Transfer of Biological Soil Suppressiveness Against *Heterodera schachtii*

A. Westphal and J. O. Becker

Department of Nematology, University of California, Riverside.
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ABSTRACT

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Heterodera schachtii-suppressive soil at a rate of either 1 or 10% (dry wt/wt) transferred suppressiveness against the beet cyst nematode to fumigated field plots when mixed into the upper 10-cm soil layer. Soil suppressiveness was established after 1 month of moist fallow and 77 days of Swiss chard cropping in the 10% transfer treatment and after 230 days in the 1% transfer treatment. The number of infective second-stage juveniles (J2) of *H. schachtii*, monitored initially at 150 degree-day intervals and later at 300 degree-day intervals, indicated the status of suppres-

siveness in the different treatments during the cropping period. In a greenhouse experiment, amending fumigated field soil with 0.1, 1.0, or 10% suppressive soil, suppressed multiplication of *H. schachtii* when soils were infested with an additional 5,000 J2. In a second greenhouse experiment, a fumigated sandy loam amended with 10 or 25% suppressive soil and a fumigated loam amended with 25% suppressive soil had significantly fewer eggs per cyst than the nonamended fumigated treatments when 1,000 J2 were added.

Additional keywords: *Beta vulgaris*, nematode infectivity, population dynamic.

Transferability is an important characteristic of biological soil suppressiveness against soilborne plant pathogens (3). Suppressive soil (1%), together with 1% alfalfa meal, transferred suppressiveness against potato scab, caused by *Streptomyces scabies*, into naturally infested conducive soil (18). Suppressive soil (0.5%) provided substantial restoration of soil suppressiveness in fumigated field plots against take-all disease of wheat (21). In successive dilutions, an equivalent of 1 ppm (vol/vol) of suppressive soil transferred suppressiveness against Fusarium wilt to a soil mixture, if intermediate dilution mixes were cultivated during the 3-month incubation between dilutions (1). Amendments of biocidally treated, disease-conducive soils or substrates with 1 to 10% disease-suppressive soils have been reported to transfer disease suppressiveness (2,7,9,10,26). Although a few nematode-suppressive soils have been studied intensively (15), transferability of soil suppressiveness against plant-parasitic nematodes has not received much attention. In a greenhouse study, the 20- to 53- μ m soil fraction of 5 kg of *Heterodera avenae*-suppressive soil from England was mixed into 2 kg of naturally cereal cyst nematode-infested South Australian soil. This resulted in infection of *H. avenae* females by fungal female parasites and, consequently, in *H. avenae* suppression (22). Ring nematode-suppressive soil (5%) added to pasteurized soil resulted in nematode suppression compared with the pasteurized and nonamended control (16).

The current study focused on a beet cyst nematode-suppressive soil at the agricultural research station, University of California, Riverside. In 1975, field 9E had been amended with *H. schachtii*-infested field soil from a sugar beet-growing area near Moreno Valley, CA, and had been cropped continuously with host plants of the nematode. After initial establishment of the nematodes and significant crop-yield reductions due to their parasitic activity, the beet cyst population declined and has remained at a low level for at least a decade (I. J. Thomason, *personal communication*; A. Westphal, *unpublished data*). Previous research demonstrated the biological nature of this soil suppressiveness (25). The objective

of this study was to determine whether the soil suppressiveness can be transferred into *H. schachtii*-conducive fumigated field plots. During the entire cropping period, the infectivity of *H. schachtii* second-stage juveniles (J2) was monitored. In addition, in greenhouse trials, we investigated whether suppressiveness of 9E soil was transferable to other fumigated soils. Preliminary results of this project have been published (23,24).

MATERIALS AND METHODS

Transfer of suppressiveness to fumigated field plots. The trial was conducted in *H. schachtii*-suppressive field 9E at the agricultural research station, University of California, Riverside. After a green-manure crop of canola (*Brassica napus* L.), the Hanford fine sandy loam soil (60.9% sand, 29.6% silt, and 9.5% clay, pH 8) had an initial *H. schachtii* population density of 13.5 eggs per g in the top 10 cm of soil. The plot area was chiseled to a depth of 45 cm in a criss-cross pattern diagonal to the orientation of the seedbeds at the end of March 1996. The area was disced and N-P-K fertilizer (15-15-15; 336 kg/ha) was incorporated with a cultimulcher. Seedbeds were prepared on 75-cm centers, allowing two seedbeds for each experimental plot. One of these rows was harvested after 77 days ("harvest row"), and the second one was used for monitoring the infectivity of *H. schachtii* and was harvested after 230 days ("sample row"). One border row separated the plots from one another. The trial was arranged in a randomized complete block design (block length 5.1 m) with six treatments and five replicates.

