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Melon–Powdery Mildew Interactions Reveal Variation in Melon Cultigens and *Podosphaera xanthii* Races 1 and 2

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Abstract. **Powdery mildew is a serious disease of melon (*Cucumis melo* L.) worldwide. Twenty-two melon cultigens have been used to define 22 reported races of the pathogen *Podosphaera xanthii* (sect. *Sphaerotheca*) *xanthii* (Castag.) U. Braun & N. Shish. Comb. nov. [syn. *Sphaerotheca fuliginea* (Schlecht. ex Fr.) Poll.]. Discrepancies in the reactions of eight cultigens to populations of *P. xanthii* races 1 and 2 in California, Japan, and Spain revealed genetic differences among them that can be used to differentiate *P. xanthii* race 1 and 2 populations in these countries. Implicit in these results is the existence of previously unknown virulence factors in these populations of *P. xanthii* races 1 and 2 that permit designation of new races of *P. xanthii* on melon. Synthesis of these results with previous reports resulted in the identification of 28 putative races of *P. xanthii* on melon that include eight variants of race 1 and six variants of race 2. Six of the cultigens exhibited resistant blisters in response to heavy infection by *P. xanthii* in field and greenhouse tests.**

Powdery mildew affects yield and quality of melon worldwide. The disease is primarily caused by two fungal species: *Podosphaera xanthii* and *Golovinomyces cichoracearum* (D.C.) Huleta (syn. *Erisyphe cichoracearum* auct. *p.p.*) (Jahn et al., 2002). Twenty-two races of *P. xanthii* and two races of *G. cichoracearum* have been reported on melon. Races 1 and 2 of *P. xanthii* were defined in 1938 when resistance to powdery mildew in 'PMR 45' was overcome in commercial production fields (Jagger et al., 1938). Race 3 was reported in 1978 (Thomas, 1978). Nineteen additional races of *P. xanthii* races have been reported since 1996 (Alvarez et al., 2000; Bertrand, 2002; Cohen et al., 2002; Hosoya et al., 2000; Lebeda and Sedláková, 2004; McCreight et al., 1987; Pitrat et al., 1998).

There are more than 30 reported sources of resistance in melon to the 22 races of *P. xanthii* (Alvarez et al., 2000; Bertrand, 2002; Cohen et al., 2002; Hosoya et al., 2000; Lebeda and Sedláková, 2004; McCreight, 2003a; McCreight et al., 1987; Pitrat et al., 1998; Sowell and Corely, 1974), but resistance genes have been reported for only four of the 22 reported races of *P. xanthii*. Genes for resistance to race 1 have been described in 20 cultigens, and 10 cultigens have genes for resistance to race 2 (Anagnostou et al., 2000; McCreight, 2003a; Pitrat, 1998). PI 124111 has one gene that confers resistance to races 1, 2, 4, and 5 (Bardin et al., 1999).

The genetic information including allelism for the resistances in the resistance sources is incomplete due in part to the minor crop status of melon, the many places around the world where the numerous reports originated, availability of germplasm for testing, different research objectives and protocols, different populations of the races used, and lack of any genetic information about the pathogen. The result has been numerous and sometimes differing or conflicting reports of genes for resistance to powdery mildew. For example, resistance in 'PMR 5' to race 1 was ascribed to the single dominant gene *Pm-1* in three reports (Bohn and Whitaker, 1964; Harwood and Markarian, 1968a; Kenigsbuch and Cohen, 1992), but a fourth report provided evidence for two dominant genes, *Pm-C* + *Pm-D* (Epinat et al., 1993). The airborne and obligate nature of the pathogen has historically made it difficult to handle more than a couple of races at any given location. Recent developments in handling the pathogen in axenic culture and long term preservation will facilitate race identification, genetic studies and breeding for resistance to powdery mildew in melon (Nicot et al., 2002).

Eleven *P. xanthii* race differentials have been frequently used worldwide. Iran H, 'Védrantais', 'Top Mark', and 'Ananas' are susceptible to *P. xanthii* races 1 and 2 (Pitrat et al., 1998). The others ('PMR 45', 'PMR 5', WMR 29, 'Edisto 47', PI 414723, MR-1, and PI 124112) are resistant to race 1, but vary in their responses to race 2 variants 2U.S. and 2F (Pitrat et al., 1998). 'PMR 45' is susceptible to race 2 while 'PMR 5', MR-1, and PI 124112 are resistant to both variants of race 2 (McCreight et al., 1987; Pitrat, 1998). 'Edisto 47' and PI 414723 are resistant to race 2F, but susceptible to race 2U.S. (McCreight et al., 1987; Pitrat, 1998). WMR 29 is resistant to race 2F, but segregates for resistance to race 2U.S. (McCreight, 2003a; McCreight et al., 1987).

