Monitoring Physiological Races of *Podosphaera xanthii* (syn. *Sphaerotheca fuliginea*), the Causal Agent of Powdery Mildew in Cucurbits: Factors Affecting Race Identification and the Importance for Research and Commerce

R. Cohen,[1,2,*] Y. Burger[2] and N. Katzir[2]

Identification of the physiological races of *Podosphaera xanthii* (syn. *Sphaerotheca fuliginea*), the causal agent of powdery mildew in cucurbits, is based upon the differing responses of various melon cultigens to the pathogen. Eight races of the pathogen have been identified to date in the USA, Africa, Europe and around the Mediterranean Sea, and four new races were reported from greenhouse melons in the major growing area of Japan. Plant responses to powdery mildew may be affected by environmental factors such as light intensity, temperature and humidity, as well as by age and nutritional status of the plants. The same factors affect the accuracy and reliability of race identification. In an attempt to overcome those obstacles, the genetic diversity of *P. xanthii* was studied using molecular markers. Unfortunately, no correlation was found between DNA polymorphism and the race of the pathogen as identified by biological tests. The usefulness of race identification as a guide for the grower in selecting appropriate cultivars is limited because changes or shifts in the pathogen population are common. Such changes may be found among growing seasons, geographic regions and hosts, and also within a single greenhouse during a single season. On the other hand, race identification is important for basic research and is especially important for the commercial seed industry, which requires accuracy in declaring the type and level of resistance to powdery mildew in its products.
KEY WORDS: *Podosphaera xanthii*; *Sphaerotheca fuliginea*; cucurbits; *Cucumis melo;* molecular markers; race identification; powdery mildew.

INTRODUCTION

Two pathogenic fungi, *Erysiphe cichoracearum* DC. ex Merat and *Sphaerotheca fuliginea* (Schlechtend: Fr.) Pollacci, are the most frequently reported powdery mildew pathogens of cucurbits (6,35). Recently, the names of the fungi were changed: *S. fuliginea* to *Podosphaera xanthii* (7), and *E. cichoracearum* to *Golovinomyces cichoracearum* (21). These new names will be used hereafter in this article. In the USA, *P. xanthii* is more widespread than *G. cichoracearum* (35). Both genera are present on cucurbits in France (6). On the island of Crete, *P. xanthii* is the predominant powdery mildew pathogen, but *G. cichoracearum* has also been found (37). In the Czech Republic and Slovakia, *G.*

Received June 24, 2003; accepted Dec. 1, 2003; http://www.phytoparasitica.org posting March 2, 2004. Contribution from the Agricultural Research Organization. No. 501/04.
[1]Dept. of Plant Pathology and [2]Dept. of Vegetable Crops, ARO, Newe Ya'ar Research Center, Ramat Yishay 30095, Israel. *Corresponding author [e-mail: ronico@volcani.agri.gov.il].

cichoracearum prevails although *P. xanthii* is also found in open fields and in greenhouses (24,25). In Israel, *P. xanthii* is the sole causal agent of the disease; *G. cichoracearum* has never been reported (15).

The identification of *P. xanthii* races on melons is based upon the differing responses of various melon (*Cucumis melo* L.) cultigens to this pathogen. Since no complete resistance to powdery mildew is available for a given set of cultivars of other cucurbit genera, the identification of powdery mildew from other cucurbits is based also on their reaction to melons. Thomas *et al.* (35) suggested using PMR 45 (resistant to race 1) and PMR 6 (resistant to races 1 and 2) as a tool for identification of race 3. Cultivar 'Ediato 45' and two accessions (WMR 29 and PI 414723) were later added to the differential set, which enabled the identification of two additional *P. xanthii* races (6,28).

However, the determination of *P. xanthii* races and the responses of melon and other cucurbit plants to powdery mildew can be problematic and confusing. Plant responses can differ according to various biotic and abiotic factors: plant age at the time of inoculation (15), purity of the pathogen isolates (29), differences in environmental conditions in greenhouses *vs* open field, cropping season, and use of shading nets (10,26) may all influence the recognition of plants as resistant or susceptible, as well as the ability to identify the pathogen race accurately.

This mini-review covers both worldwide and local distribution of *P. xanthii*, occurrence of new physiological races, factors affecting the reliability of race identification, and the importance of accurate race identification for researchers, growers and the seed industry.

