

Association of *Verticillium chlamydosporium* and *Paecilomyces lilacinus* with Root-knot Nematode Infested Soil¹

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Abstract: Population densities of *Meloidogyne incognita* and the nematophagous fungi, *Paecilomyces lilacinus* and *Verticillium chlamydosporium*, were determined in 20 northern California tomato fields over two growing seasons. *Paecilomyces lilacinus* was isolated from three fields, *V. chlamydosporium* was isolated from one field, and both fungi were isolated from 12 fields. *Verticillium chlamydosporium* numbers were positively correlated with numbers of *M. incognita* and *P. lilacinus*. *Paecilomyces lilacinus* numbers were positively correlated with *V. chlamydosporium* numbers, but they did not correlate with *M. incognita* numbers. The correlation coefficients were low ($R < 0.5$) but significant ($P < 0.05$). All *P. lilacinus* and *V. chlamydosporium* field isolates parasitized *M. incognita* eggs in vitro. In a greenhouse study, numbers of *V. chlamydosporium* and *P. lilacinus* increased more in soils with *M. incognita*-infested tomato plants than in soil with uninfested tomato plants. After 10 weeks, the Pf/Pi of second-stage juveniles in soils infested with *P. lilacinus*, *V. chlamydosporium*, and *M. incognita* was 47.1 to 295.6. The results suggest *V. chlamydosporium* and *P. lilacinus* are not effectively suppressing populations of *M. incognita* in California tomato fields.

Key words: biological control, *Lycopersicon esculentum*, *Meloidogyne incognita*, *Paecilomyces lilacinus*, tomato, *Verticillium chlamydosporium*.

Paecilomyces lilacinus (Thom) Samson and *Verticillium chlamydosporium* Goddard have been identified as egg parasites and are associated with suppression of root-knot and cyst nematodes (12,16). Their potential as biological control agents is suggested by studies in which nematode numbers 1) were low when fungus inoculum was high (9,12,16), 2) increased following suppression of *V. chlamydosporium* in field soils (15), and 3) were reduced following addition of *P. lilacinus* or *V. chlamydosporium* to soil (13,18,22). Species of *Paecilomyces* and *Verticillium* apparently are common in cyst and root-knot nematode-infested soil in many parts of the world (21), but they were not isolated from *Meloidogyne* spp. in peach orchards (24), *Tylenchulus semipenetrans* Cobb in citrus orchards (7), or *Heterodera schachtii* Schmidt in sugarbeet (*Beta vulgaris* L.) fields in California (20).

The objectives of this research were 1) to conduct a field survey to determine if *P. lilacinus* and *V. chlamydosporium* are present in California tomato soils; 2) to determine

if the presence of *P. lilacinus* and *V. chlamydosporium* could be associated with low *Meloidogyne incognita* (Kofoid & White) Chitwood populations in fields surveyed over two growing seasons; and 3) to determine if soils infested with *P. lilacinus* and *V. chlamydosporium* could be associated with soil suppressiveness in a greenhouse experiment.

MATERIALS AND METHODS

Fields sampled: Twenty commercial tomato fields (A-T) representing a range of *M. incognita* infestations (0-1,583 second-stage juveniles/kg soil) and soil types in four central California counties were selected with the assistance of farm advisers and farm managers. Eighteen of the fields were located within 180 km of San Joaquin, Stanislaus, and Yolo counties, and two were approximately 200 km farther south. Tomatoes (*Lycopersicon esculentum* Mill.) are grown in California in rotation with cotton (*Gossypium hirsutum* L.) and corn (*Zea mays* L.) in Fresno County; wheat (*Triticum aestivum* L.), sugarbeet, and dry beans (*Phaseolus lunatus* L.) in San Joaquin County; sugarbeet, peas (*Pisum sativum* L.), and dry beans in Stanislaus County; and wheat in Yolo County.

Soil in each field was sampled to a depth of 45 cm with a 2.5-cm-d Oakfield tube or

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TABLE 1. Physical and chemical characteristics of California field soils in tomato rotations.