Five *P. xanthii* race differentials and eight other sources of resistance to *P. xanthii* races 1 and 2 have been challenged with limited numbers of isolates of these races. 'Perlita', 'Seminole', PI 234607, PI 236355, and PI 179901 were resistant to *P. xanthii* race 1 in Michigan (Harwood and Markarian, 1968a, 1968b). In Spain, 'Amarillo', 'Moscatel Grande', and 'Negro' were resistant to *P. xanthii* race 1 (Floris and Alvarez, 1995), and 'Negro' was resistant to one of two isolates of *P. xanthii* race 2France (Alvarez et al., 2000). 'Earl's Knight Natsu 2', 'Earl's Miyabi Natsu 2', 'Hainan 21', and 'Quincy' were resistant to race 1 in Japan (Hosoya et al., 2000). PI 313970 was resistant to *P. xanthii* races 1 and 2U.S. in California (McCreight, 2003a).

The objective of this research was to make direct, side-by-side comparisons of these 13 cultigens and the commonly used

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P. xanthii race differentials to the same populations of *P. xanthii* in order to gain insight into the genetic differences among them for resistance to *P. xanthii*, and their potential utility as sources of resistance to *P. xanthii*. Comparative analyses of these and previously published data enabled indirect comparison of *P. xanthii* races 1 and 2 among and within different countries that provided insight into the genetic variability of *P. xanthii*. Preliminary analysis of the responses of the race differentials in two of the tests was previously reported (McCreight, 2003b).

Materials and Methods

Plant materials. 'Top Mark' and 'PMR 45' were obtained from Hollar Seed Co., Rocky Ford, Colo. Nine other *P. xanthii* race differentials (Iran H, 'Védrantais', 'PMR 5', WMR 29, 'Edisto 47', PI 414723, MR-1, PI 124111, PI 124112) originated from various other sources and were increased in a greenhouse at Salinas, Calif., by controlled self- and sib-pollination. 'Negro' was obtained from J.M. Alvarez (Centro de Investigacíon y Tecnología Agroalimentaria de Aragón, Zaragoza, Spain). The five remaining differentials, 'Fuyu 3', 'Earl's Knight Natsu 2', 'Earl's Miyabi Natsu 2', 'Hainan 21', and 'Quincy', were obtained from M. Kuzuya (Plant Biotechnology Institute, Ibaraki Agricultural Center, Iwami, Nishi-ibaraki, Japan).

PI 234607, PI 236355, and PI 179901 were obtained from the USDA, ARS, North Central Regional Plant Introduction Station, Ames, Iowa. 'Amarillo' and 'Moscatel Grande' were obtained from J.M. Alvarez. 'Perlita', Seminole', and PI 313970 originated from various other sources and were increased in a greenhouse at Salinas by controlled self- and sib-pollination.

Field tests. There were three field tests at two widely separate locations. In 2002, two field tests at the Univ. of California, Desert Research and Education Center, Holtville were direct-seeded and watered via subsurface drip irrigation. The seeding dates were 20 Mar. and 21 Aug.; powdery mildew was evaluated 18 and 19 June, and 29 Oct., respectively. Each experimental plot consisted of two hills (four seeds per hill) spaced ≈75 cm apart along rows (beds) on 2-m centers; entries were randomized in two replications. 'Top Mark' was planted in two adjacent border beds along one side and provided guards at each end of the test plots. The third field test was planted in the San Joaquin Valley, Calif., at the Univ. of California, Westside Research and Education Center, Five Points on 27 June 2003 and evaluated for powdery mildew on 21 Aug. This test was identical to the Imperial Valley tests except that the soil was pre-irrigated prior to planting and then furrow irrigated as needed.

Greenhouse and growth chamber tests. Seeds were germinated on moistened paper towels in plastic boxes at 25 °C and a 12-h photoperiod. They were transplanted into washed sand in plastic pots (10 × 10 × 10 cm deep; one seedling/pot) at the cotyledon stage of growth and immediately placed into the growth chamber or greenhouse, and grown as previously described (McCreight, 2000).

The *P. xanthii* race 1 tests (growth chamber) were arranged in nine randomized blocks (reps). The growth chamber was set at 25 °C and a 12-h photoperiod ($PPF \cong 230\ \mu mol \cdot m^{-2} \cdot s^{-1}$) for evaluation of resistance to race 1. Plants were watered daily and fertilized weekly with 15N–2.2P–12.5K–5Ca–2Mg (Peters Excel Cal-Mag; Scotts-Sierra Horticultural Products, Marysville, Ohio) at a rate of $3.6\ g \cdot L^{-1}$ to deliver $540\ mg \cdot L^{-1}$ N. The first growth chamber test was started on 17 Sept. 2002 and evaluated for powdery mildew on 18 Oct. The second growth chamber test was started on 7 Nov. 2003, and evaluated on 30 Nov. Data reported here are from the first two true leaves in both tests. No pesticides were applied to the seedlings in the growth chamber.