DISTRIBUTION OF THE PATHOGEN

Powdery mildew was first noted as a destructive disease of melon production in 1925 in the Imperial Valley of California. In their pioneering work, Jagger and Scott (cited in refs. 21 and 32) screened cantaloupe plant material from all over the world and found powdery mildew resistance in a seed-lot from India (PI 78374). A back-cross program that included field selection resulted in the introduction of the first commercial resistant melon cultivar, PMR 45, in 1936 (32). Several physiological races have been identified. The occurrence in 1938 of powdery mildew on PMR 45 grown in the Imperial Valley of California indicated the appearance of the first new race of the pathogen, which was designated race 2 (32). Genetic resistance to race 2 was identified in 1939, and led to the release of PMR 5 in 1942. Race 3 of *P. xanthii* was observed in the lower Rio Grande Valley, first in a greenhouse in 1976 and then in the field in 1977 (34); it was also reported in India in 1986 (21) and in Israel in 1996 (12). Races 1 and 4 were identified in the Czech Republic in 1997–8 (24). Recently many other races that did not fit into the differential set suggested by Bardin *et al.* (4) were found (A. Lebeda, personal communication). The occurrence of a new race, designated race 6, was suggested by Bertrand (5), who used AR Hale's Best Jumbo as a new and additional differentiating cultivar. A total of seven races of *P. xanthii* from America, Europe, Africa and Israel have been identified and described using one set of differentiating melon cultivars (4,5,28).

Four races were found in Japan in 1999 that did not fit into the differential set used at that time for race identification (4,28), and thus were considered new races and designated N1-N4 (19,20).

In a survey conducted in Israel throughout 2001 and 2002, *P. xanthii* isolates were collected from several cucurbits in various regions during different cropping seasons (9).

The most commonly found were races 1, 3, 4 and 5 (Table 1). Two isolates were unique and were previously unknown among *P. xanthii* races in Israel: one of them developed on cucumber in winter 2001 and was designated race 0; the other developed on melon grown in winter 2002 at 'En Yahav, and since it was able to infect PI 414723 it was identified as race 2 USA. No obvious conclusion regarding the distribution of *P. xanthii* races could be made from this survey. However, it seems that races 1 and 4 occurred more frequently in the winter growing season, whereas races 3 and 5 were more prevalent in the summer (Table 1) (9).

TABLE 1. Occurrence of *Podosphaera xanthii* races on cucurbits in different growing areas in Israel (9)

Location, region	Cropping season	Host	*P. xanthii* race
'En Tamar, 'Arava	Winter 2001	Squash	5
'En Tamar, 'Arava	Winter 2001	Squash	1
'En Tamar, 'Arava	Winter 2001	Watermelon	1
'En Tamar, 'Arava	Winter 2001	Melon	4
Zofar, 'Arava	Winter 2001	Melon	1
Hazeva, 'Arava	Winter 2001	Cucumber	4
Newe Ya'ar, Yizre'el Valley	Winter 2001	Melon	1
Newe Ya'ar, Yizre'el Valley	Winter 2001	Cucumber	5
Ahituv, Hefer Valley	Winter 2001	Cucumber	1
Ahituv, Hefer Valley	Winter 2001	Cucumber	0
Dor, Coastal plain	Winter 2001	Cucumber	1
Newe Ya'ar, Yizre'el Valley	Summer 2001	Melon (field)	5
Newe Ya'ar, Yizre'el Valley	Summer 2001	Melon (greenhouse)	3
Newe Ya'ar, Yizre'el Valley	Summer 2001	Melon (greenhouse)	3
NeweYa'ar, Yizre'el Valley	Summer 2001	Melon (greenhouse)	5
Newe Ya'ar, Yizre'el Valley	Summer 2001	Squash	5
Yif'at, Yizre'el Valley	Summer 2001	Melon	5
Ramat Dawid, Yizre'el Valley	Summer 2001	Squash	5
Shamerat, Western Galilee	Summer 2001	Grafted watermelon[z]	5
Kefar Haruv, Golan Heights	Summer 2001	Melon	5
Mevo Hamma, Golan Heights	Summer 2001	Melon	1
'En Yahav, 'Arava	Winter 2002	Melon	2 USA
'En Yahav, 'Arava	Winter 2002	Cucumber	4
'En Yahav, 'Arava	Winter 2002	Squash	4
'En Yahav, 'Arava	Winter 2002	Squash	1

[z]Powdery mildew on the squash (rootstock) cotyledons.

