Distribution of Mating Types of *Sphaerotheca fuliginea* in the United States

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ABSTRACT

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Mating type of *Sphaerotheca fuliginea* isolates was determined on summer squash leaves in detached leaf culture. Both mating types were found in all eight states examined (Arizona, California, Florida, Georgia, New York, North Carolina, Texas, and Virginia) and in 18 of the 27 fields examined in 1993 and 1994; therefore, the absence of one mating type is not the sole explanation for the rare sightings of cleistothecia in most areas of the United States. Cleistothecia were found on leaves collected in Michigan, indicating that both mating types also were present in this state. One mating type occurred more frequently (≥70% of the isolates tested) in 15 of these 18 fields. In 1993, 82% of the 132 isolates tested belonged to *MAT1-2*; whereas in 1994, only 31% of 155 isolates were *MAT1-2*. The frequencies of isolates resistant to triadimefon (50 µg/ml) were 0 and 63% for *MAT1-1* and *MAT1-2*, respectively, in 1993 and 25 and 62%, respectively, in 1994. Triadimefon-resistant isolates of each mating type were found in the same fields in California, Georgia, and Texas in 1994. All isolates shared identical alleles at the mating incompatibility locus. This provides strong evidence that *S. fuliginea* does not possess multiple alleles at the single mating locus.

Additional keywords: cucurbits, powdery mildew, teleomorph

Although the conidial state of *Sphaerotheca fuliginea* (Schlechtend.:Fr.) Pollacci, the causal agent of cucurbit powdery mildew, is extremely common, cleistothecia have been reported rarely. There were only three published reports of sightings in North America (9,11,16) before cleistothecia were observed on Long Island, New York, in 1989 (19). Isolates from New York were used to document that this fungus is heterothallic (20). Isolates from Florida and Michigan were found to be all one mating type during this previous study, which suggested that unequal distribution of mating types of *S. fuliginea* is a feasible explanation for the rare occurrence of cleistothecia worldwide.

Cleistothecia of *S. fuliginea* were observed for the first time in several locations in North America between 1978 and 1995, while cleistothecia were not found in other areas. The first published report of cleistothecia is from the Imperial Valley, California, where they were observed on summer squash (*Cucurbita pepo* L. var. *melopepo* (L.) Alef.) in November 1978 (16). C. E. Yarwood, who studied cucurbit powdery mildew for many years at the University of California, had been looking for cleistothecia prior to 1978 and found them near Berkeley for the first time in 1978 (D. G. Kontaxis, *personal communication*). Cleistothecia have not been observed since in the Imperial Valley, but they do occur occasionally in northern California, where cucurbits are grown for seed and thus infected plants are present for an extended period of time (D. G. Kontaxis, M. Davis, and A. O. Paulus, *personal communications*). Cleistothecia were observed on cucumber (*Cucumis sativus* L.) in a research glasshouse in Ontario, Canada, in November 1983 (11) and again in 1990 and 1991 (W. R. Jarvis, *personal communication*). However, they were not found in commercial glasshouses or fields. Cleistothecia developed on several cucurbit species in North Carolina during the fall of 1986 (9). Cleistothecia have not been found again in North Carolina (L. F. Grand and C. W. Averre, *personal communications*). Cleistothecia were observed for the first time in Indiana in September 1992 (17). They may have occurred previously in this state; however, no one looked for them before 1992 (R. X. Latin, *personal communication*). Cleistothecia were observed for the first time in Ohio in September 1995 after several years of looking (R. M. Riedel, *personal communication*). Other scientists have been searching for cleistothecia of *S. fuliginea* for several years but without any success. Cleistothecia have never been found in Florida, Georgia, South Carolina, or Arizona (K. L. Pernezny, D. R. Sumner, C. E. Thomas, and M. E. Matheron, respectively, *personal communications*).

