Effects of Fungal Communities on the Pathogenic and Saprophytic Activities of *Fusarium oxysporum* f. sp. *radicis-lycopersici*

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ABSTRACT

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The pathogenic and saprophytic activities of *Fusarium oxysporum* f. sp. *radicis-lycopersici*, as determined by the incidence of infection of tomato and by saprophytic proliferation in soil, respectively, were quantified during exposure of the pathogen to different fungal communities. Chlamydospores of the pathogen were added to soil that had been fumigated with methyl bromide-chloropicrin, and either recolonized by naturally occurring microflora or augmented with conidia of *Trichoderma harzianum, Aspergillus ochraceus,* and *Penicillium funiculosum*. In freshly fumigated, nonaugmented soil, 90% of cultivar Bonnie Best tomato seedlings were infected after 2 wk at 20 C, while only 25% were infected in freshly fumigated, augmented soil. In soils infested with the pathogen 46 days after fumigation, 1% of the plants were infected in both augmented and nonaugmented soils. When the pathogen was added to soil samples obtained at 7-day intervals after fumigation, the saprophytic proliferation of the pathogen and the incidence of host infection were correlated inversely ($r = -0.89$ to -0.94) with the natural logarithm of the total number of saprophytic fungal propagules detected in the augmented or nonaugmented soils. Mechanisms of succession and community ecology were invoked to explain the decrease in the saprophytic and pathogenic activities of the pathogen in soils during recolonization.

Additional key words: r-selected species, biological control, Fusarium crown rot of tomato.

Fusarium oxysporum Schlecht f. sp. *radicis-lycopersici* Jarvis and Shoemaker (8), the causal agent of Fusarium crown rot of tomato (*Lycopersicon esculentum* Mill.), competes as saprophyte in freshly steamed or fumigated (methyl bromide-chloropicrin) soils (12,17). Increase in the incidence of Fusarium crown rot of tomato is associated with the rapid saprophytic proliferation of the pathogen after such treatments. Natural and artificially introduced soil recolonizing fungi may reduce the severity of the epidemic by impeding saprophytic proliferation of the pathogen (7,13,17).

The saprophytic activity of a pathogen is affected by the community of its microbial associates. For example, a soilborne plant pathogen that grows poorly or not at all in untreated soil may grow readily as a saprophyte in soils in which the microbial community has been disturbed, such as by the application of a nonpersistent, broad-spectrum biocide. The succession theory of community ecology predicts that a series of communities, or seres, develop following such a perturbation (15). Specific seral plant, animal, or fungal communities have certain characteristics in common. The early successional communities are of low diversity and are usually dominated by a few species, r-selected species, which grow rapidly and quickly deplete the available resources. The success of a particular r-selected species may be dependent upon the absence of competitors (15). In more diverse communities which develop later, the few r-selected species are replaced by a number of k-selected species, which grow more slowly and utilize the remaining available resources over a longer period of time. The later successional stages are characterized by communities of increased diversity and stability (15). Usually k-selected species are found in communities composed of other k-selected species. The r-selected species, however, are unsuccessful in the presence of the diverse communities of k-selected species. Control of an r-selected pathogen may be possible either by establishing k-selected species before or after the introduction of the pathogen, or by establishing other r-selected species before the pathogen is introduced.

In the early studies of biological control, biological agents were selected for antagonism toward the pathogen in various laboratory tests outside of the soil environment (1). The results of these tests usually were not repeatable under field conditions. The reasons why such selection methods are not repeatable were summarized by Baker and Cook (1). In the present study, antagonists were selected

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because they could proliferate in freshly fumigated soil, occupy the soil adjacent to the root environment of the host, and increase the ratio of inoculum density to infection incidence (12). All of these factors were evaluated with field soil, rather than agar, as the growth medium. The selection for antagonists that are successful competitors by this method, rather than by screening for those that produce toxins or show hyperparasitism on agar plates, may result in the successful control of other plant diseases in which the epidemic involves the saprophytic growth of an r-selected pathogen.

The objectives of this study were: to determine the effect of fungal communities on the saprophytic development of *F. oxysporum* f. sp. *radicis-lycopersici* in soil, to monitor the rate of immigration of the fungal species into soils augmented or not augmented with the antagonists, and to quantify the effects of fumigation and antagonists on the activity of the pathogen in soil and on the host-pathogen interaction.

