Inheritance of Resistance to Powdery Mildew Race 1W in Watermelon

Yariv Ben-Naim and Yigal Cohen

Faculty of Life Sciences, Bar Ilan University, Ramat-Gan 52900, Israel.
Accepted for publication 24 July 2015.

ABSTRACT

Ben-Naim, Y., and Cohen, Y. 2015. Inheritance of resistance to powdery mildew race 1W in watermelon. *Phytopathology* 105:1446-1457.

Powdery mildew caused by *Podosphaera xanthii* is a major disease of watermelon in Israel. In this study, 291 accessions of *Citrullus* spp. were evaluated for resistance against *P. xanthii* race 1W. Only eight accessions exhibited high level of resistance. Inheritance of resistance against *P. xanthii* race 1W was studied by crossing three resistant accession of *Citrullus lanatus* var. *citroides* BIU 119, PI 189225, or PI 482312 with the susceptible cultivar 'Malali' or 'Sugar Baby'. Parents, F1, F2, and back cross progenies were evaluated for resistance in growth chambers at the

cotyledon stage and the 4-leaf stage and in the field, at the 15-leaf stage. Resistance at the cotyledon stage was controlled by a single, partially dominant gene, whereas at the 4-leaf stage or the 15-leaf stage resistance was controlled by three complimentary, partially dominant genes. Crosses made among these resistant accessions revealed that BIU 119 and PI 189225 carry the same genes for resistance, whereas PI 482312 shares two out of three genes with both BIU 119 and PI 189225. A breeding line with high resistance level and good fruit qualities was developed from BIU 119 × HA5500.

Additional keyword: cucurbits.

Watermelon (*Citrullus lanatus* (Thunb.) Matsum & Nakai (= *Citrullus vulgaris* Schrad. ex. Eckl. & Zeyh)) is an annual summer crop widely grown in warm regions and greatly appreciated for its large, sweet fruit. Recent archeological data suggest that watermelon was grown near the Nile River, Egypt as early as 3985 BC, before it was domesticated in West Africa (Zohary et al. 2012). Watermelon is a highly valuable fresh fruit in Israel, available 9 months a year. During the winter it is grown in the Arava Valley and fruits are marketed as early as March. In the coastal plain it is grown under plastic cover in the spring and in the open field during the summer.

C. lanatus is closely related and crossable with the diploid wild taxa *C. colocynthis* (L.) Schard., *C. ecirrhosus* Cogn., and *C. rehmii* De Winter. The wild taxon *Praecitrullus fistulosus* (Stocks) Pangalo. is not crossable with the taxa above (Levi et al. 2005, 2010).

Powdery mildew caused by *Podosphaera xanthii* (Castagne) Braun & Shishkoff (syn. *Sphaerotheca fuliginea* (Schlechtend.:Fr.) Pollacci auct.p.p.) is a major disease of watermelon in Israel, attacking the crop at all seasons and all locations. Because no resistant cultivars are available, farmers rely mainly on fungicides to control the disease. Powdery mildew reduces the number of fruits per plant, fruit size, fruit quality, flavor, and storage life (Keinath and DuBose 2004; McGrath and Thomas 1996).

Golovinomyces cichoracearum (D.C.) V.P. Heluta (formerly *Erysiphe cichoracearum* D.C.) is another powdery mildew agent of cucurbits. In Ukraine (Tomason and Gibson 2006) and the Czech Republic (Lebeda et al. 2011) both *G. cichoracearum* and *P. xanthii* occur on watermelon. *G. cichoracearum* was not found on watermelon in Israel (Cohen and Eyal 1995), the United States, or Mexico (Felix-Gastelum et al. 2005).

A set of differential melon lines (*Cucumis melo*) enables the distinction between races of *P. xanthii* (McCreight et al. 1987; Pitrat et al. 1998). Kenigsbuch and Cohen (1992) reported that in melon,

Pm-1 and *Pm-3* are responsible for resistance against race 1, while *Pm-2*, *Pm-4*, and *Pm-6* are responsible for resistance against race 2.

Powdery mildew causes economic damage in watermelon crops in the United States since 1996 (Davis et al. 2001; Keinath and DuBose 2004; McGrath 2001). Recently, outbreaks of powdery mildew races 1W, 2W, 2WU.S, and 2WF were confirmed on watermelon in many U.S. states (Davis et al. 2007; Kousik et al. 2011; Mercier et al. 2014; Zhang et al. 2011).

Extensive efforts were done to identify resistance against powdery mildew in watermelon. Davis et al. (2001) screened 110 watermelon plant introduction (PI) for resistance to race 1W of *P. xanthii* (Davis et al. 2001). They released PI 525088 as multigenic, highly resistant line to race 1W (Davis et al. 2006a). This resistance appeared to be independent in resistance to *P. xanthii* race 2W (Davis et al. 2002, 2006b; Thomas et al. 2005).

In a later study, eight accessions were found highly resistant among 1,573 accessions screened for resistance to race 1W (Davis et al. 2007). Tetteh et al. (2010) found in the same population nine accessions highly resistant to race 2W: PI 189225 exhibited polygenic inheritance of resistance (Tetteh et al. 2010) and PI 270545 carried recessive gene *pmr-1* and dominant gene *Pmr-2* for moderate resistance (Tetteh et al. 2013a). In a recent study they showed that resistance against race 2WU.S in a population derived from a cross between the resistant PI 189225 and the susceptible 'Charleston Gray' is controlled by a single dominant gene (Tetteh et al. 2013b). A screen for new sources of resistance to race 2WF in the United States revealed that most genotypes from Zimbabwe are highly resistant to this race (Zhang et al. 2011). Kim et al. (2013) reported that the Indian watermelon Arka Manik carries a single, partially dominant gene for resistance to powdery mildew race 1W.

In Israel, all commercial watermelon cultivars, diploid or triploid, are susceptible to powdery mildew. The objective of the current study was to develop watermelon lines resistant to *P. xanthii* race 1W, the most frequent race in Israel (Cohen et al. 2000). For this purpose we examined 291 accessions of *Citrullus* spp. for resistance to race 1W of *P. xanthii*. We discovered new sources of resistance effective against this race of powdery mildew, determined the mode of inheritance in three resistant accessions and developed from one accession a high-quality resistant line.