Four of six plots per block were hot-gas fumigated with methyl bromide (336 kg/ha) (11) with a commercial applicator (TriCal Inc., Hollister, CA) to reduce the soil suppressiveness to nondetectable levels (25). Suppressive 9E soil was randomly collected, passed through a 6-mm screen, and thoroughly mixed. Aliquots of this suppressive soil were sprinkled onto the seedbeds of two of the fumigated plots of each block at a rate of 1 or 10% (dry wt/wt of the upper 10-cm soil layer) and were rototilled into the upper 10 cm. The other four plots in each block were rototilled without soil amendment. All plots were kept moist at a water potential of -20 to -30 kPa with a low-volume drip-irrigation system.

During May, 1 month after amendment of plots, one nonfumigated, one fumigated, and both of the transfer treatments were

Corresponding author: J. O. Becker; Email address: ole.becker@ucr.edu

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infested with greenhouse-reared *H. schachtii*. In each plot, both seedbeds were infested at 10 planting sites in 30-cm intervals along the seedbed center. For each planting site, a 10-cm-deep soil core was taken with a bucket auger (7.6 cm in diameter). The soil was placed in a plastic bag (2-liter capacity) that contained ≈446 cysts of *H. schachtii* with ≈50,000 eggs in 250 g of a sandy potting soil. The nematodes had been raised in this potting soil on sugar beets in the greenhouse. After thoroughly mixing the soil core with the greenhouse inoculum, the infested soil was placed in the original hole. A noninfested fumigated (conductive) control and a noninfested, untreated (suppressive) control received 250 g of the same sandy potting soil that had been the substrate of *H. schachtii*-free sugar beets for the same time as the inoculum potting soil.

One month after infestation, one 5-week-old seedling of Swiss chard (*Beta vulgaris* subsp. *cicla* (L.) W. Koch 'Large White Ribbed'; Lockhart Seeds Inc., Stockton, CA) was planted in the middle of each of the planting sites in all plots. During the cropping period, insect control was conducted with spray applications of imidachloprid (52.5 g a.i./ha) as needed. After 77 days (1,350 degree days [DD], 8°C basal temperature) (8), the plant tops of the harvest row were cut off at ground level, and oven dry weights were determined. The root systems with the adhering soil core were recovered with a bucket auger (7.6 cm in diameter) to a depth of 10 cm. Cysts and soil were thoroughly shaken and washed with water from the roots over a 20-mesh screen (0.83 mm) nested on a 100-mesh screen (0.15 mm). Roots were oven dried and weighed. The recovered wash-off from the 100-mesh screen was mixed back into the rest of its original soil core. A 350-g subsample from the mixed soil core was used for cyst extraction with a modified Fenwick flotation can (6) with an extraction efficiency of ≈80% from moist soil. The cysts were counted and broken in a tissue homogenizer for egg enumeration. The plants of the sample row were trimmed to 5-cm stubble and cropped for a total of 230 days until February 1997. Three applications of 26 kg/ha and three applications of 52 kg/ha of a N-P-K fertilizer (15-30-15, Miracle Gro) were dissolved in water and supplied by overhead sprinkling as needed. Plants from the sample row were harvested as described above. For both harvests, the numbers of cysts per root dry weight and the number of eggs per cyst were determined.

Monitoring the infectivity of *H. schachtii* in field plots. During the entire length of the field trial, the nematode infectivity was monitored with a bioassay, initially in 150-DD intervals and then in 300-DD intervals, based on the soil temperature at a depth of 10 cm. For the first nine sampling dates, a cork borer (17 mm in diameter) was inserted diagonally into the root zone ≈2.5 cm from the plant stem and 10 cm deep in each of the 10 planting sites per plot. The soil cores of each plot were pooled, mixed, and used for a growth-chamber bioassay. For the final five sampling dates, one plant per sampling date was chosen at random from the sample