Cleistothecia of *S. fuliginea* on cucurbitaceous plants have been found only rarely outside of North America. They have been observed in the Moscow region of Russia (23), in Israel only in December 1946 and in January 1947 (24), in the Sudan only on three occasions in 1939 and 1943 (31), in Libya in January 1982 and January 1983 during an extensive search initiated in April 1981 (8), in Saudi Arabia (1), in India on various cultivated cucurbits (14,15), in Japan (32), in New Zealand in 1956 (4) and in 1958 (7,10), in Australia in 1968 (2), in South Australia on herbaria specimens from 1982 and 1983 (18), and in New South Wales in 1988 (18). Cleistothecia had not been found in Australia prior to 1963 (3,5). They occur commonly in Fukuoka but are uncommon in other districts of Japan (32). Cleistothecia of both *S. fuliginea* and *Erysiphe cichoracearum* DC. were found in Crimea, Russia, on melons in 1925 (6), in the Volga basin, Russia, in 1934 (26), and in Hungary in the 1970s (22). Cleistothecia have not been seen in the Scandinavian countries (12).

The introduction of a second, compatible mating type would account for the teleomorph first being observed many years after the first report of the anamorph. For example, a delay of 92 years occurred in New South Wales between reports of the anamorph and the teleomorph (18). When cleistothecia have been observed, it has been late in the growing season, several weeks after the start of powdery mildew development (9,17,19,25) (M. Davis, *personal communication*). The time required for opposite mating types to come in contact could account for this delay, rather than environmental conditions such as cold temperatures or nutritive condition of the host (18,28).

Investigating possible explanations for the rare occurrence of cleistothecia is warranted because of the commercial importance of powdery mildew and the potential impact of cleistothecia on disease management. Powdery mildew is an important disease that must be managed in most cucurbit production areas to avoid a reduction in marketable yield or quality. Cleistothecia could enable the pathogen to survive harsh environmental conditions and absence of hosts (over winter or summer) and

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ascospores could function as a primary inoculum source. Interregional movement of conidia is thought to be the source of inoculum for powdery mildew in many areas. This would account for the disease not being a problem on spring crops. A local source of inoculum, such as ascospores, could result in earlier disease onset. In addition, increased genetic diversity resulting from sexual reproduction could include, for example, new combinations of virulence genes and fungicide resistance. The primary objective of this study was to determine if both mating types of *S. fuliginea* occur in areas of the United States where cleistothecia have never been observed (Florida, Georgia, and Arizona) or have not been observed recently (Imperial Valley, California, and North Carolina). Portions of this work have been reported previously (30).

MATERIALS AND METHODS

***S. fuliginea* isolates.** Leaves with powdery mildew were collected by cooperators from 27 cucurbit plantings in eight states between 16 December 1992 and 19 September 1994 (Tables 1 and 2). Leaves were collected from a given location either at the start, the middle, or the end of the powdery mildew epidemic. For one location (Homestead, Florida), samples were collected both at the beginning and at the end of the epidemic; thus there were a total of 28 collections. Three pairs of collections came from adjacent fields in Painter, Virginia, and Eden, New York. A total of 287 isolates were obtained from individual colonies on these leaves and maintained on yellow squash cultivar Seneca Prolific cotyledon leaf disks on water agar in petri dishes until their mating type was determined. Isolates were transferred to new disks every 2 to 3 weeks. Leaves with powdery mildew also were obtained from Freeville, New York (60 leaves) and Michigan (four leaves) in 1993. Some of these leaves had cleistothecia; therefore,

Table 1. Distribution of *Sphaerotheca fuliginea* mating types in the United States in 1992 to 1993

State	Location (management[a])	Collection date	Crop	No. isolates examined	Time in epidemic	Mating type frequency (%)	
						MAT 1-1	*MAT 1-2*
AZ	Yuma (R,NF)	6/7/93	Cantaloupe	25	Mid	8	92
CA	Imperial Valley (C,T?)	5/19/93	Cantaloupe	8	Start	25	75
CA	Imperial Valley (C,T?)	5/24/93	Cantaloupe	8	Start	0	100
CA	San Diego Co. (C,T?)	6/7/93	Cucumber	2	Start	50	50
CA	San Diego Co. (C,T?)	6/7/93	Melon	5	Start	0	100
CA	All			23		13	87
FL	Homestead (C; T-4X)	12/16/92	Yellow squash	14	Mid	0	100
FL	Wellington (C,NSF)	4/7/93	Yellow squash	16	Mid	25	75
FL	All			30		13	87
GA	Tifton (R,NSF)	7/6/93	Yellow squash	6	End	83	17
NC	Clinton (C,NSF)	8/18/93	Melon	10	Start	30	70
VA	Painter (C,T-1X)[b]	8/9/93	Yellow squash	5	Start	40	60
VA	Painter (C,T-1X)	8/9/93	Zucchini squash	14	Start	21	79
VA	Painter (R,T-2X,B-2X)	8/17/93	Pumpkin	11	Mid	0	100
VA	Painter (R,NF)	8/17/93	Pumpkin	8	Mid	25	75
VA	All			38		18	82