Field	Sand (%)	Silt (%)	Clay (%)	OM (%)†	BS (%)†	pH	EC†	CEC†
Stanislaus County								
A	63	17	20	1.49	27	6.9	0.97	10.0
B	47	26	27	1.49	33	7.4	1.80	15.0
C	13	42	45	1.30	44	7.0	0.98	23.5
D	33	36	31	1.61	38	7.1	0.93	18.5
Yolo County								
E	58	25	17	0.87	31	7.2	0.79	13.0
F	50	26	24	1.05	32	5.4	4.50	15.5
G	43	30	27	1.80	35	5.8	3.40	17.5
H	37	39	24	1.74	35	6.9	0.72	18.0
I	64	19	17	1.55	31	6.9	0.43	13.0
J	53	26	21	1.55	31	6.7	0.40	16.5
San Joaquin County								
K	33	35	32	1.98	46	6.4	0.90	20.0
L	17	45	38	2.36	48	6.6	0.76	24.0
M	45	31	24	1.36	35	6.9	0.71	15.5
N	47	25	28	2.67	34	7.7	0.68	18.5
O	50	25	24	1.55	32	6.5	0.71	15.0
P	48	26	26	1.55	31	6.8	0.65	13.5
Q	37	30	33	7.44	54	7.0	0.67	38.0
R	48	26	26	8.00	42	7.6	0.90	30.0
Fresno County								
S	65	16	19	0.43	30	7.5	0.91	9.0
T	49	26	25	1.11	39	7.5	2.33	13.5

† Organic matter (OM) and base saturation (BS) percentages and electrical conductivity (EC) in mmho/cm²; cation exchange capacity (CEC) is meq/100 g soil.

with a 5-cm-d soil auger if soil was too dry for insertion of the Oakfield tube. Thirty soil cores from the Oakfield tube or five from the soil auger were taken randomly from subplots (two halves or four quadrants per 100-m² plot, one plot per field), and a 2-liter subsample per subplot was placed in a polyethylene bag and stored at 10 C for up to 7 days. The 20 fields were sampled in April and November 1986 and in April and October 1987. Texture, pH, percentage of organic matter, base saturation, electrical conductivity, and cation exchange capacity per site were determined by the Cooperative Extension Diagnostic Laboratory, University of California, Davis.

Fifteen of the fields were planted to tomato in 1986. Fields C, D, I, J, and S were not planted with tomato in 1986 but were in 1987. Only field N was planted with to-

mato both years. Soil physical and chemical characteristics varied among fields (Table 1). Sandy loams were common, but soils with large amounts of silt, clay, or organic matter were also present.

Nematodes from 100 cm³ soil per subsample were counted after elutriation (1) and sugar centrifugation (14). Material caught on a 0.35-mm-pore screen (40 mesh) during elutriation was placed on a Baermann funnel in a mistchamber, and *Meloidogyne* second-stage juveniles (J2) were counted after 7 days. Nematode extraction was completed for all samples within 7 days of collection. *Meloidogyne incognita* was the predominant *Meloidogyne* sp. in the area sampled, but perineal patterns were not examined to determine if other species were present.

Soil (20 g) from each sample was placed in 200 ml distilled water and agitated 5 minutes with a wrist-action shaker. A 1-ml aliquot was removed from the soil suspension and added to, and serially diluted in, 9-ml-water blanks. A 0.5-ml aliquot was removed from each dilution level (10⁻² to 10⁻⁶) and placed on semiselective media in petri dishes. Rose-bengal-chitin agar (8) amended with 50 mg iprodione/liter was used to determine *P. lilacinus* propagule density, and rose-bengal-chitin agar amended with 50 mg benomyl/liter was used for *V. chlamydosporium*. Fungicides were added to the rose-bengal-chitin medium to suppress rapidly growing fungi that often obscure the presence of *P. lilacinus* and *V. chlamydosporium*. Benomyl and iprodione were the most effective of a variety of fungicides in improving the selectivity of rose-bengal-chitin medium (Gaspard, unpubl.). The petri dishes were incubated at 25 ± 2 C for 7 days before fungal colonies were identified and counted. *Paecilomyces lilacinus* identification was based on conidiophore morphology and conidial color (23). *Verticillium chlamydosporium* identification was based on conidiophore morphology and the presence of dictyochlamydospores (6). Representative colonies of both fungi were subcultured from the semiselective media to potato-dextrose