row of each plot and carefully removed. The roots were separated from the cysts and soil as described before. At each sampling, the recovered soil samples were divided into three small subsamples (60- to 100-g total weight, according to availability of total soil sample) and were placed in 250-ml translucent polystyrene containers. All samples per sampling date were adjusted to a uniform moisture content; typically between 11 and 16%. After 1 day for moisture equilibration, each of the containers was seeded with one surface-sterilized (5 min in 20% commercial bleach solution, 5.25% NaOCL) radish seed (*Raphanus sativus* L. 'Cherry Belle'; Ferry-Morse, Fulton, KY). The containers were closed with a polyethylene lid to reduce evaporation and incubated for 3 days in a day and night cycle of 16 and 8 h at 28 and 23°C, respectively, in an environmental growth chamber. The radish seedlings were recovered from the soil, and J2s in the roots were counted after staining (5). The detected numbers of J2 were reported per cm of root length.

Transfer of soil suppressiveness to fumigated, initially suppressive soil in greenhouse experiments. Soil was collected randomly from the upper 10-cm soil layer of *H. schachtii*-suppressive field 9E. After passing through a 6-mm screen and mixing with silica sand (10:1, wt/wt), one part of the soil was fumigated with methyl iodide (690 kg/ha) (4), and the other part was left untreated. After aeration, fumigated soil was amended with 0.1, 1.0, or 10% (dry wt/wt) of nonfumigated, suppressive soil. Nonfumigated, suppressive soil and the fumigated equivalent served as the suppressive and conducive control, respectively. The soils were placed into 15-cm pots (Western Pulp Products Company, Corvallis, OR) and arranged in a randomized complete block design with five replicates in the greenhouse at 24 ± 3°C under ambient light. The trial was irrigated with tap water through a low-volume drip irrigation system (Netafim Irrigation Inc., Fresno, CA). After 1 month, the pots were each planted with one 5-week-old seedling of Swiss chard. Two weeks later, each pot was infested with 5,000 J2 of *H. schachtii*. After 11 weeks, plant tops were cut off at ground level and weighed after oven drying. Adhering soil and cysts were shaken and washed off the roots with water and added back into the remaining pot content. Cysts were extracted from a 350-g soil subsample and counted, and the number of eggs was determined. The remaining soil was stored for ≈1 month in plastic bags at 24 ± 3°C. The soils were repotted in 15-cm pots and planted with cabbage (*Brassica oleracea* L. 'Late Flat Dutch'; Lockhart Seeds). After 11 weeks, plant top dry weights and nematode populations were determined as described before. Both crops were fertilized with 50 ml of a nutrient solution (10 g of Miracle Gro N-P-K [15-30-15] fertilizer per 3.79 liters of water,) weekly.

Transfer of soil suppressiveness to *H. schachtii*-free soil or different textured soil in greenhouse experiments. Three soils were chosen for a transfer experiment in a randomized complete block design with six replicates. The first test soil (9C) was a

TABLE 1. Harvest data and nematode populations after 77 and 230 days of Swiss chard growth in fumigated and *Heterodera schachtii*-infested plots amended with various amounts of nematode-suppressive 9E soil

Treatment ^x			Early harvest (harvest row) ^y				Late harvest (sample row) ^y			
Fumigation	Soil	Infestation	TDW (g)	RDW (g)	Cysts/g RDW	Eggs/cyst	TDW (g)	RDW (g)	Cysts/g RDW	Eggs/cyst
+	0	+	89.1 a	13.4 b	232.3 a	121.3 a	106.9 bc	32.7 b	229.0 a	53.0 a
+	1	+	69.4 b	10.3 c	96.0 b	63.5 b	158.8 ab	37.8 b	18.4 b	18.4 b
+	10	+	69.4 b	9.9 cd	80.2 bc	37.1 cd	107.4 bc	33.1 b	18.7 b	18.6 b
–	0	+	46.5 c	6.4 e	98.8 b	35.8 cd	88.9 c	29.7 b	22.5 b	18.0 b
–	0	–	49.8 c	7.4 e	56.0 c	46.3 bc	94.8 c	28.3 b	19.5 b	26.7 b
+	0	–	83.2 ab	17.6 a	8.4 d	20.3 d	168.7 a	51.7 a	2.3 b	17.4 b
LSD ^z	...	...	14.7*	2.8*	37.1*	22.4*	55.1**	13.3*	63.0*	10.2*
P for treatment F	...	...	0.0001	0.0001	0.0001	0.0001	0.0871	0.0171	0.0001	0.0001

^x Fumigation: +, preseason fumigation with methyl bromide at 336 kg/ha; –, untreated. Soil: amendment by percent suppressive soil mixed into upper 10-cm soil layer (wt/wt). Infestation: +, potting mix contained 446 cysts (≈50,000 eggs) of *H. schachtii*; –, *H. schachtii*-free potting mix.

