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Fungi Associated with Females and Cysts of *Heterodera glycines* in a Florida Soybean Field[1]

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Abstract: Fungal colonization was determined for females and cysts of *Heterodera glycines* on soybean roots or in rhizosphere soil from a Florida soybean field. A total of 1,620 females and cysts were examined in 1991, and 1,303 were examined in 1992. More than 35 species of fungi were isolated from females and cysts. The frequency of fungi colonizing white and yellow females was low, but a high frequency of fungi was encountered in brown cysts, which increased with time of exposure of the cysts to the soil. No single fungal species predominated in the nematode females or cysts in this field. Rarely was a female or cyst colonized by more than one fungus. The common fungi isolated from the females and cysts were *Neocosmospora vasinfecta, Fusarium solani, Fusarium oxysporum, Dictyochaeta coffeae, Dictyochaeta heteroderae, Pyrenochaeta terrestris, Exophiala pisciphila, Gliocladium catenulatum; Stagonospora heteroderae,* and a black yeast-like fungus. The communities of common fungal species isolated from cysts in several regions in the southeastern United States appear to be similar.

Key words: biological control, cyst, egg, female, fungi, *Glycine max, Heterodera glycines,* mycoflora, nematode, similarity index.

The soybean cyst nematode, *Heterodera glycines* Ichinohe, is one of the most important pathogens of soybean (*Glycine max* (L.) Merr.). It occurs on soybean in Japan, China, Korea, Indonesia, Canada, the United States, Colombia, the countries within the former Soviet Union (26), and Brazil (15). It was reported also on cowpea in Egypt (5) and is believed to occur on soybean on islands in the Nile River (25). The costs of applying nematicides to control this pest are usually high, and many nematicides are no longer registered for use on soybean. Therefore, more attention is being given to alternative management tactics such as crop rotation, cultural methods, plant resistance, and biological control.

Fungal antagonists of plant-pathogenic nematodes have been studied for more than 100 years (3,29), and interest in those affecting sedentary endoparasitic nematodes has increased rapidly in recent years (28). The swollen females and cysts of cyst nematodes provide unique niches for some soil fungi. In a greenhouse study it was determined that a number of fungi were capable of invading young females and, as the females become more exposed in the soil, they were increasingly vulnerable to fungi (8,9). Some reports revealed a degree of natural control of cyst nematodes by fungi associated with females and eggs (12).

More than 150 fungal species have been isolated from the females or cysts of *H. glycines* (2,3,7–10,13,14,16,17,21,22). Extensive studies have shown a taxonomically diverse mycoflora in different locations in the United States (3,8,9,17,21), but the most common species are similar among locations. The common genera include *Exophiala, Fusarium, Gliocladium, Neocosmospora, Paecilomyces, Paraphoma, Phoma, Stagonospora,* and *Verticillium* (3,8,9,17,21). This group of "opportunistic fungi" has the greatest potential as biological control agents of cyst nematodes because they are well-adapted to compete in agricultural soil (19). However, no commercially produced biological control agent has yet been accepted widely for management of the soybean cyst nematode (16).

Ecological information about fungi associated with nematode eggs, females, and cysts, including the knowledge of fungal species composition and frequency, is im-

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portant for selecting and developing biological control agents for control of cyst nematodes. This basic information is also important for developing the potential of the soil mycoflora to suppress nematodes.

The objective of this study was to examine the species and frequency of fungi colonizing white and yellow females, and brown cysts of *H. glycines* on soybean in soil in a Florida soybean field.

Materials and Methods

A field located at the University of Florida Green Acres Agronomy Research Farm in Alachua County, Florida, was used for this study. The soil was an Arredondo fine sand (91% sand, 4.5% silt, 4.5% clay; 1.8% organic matter; pH 5.7) (4). Soybean cyst nematode obtained from another agronomy field located on the University of Florida campus in Gainesville, Florida, was introduced to the site in 1985. The soybean cyst nematode population developed poorly, suggesting that the soil could be suppressive to this nematode (4).