Differences, changes or shifts in the pathogen population may occur, not only among growing seasons, geographic regions and hosts (4,6), but also within a single greenhouse during a single season, as reported by Sowell (33) and Thomas *et al.* (35). A more complicated situation was observed at the Newe Ya'ar Research Center in Israel: several isolates were collected from different melon breeding lines with non-identified powdery mildew resistances (9). Races 2 and 3 (based on the differential cvs. 'Ananas Yoqne'am', PMR 45 and PMR 6) were identified in two greenhouses in close proximity at the same time. Adding the powdery mildew-resistant melon cv. 'Noy Yizre'el', which is not included in the common differential set for race identification (4), enabled the detection of four races or pathotypes of the same pathogen within a small area (Table 2).

Race-specific resistance to *P. xanthii* is known in melons, but has not been reported in cucumber (*Cucumis sativus* L.) or in *Cucurbita* L. The status of *P. xanthii* races in

TABLE 2. Responses of melon differential cultivars to *Podosphaera xanthii* isolated from seven different breeding lines grown in two greenhouses at Newe Ya'ar during winter 1997 (9)

Breeding line (powdery mildew source)	Greenhouse	Differential melon cultivars[z]				*P. xanthii* races[x]	
		AY	PMR 45	PMR 6	NY	Without NY	With NY
X 31	A	S[y]	S	R	**S**	2	**a**
S 58	A	S	S	R	**R**	2	**b**
X 360	A	S	S	R	**R**	2	**b**
HY 1	A	S	S	S	**S**	3	**c**
X 320	B	S	S	R	**R**	2	**b**
HY 55	B	S	S	R	**R**	2	**b**
FH 175	B	S	S	S	**R**	3	**d**

[z] AY = Ananas Yoqne'am, NY = Noy Yizre'el.

[y] S = Susceptible, R = Resistant.

[x] Race identification in the left column based on differential cultivar suggested by Thomas *et al.* (35). In the right column, use of NY (in **bold**) as an additional differentiating cultivar reveals different race identifications that are designated, for this example only, as **a**, **b**, **c** and **d**.

watermelon (*Citrullus lanatus* (Thunb.) Matsum. & Nakai) is not clear. Powdery mildew had not been a problem on watermelon in the USA until the mid-1990s, when it emerged as an important disease in major production areas (17). The reason for this change is unknown; perhaps a more virulent strain of the pathogen was introduced or became more prevalent. Only races 1 and 2 have been reported on watermelon (13,17). Y. Cohen *et al.* (13) were unsuccessful in attempting to inoculate watermelons with *P. xanthii* race 2 taken from cucumber or melon; only the pathogen taken from watermelon was capable of infecting watermelon. Based on these results it was suggested that *P. xanthii* of watermelon is a new *forma specialis,* and the suggested name for it is f.sp. *citrullus.* The availability of some watermelon accessions resistant to powdery mildew, as reported by Davis *et al.* (18), may open the opportunity to look for more specific resistances and host ranges of the powdery mildew pathogens.

ENVIRONMENTAL FACTORS AFFECTING RACE IDENTIFICATION

Environmental factors, including light intensity, temperature and humidity, can affect the severity of powdery mildew (2,30). The pathogen can be affected directly and also indirectly, by the environment influencing the host (2). The effects of various environmental factors also vary with the species of powdery mildew fungus studied and the conditions under which it is studied. This variation has led to considerable confusion as to the effect of the environment on the development of powdery mildews in general (30).