^y TDW = top dry weight; RDW = root dry weight. Plants in the harvest row were harvested after 1,350 degree days (DD); plants in the sample row were used to monitor the number of infective juveniles at the beginning of the cropping season and harvested at 2,550 DD. Means followed by the same letter within a column were not significantly different when tested with Fisher's least significant difference (LSD) at the P value indicated.

^z * and ** indicate P = 0.05 and 0.10, respectively.

Hanford coarse sandy loam soil (56% sand, 24% silt, 20% clay, pH 7.4) collected from field 9C on the agricultural research station, University of California, Riverside. This field was ≈ 200 m from *H. schachtii*-suppressive field 9E, separated by a jojoba orchard (*Simmondsia chinensis* (Link) C. Schneider). Field 9C had been cropped with various vegetable, nonhost crops of *H. schachtii* for the previous five years and with a low frequency of crucifers (*H. schachtii* host plants) during the previous five years. At the time of this trial, no beet cyst nematodes were detected in this field. The second test soil (SM) was a Camarillo loam (34% sand, 42% silt, 24% clay, pH 7.7) collected near Santa Maria, CA. A majority ($\approx 70\%$) of the crops grown in that field during the last 10 years were hosts of *H. schachtii*. The beet cyst nematode population was 15.4 eggs per g of soil. The third soil was the *H. schachtii*-suppressive sandy loam of field 9E described earlier, with a *H. schachtii* population density of 4.9 eggs per g of soil at the initiation of the experiment. All three soils were passed through a screen with 6-mm openings and mixed 10:1 (dry wt/wt) with silica sand. Test soils were fumigated with methyl iodide (500 kg/ha). After aeration, the three test soils were each mixed with nontreated *H. schachtii*-suppressive 9E soil to establish dilution ratios of the suppressive soil of 0.0, 0.1, 1.0, 10.0, or 25.0% (dry wt/wt).

The soil mixes were placed in plastic cones (120 cm³ in volume, 3.8 cm in diameter, 20.6 cm deep; Stuewe and Sons Inc., Corvallis, OR) and seeded with four seeds of mustard greens (*Brassica juncea* (L.) Czernj. 'Florida broadleaf'; Lockhart Seeds). After emergence, the plants were thinned to one seedling per cone. Four weeks after seeding, each cone was infested with 1,000 J2 of *H.*

schachtii. During the first 4 weeks, plants were fertilized with 14 ml of nutrient solution (10 g of Miracle Gro N-P-K [15-30-15] fertilizer per 3.79 liters of water,) weekly. After infestation, each cone received 1.2 g of slow-release N-P-K (17-6-10) fertilizer (Osmocote, Scotts Co., Marysville, OH). The experiment was incubated in the greenhouse at $24 \pm 3^\circ\text{C}$ under ambient light. The experiment was irrigated with tap water as needed. Eleven weeks after infestation, plant tops were cut off, and oven dry weights were determined. Nematode cysts were extracted, and the numbers of beet nematode cysts and eggs were determined.

Data analysis. All data were subjected to analysis of variance. Fisher's protected least significant difference (LSD) was used to separate means at $P = 0.05$ if the probability for treatment F was $P < 0.05$. The test was performed at $P = 0.10$ if the probability for the treatment F was between 0.10 and 0.05. In the greenhouse experiment of transfer of suppressiveness to fumigated, initially suppressive soil, the regression of the number of eggs per gram of soil to the amount of amendment of suppressive soil ($x_i = \log(x + 0.01)$) was calculated. Data were plotted, and curve fitting was performed. For all other parameters in the greenhouse experiments, Fisher's protected LSD was calculated, and additionally, linear and quadratic contrasts were determined after data transformation ($x_i = \log(x + 0.01)$).