agar (PDA) for storage. Dilution plating of soil for fungi was completed within 1 month of collection for most samples; however, soil samples collected in April 1987 were stored at 10 C for 5 months before dilution plating.

In vitro parasitism: Fifteen field isolates of *P. lilacinus* and 13 field isolates of *V. chlamydosporium* (one isolate from each tomato field that contained either fungus) were tested for their ability to parasitize *M. incognita* eggs. Ten egg masses were touched to the surface of each fungal culture sporulating on PDA or selective media. Inoculated egg masses were placed on 1.5% water agar in petri dishes and incubated at 25 C. Seven days later, egg masses were squashed in water between a microscope slide and a cover slip and viewed at 200× or 400× with a compound microscope. Eggs were considered parasitized if characteristic hyphae were present within the eggs (5). The number of parasitized eggs per egg mass was not determined.

Effect of P. lilacinus and V. chlamydosporium infested soil on M. incognita population densities: One-hundred 3-week-old 'UC82' tomato seedlings grown in 127-cm³ styrofoam cups filled with autoclaved fine sandy soil (86% sand, 8.8% clay, 5.2% silt) were inoculated with 3,000 *M. incognita* J2. Four days later, roots of five of the inoculated plants were stained with acid fuchsin (2), and the nematodes were counted. The coefficient of variation in stained roots was 17% and the average J2 penetration was 785 nematodes per root system. The *M. incognita*-infected or uninfected 4-week-old seedlings were transplanted in 400 cm³ field soil in polyvinylchloride cylinders (12.5 cm high × 10 cm d) closed at one end with nylon fabric (ca. 0.15-mm pore size). The closed end was embedded 3 cm in 915-cm³ cups filled with fine sand to improve drainage. Soils that were infested with *M. incognita*, *V. chlamydosporium*, and (or) *P. lilacinus* (A, C, D, E, G, I, J, M, O, and P) were used. Soils were stored for 12 months at 10 C before use.

Treatments were replicated four times and arranged in a randomized complete

TABLE 2. *Meloidogyne incognita* second-stage juveniles (N/100 g soil) in California tomato fields preplant (April) and postharvest (October or November) in 1986 and 1987.

Field	1986		1987		LSD
	April	November	April	October	
Stanislaus County					
A	21	187	255	2,360	1,005
B	15	192	100	2,155	1,465
C	1	20	11	205	ns
D	30	421	85	712	328
Yolo County					
E	158	692	345	597	ns
F	17	3	0	0	ns
G	17	12	27	0	ns
H	17	449	150	110	250
I	0	5	92	0	ns
J	58	66	20	806	423
San Joaquin County					
K	0	0	0	0	ns
L	0	2	42	10	39
M	0	37	7	20	ns
N	0	40	0	0	18
O	0	45	65	25	ns
P	58	80	510	1,100	ns
Q	0	82	0	0	ns
R	0	82	27	0	35
Fresno County					
S	10	5	10	580	514
T	3	214	97	1,745	ns

April 1986 values are the means of two samples per field; all other values are the means of four samples per field. LSD = Tukey's least significant difference ($P = 0.05$) for within-field comparisons; ns = values in a row that are not different ($P \leq 0.05$).

block design on a greenhouse bench (25–30 C). Ten weeks after inoculation, soil and roots from each cylinder were removed and the numbers of *P. lilacinus*, *V. chlamydosporium*, and *M. incognita* were determined as described in nematode extraction and fungal population determination.