This investigation was conducted during 1991 and 1992. In 1991, six plots, each with eight rows and a row spacing of 76 cm and row length of 9.1 m, were used. Cobb and Braxton, two soybean cultivars susceptible to soybean cyst nematode, were planted on 28 May. On 19 June, about 120 soybean plants were taken from each plot by carefully digging up their root systems. Soybean roots were washed with tap water and put in sterilized water. The young white females that contained zero or few eggs and older yellow females were removed with the aid of a stereomicroscope and transferred to sterilized water. On 3 July, about 120 soybean plants with rhizosphere soil were taken from each plot. The roots with attached soil were washed by tap water onto a sieve with 150-μm pore openings. White and yellow females were extracted from the soybean roots as described above. Brown cysts were extracted from the soil and debris remaining on the sieve by a modified sugar-flotation-centrifugation technique (11), with 1.5 kg sucrose/liter water. On 1 October, the end of the soybean season, samples of 4 kg of soil were taken with a bucket auger (10-cm-d) from the soybean rhizosphere 0–20 cm deep from each plot. Brown cysts were extracted from a subsample of about 2 kg of soil from each plot using the technique as described.

In 1992, 10 rows in each of six plots were planted with the soybean cultivar Cobb on 5 June in approximately the same sites and with same row spacing and length as in 1991. On 20 July and 9 September, white and yellow females and brown cysts were extracted using the same procedures as described for the samples of 3 July 1991. On 3 October, brown cysts were extracted by the same procedures used for the samples of 1 October 1991.

The extracted females and cysts were washed with sterilized water, treated with 0.5% NaOCl for 3 minutes, rinsed three times with sterile deionized water, and finally treated with a solution of 100 ppm streptomycin and 50 ppm chlortetracycline. The treated cysts were transferred to water agar and incubated at room temperature (23–24 C). Subcultures were made from fungal mycelium growing from the nematodes after 3–5 days, or 10–14 days for slow-growing fungi. Most subcultures were maintained at room temperature on Difco corn meal agar. However, potato dextrose agar, malt extract agar, and oat meal agar (all products of Difco Laboratories, Detroit, MI) were also used to culture certain species of fungi.

Features of fungal colonies, including growth rate and measurements of reproductive organs, were recorded for identification. Slides for measurements and morphological observations were generally prepared from the fungal cultures mounted in water or lactophenol. Slide cultures were made and semi-permanent slides were prepared (24) to observe the conidiogenous cell, conidiophore, and type of conidiogenesis of some species. Some fungal colonies were not identified because of the lack of sporulation. All observations and measurements were made with the light microscope. The percentage

frequency of white females, yellow females, or brown cysts colonized by each fungal species was recorded on each sampling date.

These frequency data on the fungal communities associated with cysts or females were used to calculate similarity indices. Similarity indices are used in ecology (23) to compare the composition of two communities on a numerical scale from 0 (dissimilar = no species in common) to 1 (identical = all species in common). Presence–absence data have been used in similarity indices comparing fungal species composition in cysts of *H. glycines* (3). The Bray and Curtis similarity index (1) uses densities of each species instead of presence–absence data to calculate the similarity between two communities. To compare fungal communities of females or cysts from two sample occasions, we used the Bray and Curtis similarity index (1) with percentage frequency data instead of density data:

$$S = \frac{2W}{A + B}$$

where S is the similarity index; A is the sum of percentage of frequency of each fungus encountered in females or cysts in one sample occasion (sampling date, stage of females or cysts, or location); B is the sum of percentage of frequencies of each fungus encountered in females or cysts in another sample occasion; and W is the sum of lowest percentage of frequency of common fungal species encountered in females or cysts in the two sample occasions. These similarity indices were used to compare composition of the fungal community between different stages of female and cyst development, between sampling dates, and between geographical locations. The latter comparison was calculated from data on brown cysts collected in the present study and that reported by Morgan-Jones et al. (21).

Results

Overall, 2,923 (1,620 in 1991 and 1,303 in 1992) females and cysts were examined, and 44% of them contained fungi. More than 35 fungal species were found, with the species composition similar in 1991 and 1992. But the fungal species and frequencies found in different stages of females and cysts were quite different (Table 1). Although some fungi were capable of colonizing young females, fungi were recovered from white and yellow females at low frequencies. Brown cysts were often colonized, and the frequency of colonization increased with the time of exposure to the soil (Fig. 1).

On each sampling date, both the number of fungal species recovered and the percentage of females or cysts colonized increased with nematode age. On 19 June 1991, when the first generation of females became mature, only four species were isolated from the white and yellow females; and only 1% of 249 white females and 3% of 118 yellow females were colonized (Table 1). On 3 July 1991, six species were isolated from 101 white females (13% colonized); eight species were isolated from 336 yellow females (5% colonized); and more than 20 species were isolated from 300 brown cysts (42% colonized). More than 30 species were isolated from 516 brown cysts (86% colonized) examined in the sample of 1 October 1991.