MATERIALS AND METHODS

An isolate of *F. oxysporum* f. sp. *radicis-lycopersici* was obtained from a diseased tomato plant collected in a south Florida field. Cultures were stored in soil tubes according to the method of Toussoun and Nelson (19). For chlamydospore production, macroconidia of the pathogen were washed from 2-wk-old cultures grown at 25 C under continuous fluorescent light (3,000 lux) on potato-dextrose agar (PDA) (Difco, Detroit, MI 48201). The macroconidia formed intercalary chlamydospores after 4 wk of incubation of 10^6 macroconidia per milliliter of autoclaved, deionized water at 28 C in the dark. Concentrations of chlamydospores of the pathogen were determined by counting 40 fields of a standard hemacytometer, and the desired dilutions were added to the soil.

The antagonists used in the artificial infestation and recolonization experiments included three isolates of *Trichoderma harzianum* Rifai, one isolate of *Penicillium funiculosum* Thom, and one isolate of *Aspergillus ochraceus* Wilhelm. The antagonists were selected as described previously (12). Conidial suspensions of each isolate of the antagonists were obtained by washing 2-wk-old cultures grown on PDA at 25 C under 12 hr of fluorescent light (2,000 lux) per day, and concentrations were determined with a standard hemacytometer.

The soil fungal communities were monitored by dilution plating of soil samples on PDA which contained 1 ml of Tergitol NPX (Sigma Chemical Co., St. Louis, MO 63178) and 50 mg of chlortetracycline hydrochloride (Sigma Chemical Co., St. Louis, MO 63178) per liter of medium (PDA-TC). The plates were incubated for 7 days at 25 C and 2,000 lux of fluorescent light. Benomyl (Benlate 50% WP, E. I. du Pont de Nemours & Co., Wilmington, DE 19898) was added to a replicate set of plates at 2.5 mg/L to inhibit the fast-growing colonies of *Trichoderma* spp. when soil dilutions in water of 1:25 or lower were used. Dilution series ranged from 1:10 to 1:10^6 (w/v), depending on the expected populations of fungi. The isolates of *F. oxysporum* f. sp. *radicis-lycopersici* from soil dilutions and plant tissue were identified by the technique of Sanchez et al (18), in which the type of lesion on tomato seedlings grown in pathogen-infested water agar is used to differentiate the isolates of the pathogen from nonpathogenic or wilt-inducing *F. oxysporum* isolates.

The experiment consisted of six treatments of combinations of fumigated or nonfumigated soil, antagonist-augmented or nonaugmented soil, and recolonized or nonrecolonized soil (Table 1). In Treatment 1, the ability of the pathogen to grow in recolonized soil and to infect host plants was determined. Pompano fine sand was treated with methyl bromide-chloropicrin (67:33, v/v) at the rate of 1 kg of fumigant to 50 kg of soil for 2 days in a sealed container. After 4 days of aeration, 20 kg of soil was placed uncovered in the greenhouse to allow natural recolonization by airborne propagules. The water content of the soil was maintained at approximately 10% by weight for the duration of the experiment. Every 7 days, at 1,500-g sample of soil was removed and five 1-g subsamples were plated on PDA-TC to monitor the fungal community. The remaining 1,495 g of sample was infested immediately with the pathogen at 1,000 chlamydospores per gram of soil. The ability of the pathogen to infect the host plants was determined by placing two germinated cultivar Bonnie Best tomato seeds in a 100-ml polypropylene beaker which contained 60 g of infested soil layered over 50 g of autoclaved sand. The beakers then were placed in growth chambers at 20 C with 12 hr of light (4,000 lux) per day. After 2 wk, the incidence of infection and the pathogen population density were determined. To determine the

TABLE 1. Treatments applied to 20-kg allotments of soil

Treatment	Soil fumigated[a]	Pathogen added[b]	Antagonists[c]	Natural recolonization[d]
1	+	Weekly	−	+
2	+	Weekly	+	+
3	+	Initially	−	−
4	+	Initially	−	+
5	+	Initially	+	+
6	−	Initially	−	N/A

[a] + = Soil fumigated with methyl bromide-chloropicrin (67:33, v/v) at 1 kg of fumigant to 50 kg of soil for 2 days and then allowed to air in the greenhouse for 4 days; − = soil not fumigated.

[b] Weekly = *Fusarium oxysporum* f. sp. *radicis-lycopersici* added at 1,000 chlamydospores per gram of soil to a 1,500-g soil sample obtained every 7 days for the duration of the experiment. Initially = *Fusarium oxysporum* f. sp. *radicis-lycopersici* added to the entire soil allotment 4 days after fumigation at 1,000 chlamydospores per gram of soil.

[c] + = Conidia of each of five antagonists (three isolates of *Trichoderma harzianum*, one isolate of *Penicillium funiculosum*, and one isolate of *Aspergillus ochraceus*) added to the entire soil allotment at 1,000 conidia of each isolate per gram of soil 4 days after fumigation; − = antagonists not added.

