Cucurbit powdery mildew of melon incited by *Podosphaera xanthii*: Global and western U.S. perspectives

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Abstract

Cucurbit powdery mildew (CPM) is a major problem of melon (*Cucumis melo* L.) production worldwide, that is mostly caused by two fungi: *Podosphaera xanthii* (*Px*; formerly *Sphaerotheca fuliginea*) and *Golovinomyces cichoracearum* (DC) V.P. Heluta (*Gc*; formerly *Erysiphe cichoracearum*). The two species may co-infect in some areas of northern Europe, but *Px* dominates in warmer climates around the world. Forty-five races of *Px* have been reported on melon based on sets of race differentials that range in number from as few as two to as many as 28. The CPM research community and seed industry are undertaking steps to define uniform sets of CPM race differentials and objective criteria for race nomenclature and designations. Breeders and pathologists must also consider another aspect of CPM that stems from its obligate parasitic nature: race stability as defined by a given set of CPM race differentials. This review summarizes the reported races of *Px* largely from the published literature. It also presents annual profiles from 2002 through 2011 of *Px* populations in the Central and Imperial valleys of California, and Yuma, Arizona. It is suggested that a large fraction of the races are not relevant to most *Px* resistance breeding, which will be done on a regional basis for subsets of races.

INTRODUCTION

Two fungi are commonly credited for inciting cucurbit powdery mildew (CPM) worldwide: *Podosphaera xanthii* (*Px*; formerly *Sphaerotheca fuliginea*) and *Golovinomyces cichoracearum* (DC) V.P. Heluta (*Ec*; formerly *Erysiphe cichoracearum*) (Shishkoff, 2000). *Px* predominates in warmer areas while *Ec* does so in cooler areas, and mixed infections (*Px* and *Gc*) have been found in Europe (Bertrand, 1991; Křístková, et al., 2009). The two CPM pathogens were confounded for many years as *Gc* (McCreight, 2004), but *Px* appears to be the predominant pathogen in major melon production areas. The increased numbers of reported *Px* races has stimulated concern over the future of breeding melons resistant to *Px*, in particular the need for a concise and objective system for *Px* race denomination and designation (see Lebeda, et al., 2012).We review here the gradual increase in the complexity of *Px*- and *Gc*-melon interactions over 87 years, expressed as pathogenic races, which has recently escalated (Fig. 1).

REPORTED PATHOLOGICAL RACES

Imperial Valley, California melon growers suffered losses to *Px* starting in 1925. Scientific breeding for resistance to *Px* was initiated in 1928 upon discovery of variation for reaction to *Px* in germplasm from India and resulted in the release of 'PMR 45' in 1934 (Jagger and Scott, 1937). Pathogenic race variation within *Px* was first observed in 1937 when 'PMR 45' was observed to be widely infected in Imperial Valley (Jagger, et al., 1938; Fig. 1). Resistance to this new form of *Px*, designated race 2, was quickly found and resulted in the release of 'PMR 5' in 1942 (Pryor, et al., 1946).

A third *Px* race on melons was observed by C.E. Thomas in the lower Rio Grande Valley of Texas in 1976 (Thomas, 1978). Race 3, as this new strain became known, did not become widespread in Texas or the U.S, but was later reported in the Punjab of India (Kaur and Jhooty, 1986) and widespread in Israel (Cohen, et al., 1996).

PI 414723 and WMR 29 revealed variation within *Px* race 2: 2US and 2F (France) in 1986 (McCreight, et al., 1987). Four *Px* races were known on melon in 1986 (Fig. 1).

By 1998, seven *Px* races, including 2US and 2F, were reported (Pitrat, et al., 1998). Race 0 revealed *Px*-resistance factors in 'Védrantais' and 'Top Mark' that had been regarded as universal *Px* susceptible genotypes (Bardin, et al., 1997). Races 4 and 5 were observed at about the same time (1997–1998) in France (M. Pitrat, pers. commun.) and Czech Republic (Krístková and Lebeda, 1999) and later in Israel (Cohen, et al., 2004). The number of reported *Px* races increased dramatically from this time (Fig. 1).

Four new races (N1, N2, N3, N4) were reported from Japan in 2000 (Hosoya, et al., 2000). Two variants each of *Px* races 2 and 3 were reported in 2002 (Cohen, et al., 2002). Bertrand (2002) reported race 6 using AR Hale's Best Jumbo.