In the samples of 20 July 1992, six fungal species were isolated from 62 white females (15% colonized), only four species were isolated from 110 yellow cysts (5% colonized), and more than 20 species were isolated from 296 brown cysts (56% colonized). In the samples of 9 September 1992, more than 11 species were isolated from 114 white females (23% colonized), only three species were isolated from 122 yellow females (3% colonized), and more than 20 species were isolated from 387 brown cysts (69% colonized). On 3 October 1992, more than 20 species were isolated from 196 of the 212 examined brown cysts (93% colonized).

The fungi isolated from white females were mainly *Rhizoctonia solani* Kühn, *Fusarium solani* (Mart.) Sacc., and *Fusarium oxysporum* Schlecht. (Table 1). The frequencies of *R. solani* in white and yellow females

TABLE 1. Percentage frequency of fungal species encountered in white and yellow females and brown cysts of *Heterodera glycines* collected from a Florida soybean field during 1991 and 1992.

Fungal species	1991						1992						
	19 June		3 July			1 Oct.	20 July			9 Sept.			3 Oct.
	W†	Y	W	Y	B	B	W	Y	B	W	Y	B	B
Chaetomium cochliodes Pall.	0	0	0	0	0	0.2	0	0	0	0	0	0	0
Curvularia lunata (Wakker) Boedijn	0	0	0	0	0.3	0	0	0	0	0	0	0	0
Dictyochaeta coffeae (Maggi and Persiani) Cabello and Arambarri	0	0	0	0	0	3.4	0	0	0.7	0	0	1.8	7.5
Dictyochaeta heteroderae (Morgan-Jones) Carris and Glawe	0	0	0	0	0	5.6	0	0	0	0	0	2.1	2.4
Drechslera fugax (Wall.) Shoemaker	0	0	0	0	0.3	0	0	0	0	0	0	0	0
Exophiala pisciphila McGinnis and Ajello	0	0	0	0	0.3	4.3	0	0	0.7	0.9	0	4.1	3.3
Fusarium equiseti (Corda) Sacc.	0	0	3.0	0	1.3	0.2	0	0	0	0	0	0.8	0.5
Fusarium oxysporum Schlecht.	0	0	2.0	2.4	8.3	6.6	0	0	1.0	1.8	0	4.4	10.8
Fusarium semitectum Berk. and Rav.	0	0	0	0.3	0	0	0	0	0	0	0	0	0
Fusarium solani (Mart.) Sacc.	0.4	0	0	0.3	5.7	11.2	0	0.9	8.4	3.5	0	11.6	27.8
Fusarium spp.	0	0	0	0	1.7	0.2	0	0	1.0	1.8	0	2.3	0.9
Gliocladium catenulatum Gilm. and Abbott	0	0	0	0	0	4.1	0	0	0	0	0	1.0	5.2
Gonytrichum macrocladum (Sacc.) Hughes	0	0	0	0	0	0	1.6	0	0	0	0	0	0
Helicomyces sp.	0.4	0	0	0	0	0	0	0	0	0	0	0	0
Humicola sp.	0	0	1.0	0	0	0	0	0	0	0	0	0	0
Myrothecium sp.	0	0	0	0	0	0	0	0	0	0	0	0.3	0
Neocosmospora vasinfecta E. F. Smith	0	0	0	0	5.3	23.3	0	0.9	10.1	4.4	0.8	18.6	22.2
Paecilomyces lilacinus (Thom) Samson	0	0	0	0	0	0.2	0	0	0	0	0	0.3	0
Papulaspora sp. 1	0	0	0	0	0	0.4	0	0	0	0	0	0	0
Papulaspora sp. 2	0	0	0	0	0	0.2	0	0	0	0	0	0	0
Paraphoma radicina (McAlp.) Morgan-Jones and White	0	0	0	0	0	0.2	0	0	0	0	0	0.5	0
Paraphoma sp.	0	0	0	0	0	0.2	0	0	0	0	0	0	0
Periconia macrospinosa Lefebvre and Johnson	0	0	0	0	0	0.2	0	0	0	0	0	0	0
Phoma chrysanthemicola Hollos	0	0	0	0	0.3	0	0	0	0	0	0	0	0
Phoma sp.	0	0	0	0	0.3	0	0	0	0	5.3	0	0.3	0
Pseudorobillarda sojae Uecker and Kulik	0	0	0	0	0	0	0	0	0	0.9	0	0	0
Pyrenochaeta terrestris (Hansen) Gorenz, Walker and Larson	0	0	0	0.3	0.3	7.6	3.2	0	6.1	0	0	4.1	8.1
Ramichloridium subulatum de Hoog	0	0	0	0	0	0.2	0	0	0	0	0	0	0
Rhizoctonia solani Kühn	0.4	0.9	1.0	0.3	1.3	0.6	0	0	2.4	0	0.8	0.8	0.9