[d] + = Soils left uncovered to allow natural recolonization by airborne inocula; − = soil placed in plastic containers to inhibit natural recolonization.

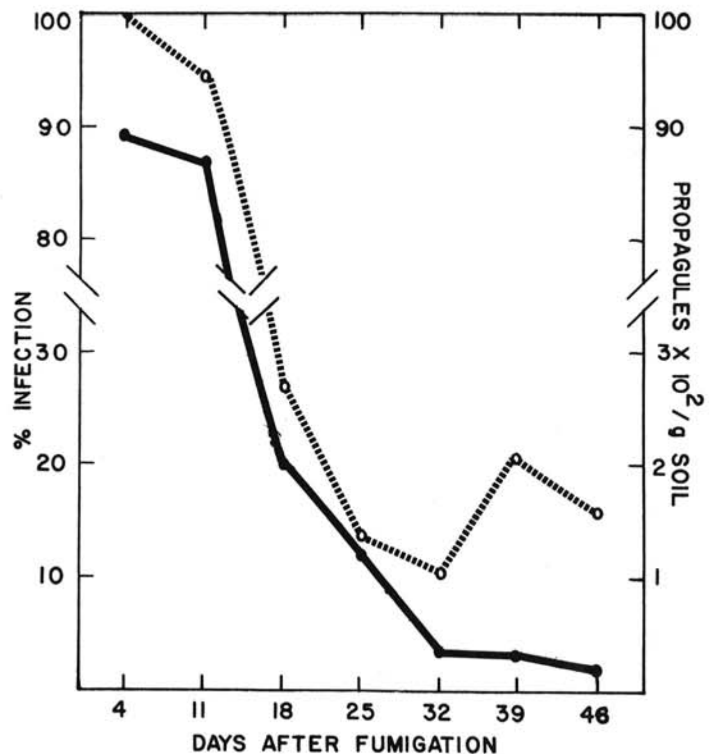

Fig. 1. The relationship of percent infection of roots of cultivar Bonnie Best tomato plants (•——•) and inoculum density of *Fusarium oxysporum* f. sp. *radicis-lycopersici* (o·····o) to time after fumigation of soils which were allowed to be recolonized naturally; the pathogen was added at 1,000 chlamydospores per gram to 1,500 g samples of soil taken every 7 days and tomato plants were maintained in the infested soil for 14 days under growth chamber conditions before infection incidence and the inoculum density of the pathogen were determined.

incidence of infection, the soil was washed from the roots; the roots and lower stems were soaked in 0.6% sodium hypochlorite for 1 min, rinsed in autoclaved deionized water, and plated on Komada's (9) medium, which is selective for *F. oxysporum*. The plates were examined after 10 days at 25 C, and plants were considered to be infected if *F. oxysporum* f. sp. *radicis-lycopersici* grew from the crown area of the seedling. The population density of the pathogen was quantified by dilution plating on Komada's (9) medium.

Treatment 2 was similar to Treatment 1 except that the entire 20 kg of soil was augmented with the antagonists 4 days after fumigation at 1,000 conidia of each antagonist isolate per gram of soil.

In Treatment 3, freshly fumigated soil was infested with the pathogen at 1,000 chlamydospores per gram of soil and placed in sealed plastic containers to inhibit recolonization by airborne microorganisms. At 7-day intervals a 1,500-g sample was removed and the pathogen population was determined by soil dilution plating on Komada's (9) medium. Infection incidence was determined as in Treatment 1 to quantify the pathogenic ability of the pathogen in soils not undergoing recolonization.

The ability of the pathogen to survive and infect the host in soils undergoing recolonization was determined in Treatment 4. Twenty kilograms of fumigated soil were placed uncovered in the greenhouse and uniformly infested with the pathogen at 1,000 chlamydospores per gram of soil. The soil was sampled every 7 days as in Treatment 3.

Treatment 5 was similar to Treatment 4 except that the antagonists' propagules were added at 1,000 conidia per isolate per gram of soil when the pathogen was added, 4 days after fumigation.

In Treatment 6, 20 kg of nonfumigated soil was infested with the pathogen and sampled every 7 days as in Treatment 3.

The experiment was repeated at least twice; 10 petri plates were used for each soil dilution and 48 tomato plants were used to determine the incidence of infection for each experiment.

