therefore, the repeatability of results. Whole-plant assays should always be performed where possible to confirm the results of leaf-disc assays and include complete sets of the pathotype and race differentials. A key aspect of the leaf-disc protocol is a unified screening methodology.

## Unified screening methodology: a proposal

Screening and evaluation protocols have been described in detail (Lebeda 1984; Lebeda and Sedláková 2010) and followed-up in the development of new differential set proposed here. The most essential points related to the screening methodology are summarized herein.

Pathotype and race differentials (Lebeda et al. 2008) are grown in pots filled with a medium conducive to healthy growth and development, and watered and fertilized accordingly; the location should be free of CPM inoculum. The universally susceptible cucumber (*C. sativus* L.) Marketer 430 (Lebeda 1984) is grown in pot culture in a second, isolated location. Heavily infected cucurbit leaves from a pure axenic culture or from a field- or greenhouse-derived sample/culture are essential, and conidia are transferred from these leaves to true leaves of Marketer 430 by tapping. Where isolation is not possible or uncertain, CPM isolates may be cultured on detached leaves in clear plastic boxes in growth chambers maintained at 24/18°C (day/night) under a 12-h photoperiod (Lebeda and Sedláková 2010; McGrath 1994).

Pathogenic variability (pathotypes, races) is screened using the leaf-disc method (Lebeda and Sedláková 2004, 2010). Leaf discs, 15 mm in diameter, are taken from 6- to 8 week-old CPM-free plants of the differentials; three to five leaf discs per plant per genotype; three plants per differential per test. The leaf discs are placed on moist filter paper in clear plastic boxes and inoculated by tapping spores onto their adaxial surfaces (Lebeda 1984). Sporulation intensity (degree of infection, DI) is evaluated 6, 8, 10, 12, and 14 days post-inoculation using a 0–4 scale (Lebeda 1984; Lebeda and Sedláková 2010). Genotypes with no or low sporulation (DI 0–1) are considered to be resistant, whereas genotypes with a DI = 2–4 are scored as susceptible. Details of this methodology have been described by Lebeda and Sedláková (2010).

## Proposals and conclusions

In this age of molecular biology, we are still missing basic "classical phytopathology" information on CPM host–pathogen interactions in general and, specifically, on pathotypes on different cucurbit species and pathogenic

races on different genotypes of one host species. We also do not have a precise and objective system for their specification and denomination. These basic data will provide the foundation for further detailed and internationally accepted studies of CPM pathogenicity variation at the individual and population levels as will facilitate our understanding of CPM pathogenicity at the genetic and molecular levels (Lebeda et al. 2008, 2009a). For these reasons, we propose that the international community of researchers working in the fields of CPM pathogenicity and plant breeding, seed, and production should consider adopting: (1) two sets of differential cucurbit genotypes for the identification of CPM pathotypes and races, respectively, and (2) an objective, efficient, uniform, comprehensive coded system for the meaningful, concise designation of CPM pathotypes (sextet code) and races (septet code). The proposed set of pathotype differentials would include six genotypes of three genera (*Cucumis*, *Cucurbita*, *Citrullus*). The proposed set of CPM race differentials includes 21 genotypes of a single species, *Cucumis melo* L. (Lebeda et al. 2008). Furthermore, we propose a uniform screening methodology based upon a leaf-disc protocol for CPM pathotype and race determinations under more uniform conditions.

Ideally, the two differential sets, systems for denomination, and leaf-disc protocol will be approved by the international community after their validation by a large number of isolates of both CPM species that originate from various cucurbits and growing areas around the world.

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