[a] C = commercial field; R = research plots; T = treated with triazole fungicide; B = treated with benzimidazole fungicide; #X = number of applications; ? = fungicide use records were not available, but triadimefon probably was applied; NF = no fungicides used; and NSF = no triazole or benzimidazole fungicides applied, only protectants used (sulfur, chlorothalonil, etc.).
[b] A sixth "isolate" from this field was a mixture of isolates of both mating types because cleistothecia formed when it was grown with both tester isolates.

Table 2. Distribution of *Sphaerotheca fuliginea* mating types in the United States in 1993 to 1994

State	Location (management[a])	Collection date	Crop	No. isolates examined	Time in epidemic	Mating type frequency (%)	
						MAT 1-1	*MAT 1-2*
CA	Imperial Valley (C,NSF)	4/11/94	Zucchini	13	Start[b]	38	62
CA	Imperial Valley (C,NSF)	4/11/94	Crenshaw melon	14	Start[c]	7	93
CA	Imperial Valley (C,NSF)	5/10/94	Squash	4	Start	100	0
CA	Imperial Valley (C,NSF)	5/10/94	Cantaloupe	3	Start	0	100
CA	Central Coast (C,NF)	7/19/94	Zucchini (golden)	12	Start	100	0
CA	All			46		48	52
FL	Homestead (C,NF)	3/24/94	Crookneck squash	20	Start	100	0
FL	Homestead (C,NF)	3/24/94	Crookneck squash	3	Start	100	0
FL	Homestead (C,T-4X)[d]	4/20/94	Crookneck squash	11	End	91	9
FL	Lantana (C,T-1X)	5/6/94	Yellow squash	10	End	90	10
FL	All			44		95	5
GA	Moultrie (C,NF)	5/27/94	Crookneck squash	8	Start	88	12
NY	Eden (C,T-2X,B-2X)	8/1/94	Winter squash	5	Start	80	20
NY	Eden (C,T-4X,B-2X)	9/19/94	Pumpkin	7	End	86	14
NY	All			12		83	17
TX	Rio Grand City (C,T-1X)	5/30/94	Melon	17	End	100	0
TX	Weslaco (R,T-3X)	5/30/94	Melon	10	End	70	30
TX	All			27		89	11
VA	Painter (C,NF)	8/9/94	Butternut squash	18	Start	11	89

[a] C = commercial field; R = research plots; T = treated with triazole fungicide; B = treated with benzimidazole fungicide; #X = number of applications; NF = no fungicides used; and NSF = no triazole or benzimidazole fungicides applied, only protectants used (sulfur, chlorothalonil, etc.).
[b] Start of mildew development in area, but collected after final harvest from a very early crop. First mildew in area.
[c] About 2 km downwind from zucchini field (previous entry in table). Fruit were starting to set. Symptoms were found in only one area of this field (about 3 m in diameter).
[d] Same field or farm as previous entry in table, resampled at the end of the powdery mildew epidemic.

Table 3. Analysis of variance for frequency of *Sphaerotheca fuliginea* mating type *MAT 1-1* as associated with location and crop characteristics of the fields where isolates were collected

Source of variation[a]	Mean square	F	Probability > F
Year	1.38	8.51	0.007
State (year)	0.21	1.65	0.179
Host crop (year)	0.82	1.16	0.364
Host genera (year)	0.10	0.56	0.576
Fungicide use (year)	0.19	1.16	0.329
Time in epidemic (year)	0.24	1.59	0.219

[a] Each independent variable nested in year was analyzed in a separate model with year.

isolates were not obtained from them for mating type determination.