The environmental conditions under which differential plants used for race identification are maintained may dramatically affect their responses to powdery mildew and, therefore, may also influence the test results. For example, the powdery mildew-resistant melon hybrid 'Revigal' and its resistant and susceptible parents were inoculated with *P. xanthii* race 1 at the third-true-leaf stage. After inoculation, the plants were maintained in the open or under shading nets transmitting 50% of natural sunlight, in the same field. When grown in the open, the resistant parent remained free of powdery mildew throughout the season, and the hybrid was only slightly affected (less than 5% of its leaves developed symptoms of powdery mildew), whereas symptoms developed on both the resistant parent

and the supposedly resistant hybrid grown under the shading nets, with 7% and 26% of the leaves affected, respectively (9,10). In another study, shading hastened the appearance of powdery mildew and increased its severity on partly resistant and susceptible squash (*Cucurbita pepo* L.) plants; shading was therefore considered a tool for facilitating the identification of resistant individuals in breeding programs for squash (26), in which race-specific resistance was not identified (11). The use of a shading net could be useful in melon breeding programs also, but the risk of incorrect race identification that may result from the shading should be taken into consideration.

The effects of sunlight on an obligatory pathogen and its reduction by a shading net or cloudy weather cannot be distinguished from the effects of other factors potentially affected by radiation level, such as leaf temperature, leaf wetness, transpiration, and rate of assimilation. All of these may affect disease development and their influence should not be underestimated (2).

Podosphaera xanthii has cardinal temperatures of 9°, 22° and 34°C (22), but temperature may affect isolates from different regions in different ways. An isolate from cantaloupes in the hot Imperial Valley of California had an optimum temperature of 25–28°C, whereas an isolate of the same species from squash in the cooler Colma area had an optimum temperature of 15°C (22). Temperature can also affect disease development within the host plant: the response of a Spanish melon cultivar, ANC-57, to *P. xanthii* race 1 was affected by temperature such that it was resistant at 26° and susceptible at 21°C. In this case resistance is controlled by one dominant gene with a temperature-conditioned response that can stimulate or inhibit the gene action (36). An opposite effect of temperature on plant resistance was presented by Hosoya *et al.* (19): four melon cultivars, 'Quincy', ENN2, EMN2 and HN21, which are resistant to race 1 of the pathogen under spring conditions, were infected during summer.

As powdery mildew fungi are obligatory parasites, disease severity and incidence depend markedly on the growing conditions of the plants. Effect of potting media and light intensity on race identification was observed in an experiment conducted at Newe Ya'ar, Israel, in which the melon cultivars Ananas Yoqne'am, PMR 45 and PMR 6 were grown in vermiculite or organic medium and under two different light intensities for 2 weeks prior to inoculation (9). Leaf disks were removed from the plants in these four treatments, placed on water agar in petri dishes and then inoculated with powdery mildew. The dishes were maintained under the same growth chamber conditions with low light intensity. Powdery mildew intensity varied among the pre-inoculation treatments, but the isolate developed under all four combinations of lighting and medium, and thus was identified as race 2 on the basis of the differentials suggested by Thomas *et al.* (35). However, a different response was observed when the cvs. 'Noy Yizre'el' and 'Dulce' were included in the biological assay as additional differentiating cultivars. Leaf disks sampled from Noy Yizre'el plants grown in organic medium under high light intensity were heavily infested, in contrast to the resistant response of Noy Yizre'el plants grown in vermiculite and under low light intensity prior to inoculation (9). These results based on additional differentiating cultivars could lead to different conclusions regarding the pathogen race.

The addition of silicon to the nutrient solution of greenhouse-grown cucumbers suppresses powdery mildew development by increasing the latent period, decreasing colony area per leaf, and reducing the germination rate of *P. xanthii* conidia on the cucumber leaves (31). Powdery mildew suppression by silicon was also affected by the temperature in the

greenhouse, the observed effect of silicon treatment being greater at 20°C than at higher temperatures. It was suggested that the temperature and the silicon acted in a synergistic manner (31).

The differing responses of a given cultivar grown under different environmental conditions (nutrition, light, temperature) demonstrate the need to grow plants used for race identification under standardized conditions, even in the pre-inoculation period.

Plant age at which the response to the disease is tested is also important. Testing plants at the cotyledon stage can be inaccurate (15). Resistance of the cotyledons is highly correlated with resistance in the field, whereas susceptibility in cotyledons is not necessarily associated with susceptibility in the true leaves. When cotyledons are susceptible, screening for resistance should be done when the plant has two true leaves (15).