RESULTS

Pathogen activity in soils undergoing recolonization (*Treatments 1 and 2*). The infection incidence of tomato by *F. oxysporum* f. sp. *radicis-lycopersici* was correlated with the final inoculum density of the pathogen in nonaugmented ($r = 0.99$) and antagonist-augmented ($r = 0.86$) soils when the pathogen was added at 1,000 chlamydospores per gram of soil to soil samples taken every 7 days during recolonization of fumigated soils. The highest infection incidence and the highest pathogen population densities occurred in soil samples infested with the pathogen 4 days after fumigation (Figs. 1 and 2). The incidence of infection eventually stabilized at approximately 1% in augmented and nonaugmented soils.

Populations of the pathogen after 2 wk incubation and infection incidence were correlated inversely ($r = -0.93$ and -0.90, respectively) with the natural logarithm of the total number of saprophytic fungal propagules detected in nonaugmented soils. The population density of the pathogen and the incidence of infection in nonaugmented soils decreased rapidly between 11 and 18 days after fumigation as natural populations of *Trichoderma* spp. increased 400-fold (Table 2).

The rate of immigration of naturally occurring fungal species was slower in soil augmented with antagonists (Table 3) than in nonaugmented soil (Table 2). Thirty-nine days after fumigation, *Cladosporium* spp. and a wet-spored *Mucor* sp. were the only species, other than the added antagonists, isolated from augmented soils; however, 10 different naturally occurring species, including *Trichoderma* spp. and *Penicillium* spp., were isolated from nonaugmented soils. Some species of fungi were isolated in freshly fumigated soil, but occurred less frequently with time. In nonaugmented soils *Cephalosporium* sp. and *Cylindrocarpon* sp. were not isolated later than 4 days after fumigation. Conversely, *Pythium* sp., *Syncephalastrum* sp., *Cunninghamella* sp., and *Rhizopus* sp. were not isolated from nonaugmented soils until 39 days after fumigation (Table 2).

The frequency of isolation of any particular species varied with time and treatment (Tables 2 and 3). *A. ochraceus* dominated augmented soils during the early stages of recolonization, and it accounted for 46% of the total number of propagules isolated 4 days after fumigation. The majority of the isolates from augmented soils 11 and 18 days after fumigation were *T. harzianum*. Beginning 18 days after fumigation, 80% of the total number of colonies were either *P. funiculosum* or *T. harzianum*. In augmented soils, the introduced species always accounted for at least 98% of the total number of fungi detected. The maximum number of fungal propagules during the recolonization of augmented or nonaugmented soils was similar (approximately 2×10^5 propagules per gram of soil).

Pathogen activity in recolonized or nonrecolonized soils (*Treatments 3 and 4*). The population of *F. oxysporum* f. sp. *radicis-lycopersici* in fumigated soils infested with the pathogen and placed in plastic containers to exclude naturally occurring recolonizers increased to 10^6 propagules per gram of soil after fumigation (Fig. 3), which was fivefold greater than the total fungal populations in any of the other treatments. By direct observation it was determined that the pathogen population consisted predominantly of microconidia. The infection incidence was approximately 100% for the duration of the experiment.

The pathogen population density increased and then decreased with time when the pathogen was added to the entire soil allotment of nonaugmented soil 4 days after fumigation (Figs. 3 and 4). The proportion of infected plants was not related to the population density of the pathogen in nonaugmented soils. When natural recolonization of fumigated soil was not inhibited, infection decreased with time and the population of the pathogen increased and then decreased (Fig. 4).

Pathogen activity in fumigated, augmented or nonfumigated soils (*Treatments 5 and 6*). When the pathogen was introduced into