Isolates MM2 and MM7, which were demonstrated to be of compatible mating types during a previous study (20), were used to determine the mating type of the unknown isolates. Isolate MM2 was designated *MAT1-1,* and isolate MM7 was designated *MAT1-2* (20). Mating type identity was checked during this study by mating MM2 and MM7 with MM64 (*MAT1-2*) and MM65 (*MAT1-1*) (20). These isolates were maintained using a detached leaf–culture technique (20). Conidia were transferred to new leaves every 2 to 4 weeks.

Fungus identification. Conidia of all isolates were examined for fibrosin bodies to confirm the identity of the powdery mildew fungus as *S. fuliginea* (13).

Matings. The isolates of unknown mating type were grown with MM2 and with MM7 on leaves of yellow squash cultivar Seneca Prolific using a detached leaf–culture technique (20). Cotyledons on water agar were used for a few matings. Although cotyledons required less time and space to set up and maintain, detached leaves generally survived longer and supported better growth of *S. fuliginea* than did cotyledons. The two isolates of each pair were inoculated in close proximity (2 to 5 mm apart) at four or six locations on a cotyledon or a detached leaf, respectively. Each inoculation site was marked with a small triangular piece of labeling tape or with a marking pen to facilitate proper placement of inoculum. These sites were examined 3 to 5 days after inoculation to determine if both isolates had become established. Then they were examined periodically until cleistothecia were formed or until the leaf died or for at least 1 month, whichever came first.

Fungicide sensitivity. Fungicide sensitivity was tested on cotyledon leaf disks from fungicide-treated summer squash seedlings. Triadimefon (formulated technical grade Bayleton 50DF, Bayer Corporation, Kansas City, MO) was dissolved in water and used at 0, 5 or 6.3, and 50 μg/ml. Blank formulation for Bayleton 50DF was used to adjust all triadimefon solutions, including 0 μg/ml, so that they contained inert ingredients of the Bayleton 50DF formulation at 50 μg/ml. Benomyl, formulated as Benlate 50DF (E. I. du Pont de Nemours, Wilmington, DE), was used at 200 μg/ml. Seedlings with expanded cotyledons (about 2 weeks after seeding) were sprayed with fungicide solutions using a DeVilbiss Model 152 atomizer (DeVilbiss Health Care, Inc., Somerset, PA) operated at 20 psi, air-dried, and 81 mm^2 disks were cut from cotyledons with a cork borer. Four disks treated with the same fungicide concentration were placed together on water agar in a single compartment of a petri dish with four sections. Disks were inoculated about 1 day after treatment. Approximately three to five conidial chains (15 to 25 conidia) of each isolate were transferred to the center of each of the disks by using an eyelash affixed to a disposable pipette.

Reference isolates of *S. fuliginea* known to be sensitive or resistant to both fungicides were included in each assay. These isolates were collected in September 1990 from a fungicide-treated research plot in Riverhead, New York. They were maintained on detached, fungicide-free leaves in petri dishes. The fungicide-resistant isolate was able to grow on leaf disks treated with triadimefon at 200 μg/ml or benomyl at 200 μg/ml.

Leaf disks were examined after incubation for 12 days using a dissecting microscope at 10.5× magnification. Isolates were considered to be resistant if they were able to grow and produce conidiophores on leaf disks treated with benomyl at 200 μg/ml or triadimefon at 50 μg/ml.

Data analysis. Analysis of variance was conducted to determine if year, state, type or species of cucurbit crop, time of collection in the epidemic, or fungicide sensitivity accounted for variation in frequency of mating types for the populations studied. These independent variables were nested within year. Time in the epidemic that the collection occurred was classified as early, middle, or late. *MAT1-1* frequency data were transformed before analysis with arcsine of the square root of these proportions (29). SuperANOVA version 1.1 for Macintosh computer was used.