Data were analyzed by correlation analysis, stepwise-regression analysis, and analysis of variance. All differences reported are significant at the 5% level.

RESULTS

Root-knot nematodes were recovered from all fields except K (Table 2). *Meloidogyne incognita* was not detected in 25% of all samples taken from the fields. Population densities in 11 of the fields did not

TABLE 3. Isolation of *Paecilomyces lilacinus* (Pl) and *Verticillium chlamydosporium* (Vc) in California tomato fields preplant and postharvest in 1986 and 1987.

Field	Colony forming units $\times 10^6$ /g soil									
	1986				1987				LSD	
	April		November		April		October		Pl	Vc
	Stanislaus County									
A	10.0	0.0	12.5	5.0	0.5	3.0	0.0	1.0	ns	ns
B	8.0	9.8	12.5	10.8	0.0	5.8	0.0	1.6	ns	ns
C	14.8	2.5	5.0	4.0	0.3	1.5	0.0	1.1	ns	ns
D	1.5	2.5	0.0	6.0	2.5	0.5	0.0	3.4	ns	ns
	Yolo County									
E	2.5	3.5	0.5	0.3	1.1	0.0	0.3	0.0	ns	ns
F	0.0	0.0	0.5	0.0	0.0	0.0	0.0	1.0	ns	ns
G	0.0	0.0	3.3	5.0	0.0	1.5	0.0	1.0	ns	ns
H	0.0	0.8	12.5	11.5	0.8	0.3	0.0	2.0	ns	ns
I	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ns	ns
J	12.5	0.0	0.8	0.0	0.0	0.3	0.0	0.1	ns	ns
	San Joaquin County									
K	12.5	0.0	15.0	0.0	2.5	0.0	0.0	0.0	13.9	ns
L	0.0	0.0	5.5	0.0	0.1	0.0	0.0	0.1	ns	ns
M	5.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	ns	ns
N	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ns	ns
O	0.0	0.0	2.5	5.0	0.0	0.0	0.0	0.0	ns	ns
P	0.0	0.0	12.5	25.0	0.0	6.0	0.0	1.8	10.4	13.8
Q	42.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ns	ns
R	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ns	ns
	Fresno County									
S	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	ns	ns
T	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	ns	ns

April 1986 values are the means of two samples per field; all other values are the means of four samples per field. LSD = Tukey's least significant difference for within-field comparisons; ns = values in a row that are not different ($P \leq 0.05$).

change ($P > 0.05$) over the 2 years of sampling. Population densities in all fields tended to be highest in postharvest samples in a given year. In some fields more nematodes were extracted in the spring of 1987 than in the fall of 1986, but these differences were not significant.

Paecilomyces lilacinus, but not *V. chlamydosporium*, was isolated from three fields; *V. chlamydosporium*, but not *P. lilacinus*, was detected in one field; and both fungi were isolated from 12 fields (Table 3). The population densities of these fungi did not vary ($P > 0.05$) in 18 of the fields over the two seasons. *Paecilomyces lilacinus* was present in 30% of the samples where *M. incognita* was absent, whereas *V. chlamydosporium* was present in 10% of the samples where *M. incognita* was absent.

Numbers of *M. incognita* J2 were posi-

tively correlated with percentage of sand, pH, and *V. chlamydosporium* numbers and were negatively correlated with base saturation (BS), cation exchange capacity (CEC), and percentages of clay, organic matter, and silt. The stepwise regression model that best explained the variation in numbers of J2 included the variables CEC, *V. chlamydosporium*, pH, percentage of clay, and percentage of organic matter (Table 4). *Paecilomyces lilacinus* numbers were positively correlated with percentage of silt and *V. chlamydosporium* numbers but were negatively correlated with percentage of sand. The stepwise regression model that best explained the variation of *P. lilacinus* population density included the variables *V. chlamydosporium*, percentage of sand, date of sample collection, electrical conductivity (EC), and pH. *Verticillium chlamydospori-*