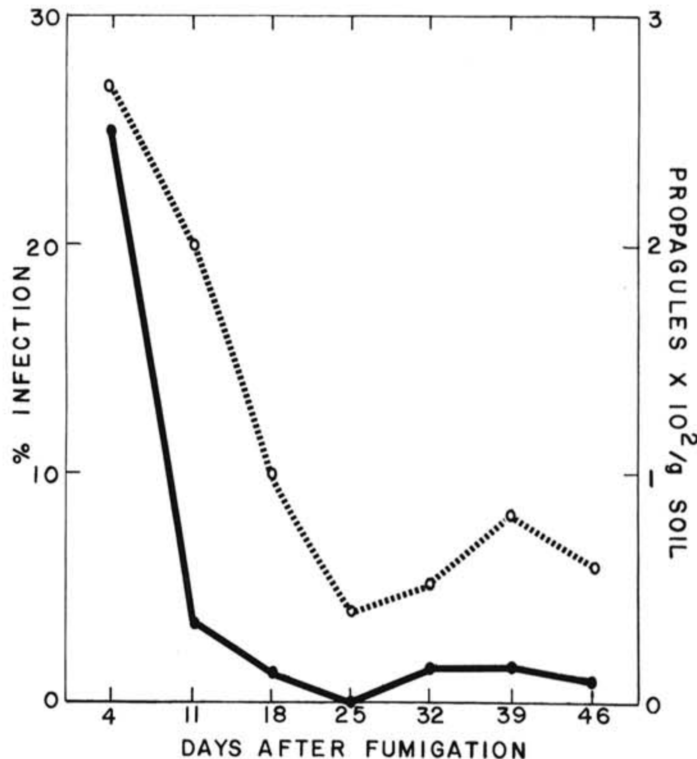

Fig. 2. The relationship of percent infection of roots of cultivar Bonnie Best tomato plants (●——●) and inoculum density of *Fusarium oxysporum* f. sp. *radicis-lycopersici* (o·····o) to time after fumigation of soils which were augmented with three isolates of *Trichoderma harzianum*, one isolate of *Aspergillus ochraceus*, and one isolate of *Penicillium funiculosum* 4 days after fumigation at 1,000 conidia of each isolate per gram of soil; the pathogen subsequently was added at 1,000 chlamydospores per gram to 1,500-g samples of soil taken every 7 days and tomato plants were maintained in the infested soil for 14 days under growth-chamber conditions before infection incidence and the inoculum density of the pathogen were determined.

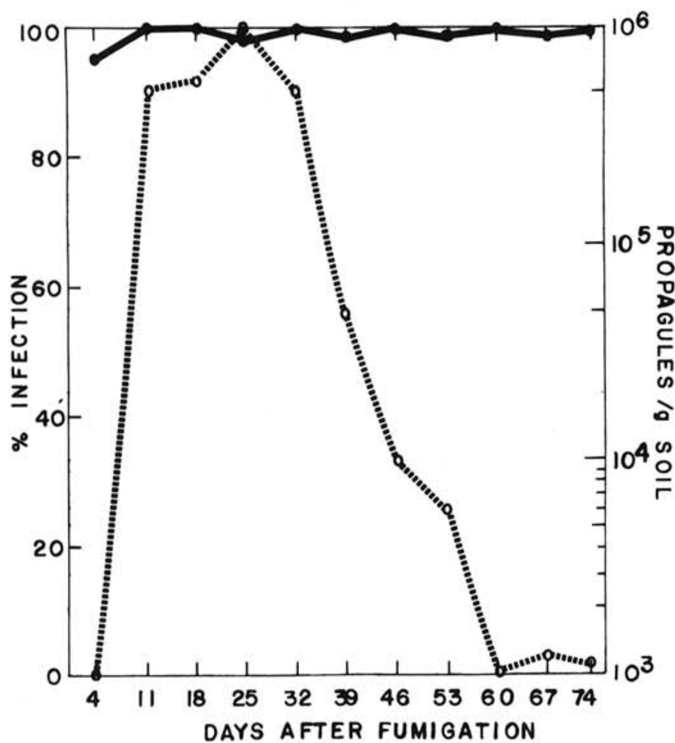

Fig. 3. The relationship of percent infection of roots of cultivar Bonnie Best tomato plants (●——●) and inoculum density of *Fusarium oxysporum* f. sp. *radicis-lycopersici* (o-----o) to time after fumigation of soils in which recolonization by other microorganisms was inhibited; the pathogen was added at 1,000 chlamydospores per gram of soil 4 days after fumigation.

soils that were either fumigated and augmented with the antagonists or nonfumigated, the pathogen populations remained relatively stable (Figs. 5 and 6). In fumigated, augmented soils the infection incidence increased to 44% 11 days after fumigation and then decreased to 23% by 39 days after fumigation. In nonfumigated soils the infection incidence remained relatively stable, and varied from 40 to 50% (Fig. 6).

DISCUSSION

Decreases in the saprophytic activity of *F. oxysporum* f. sp. *radicis-lycopersici* due to competition in naturally recolonized and artificially augmented soils similar to those observed in this study have been reported by other investigators (7,17); however, the compositions of the communities were not examined. In this study, the fungal recolonization of soils was monitored by soil dilution plating, and the theories of mechanisms of succession were invoked to explain why the pathogen population decreased when there was recolonization by other fungi.

In fumigated soils to which the pathogen was added every 7 days, there were negative correlations of infection incidence or inoculum density with the total number of fungi ($r = -0.89$ to -0.94). This agrees with Park's (16) conclusion that an organism is influenced by the entire soil community.