Race S was first observed in Imperial Valley in 2003 (McCreight, et al., 2005). Races F, G, H were found in Czech (Lebeda and Sedláková, 2006). Then, there were 20 *Px* races (Fig. 1). *Px* race SD was isolated from Imperial Valley in 2004 or 2005 (Coffey, et al., 2006), and shortly afterwards was present in a greenhouse at Salinas (J.D. McCreight, unpub. data). Races 3.5 and P6 were reported in 2005 (M. Pitrat, pers. commun.). Race 4.5 was reported in 2008 Pitrat and Besombes, 2008

Comparative studies of reported *Px* resistance sources identified in California, Japan, and Spain differentiated isolates/populations of *Px* race 1 (eight variants; seven new) and race 2 (six variants; two new) populations in these countries (McCreight, 2006).

A unique race, pxCh 1 was reported in China in 2010 (Liu, et al., 2010). Twelve new *Px* races were isolated in 2010 in Czech Republic (Lebeda, et al., 2012).

Forty-five *Px* and 13 *Gc* races have thus been reported to date on melon (Table 1). This total for *Px* ignores the variation in *Px* at the pathotype level, e.g, isolates of races S and SD vary in their ability to infect watermelon C*itrullus lanatus* (Coffey, et al., 2006).

RACE STABILITY IN CALIFORNIA AND ARIZONA

Px Race 2 was the presumed race in California after many years of the deployment of *Px* race 2-resistant cultivars. *Px* race 1 was, however, detected at the Univ. Calif. (UC), Desert Crops Res. and Ext. Ctr. (DREC), Holtville, CA 92243 in the Imperial Valley six of 10 yrs from 2002 through 2011; *Px* race S was present three years, and race 2 was present one year (Table 2). In Yuma, Arizona, *Px* race 1 was present in Spring 2003, but *Px* race S was isolated from that field via single spore transfer and was consistently present in four subsequent Spring tests (Table 2). *Px* race 1 was detected in four, Fall field tests in Yuma. *Px* race 1 was present at UC West Side Res. and Ext. Ctr., Five Points, CA 93624-0158 in the San Joaquin Valley in 2003 (ca. 460 km north of DREC); *Px* race S was found there in 2007. *Px* race S was detected at two sites in 2011 in the Davis–Woodland area, which is ca. 340 km north of Five Points. *Px* race S is becoming more widespread throughout the Central Valley of California. It remains to be seen whether the *Px* populations will be consistently race S, or vary annually, like in Imperial Valley.

DISCUSSION

The apparent challenge of 46 races of *Px* on melon is formidable for pathologists and breeders alike. It is very likely that additional races will be reported as intensive, monoculture of melon increases and new germplasm is used in melon improvement. The recent increase in number of *Gc* races is also of interest in this regard. The demonstrated genetic variation in pathogens and host is of practical significance in terms of cultivar development and, perhaps, deployment of cultivars to “manage” *Px* and *Gc* populations so that resistance genes are not rendered ineffective. The large number of races poses, too, an interesting and complex biological puzzle at the genetic and molecular level.

Genetic diversity in the Czech populations of *Px* and *Gc* are particularly of interest (Lebeda and Sedláková, 2006; Lebeda, et al., 2012) in that melon is not widely cultivated in that area of Europe, and the cultivars grown there likely, in the absence of a catalog of their types and origins, represent a narrow genetic base. The 15 *Px* and 11 *Gc* races reported in Czech Republic are unexpected in the seeming absence of selection pressure for “new” pathogenic races by a limited number of *Px* or *Gc* resistance genes in melon. The diversity in Czech Republic may, therefore, reflect natural, random genetic variation in the respective pathogen populations that is maintained on diverse cucurbit hosts (Křístková, et al., 2009) that are generally susceptible to *Px*, and a diverse array of alternate hosts.

Races N1, N2, N3, N4 may reflect selection of *Px* virulence factors by recently introduced melon germplasm in Japan. The unique *Px* race reported from China (px Ch 1) represents another unique and isolated population. There are no data on race variation of *Px* on melons across China. Notably absent are reports of *Px* variation in Mexico, Central America and Brazil, where melons are important export crops from late Fall through early Spring in U.S.A., Canada and Europe. There are not any recent CPM race data from Australia, nor from India, which is a rich source of CPM-resistant melon germplasm (Dhillon, et al., 2012; Dogimont, 2010-2012).

It is suggested that breeding cultivars resistant to many *Px* and *Gc* races be done on a regional basis, whether at one or more locations. The 15 *Px* and 11 *Gc* races identified in Czech are thus less relevant as melon production there is not significant. The general stability of races in California indicates the need to pyramid multiple *Px* resistance genes to control the predominant races in each respective region, but each region will have different sets of genes as it does horticultural and market-specific traits.