A MOLECULAR APPROACH TO RACE IDENTIFICATION

The application of molecular markers has been demonstrated to be a valuable tool for studying populations of pathogenic fungi. The genetic diversity of the two causal agents of powdery mildew in cucurbits, *P. xanthii* and *G. cichoracearum*, has been studied by this means (4,23). Bardin *et al.* (4) characterized 28 isolates of *P. xanthii* by using virulence tests, mating types and DNA polymorphism. DNA polymorphism was detected by means of *(a)* Restriction Fragment Length Polymorphism (RFLP) analysis of PCR amplicons of ribosomal genes sequences: the internal transcribed spacers (ITS) and 5.8S DNA; and *(b)* Random Amplified Polymorphic DNA (RAPD) analysis. No polymorphism was detected for the ITS sequences, through the use of 11 restriction enzymes, although the samples were collected in various geographical areas (most of them in France, but also in Africa and the USA) and from several different cucurbit crops. RAPD analysis (152 markers amplified by 22 primers) indicated a low level of polymorphism. Cluster analysis of the RAPD data did not indicate genetically distinct groups. No association was found between the results of RAPD analysis and any of the other parameters tested: virulence, mating type, geographic or host origin. Similar results were obtained in Israel for 26 local isolates of *P. xanthii*. (23). Low polymorphism was detected by RAPD and Inter-Simple Sequence Repeat (ISSR) markers. Only 2% of the RAPD primers and 10% of the ISSR primers detected polymorphism among these isolates. No association was found between DNA polymorphism and the races of the pathogen as identified by biological tests. It was suggested by Bardin *et al.* (4) that the evolution of virulence may have been independent of the RAPD markers tested.

Genetic differentiation in the French population of *G. cichoracearum* was studied by Bardin *et al.* (3), who used RFLP analysis of the ITS and RAPD analyses. In this case, cluster analysis of 147 RAPD fragments (obtained with 16 primers) revealed three distinct genetic lineages, corresponding to three rDNA haplotypes. The host ranges of the three groups differed, with one of the groups specializing more in melon. A correlation between the three groups and pathogenic races was also found. No correlation was found between pathogenic race and geographical origin.

DISCUSSION

The capability of the biological assay to identify race in *P. xanthii* is limited by the lack of balance between two factors: the relatively small genetic variation among melon

cultivars that differ in their responses to this pathogen and the genetic variability in the pathogen population, which is common in such an airborne pathogen with huge numbers of conidia (9). For instance, two isolates of *P. xanthii* that were identified as race 2 – one originating from Israel and the other from France – elicited differing plant responses when inoculated on F_2 families from crosses of PI 124111F and a susceptible line (27). This indicates that these two isolates of the same race do not carry the same virulence genes. Virulence differences between two Spanish isolates of race 2 were also reported (1).

It is possible that race 2 USA and other variants of this race have some difference(s) in their virulence genes or modifiers that may cause these differences. Another possibility is that in some of the reported cases there was a mixture of more than one pathogenic race (5). Ability to identify race depends on the number of differential genotypes available and on the knowledge of the genetic control of disease resistance. It seems that there are isolates with additional genes for pathogenicity, and that they can be identified when new differential plant genotypes become available. Including AR Hales Best Jumbo with the commonly used differential genotypes led to the identification of race 6 (5). Using the melon cultivars Noy Yizre'el with PMR 45 and PMR 6 enabled identification of four different races or pathotypes in a restricted greenhouse area in Israel (9). Using new melon accessions enabled identification of four new *P. xanthii* races that did not fit into the common differential set in Japan (19,20).

Four new races (0, 2 USA, 4 and 5) were first detected in Israel during 2001 and 2002, by exposing differential melon cultivars to Israeli isolates for the first time (9). Therefore, it would be more accurate to state that the introduction of resistant cultivars can provide a new means for detecting a new race that already exists, derived as a result of the genetic variation within the pathogen population.

The genetic background is not known for all the differential genotypes currently used for race identification. To overcome this obstacle, a group of geneticists and plant pathologists was formed in 1993 (27). The specific goals of this group are to *(a)* develop a set of melon lines with known genetic backgrounds and each possessing only one gene for powdery mildew resistance; *(b)* test these lines with different isolates of the pathogen in different locations around the world; and *(c)* conduct allelism tests among the powdery mildew resistance genes (21,27).