Corresponding author: Y. Cohen; E-mail address: yigal.cohen1@gmail.com

<http://dx.doi.org/10.1094/PHYTO-02-15-0048-R>
© 2015 The American Phytopathological Society

TABLE 1. Response to *Podosphaera xanthii* race 1W of entries 1 to 291 of watermelon accessions^a

No.	Entry	Accession	Species	Origin	Hypocotyl	Reaction cotyledons	Leaf 1
1	100	PI 164247	L	LIB	S	S	S
2	101	PI 164247	L	LIB	S	S	S
3	24	PI 164992	L	TUR	S	S	S
4	25	PI 164998	L	TUR	S	S	S
5	197	PI 165448	L	MEX	S	S	S
6	102	PI 171392	L	TUR	S	S	S
7	26	PI 172798	L	TUR	S	S	R
8	198	PI 173888	L	IND	S	S	S
9	27	PI 174105	L	TUR	S	S	S
10	199	PI 175652	L	TUR	S	S	S
11	103	PI 175659	L	TUR	S	S	S
12	28	PI 176487	L	TUR	S	S	S
13	29	PI 183125	L	IND	S	S	S
14	108	PI 186975	M	GHA	S	R	MR
15	104	PI 184800	L	AFR	S	S	S
16	105	PI 185635	L	AFR	—	—	—
17	106	PI 185635	L	GHA	—	—	—
18	107	PI 185636	L	GHA	—	—	—
19	109	PI 189225	C	ZAI	R	R	R
20	200	PI 189225	C	ZAI	—	—	—
21	110	PI 189317	L	NGA	S	S	S
22	111	PI 189318	M	NGA	S	S	S
23	112	PI 193490	***	ETH	S	S	S
24	201	PI 193963	L	ETH	S	S	S
25	6	PI 195927	N	ETH	S	S	S
26	113	PI 195928	L	ETH	S	S	S
27	202	PI 196531	L	JPN	—	—	—
28	114	PI 197416	L	ETH	S	S	S
29	115	PI 200733	L	GTM	S	S	S
30	30	PI 211917	L	IRN	S	S	S
31	203	PI 212289	L	AFG	R	S	R
32	204	PI 212596	L	AFG	S	S	R
33	205	PI 217522	F	PAK	S	S	R
34	206	PI 217938	F	PAK	S	S	R
35	207	PI 217939	L	PAK	S	S	S
36	208	PI 219691	L	PAK	S	S	S
37	31	PI 219906	L	AFG	S	S	S
38	32	PI 219907	L	AFG	S	S	S
39	33	PI 220779	L	AFG	MR	MR	MR
40	34	PI 221430	L	IRN	MR	MR	MR
41	35	PI 222137	L	ALG	S	S	S
42	36	PI 222715	L	IRN	S	S	S
43	209	PI 223764	L	AFG	S	S	S
44	116	PI 225557	M	NGA	S	S	S
45	210	PI 229605	L	IRN	S	S	S
46	7	PI 235118	N	IND	R	S	S
47	211	PI 240533	L	IRN	S	S	S
48	117	PI 241689	L	CHL	—	—	—
49	212	PI 244018	C	ZAF	S	S	S
50	37	PI 244019	L	ZAF	S	S	S
51	213	PI 246559	L	SEN	S	S	R
52	38	PI 247399	L	GRC	S	S	MR
53	214	PI 248178	L	ZAI	—	—	—
54	118	PI 249008	L	NGA	S	R	MR
55	39	PI 249009	L	NGA	S	S	S
56	119	PI 250145	F	PAK	R	R	R
57	40	PI 251244	F	IND	MR	MR	S
58	120	PI 254428	L	LBN	—	—	—
59	41	PI 254622	L	SUD	—	—	—
60	215	PI 254624	L	SUD	—	—	—
61	121	PI 254735	M	SEN	S	S	S
62	122	PI 254736	M	SEN	S	S	S
63	123	PI 254737	M	SEN	S	S	S
64	124	PI 254738	L	SEN	S	S	S
65	125	PI 254739	L	SEN	S	S	S
66	126	PI 254741	M	SEN	S	S	S
67	127	PI 254742	M	SEN	S	S	S
68	42	PI 254743	L	SEN	S	MR	S
69	128	PI 254743	M	SEN	S	S	S
70	129	PI 254744	M	SEN	—	—	—
71	43	PI 255137	L	ZAF	S	S	S
72	44	PI 255139	L	ZAF	S	S	S

(continued on next page)

^a L = *Citrullus lanatus* var. *lanatus*, M = *C. lanatus* subsp. *mucosospermus*, C = *C. lanatus* var. *lanatus* var. *citroides*, N = *C. colocynthis*, and F = *P. fistulosus*. **C. ecirrhosus*, ***C. rehmi*, and ****C. dipsaceus* (supplied as *Citrullus*). Bold R indicates resistance to powdery mildew race 1W.

TABLE 1. (continued from preceding page)

No.	Entry	Accession	Species	Origin	Hypocotyl	Reaction cotyledons	Leaf 1
73	45	PI 255662	L	AFG	S	S	S
74	216	PI 260733	L	SUD	—	—	—
75	8	PI 269365	N	AFG	S	S	S
76	88	PI 269365	N	AFG	S	MR	MR
77	217	PI 269464	L	PAK	—	—	—
78	46	PI 270548	L	GHA	S	S	S
79	131	PI 270549	L	GNA	S	S	S
80	132	PI 270550	L	GNA	S	S	S
81	133	PI 270551	L	GNA	S	S	S
82	218	PI 270562	C	ZAF	—	—	—
83	219	PI 270564	C	ZAF	—	—	—
84	220	PI 270565	L	ZAF	S	S	S
85	134	PI 271132	I	TUN	S	S	S
86	135	PI 271133	I.	TUN	S	S	S
87	136	PI 271133	L	TUN	—	—	—
88	47	PI 271750	L	GHA	S	S	S
89	48	PI 271751	L	GHA	—	—	—
90	221	PI 271752	L	GHA	—	—	—
91	262	PI 271769	L	ZAF	S	S	S
92	49	PI 271770	L	ZAF	S	S	S
93	222	PI 271773	C	ZAF	S	S	MR
94	50	PI 271774	L	ZAF	R	S	S
95	137	PI 271774	L	ZAF	—	—	—
96	51	PI 271775	L	ZAF	MR	S	S
97	138	PI 271776	L	ZAF	S	S	S
98	139	PI 271777	L	ZAF	S	S	S
99	140	PI 271778	L	ZAF	S	S	S
100	223	PI 271981	L	SOM	S	S	MR
101	224	PI 271982	L	SOM	—	—	—
102	225	PI 271986	L	SOM	—	—	—
103	52	PI 271988	L	SOM	—	—	—
104	53	PI 273479	L	ETH	S	S	S
105	54	PI 273480	L	ETH	S	S	S
106	55	PI 273481	L	ETH	S	S	S
107	164	PI 274035	L	ZAF	S	S	S
108	56	PI 274794	L	PAK	R	S	R
109	57	PI 276445	L	JOR	S	S	S
110	226	PI 278005	L	TUR	S	S	S
111	58	PI 278016	L	TUR	S	S	S
112	141	PI 278045	L	TUR	S	S	S
113	142	PI 278050	L	TUR	S	S	S
114	143	PI 278061	L	TUR	S	S	S
115	227	PI 279456	L	JPN	S	S	R
116	228	PI 295842	C	ZAF	S	S	R
117	144	PI 295845	I	ZAF	S	S	S
118	229	PI 295848	L	ZAF	S	S	S
119	145	PI 295850	C	ZAF	S	S	S
120	79	PI 296332	L	ZAF	S	S	S
121	80	PI 296335	C	ZAF	S	S	S
122	81	PI 296337	C	ZAF	S	S	S
123	78	PI 296341	C	ZAF	MR	S	S
124	165	PI 296341	C	ZAF	S	S	S
125	166	PI 296341	C	ZAF	S	S	S
126	167	PI 296342	C	ZAF	S	S	S
127	168	PI 296342	C	ZAF	S	S	S
128	169	PI 296343	C	ZAF	S	S	S
129	170	PI 296343	C	ZAF	—	—	—
130	130	PI 296466	L	PAK	—	—	—
131	146	PI 299378	C	ZAF	S	S	S
132	59	PI 306782	L	NGA	S	S	S
133	60	PI 307608	L	NGA	S	S	S
134	230	PI 307609	L	NGA	S	S	S
135	171	PI 314655	L	UZB	S	S	S
136	61	PI 319212	L	EGY	S	S	S
137	62	PI 326515	L	GHA	S	S	S
138	147	PI 331106	L	URU	S	S	S
139	232	PI 371746	F	IND	S	S	MR
140	233	PI 371747	F	IND	S	S	MR
141	234	PI 371754	F	IND	S	S	R
142	148	PI 378614	L	ZAI	S	S	S
143	149	PI 378615	L	ZAI	S	S	S
144	231	PI 381743	F	IND	S	S	MR
145	150	PI 381748	F	IND	R	R	R
146	63	PI 381749	F	IND	R	S	S