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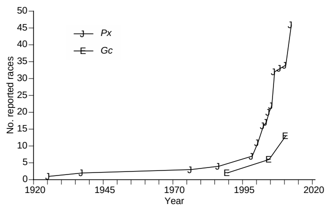

Fig. 1. Numbers of races of *Podosphaera xanthii* (*Px*) and *Golovinomyces cichoracearum* (*Gc*) on melon (*C. melo*) from 1925 through the present.

Table 1. Summary of 46 reported pathogenic races of *Podosphaera xanthii* on 37 melon cultigens.

Cultigen	Race																						
	0[y]	1J[x]	1Sp[w]	1M[v]	1IV[u]	1SJ[u]	1S[u]	1Ti[t]	1Tu[t]	2US[s]	2S[u]	2F[s]	2Z[r]	2a[q]	2b[q]	3[p]	3c[q]	3d[q]	4[o]	5[o]	3.5[n]	4.5[n]	N1[x]
Iran H	s[h]	s	–	–	s	s	s	–	–	s	s	s	s	–	–	–	–	–	s	s	–	–	–
Top Mark	R	s	–	–	s	s	s	–	–	s	s	s	–	–	–	s	–	–	s	s	–	–	–
Védrantais	R	s	–	–	s	s	s	s	s	s	s	s	–	–	–	s	–	–	s	s	s	S	–
Fuyu 3	–	s	–	–	–	–	s	–	–	s	s	s	–	s	s	s	–	–	s	s	–	–	s
PMR 45	R	R	R	R	R	R	R	R	R	s	s	s	s	–	–	s	s	s	s	s	s	S	R
PMR 5	R	R	R	R	R	R	R	R	R	R	R	R	R	–	–	s	–	–	R	R	s	S	–
PMR 6	–	–	–	–	–	–	–	–	–	–	–	–	–	R	R	–	s	s	–	–	–	–	–
WMR 29	R	R	–	–	R	R	R	R	R	H	H	R	R	–	–	–	–	–	s	s	s	S	R
Edisto 47	R	R	–	–	R	R	R	R	R	s	R	R	R	–	–	R	–	–	R	s	s	R	R
PI 414723	R	R	–	–	R	R	R	R	R	s	s	R	R	–	–	R	–	–	R	R	R	I	s
MR-1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	s	–	–
PI 124111	R	R	R	R	R	R	R	–	–	R	R	R	–	–	–	R	–	–	R	R	s	–	–
PI 124112	R	R	R	–	R	R	R	R	R	R	R	R	R	–	–	R	–	–	R	R	s	–	–
Earl’s Knight Natsu 2	–	R	–	–	–	–	s	–	–	s	–	–	–	–	–	–	–	–	–	s	–	–	s
Earl’s Miyabi Natsu 2	–	R	–	–	–	–	s	–	–	s	–	–	–	–	–	–	–	–	–	s	–	–	R
Hainan 21	–	R	–	–	–	–	R	–	–	s	–	–	–	–	–	–	–	–	–	s	–	–	R
Quincy	–	R	–	–	–	–	s	–	–	s	–	–	–	–	–	–	–	–	–	s	–	–	s
Negro	–	–	R	–	R	R	s	–	–	–	s	s	R	–	–	–	–	–	–	–	–	–	–
AR Hale’s Best Jumbo	–	–	–	–	–	–	–	s	I	–	–	R	–	–	–	–	–	–	–	R	–	–	–
Amarillo	–	–	R	–	R	s	s	–	–	–	s	–	–	–	–	–	–	–	–	–	–	–	–
Moscatel Grande	–	–	R	–	R	R	s	–	–	–	s	–	–	–	–	–	–	–	–	–	–	–	–
BG6011	–	–	–	–	–	–	–	–	–	–	–	s	R	–	–	–	–	–	–	–	–	–	–
BG 6016	–	–	–	–	–	–	–	–	–	–	–	I	R	–	–	–	–	–	–	–	–	–	–
Bellgarde	–	–	–	R	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Perlita	–	–	–	R	R	–	R	–	–	–	R	–	–	–	–	–	–	–	–	–	–	–	–
PI 179901	–	–	–	R	R	R	R	–	–	–	s	R	–	–	–	–	–	–	–	–	–	–	–
PI 234607	–	–	–	R	R	R	R	–	–	–	R	R	–	–	–	–	–	–	–	–	–	–	–
PI 236355	–	–	–	R	s	s	s	–	–	–	s	s	–	–	–	–	–	–	–	–	–	–	–
PI 313970	–	–	–	–	R	R	R	–	–	R	R	R	–	–	–	–	–	–	–	–	R	R	–
Seminole	–	–	–	R	R	–	R	–	–	–	R	R	–	–	–	–	–	–	–	–	–	–	–
Wescan	–	–	–	R	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
VA 435	–	–	–	–	–	–	–	–	–	–	–	R	–	–	–	–	–	–	–	–	–	–	–
Noy Yizre’el	–	–	–	–	–	–	–	–	–	–	–	–	–	s	R	–	s	R	–	–	–	–	–
Harukei 3	–	–	–	–	–	–	–	–	–	–	–	–	–	s	R	–	s	R	–	–	–	–	–
Nantais Oblong	–	–	–	–	–	–	–	–	–	–	–	–	–	s	R	–	s	R	–	–	–	–	–
Solartur	–	–	–	–	–	–	–	–	–	–	–	–	–	s	R	–	s	R	–	–	–	–	–
Ames 31282[f]	–	–	–	–	–	–	–	–	–	–	–	s[e]	–	–	–	s[e]	–	–	–	s[e]	s[e]	–	–