Saprophytic proliferation of the pathogen did not occur in nonfumigated soils. Nash et al (14) reported similar results when they added chlamydospores of *F. solani* f. sp. *phaseoli* to untreated soils. The lack of chlamydospore germination in natural soils was attributed to insufficient nutrients and the presence of inhibitory substances in the soil (21). Even though the saprophytic abilities of the pathogen were limited in nonfumigated soils, its pathogenic activities were greater than in fumigated and recolonized soil. This

TABLE 2. Populations of fungi that recolonized fumigated soils augmented with one isolate of *Aspergillus ochraceus*, one isolate of *Penicillium funiculosum*, and three isolates of *Trichoderma harzianum* at 1,000 conidia of each isolate per gram of soil 4 days after fumigation

	Propagules per gram of soil after fumigation[a]						
Fungi	4 days	11 days	18 days	25 days	32 days	39 days	46 days
Penicillium spp.	1.0	45.0	40.0	46.6	170.0	170.0	380.0
Trichoderma spp.		5.0	2,000.0	1,720.0	330.0	1,010.0	1,380.0
Aspergillus niger		0.1	0.5	0.8	0.3	0.3	4.3
Cladosporium spp.	5.0	12.5	6.5	8.5	9.0	10.0	28.2
Mucor spp.			0.2	0.6	0.8	0.9	0.3
Fusarium roseum			0.1	0.1	0.1	0.2	0.7
Phythium sp.						0.1	0.3
Rhizopus sp.						0.1	0.1
Cunninghamella sp.						0.1	0.1
Geotrichum sp.	0.2	5.0	2.5				
Cylindrocarpon sp.	0.1						
Cephalosporium sp.	0.1						
Fusarium solani			0.2				
Syncephalastrum sp.						0.1	1.0
Total	6.4	67.6	2,050.0	1,776.6	510.2	1,191.8	1,795.0

[a]Propagules (hundreds) per gram of air-dried soil detected in potato-dextrose agar which contained 1 ml of Tergitol NPX and 50 mg of chlortetracycline hydrochloride per liter of medium.

TABLE 3. Populations of fungi that recolonized fumigated, nonaugmented soils

	Propagules per gram of soil after fumigation[a]						
Fungi	4 days	11 days	18 days	25 days	32 days	39 days	46 days
Penicillium spp.	0.0	0.1	0.0	0.2	0.2	0.1	0.2
P. funiculosum	12.9	200.0	130.0	1,500.0	950.0	400.0	350.0
Trichoderma spp.	0.1	0.2	0.3	0.2	0.1	1.0	0.4
T. harzianum	7.3	333.0	400.0	1,350.0	110.0	723.0	430.0
A. ochraceus	17.4	250.0	27.0	19.0	23.0	213.0	62.0
Cladosporium spp.	0.2	1.2	8.0	14.6	10.0	6.6	
Mucor sp.	0.0	0.0	0.0	0.4	0.5	0.4	0.3
Total	37.9	784.5	565.3	2,884.4	1,093.8	1,344.1	852.4

[a]Propagules (hundreds) per gram of air-dried soil detected in potato-dextrose agar which contained 1 ml of Tergitol NPX and 50 mg of chlortetracycline hydrochloride per liter of medium.

phenomenon was termed induced antagonism by Welvaert (22). The practical aspect of induced antagonism is that it prolongs the effect of a soil treatment after the treatment is no longer active.

In fumigated soils in which recolonization was inhibited, the incidence of infection was nearly 100% for the duration of the experiments. The high infection incidence was attributed to the high population density of the pathogen and the high efficiency of the pathogen for host infection in the absence of competing organisms.

When the pathogen was maintained in nonaugmented soil, the pathogen population increased for 25 days and then decreased while the incidence of infection continued to decrease with time, due to the recolonization by naturally occurring organisms that reduced the pathogenic activities of the pathogen. At present, it is difficult to explain the results obtained when the pathogen was maintained in fumigated, augmented soils. The pathogen population was relatively stable, but the infection incidence increased and then decreased with time. The low incidence of infection 4 days after fumigation, when the pathogen and antagonists were first added, may have been due to antagonism by *A. ochraceus*, which was the predominant antagonist at that time. Perhaps the population of *T. harzianum*, which was dominant when the incidence of infection was high, was not as capable of restricting the pathogenic activities of the pathogen. The decrease in infection incidence with time may have been due to an effect of the combination of populations of *P. funiculosum* and *T. harzianum* during the later stages of recolonization.