(continued on next page)

TABLE 1. (continued from preceding page)

No.	Entry	Accession	Species	Origin	Hypocotyl	Reaction cotyledons	Leaf 1
147	64	PI 381750	F	IND	R	S	S
148	65	PI 381752	F	IND	S	S	S
149	151	PI 381755	F	IND	R	R	R
150	235	PI 385963	L	KEN	S	S	S
151	236	PI 385964	L	KEN	S	S	S
152	89	PI 386014	N	USA	S	MR	MR
153	90	PI 386015	N	IRN	S	MR	MR
154	91	PI 386016	N	IRN	S	MR	MR
155	9	PI 386018	N	IRN	S	S	–
156	92	PI 386019	N	IRN	S	MR	MR
157	93	PI 386024	N	IRN	S	MR	MR
158	10	PI 386026	N	IRN	S	S	S
159	94	PI 386026	N	IRN	S	MR	MR
160	1	PI 388770	N	MAR	MR	MR	S
161	237	PI 427298	F	IND	S	S	R
162	95	PI 432377	N	CYP	S	MR	MR
163	152	PI 438675	L	MEX	S	S	S
164	153	PI 442826	L	BRA	S	S	S
165	66	PI 457916	M	LIB	R	R	S
166	238	PI 482283	C	ZIM	S	S	S
167	239	PI 482293	C	ZIM	S	S	S
168	240	PI 482298	C	ZIM	S	S	MR
169	67	PI 482299	C	ZIM	MR	MR	MR
170	68	PI 482300	C	ZIM	MR	MR	MR
171	69	PI 482301	C	ZIM	MR	MR	S
172	154	PI 482312	C	ZIM	R	R	R
173	155	PI 482315	C	ZIM	S	S	S
174	156	PI 482316	C	ZIM	S	S	S
175	70	PI 482319	L	ZIM	MR	MR	S
176	71	PI 482321	L	ZIM	MR	MR	MR
177	241	PI 482326	C	ZIM	S	S	MR
178	242	PI 482335	C	ZIM	S	S	R
179	243	PI 482336	C	ZIM	S	S	S
180	82	PI 490377	L	MLI	S	S	S
181	172	PI 480378	M	MLI	S	S	S
182	83	PI 490379	L	MLI	S	S	S
183	173	PI 490380	L	MLI	S	S	S
184	174	PI 490381	M	MLI	S	S	S
185	252	PI 490382	M	MLI	S	S	S
186	175	PI 490384	M	MLI	S	S	S
187	84	PI 490385	L	MLI	S	S	S
188	176	PI 490386	M	MLI	S	S	S
189	244	PI 500303	L	ZAM	–	–	–
190	72	PI 500355	C	ZAM	MR	MR	MR
191	157	PI 505604	C	ZAM	S	S	S
192	254	PI 525088	L	EGY	S	S	MR
193	73	TB81/464	L	NGA	MR	S	S
194	74	TB81/467	L	NGA	S	S	S
195	75	TB81/472	L	NGA	MR	MR	MR
196	158	TB81/473	L	NGA	S	S	S
197	159	TB81/474	L	NGA	S	S	S
198	160	TB81/476	L	NGA	S	S	S
199	161	TB81/477	L	NGA	S	S	S
200	247	TB81/485	L	NGA	S	S	MR
201	248	TB81/486	L	NGA	S	S	MR
202	249	TB81/514	L	NGA	S	S	MR
203	250	TB81/575	L	NGA	–	–	–
204	96	TB81/728	N	NGA	–	–	–
205	97	TE81/185	N	NGA	S	R	R
206	98	TE81/192	N	NGA	S	R	R
207	19	TE81/193	N	NGA	S	S	S
208	99	TE81/194	N	NGA	S	S	S
209	20	TE81/195	N	NGA	S	S	S
210	277	CC-2	N	EGY	S	S	S
211	286	CC-3	N	EGY	S	S	S
212	287	CC-5	N	ISR	S	S	S
213	288	CC-7	N	EGY	S	S	S
214	289	CC-8	N	EGY	S	S	S
215	290	CC-9	N	ISR	S	S	S
216	18	CC-9	N	ISR	R	S	S
217	273	CC-10	N	ISR	S	S	S
218	12	CC-11	N	ISR	R	S	S
219	13	CC-14	N	ISR	R	S	S
220	14	CC-16	N	ISR	R	R	R

(continued on next page)

TABLE 1. (continued from preceding page)