The *P. xanthii* race 2 tests (greenhouse) were arranged in nine randomized blocks in 2001, and five blocks in 2003 and 2004. The plants were grown under natural daylight during the periods of 20 Aug. to 27 Sept. 2001, 9 Dec. 2003 to 13 Jan. 2004, and 17 Mar. to 28 May 2004. Plants were watered daily as needed with 15N–2.2P–12.5K–5Ca–2Mg (Peters Excel Cal-Mag) diluted to deliver $100\ mg \cdot L^{-1}$ N. The plants were treated with imidachloprid insecticide for aphid and whitefly control. Data reported here are from true leaves: 1 to 7 (2001), 1 and 2 (2003), and 4 to 12 (2004).

Pathogen culture, race identification, and inoculation. In field tests, plants were infected with inoculum from the areas surrounding the fields. Race 2U.S. of *P. xanthii* was present throughout the year on various melon cultigens and 'Grey Zucchini' squash (*Cucurbita pepo* L.) in the Salinas, Calif., greenhouse in which the *P. xanthii* race 2 tests were carried out. The *P. xanthii* race 1 strain used in the growth chamber tests was obtained from *P. xanthii* race 2 in the greenhouse described above via single spore variants and isolated as previously described (McCreight, 2003a). Air circulation fans in the greenhouse and growth chamber used for the study ensured movement of spores from source plants that were placed around and among test plants. Race determinations in the field and greenhouse tests were based upon the reactions of the 11 powdery mildew race differentials included in the field tests (Table 1).

Disease evaluation. Powdery mildew infection as evidenced by mycelial growth and sporulation was evaluated on true leaves using a 1 to 9 scale as follows: 1 = no evidence of disease; 2 = trace of hyphae, no detectable sporulation; 3 = hyphae restricted, no detectable sporulation; 4 = few colonies present, sporulation; 5 = scattered colonies, sporulation; 6 = numerous colonies, sporulation; 7 = ≈50% of adaxial surface covered with hyphae and spores, few colonies on abaxial surface, abundant sporulation; 8 = >50% of adaxial surface covered with hyphae and spores, scattered colonies on abaxial surface, abundant sporulation; and 9 = >75% of adaxial surface covered with hyphae and spores, numerous or coalesced colonies on abaxial surface.

Disease evaluations were done on a plot basis in the field tests. Individual leaves were evaluated in growth chamber and greenhouse tests. Mean disease rating <4.0 was considered resistant and a mean rating ≥4.0 was considered susceptible.

Results

Race 1–Field tests. Reactions of the powdery mildew race differentials indicated the presence of race 1 in the three field tests: Iran H, 'Védrantais', and 'Top Mark' were susceptible; 'PMR 45' and seven other race 1–resistant differentials included in the field tests were resistant (Table 1). The reappearance of race 1 in the Imperial Valley was previously noted (Thomas et al., 1984).

'Perlita' and 'Seminole' were highly resistant to *P. xanthii* race 1 in both Imperial Valley field tests, but were not included in the San Joaquin Valley test (Table 1). The original descriptions of these cultivars omitted details about *P. xanthii* race specificity (Patterson, 1964; Whitner, 1960), but Harwood and Markarian (1968b) evaluated their responses to *P. xanthii* race 1 in Michigan. They concluded from genetic data that 'Perlita' has *Pm-1*, an allele of *Pm-1*, or a closely linked gene (Harwood and Markarian, 1968a). 'Seminole' was completely resistant to *P.*

Table 1. Expected disease reactions and mean disease ratings of 17 melon *P. xanthii* race differentials and eight additional reported sources of resistance to *P. xanthii* races 1 and 2 in field, growth chamber, and greenhouse tests, in the years 2001 to 2004.[z]