The mechanisms by which environmental conditions may alter powdery mildew development and race identity are not clear. Despite extensive studies on the occurrence and inheritance of genes for resistance to powdery mildew in muskmelon, only a few studies have addressed the question of their nature (21). Cohen and Eyal (14,16) showed that reduced *P. xanthii* growth on PI 124111 was associated with a hypersensitive reaction of the epidermal cells of the host in response to a challenge inoculation. Callose deposition and lignification were suggested as mechanisms involved in powdery mildew resistance in a wide range of melon genotypes (16). This mechanism is probably related to papilla formation (Y. Cohen, personal communication), which is known to be a general defense mechanism of plant cells against invading microorganisms (2). Papilla formation has been reported as a resistance mechanism of barley, oat, sugar beet and grapes against powdery mildews. Papilla formation and fungal penetration can be affected by environmental conditions. When wheat plants were placed in the dark during the first 3 or 4 days after inoculation, the pathogen attack resulted in more severe disease than when the plants were exposed to normal daylight. These results can be interpreted as indicating faster or easier

penetration through a weak or thin epidermis layer, caused by the lack of photosynthesis during the dark period. Whether the pathogen penetrates the host mechanically or enzymatically, it needs more energy to do so when the cuticle and epidermal cell wall are thicker. This finding demonstrates how changes in host anatomy that are brought about by environmental conditions may alter pathogen development (2) and, consequently, affect race identification.

The above examples show how various biotic and abiotic factors can affect *P. xanthii* race identification. These examples illustrate first the need for a clear definition of the term 'resistance' as related to this particular host–pathogen interaction, and secondly the need for standardized race identification tests. To date, there are no standard methods for race identification or for characterization of the responses of plants to the disease, *i.e.*, there is no standard definition of resistance to cucurbit powdery mildew. The absence of standardization may lead to differing conclusions if a given cultivar or breeding line is tested at different locations.

It was suggested that the term 'resistance' be used to denote cases in which host genotypes show considerably less growth and sporulation of the pathogen, recognizing that even the most resistant genotype will exhibit some evidence of the disease under extreme pressure (21). Plants to be tested should be grown under standard conditions (potting mixture, fertilization, light intensity, temperature, humidity) and should be tested at a certain age by a standard method. Such a method could be a leaf disk assay (6,8), which facilitates the use of an accurate sampling and inoculation system in which the tested samples are maintained under standard conditions and subjected to standardized disease evaluation. A single conidium culture of each isolate to be tested is required to ensure the purity of the culture and the reliability of the test (30).

Is monitoring pathogen races important? It seems that the knowledge gained through the years, worldwide, is significant mainly from the point of view of basic genetic studies. Future studies will probably be aimed at implementing novel molecular procedures for identifying and isolating resistance genes. On the other hand, it has been shown that population shifts of fungal races are not necessarily caused by the introduction of new resistant melon cultivars (19). Therefore, monitoring fungal races to determine which resistant gene(s) should be introduced in melon breeding programs would not be reasonable.

In contrast to the importance of race identification for scientific purposes, the value of identification for growers varies with their global location. Plants in grower's fields may be exposed to huge amounts of conidia of several different races, which can infect plants and initiate disease at various growth stages of the crop. A microcosm of such a phenomenon occurred at the Newe Ya'ar Research Center, where four different *P. xanthii* races were found at the same time in two greenhouses located less than 100 m apart (9).

The problematic race identification of *P. xanthii* discussed in this article has special importance for the seed industry and seed commerce. Since plants may be bred at one location and then grown commercially elsewhere in the world where different races may occur and environmental conditions are different, breeders need a uniform method for determining the type and level of resistance to powdery mildew, and must adopt a commonly recognized way of declaring the type and level of plant response to powdery mildew.