The population density of the total number of fungi that were detected increased rapidly after fumigation and then decreased with time. Kreutzer (10) attributed the rapid increase in populations of recolonizing fungi to the availability of nutrients. Wilson (23) hypothesized that the rapid increase in organisms following fumigation or other severe perturbation was the result of growth at noninteractive stages of recolonization, when competition was low because of the large niche space available.

The changes in species composition and dominance in nonaugmented soils were attributed to different stages of recolonization. Fungal succession in treated soil has been the subject of several reviews (2,10,22). The succession usually is determined by the available carbon source (5). Also there are instances in which single species remain dominant during the entire exploitation of the substrate (3,6,11,20). This occurs when a species is introduced artificially at high inoculum densities to a substrate prior to colonization by other organisms, as in antagonist-augmented soils. Bruehl and Lai (3) reported that the advantage of prior colonization of wheat straw increased the competitive saprophytic ability of several fungi. The importance of prior colonization in soil systems is evident in these studies by the decreased immigration rates by naturally occurring fungal species in amended soils. In addition, when the pathogen was added to freshly fumigated soil, it was able to proliferate for up to 25 days after fumigation; conversely, when added to fumigated soils which had undergone recolonization for 25 days, it was unable to compete as a saprophyte.

The apparent contradiction between the results of this study and those reported in the literature regarding the occurrence of succession in natural soils but not in augmented soils, may be explained by examining different models of the mechanisms of succession, as proposed by Connell and Slatyer (4). In the facilitation model, which explains why secondary invaders are detected only after a plant pathogen has invaded the healthy tissue of the host, later species can become established only after earlier inhabitants have suitably modified the environment. According to the tolerance model, which is similar to Garrett's (5) model, species in a succession can become established because they can utilize nutrients at lower levels than earlier recolonizers. In the inhibition model, later species cannot become established until the death of the earlier species. The results of this study and those reported in the literature indicate that successions in artificially infested substrates follow the inhibition model, but that in nonaugmented substrates succession follows the tolerance model.

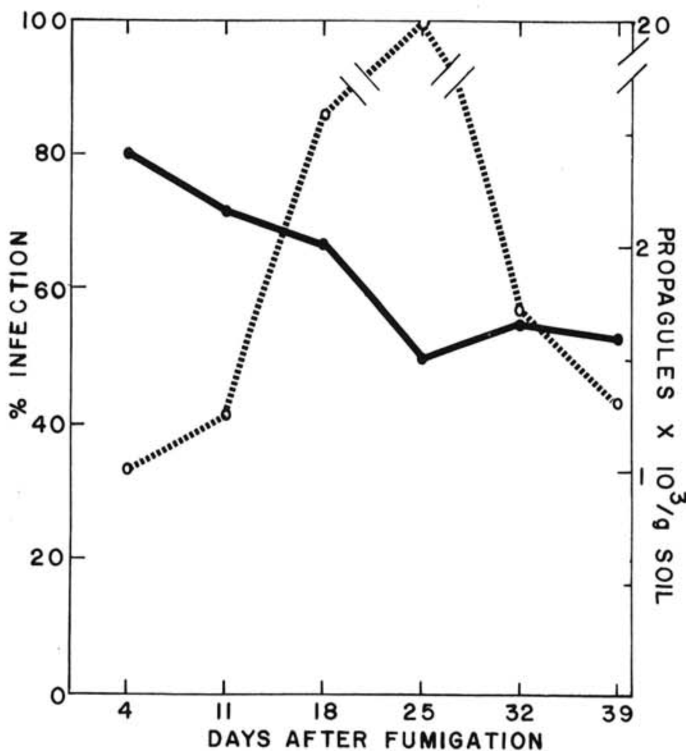

Fig. 4. The relationship of percent infection of roots of tomato cultivar Bonnie Best tomato plants (•——•) and inoculum density of *Fusarium oxysporum* f. sp. *radicis-lycopersici* (o----- o) to time after fumigation of soils in which recolonization by other microorganisms was not inhibited; the pathogen was added at 1,000 chlamydospores per gram of soil 4 days after fumigation.