	Race 1						Race 2[y]				
							2S	2U.S.		2F	
	Expected	Field[x]			Growth chamber[w]			Expected		Expected	
Cultigen	reaction[v]	IV02S	IV02F	SJV03	2002	2003	2001	reaction	2003	reaction	2004
Commonly tested race differentials											
Iran H	s[u]	9.0	6.5	9.0	8.9	8.5	8.6	s[u]	7.1	s[u]	8.8
Védrantais	s[u]	4.5	6.5	–	8.4	7.9	7.9	s[u]	4.2	s[u]	8.6
Top Mark	s[u]	5.0	5.5	8.0	8.4	6.6	8.4	s[u]	6.9	s[u]	9.0
Fuyu 3	s[t]	–	–	–	–	8.7	–	s[t]	7.6	s[t]	–
PMR 45	R[u]	1.0	2.0	1.0	1.0	1.0	8.4	s[u]	6.4	s[u]	8.5
PMR 5	R[u]	1.0	1.0	1.0	1.0	1.0	2.7	R[u]	1.3	R[u]	1.0
WMR 29	R[u]	1.0	1.0	1.0	1.0	1.0	7.0	H[u]	6.4	H[u]	7.7
Edisto 47	R[u]	–	1.0	1.0	1.0	1.0	7.7	s[u]	5.5	R[u]	3.4
PI 414723	R[u]	1.0	1.0	1.0	1.0	1.0	3.3	s[u]	4.1	R[u]	1.5
MR-1	R[u]	1.0	1.0	1.0	1.0	1.0	1.1	R[u]	1.4	R[u]	1.1
PI 124111	R[u]	1.0	1.0	–	1.0	–	1.0	R[u]	–	R[u]	1.0
PI 124112	R[u]	1.0	1.0	1.0	1.0	1.0	1.1	R[u]	1.1	R[u]	1.0
Other race differentials											
Earl's Knight Natsu 2	R[t]	–	–	–	–	7.3	–	–	7.3	–	–
Earl's Miyabi Natsu 2	R[t]	–	–	–	–	8.2	–	–	4.0	–	–
Hainan 21	R[t]	–	–	–	–	1.2	–	–	7.5	–	–
Quincy	R[t]	–	–	–	–	8.2	–	–	7.8	–	–
Negro	R[s]	1.0	1.0	1.0	6.5	–	8.4	–	–	–	7.4
Other sources of resistance to race 1 and race 2											
Amarillo	R[s]	1.0	–	6.5	8.7	–	8.6	–	–	–	8.8
Moscatel Grande	R[s]	1.0	1.0	1.0	5.7	–	8.2	–	–	–	8.6
Perlita	R[r]	1.0	1.0	–	1.0	–	2.1	R[r]	–	R[r]	1.0
PI 179901	R[r]	1.0	1.0	1.0	1.0	–	6.6	R[q]	–	R[q]	3.5
PI 234607	R[r]	1.0	–	1.0	1.0	–	1.7	R[q]	–	R[q]	1.0
PI 236355	R[r]	5.5	–	9.0	8.5	–	8.4	–	–	–	9.0
PI 313970	R[p]	1.0	1.0	1.0	1.2	1.0	2.1	R[p]	1.7	R[p]	1.0
Seminole	R[r]	1.0	1.0	–	1.0	–	1.4	R[r]	–	R[r]	1.0

[z] Rated on a 1 (no disease) to 9 (infected, abundant sporulation) scale; see text for description; resistant < 4.0; susceptible ≥ 4.0.

[y] Data reported here are from true leaves 1 to 7 (2001), 1 and 2 (2003), and 4 to 12 (2004).

[x] IV02S, Imperial Valley, Spring 2002; IV02F, Imperial Valley, Fall 2002; SJV03, San Joaquin Valley, 2003.

[w] Data from first two true leaves.

[v] Based on previous reports: s = susceptible; H = heterogeneous; R = resistant; – = not tested.

[u] Pitrat et al., 1998.

[t] Hosoya et al., 2000.

[s] Floris and Alvarez, 1995.

[r] Harwood and Markarian, 1968a.

[q] Sowell and Corley, 1974.

[p] McCreight, 2003a.

xanthii race 1 in greenhouse and field tests in one study (Markarian and Harwood, 1967), but was variable in a second study where 92% of the 'Seminole' plants were completely free of mildew (Harwood and Markarian, 1968b). They concluded after further analysis that 'Seminole' possessed one partially dominant gene (*Pm*^{4}), one almost completely dominant gene (*Pm*^{5}), and at least one minor gene for resistance to *P. xanthii* race 1 (Harwood and Markarian, 1968a). These differing results indicate possible variation in virulence factors within the *P. xanthii* race 1 population in Michigan.

PI 179901, PI 234607, and PI 236355 were resistant to *P. xanthii* race 1 in Michigan when each was found to have two dominant genes for resistance to *P. xanthii* race 1 in crosses with 'PMR 45' and 'PMR 5' (Harwood and Markarian, 1968a). In these field tests, PI 179901 and PI 234607 were resistant, and PI 236355 was susceptible (Table 1). The differential responses of PI 236355 indicate different virulence factors in populations of *P. xanthii* race 1 in Michigan and California. Based on this difference, the Michigan *P. xanthii* population is designated race 1Michigan (1M) (Table 2).