Table 1. (continued)

	N2[x]	N3[x]	N4[x]	6[m]	F[l]	G[l]	H[l]	P6[n]	S[k]	SD[j]	pxCh 1[i]	Czech 2010 races[h]											
												10	33	36	44	45	51	52	53	54 2	55 2	56 2	59
Iran H	–	–	–	–	s	s	s	–	–	–	R	s	s	s	s	s	s	s	s	s	s	s	s
Top Mark	–	–	–	–	–	–	–	–	s	s	–	–	–	–	–	–	–	–	–	–	–	–	–
Védrantais	–	–	–	s	s	s	s	s	–	–	s	s	s	s	s	s	s	s	s	s	s	s	s
Fuyu 3	s	s	s	–	–	–	–	–	s	–	s	–	–	–	–	–	–	–	–	–	–	–	–
PMR 45	s	R	R	s	s	s	s	s	s	s	R	s	R	s	s	s	s	s	R	s	s	s	s
PMR 5	–	–	–	R	s	s	s	R	s	s	s	s	R	s	s	s	s	s	R	R	s	R	s
PMR 6	–	–	–	–	–	–	–	–	s	s	R	R	R	R	R	s	s	R	R	R	R	R	R
WMR 29	R	R	R	s	s	s	R	s	s	s	R	R	R	s	R	s	s	R	R	s	s	R	s
Edisto 47	R	s	s	s	s	s	s	s	s	s	–	s	R	R	R	s	R	s	R	R	s	R	s
PI 414723	s	s	R	R	s	s	s	s	s	s	–	s	R	s	s	s	s	s	s	s	s	R	s
MR-1	–	–	–	–	s	R	s	R	s	s	R	R	R	R	R	s	R	R	R	R	R	R	s
PI 124111	–	–	–	–	–	–	–	–	?	?	–	R?	R	R	R	R	R	R	R	R	R	R	R
PI 124112	–	–	–	R	s	s	s	R	s	s	s	R	R	R	R	s	R	R	R	R	R	R	R
Earl's Knight Natsu 2	R	–	–	–	–	–	–	–	s	s	–	–	–	–	–	–	–	–	–	–	–	–	–
Earl's Miyabi Natsu 2	R	–	–	–	–	–	–	–	s	s	–	–	–	–	–	–	–	–	–	–	–	–	–
Hainan 21	s	–	–	–	–	–	–	–	s	s	–	–	–	–	–	–	–	–	–	–	–	–	–
Quincy	R	–	–	–	–	–	–	–	s	s	–	–	–	–	–	–	–	–	–	–	–	–	–
Negro	–	–	–	–	–	–	–	–	s	s	–	s	s	s	R	s	s?	s	s	s	s	s	s
AR Hale's Best Jumbo	–	–	–	s	–	–	–	–	s	s	–	s	s	s	s	s	s	s	s	s	s	s	s
Amarillo	–	–	–	–	–	–	–	–	s	s	–	s	s	s	s	s	s	s	s	s	s	s	s
Moscatel Grande	–	–	–	–	–	–	–	–	s	s	–	–	–	–	–	–	–	–	–	–	–	–	–
BG6011	–	–	–	–	–	–	–	–	s	s	–	–	–	–	–	–	–	–	–	–	–	–	–
BG 6016	–	–	–	–	–	–	–	–	?	s	–	–	–	–	–	–	–	–	–	–	–	–	–
Bellgarde	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Perlita	–	–	–	–	–	–	–	–	s	s	–	–	–	–	–	–	–	–	–	–	–	–	–
PI 179901	–	–	–	–	–	–	–	–	s	s	–	s	s	s	R	s	s	s	s	s	s	s	s
PI 234607	–	–	–	–	–	–	–	–	s	s	–	R	R	R	R	s	R	R	R	R	R	R	R
PI 236355	–	–	–	–	–	–	–	–	s	s	–	s	s	s	s	s	s	s	s	s	s	s	s
PI 313970	–	–	–	–	s	–	–	–	R	s	–	R	R	s	R	s	s	s	s	s	s	R	s
Seminole	–	–	–	–	–	–	–	–	s	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Wescan	–	–	–	–	–	–	–	–	s	–	–	–	–	–	–	–	–	–	–	–	–	–	–
VA 435	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Noy Yizre'el	–	–	–	–	–	–	–	–	–	–	–	R	R	R	R	s	s	R	R	R	R	s	R
Harukei 3	–	–	–	–	–	–	–	–	–	–	s	–	–	–	–	–	–	–	–	–	–	–	–
Nantais Oblong	–	–	–	–	s	s	s	–	–	–	–	s	s	s	s	s	s	s	s	s	s	s	s
Solartur	–	–	–	–	s	s	s	–	–	–	–	s	s	s	s	s	s	s	s	s	s	s	s
Ames 31282[f]	–	–	–	–	–	–	–	–	s[d]	s[d]	R	–	–	–	–	–	–	–	–	–	–	–	–