RESULTS AND DISCUSSION

Both mating types of *S. fuliginea* were found in all eight states sampled and in 18 of the 27 fields sampled (Tables 1 and 2); therefore, the absence of one mating type is not the sole explanation for the lack of sightings of cleistothecia in most areas of the United States. Locations with both mating types included the Imperial Valley, California, and North Carolina, where cleistothecia have not been found since they were first observed in fall 1978 and 1986, respectively. In addition, cleistothecia were found on two leaves from central New York and one leaf from Michigan in 1993, thereby confirming the presence of both mating types in those areas. Although both mating types evidently were present in Michigan in 1993, only *MAT1-1* had been found in 1991 (20). Three of the fields with one mating type detected in 1994 were in areas where both mating types had been found in other fields that year (Imperial Valley, California, and southern Texas). Only one mating type was found in three of four collections from two of three fields in Homestead, Florida. Surprisingly, it was not the same mating type in the 2 years: only *MAT1-2* was found in December 1992 at the end of the fall growing season, whereas *MAT1-1* was found almost exclusively in March and April 1994. Only *MAT1-1* had been found in March and April 1992 in Homestead (20). Only one isolate from Homestead in 1994 was *MAT1-2*. These apparent shifts in the mating type that dominated prompted a check of the mating type of the tester isolates to confirm that they had not been mislabeled, although this was unlikely because they were transferred at different times.

One mating type occurred more frequently (≥70% of the isolates tested) in 15 of the 18 fields with both mating types (Tables 1 and 2). As a result, the chance of the two mating types occurring together on a leaf would be lower than if they occurred at the same frequency. This could affect cleistothecial occurrence because there would be fewer locations with both mating types and more time would be required for this chance event. Any time delay could be detrimental to cleistothecial formation in areas such as Arizona and Florida, where powdery mildew develops over a shorter period of time (3 to 4 weeks) than in northern states (6 to 8 weeks). However, cleistothecia have been found every year on Long Island despite the unequal frequency of the two mating types (M. T. McGrath, *personal observation*). Unequal frequency therefore is unlikely to be the sole explanation for cleistothecia not being found in several other areas in the northern United States.

MAT1-2 occurred more frequently than *MAT1-1* in 1993 (82% of the 132 isolates tested), whereas *MAT1-1* occurred more frequently in 1994 (69% of the 155 isolates tested). Year was the only variable examined that accounted for variation in mating type frequency in the *S. fuliginea* populations (Table 3). In a previous study, *MAT1-1* was found to be more common in 1989 and 1991 on Long Island and in 1992 in Florida (20). This suggests that neither mating type is associated with reduced fitness, although data from a particular

Table 4. Mating type and fungicide sensitivity of *Sphaerotheca fuliginea* isolates collected in the United States in 1993 and 1994[a]

		Mating type *MAT 1-1*			Mating type *MAT 1-2*		
Year	State	Total	Triadimefon resistant (%)	Benomyl resistant (%)	Total	Triadimefon resistant (%)	Benomyl resistant (%)
1993	AZ	3	0	0	21	76	0
1993	CA	3	0	0	20	85	0
1993	GA	5	0	0	1	100	0
1993	FL	4	0	0	12	92	0
1993	NC	3	0	0	7	0	14
1993	VA	8	0	0	32	44	0
1994	CA	14	29	7	14	64	0
1994	FL	36	36	36	2	0	50
1994	GA	7	43	29	1	100	0
1994	TX	18	38	0	3	33	0
1994	VA	2	0	0	15	67	0

[a] Fungicide sensitivity was not determined for all isolates listed in Tables 1 and 2.

year would suggest the opposite. This apparent shift in the relative frequency of the two mating types between 1993 and 1994 could be partially due to differences in the populations examined in terms of geographical location and crop. *MAT1-1* was found more commonly on yellow crookneck squash in south Georgia in both 1993 (83%) and 1994 (88%). However, on yellow crookneck squash in east central Florida, *MAT1-2* was found more commonly in 1993 (75%), whereas *MAT1-1* was found more commonly in 1994 (90%) and in 1992 (85%) (20).

Although mating type frequency appeared to be affected by crop, this may have been chance variation since there is no obvious biological explanation for host specificity being linked to mating type. For example, in a field in Weslaco, Texas, only *MAT1-2* was found on Hales Best 36, while only *MAT1-1* was found on Toledo (Casaba) and Meckty White. Two collections were made in the Imperial Valley on 10 May 1994. Only *MAT1-1* was found on squash, and only *MAT1-2* was found on cantaloupe.