No.	Entry	Accession	Species	Origin	Hypocotyl	Reaction cotyledons	Leaf 1
221	274	CC-16	N	ISR	S	S	S
222	15	CC-17	N	ISR	R	S	R
223	275	CC-17	N	ISR	S	S	S
224	276	CC-19	N	ISR	S	S	S
225	278	CC-20	N	ISR	S	S	S
226	279	CC-21	N	ISR	S	S	S
227	280	CC-22	N	ISR	S	S	S
228	281	CC-23	N	ISR	S	S	S
229	282	CC-24	N	ISR	S	S	S
230	16	CC-25	N	ISR	R	R	S
231	17	CC-27	N	ISR	R	S	S
232	283	CC-27	N	ISR	S	S	S
233	284	CC-28	N	ISR	S	S	S
234	285	CC-29	N	ISR	S	S	S
235	183	CIT 115/1978	C	CHN	S	S	S
236	184	CIT 116/1978	C	CHN	—	—	—
237	185	CIT 119/1980	C	PRT	S	S	S
238	195	CIT 121/1977	C	ZAF	S	S	S
239	22	CIT 127/1970	C	ZAF	S	S	S
240	87	CIT 141/1975	N	SEN	S	MR	MR
241	186	CIT 35/1976	C	BRA	S	S	S
242	187	CIT 63/1975	C	ITA	S	S	S
243	188	CIT 65/1976	C	ITA	S	S	S
244	189	CIT 68/1975	C	ITA	S	S	S
245	190	TETRA 1	L	USA	S	S	S
246	191	TETRA 2	L	USA	S	S	S
247	192	TETRA 3	L	USA	S	S	S
248	193	TETRA 4	L	USA	S	S	S
249	258	Crimson sweet	L	ISR	S	S	S
250	253	G200	L	USA	—	—	—
251	267	HA 1032	L	ISR	S	S	S
252	265	HA 6008	L	ISR	S	S	S
253	268	HA 1042	L	ISR	S	S	S
254	266	HA 5603	L	ISR	S	S	S
255	269	HAZERA-8	L	ISR	S	S	S
256	196	King of heart	L	USA	S	S	S
257	162	L. W 1298	M	AFR	R	R	R
258	23	L. WILD	*	ZAF	S	S	S
259	4	LOT 88-151	N	EGY	S	S	S
260	5	M-1411	N	ISR	S	S	S
261	271	M-1411	N	ISR	S	S	S
262	272	M-1535	N	ISR	S	S	S
263	256	Malali	L	ISR	S	S	S
264	255	Mini Pool	L	ISR	S	S	S
265	11	Plot 372	N	NGA	R	R	S
266	245	Quality Tri	L	TWN	S	S	MR
267	246	Queen of hearts	L	USA	—	—	—
268	257	Sugar Baby	L	ISR	S	S	S
269	261	Summit	L	ISR	S	S	S
270	21	WIR-4339	N	SUN	R	S	—
271	76	1 wir-3706	C	SUM	S	S	S
272	85	69/1978	L	ITA	—	—	—
273	194	71/352	L	ZAF	S	S	R
274	77	77046 J. 14	**	ZAF	—	—	—
275	163	77125 N. 16	L	ZAF	S	S	S
276	3	ACC.62.023	N	ITA	R	S	S
277	259	Calhoun Gray	L	ISR	S	S	S
278	264	China 6/2/3	L	ISR	S	S	S
279	260	Charelston Gray	L	ISR	S	S	S
280	86	234	N	HUN	S	S	S
281	2	284	N	EYG	R	MR	MR
282	270	284	N	ISR	S	S	S
283	263	HA 5500	L	ISR	S	S	S
284	177	32776	L	TUR	—	—	—
285	178	33344	L	TUR	S	S	S
286	179	37073	L	TUR	S	S	S
287	180	38225	L	TUR	S	S	S
288	181	38480	L	TUR	S	S	S
289	182	38940	L	TUR	S	S	S
290	251	83508	L	ZAF	S	S	S
291	291	BIU 119	C	Unknown	R	R	R

In a preliminary study, we reported that among 250 accessions of *C. lanatus* and *C. colocynthis*, two entries were resistant to *P. xanthii* race 1W (Cohen et al. 2000).

MATERIALS AND METHODS

Plants. A total of 291 *Citrullus* spp. and *Parecitrulus fistulosus* accessions were obtained in 1998 from the USDA via the Israel Gene Bank. The accessions, originating from 44 countries, included six main species/subspecies: *C. lanatus* var. *lanatus* (including subsp. *mucosospermus*); *C. lanatus* var. *citroides*; *C. colocynthis*; *C. rehmi*; *C. ecirrhosus*; and, *P. fistulosus*. Plants were grown from seeds in Speedling trays (1 × 1 inch filled with 2:1 peat:vermiculite, vol/vol) in the greenhouse (23 to 30°C). About six to eight seeds of each accession were seeded. After germination plants were fertilized once a week with 1% N: P: K solution.

Pathogen and inoculation. Conidia were collected from powdery mildew-infected watermelon plants in the field. Microscopic examination of spore germination confirms it as *P. xanthii*.

The following melon (*Cucumis melo*) differential cultivars were included in all tests to determine the race identity of *P. xanthii*: ‘Dulche’, ‘Hemed’, ‘Anannas-Yokneam’ (AY), ‘WNR-18’, ‘Noy-Izrael’, PI 124111, PI 124112, ‘Ein Dor’ (=‘PMR 45’), ‘PMR 5’, and ‘PMR 6’ (Kenigsbuch and Cohen 1992; McCreight et al. 1987; Pitrat et al. 1998). Accessions were evaluated for resistance to powdery mildew race 1W at the cotyledon stage during 1999 (Cohen et al. 2000); the resistant accessions were propagated by self-pollination and re-examined for resistance to race 1W during 2008 to 2012. Inoculation at the cotyledon stage and the 4-leaf stage was done in the greenhouse by dusting fresh conidia from infected susceptible Malali plants over the test plants (~150 conidia/cm²). The resistant plants were selected and planted (April or August) in the field in a net-house (6 × 50 m). Spreader plants (melon AY and watermelon Malali) infected with *P. xanthii* race 1W were planted in the net-house to facilitate infection of the selected watermelon plants. Once a week, plants were blown with a back-pack mechanical blower to enhance conidial dispersal in the house.

Resistance to powdery mildew in original accessions.

Inoculation was done at the cotyledon stage and disease was recorded at 10 days postinoculation (dpi) from the hypocotyl, cotyledons, and leaf one. The following visual categorical scale was used to rate the reaction to infection: R = resistant, no fungal colonies were seen; MR = moderately resistant, a few colonies with sparse sporulation were visible; S = susceptible, abundant colonies with profuse sporulation were visible. Thirty-four accessions (out of the 291) did not germinate or experienced early death of seedlings.

In some experiments, resistance/susceptibility was evaluated by counting the number of conidia produced by *P. xanthii* per unit leaf area. For spore yield determination, two leaf discs (14 mm diameter) were removed from each leaf, placed in 2 ml of water containing 0.1% Tween-20, and agitated for 10 min, and the number of conidia was counted with the aid of a cytometer.

Resistance to powdery mildew in progeny plants. Parents, F1, F2, and back cross (BC) progeny plants were grown in Speedling trays and inoculated at the cotyledon stage or the 4-leaf stage by dusting fresh conidia as described above. Evaluation of disease development was done at 10 dpi by using the following 0 to 4 visual scale: 0 = no disease; 0.1, 0.2... 0.9 = 10, 20... 90% of the plant surface exhibit chlorotic or necrotic symptoms with sparse mycelium lacking conidia; 1 to 1.9 = 5 to 25% of the plant surface is occupied with discrete sporulating fungal colonies, with or without chlorosis; 2 to 2.9 = 25 to 50% of the plant surface is occupied with coalescing, sporulating fungal colonies; and 3 to 4 = 51 to 100% of the plant surface is occupied with coalesced, heavily sporulating fungal colonies. The same visual scale was used to also evaluate the disease in mature plants in the field.

RESULTS

Disease resistance in original accessions. Table 1 presents the response of 291 accessions of *Citrullus* spp. to powdery mildew

Fig. 1. Mature fruits of the three resistant watermelon accessions used in the present study.