um numbers were positively correlated with numbers of J2 and *P. lilacinus* but were negatively correlated with BS, CEC, and percentage of organic matter. The stepwise regression model that best explained the variation of *V. chlamydosporium* population density included the variables nematode numbers, *P. lilacinus*, percentage of sand, BS, percentage of organic matter, CEC, percentage of clay, date of sample collection, and percentage of silt. Although the *P* values for the stepwise regression models in Table 4 were significant ($P \leq 0.05$), only a small portion of the variation was explained by these equations ($R^2 \leq 0.25$).

In vitro parasitism: All isolates of *P. lilacinus* and *V. chlamydosporium* parasitized eggs of *M. incognita* in vitro. Less than 50% of the eggs present in individual egg masses were parasitized in most cases. Eggs in all stages of development were parasitized.

Effect of P. lilacinus and V. chlamydosporium infested soil on M. incognita population densities: After 10 weeks in the greenhouse, root-knot nematodes were not detected in the 10 field soils that were stored for 12 months and planted with uninfected tomato seedlings. These nematodes were detected in soils to which infected seedlings had been planted. The Pf/Pi (total final number of J2 extracted/initial number of J2 in roots/785 cm³ soil) was 47.1 to 295.6. Propagule densities for *P. lilacinus* and *V. chlamydosporium* were higher ($P \leq 0.05$) at the end of the experiment than at the beginning in most soils planted to *M. incognita*-infected tomato but not in soils planted with uninfected tomato seedlings (Fig. 1).

DISCUSSION

The results indicate that *P. lilacinus* and *V. chlamydosporium* occur in many tomato fields in California. Various soil factors were correlated with the presence of these fungi, but these correlations were low. The low correlations observed in the field data may be explained by the small number of observations per field, variation in the

TABLE 4. Stepwise regression statistics for prediction of *Meloidogyne incognita*, *Paecilomyces lilacinus*, and *Verticillium chlamydosporium* population densities.

Dependent variable	R^2	Independent variable†	<i>P</i> -value
<i>M. incognita</i>	0.250		0.0001
		CEC	0.0066
		<i>V. chlamydosporium</i>	0.0001
		pH	0.0001
		Clay %	0.0001
		Organic matter %	0.0001
<i>P. lilacinus</i>	0.064		0.0001
		<i>V. chlamydosporium</i>	0.0001
		Sand %	0.1179
		Date	0.1044
		EC	0.0125
		pH	0.0284
<i>V. chlamydosporium</i>	0.224		0.0001
		<i>M. incognita</i>	0.0001
		<i>P. lilacinus</i>	0.0006
		Sand %	0.1327
		Base saturation	0.0001
		Organic matter %	0.0001
		CEC	0.0002
		Clay %	0.0612
		Date	0.0264
		Silt %	0.0920

† CEC = cation exchange capacity; date = date of sample collection; EC = electrical conductivity. *P*-values of independent variables indicate the significance of each variable to the model. Independent variables are listed in the order they were entered.

cropping history, or variation in the microbial community of each field. Certain organic substrates enhance the parasitic activity of *P. lilacinus* and *V. chlamydosporium* (18,22); however, in this study, only total organic matter was measured. Variation among fungal isolates could also have contributed to the low correlation in the field data. *Paecilomyces lilacinus* and *V. chlamydosporium* isolates from different geographical areas vary in growth rate and parasitic ability (4,9,11,17,21). All of the tomato field isolates of *P. lilacinus* and *V. chlamydosporium* parasitized *M. incognita* eggs in vitro, but the variation in virulence is unknown.