Isolates of both mating types were found to be resistant to triadimefon (50 μg/ml); however, resistance was much more common in *MAT1-2* isolates (Table 4). Of the isolates collected in 1993, 59 of 93 *MAT1-2* isolates were able to grow on disks from leaves treated with triadimefon at 50 μg/ml, whereas all 26 *MAT1-1* isolates tested were sensitive to this concentration. In sharp contrast, the numbers of triadimefon-resistant isolates detected in 1994 were 21 of 35 *MAT1-2* isolates and 26 of 77 *MAT1-1* isolates. Triadimefon-resistant isolates of each mating type were found in 1994 in a field in Georgia, a field in Weslaco, Texas, and in two fields in the Imperial Valley, California, in April. Consequently, applying this fungicide to these populations would not be expected to prevent sexual reproduction. Sixteen *MAT1-1* isolates were resistant to benomyl (200 μg/ml) in 1994; 10 of these were also resistant to triadimefon. Only two *MAT1-2* isolates were sensitive to benomyl (one in 1993 and one in 1994). Benomyl-resistant isolates of each mating type were found in 1994 in a field in Florida. Fungicide usage and occurrence of fungicide resistance in the fields included in the present study are examined in another paper (21).

There is strong evidence that *S. fuliginea* does not possess multiple alleles at the mating incompatibility locus. All of the isolates tested were able to mate with one of the two tester isolates in this study and in a previous study (20). Only two of 352 isolates tested in these two studies produced cleistothecia with both tester isolates; this was most likely because they were a mixture of at least two isolates. *MAT1-1* and *MAT1-2* tester isolates produced cleistothecia only when mated with "–" and "+" mating type isolates, respectively, from France (M. Bardin, *unpublished*; 27), providing additional data to support the conclusion that all *S. fuliginea* isolates share identical alleles at the mating incompatibility locus.

A more intensive search for cleistothecia in areas where they have not been found but where both mating types have been reported is needed. If cleistothecia are found, then most likely the second mating type was introduced recently to these areas. If cleistothecia are not found, then their development is affected by factors other than mating type distribution.

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LITERATURE CITED

1. Abul-Hayja, Z. M., and Trabulsi, I. Y. 1981. *Sphaerotheca fuliginea* on cucurbits in Saudi Arabia. Trans. Br. Mycol. Soc. 76:506.
2. Alcorn, J. L. 1968. Cucurbit powdery mildew on papaw. Queensl. J. Agric. Animal Sci. 25:161-164.
3. Ballantyne, B. 1963. A preliminary note on the identity of cucurbit powdery mildews. Aust. J. Sci. 25:360-361.
4. Boesewinkel, H. J. 1976. Cleistothecia of powdery mildews in New Zealand. Trans. Br. Mycol. Soc. 67:143-146.
5. Clare, B. G. 1958. The identity of the cucurbit powdery mildew of South-Eastern Queensland. Aust. J. Sci. 20:273-274.
6. Deckenbach, K. N., and Koreneff, M. S. 1927. Contribution to the study of the mildew fungi of plantation crops in Crimea. Bolezni Rast. 16:155-160.
7. Dingley, J. M. 1959. New records of fungous disease in New Zealand, 1957/58. N.Z. J. Agric. Res. 2:380-386.
8. El-Ammari, S. S., and Khan, M. W. 1985. *Sphaerotheca fuliginea* (perithecial stage) on cucurbits. FAO Plant Prot. Bull. 33:42-43.
9. Grand, L. F. 1987. Teleomorph of *Sphaerotheca fuliginea* on cucurbits in North Carolina. Mycologia 79:484-486.
10. Hammett, K. R. W. 1977. Taxonomy of Erysiphaceae in New Zealand. N.Z. J. Bot. 15:687-711.
11. Jarvis, W. R., and Slingsby, K. 1984. Cleistothecia of *Sphaerotheca fuliginea* on cucumber in Ontario. Plant Dis. 68:536.
12. Junell, L. 1966. A revision of *Sphaerotheca fuliginea* ([Schlecht.] Fr.). Poll. S. Lat. Sv. Bot. Tidskr. 60:365-392.
13. Kable, P. K., and Ballantyne, B. J. 1963. Observations on the cucurbit powdery mildew in the Ithaca district. Plant Dis. Rep. 47:482.
14. Khan, A., Akram, M., and Khan, A. M. 1978. Perithecia of *Sphaerotheca fuliginea* (Schlecht) Poll. from certain cultivated cucurbits. Acta Bot. Indica 6:103-105.
15. Khan, M. W., and Khan, A. M. 1970. Studies on the cucurbit powdery mildew. I. Perithecial production in cucurbit powdery mildew in northern India. Indian Phytopathol. 23:497-502.
16. Kontaxis, D. G. 1979. Cleistothecia of cucurbit powdery mildew in California--A new record. Plant Dis. Rep. 63:278.
17. Latin, R. X. 1993. Occurrence of cleistothecia of *Sphaerotheca fuliginea* on pumpkin in Indiana. Plant Dis. 77:647.
18. Letham, D. B., and Priest, M. J. 1989. Occurrence of cleistothecia of *Sphaerotheca fuliginea* on cucurbits in South Australia and New South Wales. Australas. Plant Pathol. 18:35-37 (Cf. Braun, U. 1987. A monograph of the Erysiphales (powdery mildews). Nova Hedwigia, Beiheft 89. J. Cramer: Berlin.).
19. McGrath, M. T. 1991. Cleistothecia of the powdery mildew fungus *Sphaerotheca fuliginea* observed on pumpkin in New York. Plant Dis. 75:1075.
20. McGrath, M. T. 1994. Heterothallism in *Sphaerotheca fuliginea*. Mycologia 86:517-523.