'Amarillo', 'Moscatel Grande', and 'Negro' were resistant to *P. xanthii* race 1 in Spain and shown to possess three unique dominant genes: *Pmy*^{1} or *Pmz*^{1}, *Pmy* + *Pmz*, and *Pmx*, respectively (Floris and Alvarez, 1995). 'Moscatel Grande' and 'Negro' were resistant in the field tests (Table 1). In contrast, 'Amarillo' was resistant in the spring Imperial Valley test, but susceptible in the San Joaquin Valley test (Table 1). These data confirm the genetic differences for resistance to *P. xanthii* between 'Amarillo', 'Moscatel Grande', and 'Negro' (Floris and Alvarez, 1995). They also indicate differences in virulence factors between the

P. xanthii race 1 populations in Spain and California. The Spanish *P. xanthii* population is, therefore, designated race 1Spain (1Sp) (Table 2).

PI 313970, which has a recessive gene for resistance of true leaves to race 1 (McCreight, 2003a), was resistant to race 1 in the field tests.

In the San Joaquin Valley field test, PI 313970, MR-1, and PI 124112 exhibited water-soaked spots and raised blisters (data not shown) to heavy mildew infection, which was evidenced by the mean disease ratings ≥8.0 of Iran H and 'Top Mark'. PI 313970, PI 124111 (from which MR-1 was derived), and PI 124112 were previously noted to exhibit resistant blisters in response to *P. xanthii* race 2 in greenhouse tests at Salinas (McCreight, 2003a). The resistant blisters on these three melon cultigens were similar to those described on hops (*Humulus lupulus* L.) in response to heavy powdery mildew infection incited by *Sphaerotheca humuli* DC. (Burr) (Royle, 1978).

RACE 1–GROWTH CHAMBER. Iran H, 'Védrantais', 'Top Mark', and 'Fuyu 3' were highly susceptible to *P. xanthii* race 1 in the growth chamber (Table 1). 'PMR 45' and the seven other common powdery mildew race differentials were highly resistant in the growth chamber (Table 1).

'Earl's Knight Natsu 2', 'Earl's Miyabi Natsu 2', 'Hainan 21', and 'Quincy' were resistant to *P. xanthii* race 1 on leaf disks in Japan (Hosoya et al., 2000). The inheritance of their resistances to *P. xanthii* race 1 in Japan has not been reported; they are all F_1 hybrids. Three of these four cultivars were, in contrast to their reactions in Japan, highly susceptible to *P. xanthii* race 1 in this study; only 'Hainan 21' was resistant (Table 1). These data are additional evidence of new virulence factors in geographically isolated populations of race 1. The Japanese *P. xanthii* population is, therefore, designated race 1Japan (1J) (Table 2).

'Perlita', PI 179901, PI 234607, PI 313970, and 'Seminole' were highly resistant to *P. xanthii* race 1 in the growth chamber (Table 1), consistent with their previously reported responses to *P. xanthii* race 1 (Harwood and Markarian, 1968a, 1968b; McCreight, 2003a), and their responses in the field tests (Table 1).

'Amarillo', 'Moscatel Grande', and 'Negro', which exhibited dominant genes for resistance to *P. xanthii* race 1 in Spain (Floris and Alvarez, 1995), were susceptible in the growth chamber (Table 1). 'Moscatel Grande' and 'Negro' were not as susceptible as Iran H, 'Védrantais', or 'Top Mark', whereas 'Amarillo' was highly susceptible and comparable to Iran H, 'Védrantais', and 'Top Mark' (Table 1). These data reveal differences in their resistance genes and additional evidence of new virulence factors within *P. xanthii* race 1 populations. The isolate of *P. xanthii* used in the growth chamber is designated race 1Salinas (1S) (Table 2).

PI 236355 was highly susceptible to *P. xanthii* race 1 in the growth chamber (Table 1). It was previously found to possess two dominant genes for resistance to *P. xanthii* race 1 in Michigan; one possibly linked to *Pm-1*, the other possibly similar to a gene in PI 124111 (Harwood and Markarian, 1968a).

Synthesis of these *P. xanthii* race 1 results with previous reports (Bertrand, 2002; Floris and Alvarez, 1995; Harwood and Markarian, 1968a; Hosoya et al., 2000; Pitrat et al., 1998; Sowell and Corley, 1974) resulted in the recognition of eight variants of *P. xanthii* race 1 on melon cultigens (Table 2). Race 1 Imperial Valley (1IV) is distinguished by the susceptible reaction of PI 236355, and the resistant reactions of 'Amarillo', 'Moscatel Grande', and 'Negro' (Tables 1 and 2). Race 1 San Joaquin Valley (1SJ) is distinguished by the susceptible reaction of 'Amarillo' and the resistant reactions of 'Moscatel Grande' and 'Negro' (Tables 1 and 2). Variants 1Ti and 1Tu are based on the different reactions of AR Hale's Best Jumbo leaf disks to race 1 populations from Tifton, Ga. (1Ti), to which it was susceptible, and Tunisia (1Tu), to which it expressed an intermediate level of susceptibility (Bertrand, 2002).