RESULTS

Transfer of suppressiveness to fumigated field plots. At the early harvest after 77 days (1,350 DD), the numbers of cysts per

Fig. 1. Growth-chamber radish bioassay for infective *Heterodera schachtii* juveniles present in field plots of the suppressiveness transfer trial. Soil bioassay samples were collected at 150 or 300 degree-day intervals from the root zone of Swiss chard. Shown are the means of four experimental treatments: one nontreated suppressive treatment and one fumigated, conducive treatment, as well as two fumigated treatments amended with either 1 or 10% suppressive soil. These treatments were all infested with *H. schachtii* prior to planting. The noninfested, fumigated and noninfested, untreated controls were included in the statistical analysis but are not shown. Least significant differences are indicated as * ($P = 0.05$) and † ($P = 0.10$); NS = not significant.

gram of root dry weight in the treatments with 1 or 10% soil transfer to fumigated plots were not significantly different from the infested, nonfumigated treatment. The number of cysts per gram of root dry weight was 2.4-fold higher in the infested, fumigated treatment than in the infested, nonfumigated treatment (Table 1). The numbers of eggs per cyst in the 10% transfer and infested, nonfumigated treatments were not statistically different but were significantly lower than in the infested, fumigated treatment. The number of eggs per cyst in the 1% transfer was significantly higher than in the 10% transfer treatment, but significantly lower than in the infested, fumigated treatment. The number of eggs per cyst was 3.4-fold higher in the infested, fumigated treatment than in the infested, nonfumigated treatment.

At the late harvest (2,550 DD), both the 1 and 10% transfer treatments had low levels of cysts per gram of root dry weight similar to the infested, nonfumigated treatment (Table 1). The number of cysts per gram of root dry weight was significantly higher (≈ 11.5 -fold) in the infested, fumigated treatment than in the other infested treatments (Table 1). The numbers of cysts per gram of root dry weight in the transfer treatments and the infested, nonfumigated treatment were not significantly different from those in

the noninfested, nonfumigated control (Table 1). The number of eggs per cyst was 2.9-fold higher in the infested, fumigated treatment than the average of the 1 and 10% transfer and infested, nonfumigated treatments.

Monitoring the infectivity of *H. schachtii* in field plots with the radish bioassay. At planting and both harvest dates for the field trial, the number of J2 detected in the radish roots of the bioassay were indicative of the suppressive conditions for *H. schachtii*. At planting, the transfer treatments had numbers of J2 similar to the infested, fumigated treatment. Nine times more J2 were detected in radish roots in the infested, fumigated control than in the infested, nonfumigated control (Fig. 1). At 450 DD, the number of J2 in the 10% soil transfer treatment was no longer significantly different from that in the infested, nonfumigated treatment. At the early harvest (1,350 DD), the number of J2 was not significantly different in the 10% soil transfer and infested, nonfumigated treatments. Only in the infested, fumigated control were significantly more J2 detected by the radish bioassay. At the late harvest (2,550 DD), there was no significant difference among the numbers of J2 in the transfer treatments and infested, nonfumigated treatment. The number of J2 in the radish roots in the infested, fumigated treatment

Fig. 2. Effect of suppressive soil amendment rates to fumigated, conducive 9E soil on number of *Heterodera schachtii* eggs per gram of soil in greenhouse trials. Amended soils were infested with 5,000 J2 per pot and cropped to **A**, Swiss chard followed by **B**, cabbage. Regression was calculated for eggs per gram of soil to the log-transformed amendment rate.

TABLE 2. *Heterodera schachtii* population densities at harvests of two consecutive crops in fumigated, infested soil amended with various amounts of suppressive 9E soil in a greenhouse experiment^w

Treatment ^x	First crop: Swiss chard				Second crop: cabbage			
	Plant TDW (g)	Cysts/g soil	Eggs/cyst	J2/cm	Plant RDW (g)	Cysts/g soil	Eggs/cyst	J2/cm
0.0	6.6	1.4	113.6	3.9	0.2	2.6	91.1	22.1
0.1	5.5	0.9	97.1	2.5	0.3	1.4	96.1	5.4
1.0	6.7	0.7	52.2	2.0	0.3	0.9	56.0	4.2
10.0	4.9	0.6	35.8	0.4	0.3	0.7	71.8	0.9
100.0	4.8	0.5	18.5	0.2	0.4	0.6	62.4	0.9
LSD ^y	NS	0.3	29.2	2.3	NS	0.5	NS	9.0
P for treatment F	0.2114	0.0004	0.0001	0.0291	0.5238	0.0003	0.9326	0.0466
Contrast ^z								
P linear	0.0650	0.0001	0.0001	0.0039	0.1388	0.0001	0.5534	0.0058
Quadratic	0.8073	0.0194	0.3801	0.7205	0.9150	0.0082	0.9290	0.0938

^w All treatments initially were infested with 5,000 second-stage juveniles (J2) of *H. schachtii*. TDW = top dry weight; RDW = root dry weight. *H. schachtii* Populations of *H. schachtii* cysts and eggs were measured at harvest. After harvest of the first crop, soils were planted with cabbage without further treatments.