TABLE 2. Phenotypic characteristics of three watermelon accessions resistant to powdery mildew 1W used in this study

Character	Accession		
	BIU 119	PI 189225	PI 482312
Fruit shape	Flat round	Round	Flat round
Fruit weight, kg	12–21	6–7	10–16
Flesh color	Yellow	Yellow	Yellow
Rind thickness, cm	3–3.5	2.5–3	3–3.5
Seed color	Khaki	Red	Green or red
Flowering	Andromonoecious	Monoecious	Andromonoecious
Days to maturity	120	110	120
Total soluble solids, %	3.5	3	3.5

incited by *P. xanthi* race 1W. Most entries were susceptible, classified as SSS showing colonies of powdery mildew on hypocotyl, cotyledons, and first true leaf. A few entries were classified SSR, SRR, RSS, RSR, or RRS (Table 1). High level of resistance, RRR, was expressed by three accessions of *C. lanatus* var. *citroides*, three accessions of *Praecitrullus fistulosus*, one accession of *C. colocynthis*, and one accession of *C. lanatus* subsp. *mucospermus*. PI 525088 (reported resistant by Davis et al. 2006a) was susceptible.

Further experiments were conducted with only the three resistant accessions of *C. lanatus* var. *citroides*: BIU 119, PI 189225, and PI 482312. Their fruits are shown in Figure 1 and their phenotypic features are given in Table 2.

Quantitative assays for disease resistance. BIU 119, PI 189225, and PI 482312 developed significantly less disease (Fig. 2A) and allowed for a significantly reduced sporulation (Fig. 2B) compared with the commercial watermelon cultivars HA5500, Crimson Sweet, Malali, or Sugar Baby.

The response of BIU 119, PI 189225, PI 482312, and Malali to inoculation with increasing inoculum doses of *P. xanthii* is shown in Figure 3. The susceptible Malali produced heavy disease in hypocotyls, cotyledons, and first true leaf when inoculated with a low dose of ~33 spores/cm². Much lower disease levels compared with Malali were seen in all three resistant accessions at all five inoculum doses tested.

Inheritance of resistance. Crosses were made between each resistant accession and the susceptible cultivars Malali or Sugar Baby. The response to powdery mildew of the parents and their F1 progeny plants in the field is shown in Figure 4A. F1 plants of all

crosses were moderately resistant. The relationship between leaf position and disease severity in field-grown 15-leaf parental and F1 plants of the cross Malali × PI 189225 is shown in Figure 4B. Disease severity on leaves of the resistant parent did not exceed a value of 0.5 compared with 1.0 to 3.1 in the susceptible parent. F1 plants showed values ranging between 0.5 and 2. The two oldest and two youngest leaves showed less disease compared with middle leaves (Fig. 4B).

Data on the inheritance of disease resistance are given in Tables 3, 4, and 5. They show the segregation of powdery mildew resistance in the offspring plant populations obtained from three crosses made between each resistant accession and a susceptible commercial cultivar. Response to the disease was estimated in F1, F2, and BC plants at the cotyledon stage, 4-leaf stage, and 15-leaf stage plants in the field.

Resistance at the cotyledon stage (Table 3) was controlled by a single, partially dominant gene in all three resistant accessions. The F2 progeny plants segregated R/MR/S (resistant; moderately resistant; susceptible) at a ratio of 1/2/1, the BCr at 1/1/0 and the BCs at 0/1/1.

A different mode of inheritance was observed at the 4-leaf stage (Table 4). F1 plants were moderately resistant and the F2 population segregated R/MR/S at a ratio of 7/37/20, suggesting that resistance is controlled by the complementary (additive) action of five or six partially dominant alleles donated by three genes. Plants showing the MR response probably carried three or four partially dominant alleles.

The mode of inheritance in adult plants in the field was slightly different from the previous model. F2 populations segregated

Fig. 2. Development of powdery mildew on seven accessions of *Citrullus* spp. Potted plants at their 4-leaf stage were inoculated with ~150 conidia/cm² of *Podosphaera xanthii*. **A**, Disease severity at 12 days postinoculation (dpi). **B**, Spore yield at 13 dpi. Different letters on bars indicate significant difference between means at $\alpha = 0.05$. Pearson correlation coefficient between disease severity and spore yield is 0.90.

R/MR/S at a ratio of 1/43/20 (Table 5). Only 1 out of 64 F2 plants (9 resistant out of 525 F2 plants in three crosses) was fully resistant to powdery mildew, suggesting that three partially dominant complementary genes are responsible for resistance, regardless of the source of resistance.

The nine resistant plants (Table 5) were self-pollinated and their pedigree plants were all found to be resistant to powdery mildew race 1W under field conditions in the following season.

Allelic relationships. To verify whether or not the three resistant accessions carry the same genes for resistance they were crossed with each other and their progeny plants tested for resistance at the cotyledon stage in the greenhouse and the 15-leaf stage under field conditions.

F1, F2, and BCs progeny plants of all three crosses were resistant at the cotyledon stage (data not shown), suggesting that all accessions share the same partially dominant gene for resistance.

At the 15-leaf stage in the field, all offspring plants of the cross PI 189225 × BIU 119 were resistant (Table 6, cross A), suggesting that both parents carry the same resistance genes against *P. xanthii*. However, PI 482312 was only partially allelic for resistance with either PI 189225 (Table 6, cross B) or BIU 119 (Table 6, cross C) under field conditions. F1 and E1 (reciprocal cross) plants of cross B and cross C were moderately resistant, the F2 and E2 (reciprocal cross) progeny plants of both cross B and cross C segregated R/MR at a ratio of 7/9 and the BC offspring plants segregated 1/1R/MR, suggesting that PI 482312 shares two out of three genes with either PI 189225 or BIU 119.

Advanced breeding lines. BIU 119 was used to produce a resistant breeding line by crossing with the elite watermelon HA5500 as a recurrent parent. After a series of four BCs to HA5500, selection for resistance, and self-pollination, a highly resistant breeding line (TSS 11%) was developed. The fruit shape, color, and resistance to powdery mildew race 1W are shown in Figure 5.

DISCUSSION

The present study confirms that resistance against powdery mildew in watermelon could be transferred from wild resistant watermelon accessions into elite susceptible cultivars. The advanced breeding line we produced has high levels of resistance to powdery mildew and good fruit qualities (Fig. 5).

Of 291 watermelon accessions examined, only eight were highly resistant to powdery mildew race 1W. The resistant accessions PI 189225, PI 482323, and BIU 119 were crossed with susceptible parents to follow the mode of inheritance of resistance against the disease.

These accessions and their self-pollinated pedigree plants were resistant to the disease, showing no disease or reduced number of powdery mildew colonies on the hypocotyl, cotyledons, or the first true leaf. The mode of inheritance of resistance against race 1W in all crosses was strongly dependent on plant organ and plant age at time of inoculation. When inoculated at the cotyledon stage, 25% of the F2 plants were resistant, 50% moderately resistant, and 25% susceptible, suggesting on a single, partially dominant gene controlling resistance. When inoculated at the 4-leaf stage, F2 plants segregated 7/37/20 R/MR/S, BCs segregated 1/1 R/MR, and BCs segregated 1/7 MR/S. This indicated that three genes are responsible for resistance: full resistance is achieved by the complementary (additive) action of five or six partially dominant alleles. Plants showing intermediate resistance probably carry three or four dominant alleles (Table 7).