RACE 2–GREENHOUSE. The differentials indicated *P. xanthii* race 2 in the greenhouse tests. The population at Salinas differed from the population of *P. xanthii* race 2 at Riverside, Calif., which infected PI 414723 and resulted in the differentiation of two variants of race 2: 2U.S. and 2France (McCreight et al., 1987; Pitrat et al., 1998). In this study at Salinas, PI 414723 was resistant in 2001 and 2004 and susceptible in 2003 (Table 1). The difference in populations is also shown by the reactions of 'Edisto 47' in the three tests: susceptible in 2001 and 2003, and resistant in 2004. The reactions of the *P. xanthii* race differentials indicate that the 2003 population was similar to race 2U.S. and the population in 2004 was race 2France (2F). The population present in 2001 was unique and was, therefore, designated race 2Salinas (2S) (Table 2).

'Earl's Knight Natsu 2', 'Hainan 21', and 'Quincy' were highly susceptible to *P. xanthii* race 2U.S. (2003 test), and 'Earl's Miyabi Natsu 2' was susceptible at a low level (Table 1). Hosoya et al. (2000) isolated *P. xanthii* race 2U.S. at low frequencies (<4%) from 'Earl's Knight Natsu 2' samples) and 'Earl's Miyabi Natsu 2', but not from 'Hainan 21' or 'Quincy'. They did not report the reactions of these four hybrids to race 2U.S. (Hosoya et al., 2000).

'Perlita' and 'Seminole' were highly resistant to *P. xanthii* race 2S and 2F (Table 1). PI 313970 was resistant to *P. xanthii* race 2U.S. as previously reported (McCreight, 2003a), and was resistant to 2S and 2F (Table 1).

'Amarillo', 'Moscatel Grande', 'Negro', and PI 236355 were highly susceptible to *P. xanthii* race 2US and 2F; mean disease ratings ranged from 7.4 to 8.8 (Table 1). 'Negro' varied in its reaction to two Spanish isolates of *P. xanthii* race 2F: susceptible to one from Málaga, resistant to one from Zaragoza (Alvarez et al., 2000). Thus, the *P. xanthii* race 2F isolate in the 2004 test is similar to the Málaga isolate. The Zaragoza isolate is designated 2Zaragoza (2Z), one of six variants of race 2 (Table 2).

Sowell and Corley (1974) reported PI 179901 and PI 234607 resistant to *P. xanthii* race 2 in Georgia. PI 179901 was susceptible to *P. xanthii* race 2S and moderately resistant to 2F in this study (Table 1). PI 234607 was resistant to *P. xanthii* race 2S and 2F (Table 1). These data suggest that the Georgia population of *P. xanthii* race 2 was similar to race 2F.

Some individuals of PI 313970, PI 124111, MR-1, and 'Seminole' exhibited resistant blisters in response to *P. xanthii* race 2U.S.: eight of nine PI 313970 plants had blisters, while only three plants each of PI 124111, MR-1, and one plant of 'Seminole' had blisters. The blisters appeared long after susceptible cultigens such as 'Top Mark' were heavily infected. There were incipient blisters on a few individuals when the 2F test was terminated: two of five PI 313970, and one of five plants each of PI 124111 and MR-1. In both of these tests, powdery mildew infection was heavy as indicated by mean disease ratings >8.0 for Iran H and 'Top Mark' (Table 1). PI 313970, PI 124111, and MR-1 were previously reported to exhibit resistant blisters in response to *P. xanthii* race 2U.S. in the late stages of infection in greenhouse tests (McCreight, 2003a).

Table 2. Summary of reactions of melon cultigens to 28 putative races of *Podosphaera xanthii* based on previous reports and present results.