^x Percent suppressive, fumigated soil (wt/wt). Methyl iodide-fumigated (690 kg/ha), originally *H. schachtii*-suppressive soil, was amended with nonfumigated *H. schachtii*-suppressive soil.

^y Fisher's protected least significant difference at $P = 0.05$; NS = nonsignificant.

^z Orthogonal contrasts were calculated after transformation of soil amendment amount by $xi = \log(x + 0.01)$.

was 180-fold higher than the average in the two transfer treatments and infested, nonfumigated treatment (Fig. 1).

Transfer of soil suppressiveness to fumigated, initially suppressive soil in greenhouse experiments. At the first harvest, soil amended with nematode-suppressive 9E soil had a significantly lower *H. schachtii* population than the nonamended, fumigated (conductive) control. The interrelation between amount of soil amendment and number of *H. schachtii* eggs per gram soil was described by a significant regression (Fig. 2A). Nematode reproduction in the 10% transfer treatment was not significantly different from the suppressive control (Table 2). Significantly fewer J2 were detected in the 10% soil transfer treatment than in the conducive control (Table 2). The amendment amount in suppressive soil had a quantitative suppressive effect on nematode population densities (linear contrast $P = 0.05$). At the second harvest, all transfer treatments had significantly lower cyst populations than the conducive control with a quantitative effect of soil amendment amount (linear contrast $P = 0.05$) (Table 2). The number of eggs per gram of soil was described by a significant regression (Fig. 2B). The infectivity of the J2 was significantly higher in the conducive control than in any other treatment (Table 2). The plant dry weights were not significantly different among the treatments (Table 2).

Transfer of soil suppressiveness to *H. schachtii*-free soil or different textured soil in greenhouse experiments. Amendment of fumigated soils with *H. schachtii*-suppressive 9E soil resulted in fewer numbers of eggs per cyst in all three soils. This effect was significant with 0.1% suppressive soil amendment in the fumigated, originally suppressive 9E soil; at 10% in the sandy loam 9C soil; and at 25% in the SM loam (Table 3). The number of cysts per 100 cm³ of soil was significantly reduced only in the SM loam at the highest amendment rate.

DISCUSSION

Biological suppressiveness against *H. schachtii* was transferable with small portions of soil under both field and greenhouse conditions. After 1 month of moist fallow and 77 days of the host crop Swiss chard, 10% of suppressive soil mixed into methyl bromide-fumigated field plots was sufficient to suppress nematode multiplication to the level of the infested, nonfumigated treatment. After 230 days, 1% of suppressive soil had transferred the *H. schachtii* suppressiveness to a similar level. At this later date, the plant top dry weights in the 1% suppressive soil transfer treatment were not significantly different from the noninfested, fumigated control, indicating an efficient protection of the host crop from beet cyst nematode damage. The amounts of soil necessary to

transfer cyst nematode suppressiveness were considerably smaller than the ones used for previously reported greenhouse experiments (19,22). The onset of *H. schachtii* suppressiveness was rapid when compared with the transfer of suppressiveness against take-all disease of wheat into fumigated field plots with similar amounts of suppressive soil. After one cropping cycle of wheat, transfer of take-all suppression was not sufficient to keep plants alive until harvest (21). Only in the second year was suppression of the take-all disease attributable to the transfer of suppressive soil (3). Furthermore, the time necessary for the *H. schachtii* suppressiveness to be expressed was significantly shortened when compared with the onset of population density decline under host crops in initially conducive plots in field 9E (25). In those trials, the *H. schachtii* population level started to decline in the third cropping period of host plants whereas, in the transfer experiments, *H. schachtii* suppression was observed in the first cropping period.

Measuring the infectivity of *H. schachtii* J2 in the radish bioassay was valuable for monitoring the development of nematode suppressiveness in different treatments. The infectivity decreased earlier in the 10% transfer treatment than in the 1% transfer treatment and remained low for the rest of the monitoring time. Therefore, nematode infectivity seemed to reflect the development of *H. schachtii* suppressiveness. The 1% soil amendment presumably transferred fewer nematode antagonists into the plots than the 10% transfer. Whether this was merely a quantitative effect that was the result of introducing fewer propagules of one or more suppressive organisms or also a qualitative difference that was the result of leaving out certain components of a community or population structure, has not yet been determined.