TABLE 1. *Continued*

Fungal species	1991						1992					
	19 June		3 July		1 Oct.		20 July			9 Sept.		3 Oct.
	W†	Y	W	Y	B	B	W	Y	B	W	Y	B	B
Scytalidium lingicola Pesante	0	0	0	0	0.3	0	0	0	0	0	0	0	0
Stagonospora heteroderae Carris, Glawe and Morgan-Jones	0	0	0	0	0	5.8	0	0	0.3	0	0	1.0	4.2
Trichoderma lignorum (Tode) Harz	0	0	0	0	0	0	1.6	0	0.3	0	0	0	0
Sterile fungus 1 (a black yeast-like fungus)	0	2.6	0	0	9.0	10.3	6.5	0.9	13.5	2.6	0.8	17.1	5.7
Sterile fungus 2 (an extremely slow-growing fungus)	0	0	0	0	0	0	1.6	0	6.6	0	0	1.3	0
Others‡	0	0	4.0	0.9	8.0	4.1	1.6	0.9	5.1	2.7	0	3.4	6.3
Total females or cysts examined	249	118	101	336	300	516	62	110	296	114	122	387	212
Number of females or cysts without fungi	246	114	90	321	173	73	53	106	130	88	119	116	14
Percentage of females or cysts without fungi	98.8	96.6	89.1	95.5	57.7	14.2	85.5	96.4	43.9	77.2	97.5	30.7	6.6
Number of females or cysts each colonized by more than one fungus	0	0	0	0	1	17	1	0	1	1	0	22	25

† W = white females, Y = yellow females, B = brown cysts.
‡ Fungi that would not sporulate and could not be identified.

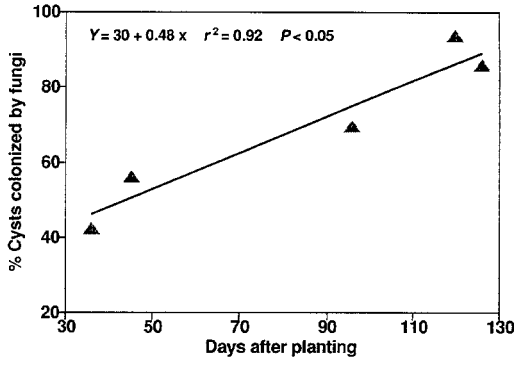

FIG. 1. Relationship between sampling date (x) and the percentage of brown cysts of *Heterodera glycines* with fungi (Y) in a Florida soybean field in 1991 and 1992.

and brown cysts in samples in 1991 were similar and did not increase with time of exposure to soil. *Neocosmospora vasinfecta* E. F. Smith, *Phoma* sp., *Pyrenochaeta terrestris* (Hansen) Gorenz, Walker and Larson, and a black yeast-like fungus were also encountered at a relatively high frequency in white females in the samples collected in 1992, but not in 1991. The fungi most frequently encountered in yellow females were *Fusarium* spp., *R. solani, N. vasinfecta,* and the black yeast-like fungus. The common species encountered in brown cysts were *N. vasinfecta, F. oxysporum, F. solani, Dictyochaeta heteroderae* (Morgan-Jones) Carris and Glawe, *D. coffeae* (Maggi and Persiani) Cabello and Arambarri, *Exophiala pisciphila* McGinnis and Ajello, *Gliocladium catenulatum* Gilm. and Abbott, *P. terrestris,* and *Stagonospora heteroderae* Carris, Glawe and Morgan-Jones. *Dictyochaeta heteroderae, D. coffeae, G. catenulatum,* and *S. heteroderae* were isolated only from brown cysts. Numerous other fungi were isolated from brown cysts at low frequency (Table 1).