	Race[z]																										
Cultigen	0	1J	1Sp	1M	1IV	1SJ	1S	1Ti	1Tu	2US	2S	2F	2Z	2a	2b	3	3c	3d	4	5	N1	N2	N3	N4	6	F	G	H
Iran H	s[y]	s	–	–	s	s	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	s	s
Fuyu 3	–	s	–	–	–	–	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	R	s	R	R	s	s	s	s
PMR 5, PMR 6	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	s	s	s	R	R	R	R	R	R	R	s	s	s
WMR 29	R	R	–	–	R	R	R	R	R	H	H	R	R	–	–	–	–	–	s	s	R	R	R	R	s	s	s	R
Edisto 47	R	R	–	–	R	R	R	R	R	s	R	R	R	–	–	R	–	–	R	s	R	R	s	s	s	s	s	s
PI 414723	R	R	–	–	R	R	R	R	R	s	s	R	R	–	–	R	–	–	R	R	s	s	s	R	R	s	s	s
PI 124111, MR-1	R	R	R	R	R	R	R	–	–	R	R	R	–	–	–	R	–	–	R	R	–	–	–	–	–	–	R	–
PI 124112	R	R	R	–	R	R	R	R	R	R	R	R	R	–	–	R	–	–	R	R	–	–	–	–	R	s	R	s
Earl's Knight Natsu 2	–	R	–	–	–	–	s	–	–	s	–	–	–	–	–	–	–	–	–	s	s	R	–	–	–	–	–	–
Earl's Miyabi Natsu 2	–	R	–	–	–	–	s	–	–	s	–	–	–	–	–	–	–	–	–	s	R	R	–	–	–	–	–	–
Hainan 21	–	R	–	–	–	–	R	–	–	s	–	–	–	–	–	–	–	–	–	s	R	s	–	–	–	–	–	–
Quincy	–	R	–	–	–	–	s	–	–	s	–	–	–	–	–	–	–	–	–	s	s	R	–	–	–	–	–	–
AR Hale's Best Jumbo	–	–	–	–	–	–	–	s	I	–	–	R	–	–	–	–	–	–	–	R	–	–	–	–	s	–	–	–
Amarillo	–	–	R	–	R	s	s	–	–	–	s	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Moscatel Grande	–	–	R	–	R	R	s	–	–	–	s	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Negro	–	–	R	–	R	R	s	–	–	–	s	s	R	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
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	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Seminole	–	–	–	R	R	–	R	–	–	–	R	R	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Wescan	–	–	–	R	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
VA 435	–	–	–	–	–	–	–	–	–	–	–	R	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Noy Yizre'el	–	–	–	–	–	–	–	–	–	–	–	–	–	s	R	–	s	R	–	–	–	–	–	–	–	–	–	–

[z] See text for details and references.

[y] s = susceptible, R = resistant, H = heterogeneous, I = intermediate; "–" = not tested.

Discussion

Susceptibility of the eight cultigens previously found resistant to *P. xanthii* race 1 (seven cultigens) and *P. xanthii* race 2 (one cultigen) was unexpected. Error at some point in seed regeneration and maintenance could account for the complete susceptibility of PI 236355 to race 1 in the field and growth chamber. The rating scale used by Floris and Alvarez (1995) may account for the discrepancy of 'Moscatel Grande' and 'Negro' where presence of sporulation on <10% of affected tissue, or an average of <1 conidium from a 1-cm-diameter leaf disk was regarded as resistant (Floris and Alvarez, 1991). In the present study, any discernable sporulation resulted in a minimum rating of 4, the low end of susceptibility. Regardless, the reaction of 'Amarillo' in these tests was inconsistent: highly resistant in one field test (IV02S; Table 1); susceptible at a low level in a second field test (SJ03; Table 1) where 'Moscatel Grande' and 'Negro' were highly resistant; and highly susceptible (mean rating ≥7.0) in the 2002 growth chamber test where 'Moscatel Grande' and 'Negro' expressed low susceptibility (4.0 ≤ mean rating ≤ 6.0). Moreover, 'Earl's Knight Natsu 2', 'Earl's Miyabi Natsu 2', and 'Quincy' were highly susceptible, whereas 'Hainan 21' proved resistant to race 1. Hosoya et al. (2000) isolated *P. xanthii* race 1 from 'Earl's Knight Natsu 2', 'Earl's Miyabi Natsu 2', and 'Quincy' in a survey, but found them and 'Hainan 21' resistant to race 1 in leaf disk assays where any detectable sporulation was considered susceptible (Hosoya et al., 1999). There is no obvious explanation for the susceptible reaction of PI 179901 to *P. xanthii* race 2.

Environmental factors are a potential cause of discrepancies between these results and previous reports. Inoculum source, light intensity, temperature and growing media can affect disease severity and race identification of powdery mildew of melon incited by *P. xanthii*, and may reveal or mask the action of host resistance and pathogen virulence factors (Cohen et al., 2004). Examination of the mean disease ratings of Iran H and 'Top Mark' shows the variability of *P. xanthii* race 1 on two highly susceptible cultigens that may be attributable in part to environmental differences between years, field locations, and growth chamber (Table 1). In contrast, 'PMR 45', 'PMR 5', WMR 29, 'Edisto 47', PI 414723, MR-1, PI 124111, and PI 124112 were consistently highly resistant to *P. xanthii* race 1 (Table 1). In Japan, high summer temperatures (>35 °C) may have caused a breakdown of resistance that enabled race 1 to sporulate on 'Quincy' (3% of isolates), 'Earl's Knight Natsu 2' (10% of isolates) and 'Earl's Miyabi Natsu 2' (3% of isolates) (Hosoya et al., 2000). These three cultivars were highly susceptible to race 1S in a growth chamber study at 25 °C (Table 1), whereas they were resistant to race 1J at 26 °C (Hosoya et al., 2000).