[z]Race 1: 1J, Japan; 1Sp, Spain; 1M, Michigan; 1IV, Imperial Valley, Calif.; 1SJ, San Joaquin Valley, Calif.; 1S, Salinas; 1Ti, Tifton , Ga.; 1Tu, Tunisia. Race 2: 2US, U.S.A.; 2S, Salinas, Calif.; 2F, France; 2Z, Zaragoza
[y]Bardin, et al., 1999; Bardin, et al., 1997; Bertrand, 1991; Krístková and Lebeda, 1999; 1999; Mohamed, et al., 1995
[x]Hosoya, et al., 2000
[w]Floris and Alvarez, 1995
[v]Harwood and Markarian, 1968
[u]McCreight, 2006
[t]Bertrand, 2002
[s]McCreight, et al., 1987
[r]Alvarez, et al., 2000
[q]Cohen, et al., 1996; Cohen, et al., 2002
[p]Thomas, 1978
[o]Bardin, 1996; Bardin, et al., 1999; Cohen, et al., 2002; Pitrat, et al., 1998
[n]M.Pitrat, pers. commun.; Pitrat and Besombes, 2008
[m]Bertrand, 2002
[l]Lebeda and Sedláková, 2004
[k]McCreight and Coffey, 2011
[j]Coffey, et al., 2006
[i]Liu, et al., 2010
[h]Lebeda, et al., 2012
[g]s = susceptible, R = resistant, H = heterogeneous, I = intermediate, ? = uncertainty; "–" = not tested.
[f]Ames 31282 is the correct designation for PI 134198 in Liu et al., 2010 (K.R. Reitsma, pers. commun.); see http://www.ars-grin.gov/cgi-bin/npgs/acc/display.pl?1898811 and http://www.ars-grin.gov/cgi-bin/npgs/acc/display.pl?1812862
[e]J.Fauve, Harris Moran Clause, pers. commun.
[d]J.D. McCreight, unpubl. data

Table 2. Pathogenic races of cucurbit powdery mildew incited by *Podosphaera xanthii* in different seasons at four locations in California, and Yuma, Arizona; 2002 through 2011.

		Year									
Location	Season	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011
California											
Imperial Valley	Spring	1	S	1	S	1	1	1SJ	S	1/2[z]	1
	Fall	1	–	1	–	1[y]	1[y]	–	–	–	–
Five Points	Summer	–	1SJ	–	–	–	S	–	–	–	–
	Fall	–	1	–	–	–	–	–	–	–	–
Davis		–	–	–	–	–	–	–	–	2[x]	S[x]
Woodland		–	–	–	–	–	–	–	–	2[w]	S
Arizona											
Yuma	Spring	–	1/S[v]	S	S	–	S	S	–	–	–
	Fall	–	1	1	–	1[y]	1[y]	–	–	–	–

[z]'PMR 45' did not germinate; race 1 or 2 based on reactions of other lines.
[y]Plants infected with *Cucurbit yellow stunting disorder virus*.
[x]J. Mercier, Harris Moran Clause, pers. commun.
[w]H. Bouzar, Sakata Seed America, pers. commun.
[v]*Px* race 1 detected in a field test at Univ. Ariz., Yuma Agric. Res. Ctr. (YARC); *Px* race S isolated via single spore transfer from a field sample at YARC.