Of the 525 F2 plants inoculated (in all three crosses) at the 4-leaf stage, 59 plants were highly resistant. Nine of them remained highly resistant when transferred and grown in the field while the other 50 plants became moderately resistant, changing the

segregation ratio to 1/43/20 R/MR/S. This suggests that resistance is controlled by the complementary/additive action of three partially dominant genes. In parents-offspring F2/F3 tests, F3 plants derived from the resistant F2 individuals were all resistant. We assume that when all six partially dominant alleles are present at the mature stage (1/64, Table 7) reaction to disease will be highly resistant; three to five alleles (43/64) will mediate moderate resistance, and zero to two alleles (20/64) will contribute no resistance.

The allelic relationship between the three sources of resistance was examined by their intercrossings. BIU 119 and PI 189225 were fully allelic for resistance, although different in other traits (Table 2). PI 482312 shares two resistance genes with the other two accessions. We propose that BIU 119 and PI 189225 carry the genes A, B, and C for resistance whereas PI 482312 carry the resistance genes A, B, and D. Combining A, B, C, and D may enhance resistance against powdery mildew race 1W to a maximal level.

Fig. 3. The effect of inoculum dose on powdery mildew development in susceptible and resistant watermelon accessions. Plants at the first leaf stage were inoculated by overhead dusting of conidia of *Podosphaera xanthii* at the indicated doses and evaluated for disease development at 10 days post-inoculation. **A, B, and C,** Disease severity records taken from the hypocotyls, cotyledons, and leaf 1, respectively. Bars indicate standard deviation of the mean. The susceptible cultivar Malali showed significantly ($\alpha = 0.05$) higher disease index values compared with all resistant accessions at all inoculum doses (analysis not shown).

Fig. 4. A, Development of powdery mildew race 1W on parents and F1 hybrid plants under field conditions. Different letters on bars indicate significant difference between means at $\alpha = 0.05$. **B,** Effect of leaf age on development of powdery mildew in detached leaves of parental and F1 progeny plants. Leaves were detached from 10-leaf field-grown plants, placed on wet filter paper in transparent plastic plates ($20 \times 20 \times 3$ cm), dust-inoculated with conidia of *Podosphaera xanthii* (~ 150 conidia per cm^2), incubated in a growth chamber at 21°C , 12 h light/day, and evaluated for disease development at 10 days postinoculation. Different letters on bars indicate significant difference between means at $\alpha = 0.05$.

TABLE 3. Inheritance of resistance to powdery mildew race 1W in watermelon^a

Pedigree	Generation	Disease index, 0 to 4 visual scale							Ratio observed			Ratio expected			Model analysis			df	χ^2	P
		Resistant		Moderately resistant			Susceptible													
		0.0–0.5	0.6–0.9	1.0–1.4	1.5–1.9	2.0–2.4		2.5–2.9	3.0–4.0											
Cross A																				
PI 189225	Pr	29	—	—	—	—	—	—	29	0	0	—	—	—	—	—	—	—	—	—
Sugar Baby	Ps	—	—	—	—	—	—	35	0	0	35	—	—	—	—	—	—	—	—	—
Pr × Ps	F1	5	20	33	3	—	—	—	25	36	0	—	—	—	—	—	—	—	—	—
Pr × Ps	F2	33	27	46	19	9	6	41	60	80	41	45	91	45	1	2	1	2	6.43	0.04
(Pr × Ps) × Pr	BCr	58	4	8	—	1	—	—	62	9	0	52	17	0	3	1	0	1	5.69	0.017*
(Pr × Ps) × Ps	BCs	—	—	—	3	7	—	44	0	10	44	0	13	41	0	1	3	1	0.98	0.32*
Cross B																				
BIU-119	Pr	54	—	—	—	—	—	—	54	0	0	—	—	—	—	—	—	—	—	—
Malali	Ps	—	—	—	—	—	—	44	0	0	44	—	—	—	—	—	—	—	—	—
Pr × Ps	F1	4	8	11	16	20	21	—	12	68	0	—	—	—	—	—	—	—	—	—
Pr × Ps	F2	30	17	42	20	20	10	61	47	92	61	50	100	50	1	2	1	2	3.24	0.2*
(Pr × Ps) × Pr	BCr	12	15	21	—	—	—	—	27	21	0	24	24	0	1	1	0	1	0.75	0.384*
(Pr × Ps) × Ps	BCs	—	—	8	10	5	3	18	0	26	18	0	22	22	0	1	1	1	1.45	0.23*
Cross C																				
PI 482312	Pr	42	—	—	—	—	—	—	42	0	0	—	—	—	—	—	—	—	—	—
Malali	Ps	—	—	—	—	—	—	39	0	0	39	—	—	—	—	—	—	—	—	—
Pr × Ps	F1	1	—	24	32	9	2	2	1	67	2	—	—	—	—	—	—	—	—	—
Pr × Ps	F2	53	—	60	24	25	14	61	53	123	61	59	119	59	1	2	1	2	0.83	0.66*
(Pr × Ps) × Pr	BCr	17	—	16	14	—	—	—	17	30	0	24	24	0	1	1	0	1	3.53	0.06*
(Pr × Ps) × Ps	BCs	—	—	9	19	8	19	18	0	55	18	0	37	36	0	1	1	1	17.75	E-2.5105

^a Three resistant genotypes were crossed with the commercial susceptible Sugar Baby, and the cotyledons of the progeny plants were scored for resistance in the greenhouse. * Indicates model analysis accepted ($P \geq 0.05$) in seven of nine cases.