In this study, isolates of *P. lilacinus* and *V. chlamydosporium* not detectable with the semiselective media may have been present

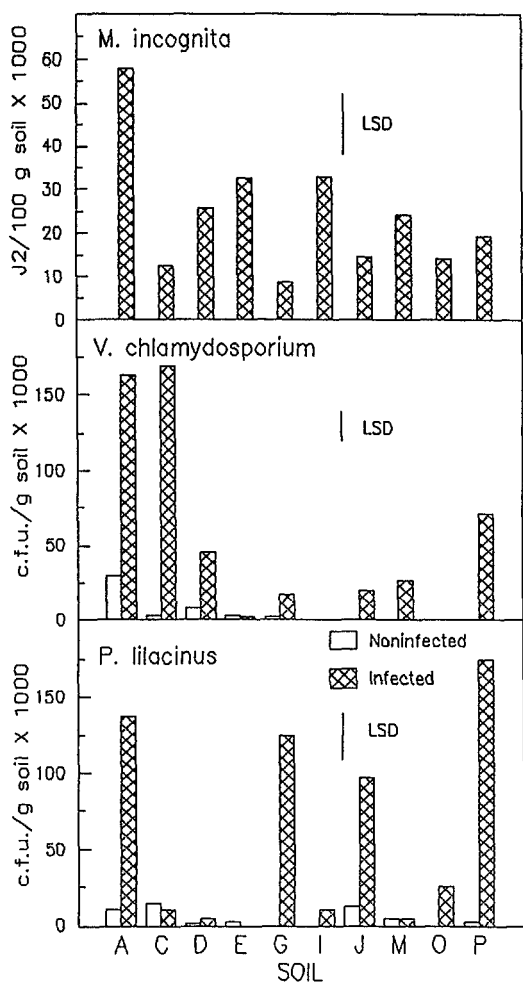


FIG. 1. Final population densities of *Meloidogyne incognita*, *Paecilomyces lilacinus*, and *Verticillium chlamydosporium* in 10 tomato field soils planted with *M. incognita*-infected tomato seedlings and uninfected seedlings under greenhouse conditions. Tukey's least significant difference (LSD) bar indicates differences among all means ($P = 0.05$).

in the tomato soils. Media amended with benomyl or iprodione permitted consistent isolation of *P. lilacinus* and *V. chlamydosporium* from most soils surveyed. All *V. chlamydosporium* isolates grew well on the benomyl-amended medium, but four isolates were also obtained on iprodione-amended medium. Benomyl is used in another *P. lilacinus*-selective medium (19), but *P. lilacinus* was not detected on benomyl-amended medium used in this study.

Paecilomyces lilacinus and *V. chlamydospori-*

um are facultative parasites of nematodes. Isolates of *P. lilacinus* parasitize invertebrate as well as vertebrate animals (21). In our study, incidence of *P. lilacinus* was not correlated with *M. incognita* densities and was present in one field where *M. incognita* was not found. In microplot experiments in Florida, *P. lilacinus* failed to control *M. javanica*, but the fungus maintained high propagule densities in inoculated soil and was also present at lower levels in plots not infected with the fungus or the nematode (10). *Verticillium chlamydosporium* also uses numerous nutrient sources (21). In contrast to *P. lilacinus*, *V. chlamydosporium* numbers were positively but weakly correlated with *M. incognita* numbers.

The stimulating effect of *M. incognita*-infected plants on *P. lilacinus* and *V. chlamydosporium* numbers in the greenhouse indicated that these nematodes may be an important substrate for these fungi. Additional evidence is required, however, to determine if the increase in fungal population densities resulted from parasitism of nematode eggs or utilization of other substrates associated with nematode-infected roots.

Verticillium chlamydosporium chlamydo-spore level was negatively correlated with *Heterodera avenae* reproduction in cereal monoculture (3). The absence of a negative correlation in this study may indicate that the egg parasites are not suppressing *M. incognita* in the tomato soils studied. In studies on the cereal cyst-nematode system, the increase in nematode numbers after antagonists were suppressed with a formalin drench provided some experimental evidence of biological control (15). A similar approach could be used to measure the impact of *P. lilacinus* and *V. chlamydosporium* on root-knot nematode population density in California tomato soils.

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