The similarity indices between sampling dates for the fungi in white females, yellow females, or brown cysts are listed (Table 2). The average of similarity indices of the fungi in brown cysts at different sampling occasions was 0.54, with a standard deviation (SD) of 0.12. In contrast, the averages of the similarity indices for fungi in white or yellow females versus white females, yellow females, or brown cysts were low

TABLE 2. Similarity indices between sampling dates for fungi in white and yellow females and brown cysts of *Heterodera glycines* collected from a Florida soybean field during 1991 and 1992.

	White females			Yellow females				Brown cysts				
	1991	1992		1991		1992		1991		1992		
	3 July	20 July	9 Sept.	19 June	3 July	20 July	9 Sept.	3 July	1 Oct.	20 July	9 Sept.	3 Oct.
White females	(0.03 ± 0.04; n = 6)†			(0.12 ± 0.09; n = 16)				(0.17 ± 0.12; n = 20)				
19 June 1991	0.07	0	0.03	0	0.17	0.21	0.17	0.04	0.02	0.03	0.02	0.10
3 July 1991		0	0.11	0.12	0.30	0	0.12	0.16	0.06	0.06	0.08	0.06
20 July 1992			0.03	0	0	0.09	0.09	0.24	0.19	0.33	0.25	0.15
9 Sept. 1992				0.19	0.15	0.20	0.12	0.44	0.24	0.33	0.31	0.22
Yellow females				(0.26 ± 0.20; n = 6)				(0.08 ± 0.03; n = 20)				
19 June 1991					0.08	0.25	0.54	0.15	0.07	0.11	0.09	0.06
3 July 1991						0.08	0.09	0.14	0.07	0.06	0.08	0.06
20 July 1992							0.53	0.12	0.06	0.09	0.07	0.05
9 Sept. 1992								0.11	0.05	0.05	0.06	0.04
Brown cysts									(0.54 ± 0.12; n = 10)			
3 July 1991									0.43	0.40	0.48	0.42
1 Oct. 1991										0.53	0.73	0.74
20 July 1992											0.63	0.43
9 Sept. 1992												0.61

† The values in parentheses are average similarity indices ± standard deviations for the group of data directly beneath.

(Table 2). The average of the similarity indices for fungi in brown cysts in our study compared with the fungi of brown cysts from other locations surveyed by Morgan-Jones et al. (21) was 0.4, whereas the average in brown cysts among the soils collected by Morgan-Jones et al. was 0.66 (Table 3).

DISCUSSION

The fungi isolated from the females and cysts by the methods used in our study and others (3,8,9,16,17,21,22) are typically opportunists. Obligate parasites of females or eggs of the nematodes generally are not isolated by these methods. The species of *Cylindrocarpon, Exophiala, Fusarium, Gliocladium, Paecilomyces, Phoma,* and *Verticillium* were among the fungi most frequently encountered from nematode cysts in other studies (19,20). These species appear to colonize eggs of a range of plant-parasitic nematodes (20). In addition, species of *Stagonospora* and *Paraphoma* also have been isolated frequently from cysts of *H. glycines* (3). The most common species isolated in our study, except for *N. vasinfecta* and the black yeast-like fungus, also were in these groups of fungi. *Pyrenochaeta terrestris* was probably identified as *Phoma terrestris* Mont. in some studies (9). *Dictyochaeta heteroderae* (as *Codinaea heteroderae* Morgan-

TABLE 3. Similarity indices between locations and sampling dates for fungi in brown cysts of *Heterodera glycines* collected in different locations in the southeastern United States at different times.

	Brown cysts from dried soil in 1981†			Brown cysts from a Florida field soil				
				1991		1992		
	Mississippi	Alabama	Missouri	3 July	1 Oct.	20 July	9 Sept.	3 Oct.
1981	(0.66 ± 0.06; n = 6)‡			(0.41 ± 0.08; n = 8)		(0.40 ± 0.10; n = 12)		
Florida	0.64	0.56	0.63	0.31	0.39	0.21	0.31	0.54
Mississippi		0.71	0.68	0.31	0.39	0.27	0.38	0.47
Alabama			0.72	0.35	0.49	0.32	0.44	0.44
Missouri				0.49	0.51	0.37	0.47	0.52
1991						(0.55 ± 0.14; n = 6)§		
1992						(0.56 ± 0.09; n = 3)§		

† Data cited from Morgan-Jones et al. (1981).
‡ The values in parentheses are average similarity indices ± deviations for the group of data directly beneath.
§ Calculated from Table 2.