REFERENCES

1. Alvarez, J.M., Gomez-Guillamon, M.L., Tores, J.A., Canovas, I. and Floris, E. (2000) Virulence differences between two Spanish isolates *of Sphaerotheca fuliginea* race 2 on melons. *Acta Hortic.* 510:67-69.
2. Aust, H.J. and Hoyningen-Huene, J. (1986) Microclimate in relation to epidemics of powdery mildew. *Annu. Rev. Phytopathol.* 24:491-510.
3. Bardin, M., Carlier, J. and Nicot, P.C. (1999) Genetic differentiation in the French population of *Erysiphe cichoracearum*, a causal agent of powdery mildew of cucurbits. *Plant Pathol.* 48:531-540.
4. Bardin, M., Nicot, P.C., Normand, P. and Lemaire, J.M. (1997) Virulence variation and DNA polymorphism in *Sphaerotheca fuliginea*, causal agent of powdery mildew of cucurbits. *Eur. J. Plant Pathol.* 103:545-554.
5. Bertrand, F. (2002) AR Hale's Best Jumbo, a new differential melon variety for *Sphaerotheca fuliginea* races in leaf disk tests. *in:* Maynard, D.N. [Ed.] Cucurbitaceae 2002. ASHS Press, Alexandria, VA, USA. pp. 234-237.
6. Bertrand, F. and Pitrat, M. (1989) Screening of a muskmelon germplasm for susceptibility to 5 pathogens of powdery mildew. *in: Proc. Cucurbitaceae 89. Evaluation and Enhancement of Cucurbit Germplasm* (Charleston, SC, USA), pp. 140-142
7. Braun, U., Shishkoff, N. and Takamatsu, S. (2001) Phylogeny of *Podosphaera* sect. *Sphaerotheca* subsect. *Magnicellulatae* (*Sphaerotheca fuliginea* s.lat.) inferred from rDNA ITS sequences – a taxonomic interpretation. *Schlechtendalia* 7:45-52.
8. Cohen, R. (1993) A leaf disk assay for detection of resistance of melon to *Sphaerotheca fuliginea* race 1. *Plant Dis.* 77:513-517.
9. Cohen, R,. Burger, Y. and Shraiber, S. (2002) Physiological races of *Sphaerotheca fuliginea*: Factors affecting their identification and the significance of this knowledge. *in:* Maynard, D.N. [Ed.] Cucurbitaceae 2002. ASHS Press, Alexandria, VA, USA. pp. 181-187.
10. Cohen, R., Burger, Y., Shraiber, S., Elkind, Y. and Levin, E. (1996) Influence of the genetic background and environmental conditions on powdery mildew of melons. *Phytoparasitica* 24:162 (abstr.).
11. Cohen, R., Hanan, A. and Paris, H.S. (2003) Single-gene resistance to powdery mildew in a zucchini squash (*Cucurbita pepo). Euphytica* 130:433-441.
12. Cohen, R., Katzir, N., Shraiber, S., Yarden, O. and Greenberg, R. (1996) Occurrence of *Sphaerotheca fuliginea* race 3 on cucurbits in Israel. *Plant Dis.* 80:334.
13. Cohen, Y., Baider, A., Petrov, L., Sheek, L. and Voloisky, V. (2000) Cross-infectivity of *Sphaerotheca fuliginea* to watermelon, melon, and cucumber. *Acta Hortic.* 510:85-88.
14. Cohen, Y. and Eyal, H. (1988) Epifluorescence microscopy of *Sphaerotheca fuliginea* race 2 on susceptible and resistant genotypes of *Cucumis melo. Phytopathology* 78:144-148.
15. 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.
16. Cohen, Y., Eyal, H. and Hanania, J. (1989) Ultrastructure, autofluorescence, callose deposition and lignification in susceptible and resistant muskmelon leaves infected with the powdery mildew fungus *Sphaerotheca fuliginea. Physiol. Mol. Plant Pathol.* 36:191-204.
17. Davis, A.R., Brouton, B.D., Pair, S.D. and Thomas, C.E. (2001) Powdery mildew: An emerging disease of watermelon in the United States. *Cucurbit Genet. Coop. Rep.* 24:42-48.
18. Davis, A.R., Thomas, C.D., Levi, A., Bruton, B.D. and Pair, S.D. (2002) Watermelon resistance to powdery mildew race 1. *in:* Maynard, D.M. [Ed.] Cucurbitaceae 2002. ASHS Press, Alexandria, VA, USA. pp. 192-198.
19. Hosoya, K., Kuzuya, M., Murakami, T., Kato, K., Karisawa, K. and Ezura, H. (2000) Impact of resistant melon cultivars on *Sphaerotheca fuliginea. Plant Breed.* 119:286-288.
20. Hosoya, K., Narisawa, K., Pitrat, M. and Ezura, H. (1999) Race identification in powdery mildew (*Sphaerotheca fuliginea*) on melon (*Cucumis melo*) in Japan. *Plant Breed.* 118:259-262.
21. Jahn, M., Munger, H.M. and McCreight, J.D. (2002) Breeding cucurbit crops for powdery mildew resistance. *in:* Belanger, R.R., Bushnell, W.R., Dik, A.J. and Carver, L.W. [Eds.] The Powdery Mildews, A Comprehensive Treatise. APS Press, St. Paul, MN, USA. pp. 239-248.
22. Jarvis, W.R., Gubler, W.D. and Grover, G.G. (2002) Epidemiology of powdery mildew in agricultural pathosystems. *in:* Belanger, R.R., Bushnell, W.R., Dik, A.J. and Carver, L.W. [Eds.] The Powdery Mildews, A Comprehensive Treatise. APS Press, St. Paul, MN, USA. pp. 169-199.
23. Katzir, N., Cohen, R., Greenberger, R., Shraiber, S., Tzuri, G., Ben Zeev, I.S. *et al.* (2000) Variability among Israeli isolates of *Sphaerotheca fuliginea:* virulence races, DNA polymorphism, and fatty acid profiles. *Cucurbit Genet. Coop. Rep.* 23:30-31.

