Suppression of *Fusarium roseum* 'Avenaceum' by Soil Microorganisms

Y. S. Lin and R. J. Cook

Research assistant, Department of Plant Pathology, Washington State University; and plant pathologist, Agricultural Research, Science and Education Administration, U.S. Department of Agriculture, Washington State University, Pullman, WA 99164, respectively.

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ABSTRACT

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Fusarium roseum 'Avenaceum' is a highly virulent root pathogen of lentils, but severity of disease is suppressed by natural soil. The suppressive effect of natural soil was eliminated by moist heat (60 C for 30 min) treatment, but not by soil treatment with Bay 22555, pentachloronitrobenzine, or benomyl. Suppression was less apparent when the dosage of inoculum of Avenaceum was increased in soil. Within 8 wk the suppressivity gradually returned to heat-treated soil exposed to airborne contaminants; it returned immediately to treated soil amended with 1% (w/w) nontreated soil. The suppressive effect could not be attributed to induced host resistance. Instead, antagonists were shown to act against Avenaceum in the inoculum substrate in soil. Inoculum that had been buried 48–72 hr in nontreated soil, then transferred to heat-treated soil, no longer produced disease or supported growth of Avenaceum from the food base into the soil as did similar inocula from treated soil. Isolations from the inoculum substrate recovered from nontreated soil yielded species of common, fast-growing fungi; these included *Mucor plumbeus, Mucor hiemalis, Trichoderma viride,* and *Penicillium* spp. which singly and in combinations controlled lentil root rot caused by Avenaceum when added to treated soil. In contrast, several other isolates of soilborne fungi and bacteria did not control the disease. The inhibition of Avenaceum in the inoculum food base apparently was due to competition between Avenaceum and certain common, fast-growing fungi for the food base needed by Avenaceum to produce disease.

Additional key words: biological control.

Fusarium roseum Lk. ex. Fr. emend. Snyd. & Hans. 'Avenaceum' (hereafter called Avenaceum) is pathogenic to many crops, including subterranean clover (7), sweet clover, alfalfa (9), squash fruit (8), carnations (19), oats, wheat, grasses (4,5,11), and lentils (13). The root rot caused in lentils by Avenaceum was discovered first in eastern Washington in 1973, and was particularly common in crops following bluegrass (13). Usually, however, the disease is rare under field conditions. On the other hand, Avenaceum produces an extremely severe root rot of lentils if the soil is fumigated first with methyl bromide and then reinfested with the fungus (13). Apparently, the absence of root rot of lentils caused by this fungus in natural soil in eastern Washington is due to suppression associated with the soil microbiota.

The occurrence of more severe root disease in fumigated or heat-treated compared with nontreated soil is a well-recognized phenomenon (10). However, whether the soil microbiota affects the pathogen indirectly (for example, through increased host resistance) or directly (for example, through competition, antibiosis, or hyperparasitism) is known in only a very few cases. The lentil-Avenaceum system (13) offered a unique opportunity to investigate the mechanisms of suppression of a root disease by the soil microbiota because incidence of disease in treated soil (100% seedling blight) contrast sharply with that in nontreated soil (virtually no symptoms apparent except by close inspection of the lentil roots). The present study was undertaken to determine the mechanism(s) involved in the suppressive effect of untreated soil on root rot of lentils caused by Avenaceum.

MATERIALS AND METHODS

The pathogen. Avenaceum was isolated from diseased lentil plants sampled from the field. All cultures and transfers were single spored to maintain the wild (sporodochial) type and avoid the common laboratory (pionnotal) type. Inoculum for greenhouse and laboratory experiments was grown on autoclaved oat kernels or lentil stems in jars at 22 C for 2 wk in the laboratory, dried (on a laboratory table), ground to a coarse texture, and blended with the soils, generally at 0.1% (w/w).

The soil. All soils tested to date have been suppressive to Avenaceum. For the present study, we chose a Palouse silt loam collected from the top 20-cm of a lentil field cropped to wheat and lentils (in lentils at the time of collection) near Fairfield, Washington. The soil was blended, passed through a sieve (4 mm^2), and stored at 8–10% (−15 to −25 bars) moisture content (w/w) in a large can in the greenhouse until use.

Selective treatment of the soil. Steam-air treatment (2) of soil was used to eliminate organisms selectively. A double-walled Plexiglas cylinder containing 2 kg of soil was connected to a steam-air mixture to provide heat-treatment temperatures of 40, 50, 55, 60, 70, and 100 C for 30 min. After treatment, cool air was substituted for the steam-air to provide a rapid return to ambient temperature.

Chemicals also were used to selectively eliminate or inhibit the organism(s). Benomyl (methyl 1-[butylcarbamoyl]-2-benzimidazolecarbamate) was mixed (as active ingredient) at 0, 0.25, 0.50, 0.75, and 1.0 ppm into soil amended with 0.1% (w/w) oat inoculum. Pentachloronitrobenzene (PCNB as a 75% wettable powder) was added at 0, 0.25, 0.05, 0.10, and 1.0% (w/w) to similar soil. Bay 22555 [sodium *p*-(dimethylamino)-benzenediazosulfonate] was added as a drench to provide 110 ppm (active ingredient basis) in the soil in 10-cm-diameter clay pots. The drench was applied 24 hr before infestation of the soil with 0.1% oat inoculum.

Rating of suppressive effect. The suppressive effect of treated and nontreated soils was rated by counts of surviving plants of 24 test lentil plants in each treatment. The surviving plants included healthy plants, plants with slight lesions on their root system, and

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plants with the taproot destroyed but able to survive by production of secondary roots (12).