TABLE 4. Inheritance of resistance to powdery mildew race 1W in watermelon^a

Pedigree	Generation	Disease index, 0-4 visual scale							Ratio observed			Ratio expected			Model analysis			df	χ^2	P
		Resistant		Moderately resistant				Susceptible	R	MR	S	R	MR	S	R	MR	S			
		0.0–0.0.5	0.6–0.9	1.0–1.4	1.5–1.9	2.0–2.4	2.5–2.9													
Cross A																				
PI 189225	Pr	31	—	—	—	—	—	—	31	0	0	—	—	—	—	—	—	—	—	—
Sugar Baby	Ps	—	—	—	—	—	—	—	0	0	38	—	—	—	—	—	—	—	—	—
Pr × Ps	F1	—	—	4	22	21	10	7	0	57	7	—	—	—	—	—	—	—	—	—
Pr × Ps	F2	6	9	21	19	31	21	65	15	92	85	18	100	54	7	37	20	2	3.385	0.184*
(Pr × Ps) × Pr	BCr	16	20	17	12	2	—	—	36	31	0	33	34	0	1	1	0	1	0.54	0.46*
(Pr × Ps) × Ps	BCs	—	—	—	—	3	7	44	0	10	44	0	7	47	0	1	7	1	1.47	0.22*
Cross B																				
BIU 119	Pr	23	—	—	—	—	—	—	23	0	0	—	—	—	—	—	—	—	—	—
Malali	Ps	—	—	—	—	—	—	21	0	0	25	—	—	—	—	—	—	—	—	—
Pr × Ps	F1	—	—	11	38	5	6	1	0	60	1	—	—	—	—	—	—	—	—	—
Pr × Ps	F2	11	10	25	19	10	17	41	21	72	41	15	78	41	7	37	20	2	2.85	0.24*
(Pr × Ps) × Pr	BCr	37	—	26	1	—	—	—	37	26	0	32	32	0	1	1	0	1	1.9	0.168*
(Pr × Ps) × Ps	BCs	—	—	—	—	—	2	38	0	2	38	0	5	35	0	1	7	1	2.06	0.151*
Cross C																				
PI 482312	Pr	42	—	—	—	—	—	—	42	0	0	—	—	—	—	—	—	—	—	—
Malali	Ps	—	—	—	—	—	—	39	0	0	39	—	—	—	—	—	—	—	—	—
Pr × Ps	F1	—	—	14	26	30	8	7	0	78	7	—	—	—	—	—	—	—	—	—
Pr × Ps	F2	—	23	27	41	42	21	65	23	131	65	24	126	69	7	37	20	2	0.47	0.79*
(Pr × Ps) × Pr	BCr	—	28	16	4	—	—	—	28	20	0	24	24	0	1	1	0	1	0.065	0.8*
(Pr × Ps) × Ps	BCs	—	—	—	—	2	18	50	0	20	50	0	9	61	0	1	7	1	3.17	0.075*

^a Three resistant genotypes were crossed with the susceptible commercial cultivars Sugar Baby or Malali and progeny plants were scored for resistance at the 4-leaf stage in the greenhouse. * Indicates model analysis accepted ($P \geq 0.05$).

TABLE 5. Inheritance of resistance to powdery mildew race 1W in watermelon^a

Cross	Generation	Ratio observed			Ratio tested			Model analysis			df	χ^2	P
		R	MR	S	R	MR	S	R	MR	S			
PI 482312 × Malali	F2	4	150	65	3	147	69	1	43	20	2	0.626	0.73*
BIU 110 × Sugar Baby	F2	1	90	43	2	91	41	1	43	20	2	1.01	0.74*
PI 189225 × Sugar Baby	F2	4	103	65	3	116	53	1	43	20	2	4.5	0.105*

^a Three resistant genotypes were crossed with the susceptible cultivars Malali or Sugar Baby. F2 progeny plants that were scored resistant or moderately-resistant at the 4-leaf stage in the greenhouse were transferred to the field and again scored for resistance at the 15-leaf stage. * Indicates model analysis accepted ($P \geq 0.05$).

TABLE 6. The allelic relationships between three accessions of *Citrullus* spp., each carrying three partially dominant genes for resistance against powdery mildew race 1W^a

	Generation	Ratio observed			Ratio expected			Model analysis			df	χ^2	P	Genes
		R	MR	S	R	MR	S	R	MR	S				
Cross A														
PI 189225	Pr-1	55	0	0	1	0	0	55	0	0	—	—	—	Fully allelic
BIU 119	Pr-2	47	0	0	1	0	0	47	0	0	—	—	—	
BIU 119 × PI 189225	F1	66	0	0	1	0	0	66	0	0	—	—	—	
PI 189225 × BIU 119	E1	55	0	0	1	0	0	55	0	0	—	—	—	
BIU 119 × 189225	F2+E2	164	0	0	1	0	0	164	0	0	—	—	—	
(BIU 119 × PI 189225) × BIU 119	BC Pr-1	41	0	0	1	0	0	1	0	0	—	—	—	
(BIU 119 × PI 189225) × PI 189225	BC-Pr-2	42	0	0	1	0	0	1	0	0	—	—	—	
Cross B														
PI 189225	Pr-1	41	1	0	—	—	—	—	—	—	—	—	—	Partially allelic
PI 482312	Pr-2	25	2	0	—	—	—	—	—	—	—	—	—	
PI 482312 × PI 189225	F1	3	45	0	—	—	—	—	—	—	—	—	—	
PI 189225 × PI 482312	E1	1	27	0	—	—	—	—	—	—	—	—	—	
BIU 119 × 189225	F2+E2	73	62	0	64	81	0	7	9	0	1	0.005	0.016	
(PI 190225 × PI 482312) × PI 482312	BC Pr-1	20	21	0	21	20	0	1	1	0	1	1.35	0.75*	
(PI 189225 × PI 482312) × PI 189225	BC Pr-2	25	9	0	17	17	0	1	1	0	1	5.79E-05	0.006	
Cross C														
PI 482312	Pr-1	47	2	0	—	—	—	—	—	—	—	—	—	Partially allelic
BIU 119	Pr-2	39	2	0	—	—	—	—	—	—	—	—	—	
PI 482312 × BIU 119	F1	2	32	0	—	—	—	—	—	—	—	—	—	
BIU 119 × PI 482312	E1	6	48	0	—	—	—	—	—	—	—	—	—	
PI 189225 × BIU 119	F2+E2	83	59	0	62	80	0	7	9	0	1	2.27E-07	0.003	
(BIU 119 × PI 482312) × PI 482312	BC Pr-1	37	25	0	31	31	0	1	1	0	1	2.3	0.13*	
(BIU 119 × PI 482312) × BIU 119	BC Pr-2	66	49	0	58	57	0	1	1	0	1	2.3	0.14*	

^a The resistant accessions were intercrossed and the progeny plants were scored for resistance at the 15-leaf stage in the field. * Indicates model analysis accepted ($P \geq 0.05$).

Fig. 5. A, Fruit shape, flesh color, and resistance to powdery mildew of an advance watermelon breeding line 35 developed in this study. Its pedigree is [(BIU 119 × HA5500, F2) × HA5500) self, BCs ×4]. **B,** Response to powdery mildew race 1W in a net-house in the field. Upper part: resistant line 35; lower part: susceptible cultivar HA5500.

TABLE 7. Segregation of partially dominant resistance alleles in a three-gene proposed model^a

Gametes	ABC	ABc	AbC	Abc	aBC	aBc	abC	abc
ABC	ABC	ABc	AbC	Abc	aBC	aBc	abC	abc
ABc	ABC	ABc	AbC	Abc	aBC	aBc	abC	abc
AbC	ABC	ABc	AbC	Abc	aBC	aBc	abC	abc
Abc	ABC	ABc	AbC	Abc	aBC	aBc	abC	abc
aBC	ABC	ABc	AbC	Abc	aBC	aBc	abC	abc
aBc	ABC	ABc	AbC	Abc	aBC	aBc	abC	abc
abC	ABC	ABc	AbC	Abc	aBC	aBc	abC	abc
abc	ABC	ABc	AbC	Abc	aBC	aBc	abC	abc

^a The complementary action of six alleles is required for full resistance of watermelon against *Podosphaera xanthii* race 1W. Lower levels of resistance are obtained by the complementary action of three to five alleles. The complementary action of one to two alleles contributes no visible resistance. All three resistant accessions share the resistance genes A and B. The third resistance gene in accessions BIU 119 and PI 189225 is C, whereas the third resistance gene in accession PI 482312 is D (not shown in the Table).