The establishment of *H. schachtii* suppressiveness into fumigated 9E and 9C soil occurred rapidly, presumably because of similar soil texture as well as physical and chemical characteristics. However, the transfer of suppressiveness into the SM soil was more difficult and was achieved only at the highest amendment ratio. The restriction of soil suppressiveness to certain soil textures had been reported for fungal disease-suppressive soils (3). For example, in a study with take-all disease-suppressive soil, it was demonstrated that organisms antagonistic to *Gaeumannomyces graminis* could be present in a soil with a certain texture without expressing suppressiveness. When the conducive soil was mixed at a rate of 1% into fumigated soil with a drastically different soil texture that naturally hosted suppressiveness, the disease was diminished (2).

Competitive, slow-growing microorganisms typically dominate natural, undisturbed soil ecosystems (20). Such microorganisms are able to utilize complex carbon sources and compete success-

TABLE 3. *Heterodera schachtii* population densities 11 weeks after seeding with mustard greens in three fumigated, nematode-infested soils amended with various amounts of suppressive 9E soil in a greenhouse experiment ^w

Treatment ^x	SL suppressive			SL with no cysts			Loam with cysts		
	RDW (g)	Cysts/100 cm ³	Eggs/cyst	RDW (g)	Cysts/100 cm ³	Eggs/cyst	RDW (g)	Cysts/100 cm ³	Eggs/cyst
0.0	2.5	80.1	40.8	2.2	35.6	120.6	2.1	149.5	94.6
0.1	2.1	60.8	15.8	2.5	28.9	128.2	2.9	161.8	106.1
1.0	1.0	67.8	20.6	2.0	17.4	110.4	2.7	139.6	126.4
10.0	1.6	73.1	31.0	1.4	13.9	58.9	2.8	88.6	79.3
25.0	1.5	67.8	20.8	1.7	23.3	42.7	2.9	70.4	61.0
LSD ^y	1.0	NS	16.4	NS	NS	47.2	NS	62.8	31.4
<i>P</i> for treatment <i>F</i>	0.0493	0.4866	0.0281	0.1605	0.2706	0.0027	0.9353	0.0283	0.0039
Contrast ^z									
<i>P</i> linear	0.0296	0.5576	0.2244	0.0485	0.1062	0.0002	0.5700	0.0043	0.0191
Quadratic	0.0883	0.3475	0.0910	0.9170	0.1598	0.1894	0.6705	0.2724	0.0049

^w All soil mixes were infested with 1,000 second-stage juveniles (J2) of *H. schachtii* 4 weeks after seeding of soil with mustard greens. Test soils were collected from three field sites with either different soil textures or different nematode infestation histories: SL suppressive = sandy loam, originally cyst-nematode suppressive; SL with no cysts = sandy loam, originally no cyst nematodes present; loam with cysts = loam, originally cyst nematodes present. RDW = root dry weight.

^x Percent suppressive, fumigated soil (wt/wt). All soils were fumigated with methyl iodide (500 kg/ha) before untreated suppressive 9E soil was added.

^y Fisher's protected least significant difference at $P = 0.05$; NS = nonsignificant.

^z Orthogonal contrasts were calculated after transformation of soil amendment amount by $xi = \log(x + 0.01)$.

fully with other microbes, often by producing inhibitory metabolites. Microbiostasis can impede microbial colonization (12,17) and may interfere with the activity of nematode antagonists in the nonfumigated soils. This biological phenomenon is active against fungi, bacteria, and actinomycetes (12), and general microbial competition has been considered a core problem in attempts to establish biocontrol organisms (3,14). Alien microorganisms face the challenge of replacing at least parts of native microbial communities that occupy essential resources, and defending their niche with chemical (e.g., antibiotics, siderophores) or physical (e.g., pH, space) means. Autoclaving of soil reduced the microbiostatic effect on introduced microbial organisms (13), and other published research indicates that biocidal disturbances may be crucial to successfully transferring disease suppressiveness (2,7,9,10,26). On the other hand, it is perhaps only indicative of our poor understanding of soil microbial communities, their structure, and interactions that we still have to rely on drastic, nonselective forces to transfer soil suppressiveness to agroecosystems.

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