Genetic variation for virulence among *P. xanthii* race 1 populations could explain the observed discrepant reactions. This was previously found to occur for *P. xanthii* race 2 based on discrepancies in the reactions of WMR 29 and PI 414723 to U.S. and French *P. xanthii* race 2 populations (McCreight et al., 1987), and the reactions of 'Negro', BG 6011 and BG 6016 to *P. xanthii* race 2F isolates from two different regions of Spain (Alvarez et al., 2000). The reactions of 'Amarillo', 'Moscatel Grande', 'Negro', 'Earl's Knight Natsu 2', 'Earl's Miyabi Natsu 2', and 'Quincy' in the present study indicate differences in virulence factors between race 1 populations in Japan, Spain and the U.S. A source of resistance to one population of *P. xanthii* race 1 or race 2 may, as shown here, be susceptible to other populations of these respective *P. xanthii* races as defined by the 11 differentials included in these studies. Thus, not only can the same race, as defined by specific differential hosts, occur in different genetic backgrounds (Bardin et al., 1997), they may include one or more virulence factors not detected by the differentials (Brown, 2002). Moreover, *P. xanthii* pathotypes have been defined by their ability to infect more than one cucurbit species, and races cross over pathotype definitions (Bardin et al., 1997; Křístková and Lebeda, 1999; Křístková et al., 2004; Lebeda and Sedláková, 2004).

Twenty-eight putative races of *P. xanthii* have been recognized on melon (Table 2) based on these results and previous reports (Alvarez et al., 2000; Bertrand, 1991, 2002; Cohen, 2002; Floris and Alvarez, 1995; Harwood and Markarian, 1968a; Hosoya et al., 2000; Mohamed et al., 1995; Pitrat et al., 1996, 1998; Sowell and Corley, 1974; Thomas, 1978). Race 0 of *P. xanthii* was first observed in France (F. Bertrand, personal communication), but not recognized as such until later (Bardin et al., 1997), after it was observed in Sudan (Mohamed et al., 1995). Four of 410 accessions from the Middle East were highly susceptible to *P. xanthii* race 0, and Pitrat et al. (1996) concluded that as a general rule melon is resistant to *P. xanthii* race 0. Races 4 and 5 of *P. xanthii* were discovered in France (Bardin, 1996) and Israel (Cohen et al., 2002). Eight of the races were designated as variants of race 1 because the reactions of eight melon differentials (‘PMR 45’, ‘PMR 5’, WMR 29, ‘Edisto 47’, PI 414723, MR-1, PI 124111, and PI 124112) have been consistent worldwide although the reactions of some of them are incomplete (Table 2). A more complete data set might reveal similarity of races 1Ti and 1Tu with other race 1 variants, or race 2S with race 3. Races 4, 5, and 6 may likewise be considered variants of race 2. Races N1, N2, N3, and N4 were discovered in Japan (Hosoya et al., 2000). Bertrand (2002) proposed a new race (race 6) based on the reactions of AR Hale’s Best Jumbo to different populations of *P. xanthii* race 5 in France. The putative races 2a and 2b were not very well characterized (Cohen et al., 2002); they could be identical to the other variants of races 2, 4, 5, and 6 (Table 2). Likewise, putative races 3c and 3d (Cohen et al., 2002) could be variants of race 3, or races F, G, or H (Table 2). Race F observed in Czech is the first to overcome all of the commonly used melon race differentials (Lebeda and Sedláková, 2004).

The resistant blister reaction reactions of PI 313970, PI 124111, MR-1, and PI 124112 reveal additional complexity to the response of melon to *P. xanthii*; its inheritance remains to be demonstrated. In hops, a single dominant gene confers the resistant blister response to any isolate of *S. humuli* regardless of the presence of other race-specific genes (Liyanage et al., 1973).

There remains much research to be done before a clear understanding of the melon–*P. xanthii* powdery mildew system is fully elucidated and a robust, durable resistance strategy developed. It is likely that more virulence factors will emerge as new resistance genes in exotic germplasm resources are exploited. Melon breeders are urged to verify, alongside as many of the race differentials as possible, the reactions of their resistance sources to populations of the races to which they are breeding resistance, and to verify the performance of their candidate resistance sources in the areas where the cultivars will be grown.

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