LITERATURE CITED

- Cohen, Y., Baider, A., Petrov, L., Shek, L., and Voloisky, V. 2000. Cross-infectivity of *Sphaerotheca fuliginea* to watermelon, melon and cucumber. Proceedings of 7th EUCARPIA Meeting on Cucurbit Genetics and Breeding. N. Katzir and H. S. Paris, eds. Acta Hort. 510:85-88.
- Cohen, Y., and Eyal, H. 1995. Differential expression of resistance to powdery mildew incited by race 1 or 2 of *Sphaerotheca fuliginea* in *Cucumis melo* genotypes at various stages of plant development. Phytoparasitica 23:223-230.
- Davis, A. R., Bruton, B. D., Pair, S. D., and Thomas, C. E. 2001. Powdery mildew: An emerging disease of watermelon in the United States. Cucurbit Genet. Coop. 24:42-48.
- Davis, A. R., Levi, A., Tetteh, A., Wehner, T., Russo, V., and Pitrat, M. 2007. Evaluation of watermelon and related species for resistance to race 1W powdery mildew. J. Am. Soc. Hortic. Sci. 132:790-795.
- Davis, A. R., Levi, A., Wehner, T., and Pitrat, M. 2006a. PI525088-PMR, a melon race 1 powdery mildew-resistant watermelon line. HortScience 41: 1527-1528.
- Davis, A. R., Tetteh, A., Wehner, T., Levi, A., and Pitrat, M. 2006b. Watermelon resistance to powdery mildew race 1 and race 2. Pages 412-420 in: Proc. Cucurbitaceae. G. J. Holmes, ed. Universal Press, Raleigh, NC.
- Davis, A. R., Thomas, C. E., Levi, A., Bruton, B. D., and Pair, S. D. 2002. Watermelon resistance to powdery mildew race 1. Cucurbitaceae 2: 192-198.
- Felix-Gastelum, R., Apodaca-Sanchez, M. A., and Martinez-Valenzuela, M. C. 2005. *Podosphaera* (sect. *Sphaerotheca*) *xanthii* (Castagne) U. Brawn and N. Shishkoff on cucurbits in northern Sinaloa, Mexico. Rev. Mex. Fitopatol. 23:162-168.
- Keinath, A. P., and DuBose, B. 2004. Evaluation of fungicides for prevention and management of powdery mildew on watermelon. Crop Prot. 23:35-42.
- Kenigsbuch, D., and Cohen, Y. 1992. Inheritance and allelism of genes for resistance against races 1 and 2 of *Sphaerotheca fuliginea* in muskmelons. Plant Dis. 76:626-629.
- Kim, K. H., Ahn, S. G., Hwang, J. H., Choi, Y. M., Moon, H. S., and Park, Y. H. 2013. Inheritance of resistance to powdery mildew in the watermelon and development of a molecular marker for selecting resistant plants. Hortic. Environ. Biotechnol. 54:134-140.
- Kousik, C. S., Donahoo, R. S., Webster, C. G., Turechek, W. W., Adkins, S. T., and Roberts, P. D. 2011. Outbreak of cucurbit powdery mildew on watermelon fruit caused by *Podosphaera xanthii* in Southwest Florida. Plant Dis. 95:1586.
- Lebeda, A., Kristkova, E., and Sedlakova, B. 2011. Gaps and perspectives of pathotype and race determination in *Golovinomyces cichoracearum* and *Podosphaera xanthii*. Mycoscience 52:159-164.
- Levi, A., Harris, K. R., Wechter, W. P., Kousik, C. S., and Thies, J. A. 2010. DNA markers and pollen morphology reveal that *Praecitrullus fistulosus* is more closely related to *Benincasa hispida* than to *Citrullus* spp. Genet. Resour. Crop Evol. 57:1191-1205.
- Levi, A., Thomas, C. E., Simmons, A. M., and Thies, J. A. 2005. Analysis based on RAPD and ISSR markers reveals closer similarities among *Citrullus* and *Cucumis* species than with *Praecitrullus fistulosus* (Stocks) Pangalo. Genet. Resour. Crop Evol. 52:465-472.
- McCreight, J. D., Pitrat, M., Thomas, C. E., Kishaba, A. N., and Bohn, G. W. 1987. Powdery mildew resistance genes in muskmelon. J. Am. Soc. Hortic. Sci. 112:156-160.
- McGrath, M. T. 2001. Distribution of cucurbit powdery mildew races 1 and 2 on watermelon and muskmelon. Abstr. Phytopathology 91(suppl.):197.
- McGrath, M. T., and Thomas, C. E. 1996. Powdery mildew. Pages 28-30 in: Compendium of Cucurbit Diseases. T. A. Zitter, D. L. Hopkins, and C. E. Thomas, eds. American Phytopathological Society, St. Paul, MN.
- Mercier, J., Muscara, M. J., and Davis, A. R. 2014. First Report of *Podosphaera xanthii* race 1W causing powdery mildew of watermelon in California. Plant Dis. 98:158.
- Pitrat, M., Dogimont, C., and Bardin, M. 1998. Resistance to fungal diseases of foliage in melon. Pages 167-173 in: Cucurbitaceae '98: Evaluation and Enhancement of Cucurbit Germplasm. J. D. McCreight, ed. ASHS Press, Alexandria, VA.
- Tetteh, A. Y., Wehner, T. C., and Davis, A. R. 2010. Identifying resistance to powdery mildew race 2W in the USDA-ARS watermelon germplasm collection. Crop Sci. 50:933-939.
- Tetteh, A. Y., Wehner, T. C., and Davis, A. R. 2013a. Inheritance of resistance to powdery mildew race 2 in *Citrullus lanatus* var. *lanatus*. HortScience 48: 1227-1230.
- Tetteh, A. Y., Wehner, T. C., and Davis, A. R. 2013b. Inheritance of resistance to the new race of powdery mildew in watermelon. Crop Sci. 53: 880-887.

- Thomas, C. E., Levi, A., and Caniglia, E. 2005. Evaluation of US plant introductions of watermelon for resistance to powdery mildew. *HortScience* 40:154-156.
- Tomason, Y., and Gibson, P. T. 2006. Fungal characteristics and varietal reactions of powdery mildew species on cucurbits in the steppes of Ukraine. *Agron. Res.* 4:549-562.
- Zhang, H., Guo, S., Gong, G., Ren, Y., Davis, A. R., and Xu, Y. 2011. Sources of resistance to race 2WF powdery mildew in US watermelon plant introductions. *HortScience* 46:1349-1352.
- Zohary, D., Hopf, M., and Weiss, E. 2012. *Domestication of Plants in the Old World*. Oxford University Press, New York.