21. McGrath, M. T., Staniszewska, H., Shishkoff, N., and Casella, G. 1996. Fungicide sensitivity of *Sphaerotheca fuliginea* populations in the United States. Plant Dis. 80:697-703.
22. Nagy, G. S. 1976. Studies on powdery mildews of cucurbits. II. Life cycle and epidemiology of *Erysiphe cichoracearum* and *Sphaerotheca fuliginea.* Acta Phyto. Acad. Sci. Hung. 11:205-210.
23. Osnitskaya, E. A. 1959. The biological reasons for preventive measures against powdery mildew of cucumber in hothouses and forcing beds. Tr. Inst. Ovoshch. Khoz. 2:121-137.
24. Palti, J. 1961. Prediction of powdery mildew outbreaks on cucurbits on the basis of seasonal factors and host age. Bull. Res. Counc. Israel 10D:236-249.
25. Randall, T. E., and Menzies, J. D. 1956. The perithecial state of the cucurbit powdery mildew. Plant Dis. Rep. 40:255.
26. Rodigin, M. N. 1936. Note on the powdery mildews of cucurbits (*Sphaerotheca fuliginea* (Schl.) Poll. and *Erysiphe cichoracearum* Fr.). Sovet. Bot. 5:120-123.
27. Shishkoff, N., and McGrath, M. T. 1995. Mating compatibility of French isolates with American isolates of the cucurbit powdery mildew fungus. Page 37 in: Long Island Hortic. Res. Lab. 1995 Annu. Rep.
28. Smith, C. G. 1970. Production of powdery mildew cleistocarps in a controlled environment. Trans. Br. Mycol. Soc. 55:355-365.
29. Snedecor, G. W., and Cochran, W. G. 1980. Statistical Methods. 7 ed. Iowa State University, Ames.
30. Staniszewska, H., and McGrath, M. T. 1993. Influence of mating type distribution and temperature on the occurrence of cleistothecia in *Sphaerotheca fuliginea.* (Abstr.) Phytopathology 83:697.
31. Tarr, S. A. J. 1955. The Fungi and Plant Diseases of the Sudan. Commonw. Mycol. Inst., Kew, Surrey, England.
32. Uozumi, T., and Yoshii, H. 1952. Some observations on the mildew fungus affecting the cucurbitaceous plants. Ann. Phytopathol. Soc. Jpn. 16:123-140.