Jones) was reported with a relative high frequency from a Florida soil (21). *Neocosmospora vasinfecta* was the most frequently occurring species from brown cysts in our study. This fungus is probably adapted to the high temperature of a tropical or subtropical climate (6), but its impact on eggs in cysts of the soybean cyst nematode is unclear.

The frequencies of fungi in young females were much lower in our field study than in those reported in previous greenhouse studies (8,9). It is possible that more favorable conditions existed in the greenhouse. The frequency of fungi in yellow females was lower than that in white females (Table 1). This suggests that resistance to fungal infections may increase as females change from white to yellow.

The similarity indices between fungi in brown cysts in our study and fungi of brown cysts reported by Morgan-Jones et al. (21) were much lower (0.4) than indices for fungi in brown cysts among soil samples from various locations in the study of Morgan-Jones et al. (0.66), even though one soil sample in that study was also from Florida. This suggests that the fungi are influenced greatly by environmental conditions or by methodology. Morgan-Jones et al. (21) extracted cysts from air-dried soils stored for a period of time, rather than processing these soils immediately after collection, as we did in this study.

Under field conditions, no significant difference was observed between the group of similarity indices that were calculated for fungi in brown cysts from two sampling dates within a year (1991 vs. 1991, 1992 vs. 1992) and the group of similarity indices that were calculated from two dates in different years (1991 vs. 1992) (Table 2). This suggested that the environmental conditions between the two growing seasons were similar. The similarity index for fungi in brown cysts between two sampling dates however was negatively correlated with the length of time between the dates without considering the year (Fig. 2). The fungi may have been affected by either the seasonal changes in field conditions, including the climate and cultural

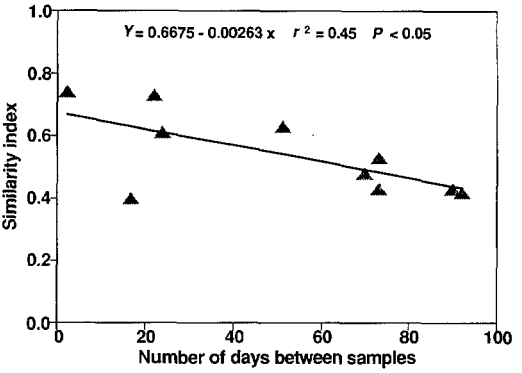

FIG. 2. Relationship between the length of time between two sampling dates (x) and the similarity index (Y) of fungi in brown cysts of *Heterodera glycines* between those two dates in a Florida soybean field in 1991 and 1992. The days between sampling dates were calculated without considering the years; for example, the time between 1 October of 1991 and 3 October of 1992 is 2 days rather than a year plus 2 days; the corresponding similarity index associated with these two sampling dates is 0.74 (see Table 2).

conditions, or the condition of cysts in soil, or both. Between the dates 1 October 1991 and 3 October 1992, for example, the length of time was considered to be 2 days rather than 2 days plus 1 year; the environmental conditions, the condition of cysts, and the exposure periods of the cysts to the soil were similar; therefore the similarity index was as high as 0.74 (Table 2). In contrast, between the dates 3 July and 1 October in the same year of 1991, the length of time was 90 days; the environmental conditions, the condition of cysts, and the exposure periods of cysts to the soil were much more different; and the similarity index was as low as 0.43. The similarity indices for fungi in white or yellow females versus white females, yellow females, or brown cysts was low because no one single fungal species predominated and none infected the females consistently.

Although several species occurred more frequently than others, no single species predominated in white and yellow females and in brown cysts. Our study and previous work (3,9,18) indicate that cysts colonized by one fungus are not readily colonized by other fungi. Only 2 of 525 white females, none of the yellow females, and 66 of 1,711 brown cysts were colonized by more than one fungus (Table 1). Because

of this and because these opportunistic fungi are affected greatly by the environmental conditions, it may be important to create an environment favoring the development of nematode-pathogenic fungi in order to stimulate rapid colonization of cysts of soybean cyst nematode. For example, addition of crustacean chitin to soil improved the control of soybean cyst nematode (27). The impact of soil amendments on manipulating the soil mycoflora to control soybean cyst nematode needs further investigation.

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