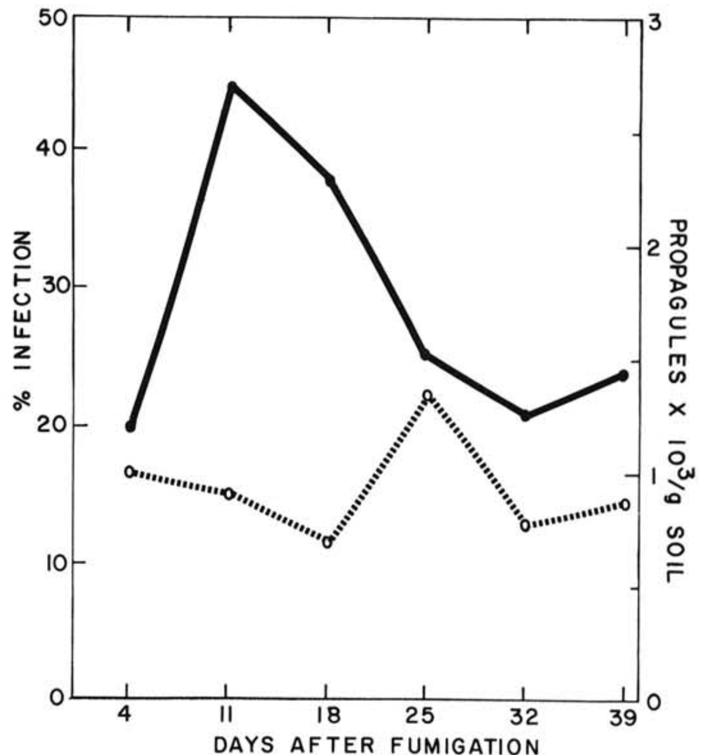

Fig. 5. The relationship of percent infection of roots of cultivar Bonnie Best tomato plants (•——•) and inoculum density of *Fusarium oxysporum* f. sp. *radicis-lycopersici* (o------o) to time after fumigation of soils which were augmented with three isolates of *Trichoderma harzianum*, one isolate of *Aspergillus ochraceus*, and one isolate of *Penicillium funiculosum* at 1,000 conidia of each isolate per gram of soil; the pathogen was added 4 days after fumigation at 1,000 chlamydospores per gram of soil.

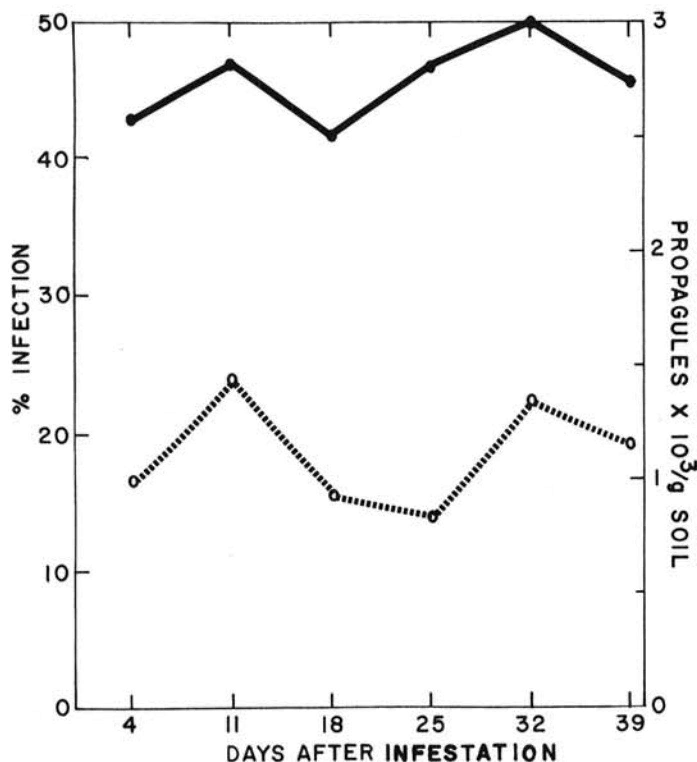

Fig. 6. The relationship of percent infection of roots of cultivar Bonnie Best tomato plants (•—— •) and inoculum density of *Fusarium oxysporum* f. sp. *radicis-lycopersici* (o-----o) to time in nonfumigated soils; the pathogen was added at 1,000 chlamydospores per gram of soil on day 4.

A basic principle of community ecology is that the success of a species, such as a plant pathogen, is dependent upon its ability to interact successfully with the abiotic and biotic factors of its environment. Because fumigation practices create an environment conducive to the proliferation of the pathogen, a possible means of control is to establish a community which is inhibitory to the pathogen in the treated soil. *F. oxysporum* f. sp. *radicis-lycopersici* is an r-selected species, as indicated by the rapid increase and then decrease of its population in the absence of other organisms in treated soil; therefore, its ability to compete as a saprophyte is dependent upon the total population density of all interacting soil microorganisms (15). The saprophytic proliferation of the pathogen was controlled by adding r-selected antagonists to freshly fumigated soil before the reinvasion of the pathogen could occur. By the application of the basic concepts of community ecology to the control of plant disease and the utilization of composites of antagonists, the success of biological control applications may increase, and disease control in the field may be realized more frequently.

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