24. Kirstkova, E., Lebeda, A. and Katovska, J. (2002) Response of *Cucumis melo* genotypes MR-1 and PI 124112 to Czech isolates of cucurbit powdery mildew. *Acta Hortic.* 588:181-184.
25. Kirstkova, E., Lebeda, A., Sedlakova, B. and Duchoslav, M. (2002) Distribution of cucurbit powdery mildew species in the Czech Republic. *Plant Prot. Sci.* 38(Special Issue 2):415-416.
26. Leibovich, G., Cohen, R. and Paris, H.S. (1996) Shading of plants facilitates selection for powdery mildew resistance in squash. *Euphytica* 90:289-292.
27. McCreight, J.D. and Pitrat, M. (1993) Club Mildew: Working group on resistance of melon to powdery mildew. *Cucurbit Genet. Coop. Rep.* 16:39.
28. Mohamed, Y.F., Bardin, M., Nicot, P.C. and Pitrat, M. (1995) Causal agents of powdery mildew of cucurbits in Sudan. *Plant Dis.* 79:634-636.
29. Nicot, P.C., Bardin, M. and Dik, A.J. (2002) Basic methods for epidemiological studies of powdery mildew: Culture and preservation of isolates, production and delivery of inoculum, and disease assessment. *in:* Belanger, R.R., Bushnell, W.R., Dik, A.J. and Carver, L.W. [Eds.] The Powdery Mildews, A Comprehensive Treatise. APS Press, St. Paul, MN, USA. pp. 83-99.
30. Schnathorst, W.C. (1965) Environmental relationships in the powdery mildews. *Annu. Rev. Phytopathol.* 3:343-363.
31. Schuerger, A.C. and Hammer, W. (2003) Suppression of powdery mildew on greenhouse-grown cucumber by addition of silicon to hydroponic nutrient solution is inhibited by high temperature. *Plant Dis.* 87:177-185.
32. Sitterly, W.R. (1979) Powdery mildew of Cucurbits. *in:* Spencer, D.M. [Ed.] The Powdery Mildews. Academic Press, New York, NY. pp. 359-379.
33. Sowell, G. Jr. (1982) Population shift of *Sphaerotheca fuliginea* from race 2 to race 1 in southeastern United States. *Plant Dis.* 66:130-131.
34. Thomas, C.E. (1978) A new biological race of powdery mildew of cantaloupes. *Plant Dis. Rep.* 62:223.
35. Thomas, C.E., Kishaba, E., McCreight, J.D. and Nugent, P.E. (1984) The importance of monitoring races of powdery mildew on muskmelon. *Cucurbit Genet. Coop. Rep.* 7:58-59.
36. Tores, J.A., Gomez-Guillamon, M.L. and Canova, I. (1996) Temperature-conditioned response to *Sphaerotheca fuliginea* race 1 in the Spanish melon ANC-57. *Cucurbit Genet. Coop. Rep.* 19:59-60.
37. Vakalounakis, E.K. and Papadakis, A. (1994) Species spectrum, host range and distribution of powdery mildew on Cucurbitaceae in Crete. *Plant Pathol.* 43:813-818.