Return of suppressive effect to soil after pasteurization. Batches of heat-treated soil were amended at time zero with either sterile oats (0.1%, w/w), live oat inoculum (0.1%, w/w), or no inoculum and each batch was distributed among 16 pots. Seeds were then sown at 0, 2, 3, and 8 wk after soil treatment using four pots per sowing to determine the time required for a return of suppressiveness. Additional (fresh) oat inoculum (0.1%, w/w) was added at the time of planting.

In another study, soil was heat-treated at 60 C for 30 min, allowed to cool for 1 day, and then amended with 1% nontreated soil and 0.1% ground oat inoculum. Treated soil with oat inoculum only served as the control. The soil was distributed among four pots

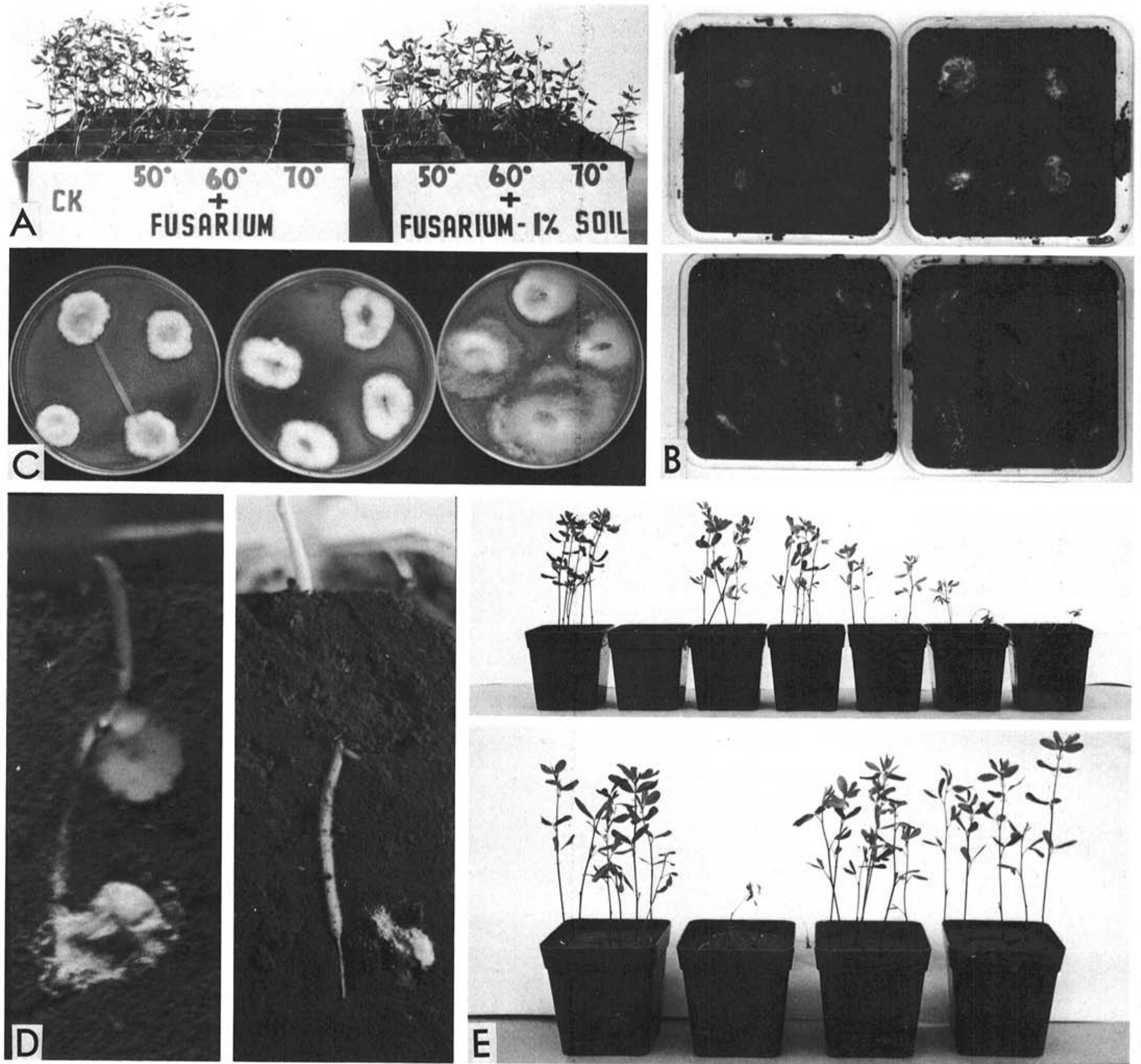

Fig. 1. Influence of microorganisms from soil on pathogenicity of *Fusarium roseum* 'Avenaceum' to lentil, and evidence that the suppressive effect of the microorganisms acts against the pathogen in the inoculum substrate. **A)** Elimination of the suppressive effect by heat-treatment of soil at 50, 60, or 70 C/30 min, and its restoration by mixing 1% (w/w) nontreated soil with 99% treated soil. All pots contained 0.1% (w/w) of oat inoculum of the pathogen. **B)** Saprophytic growth and associated sporodochia of *F. roseum* 'Avenaceum' from oat-kernel substrate (top row) and lentil-stem substrate (bottom row) in nontreated (left) and heat-treated (60 C/30 min) soil (right). **C)** Growth of *F. roseum* 'Avenaceum' from oat kernels buried for 48 hr in natural soil, then recovered and plated on PDA. From left to right: kernels not buried (Ck); kernels recovered from soil and surface sterilized before plating; kernels washed but not surface sterilized before plating. **D)** Damage to lentil seedlings caused by *F. roseum* 'Avenaceum' in heat-treated (60 C/30 min) (left) and natural (right) soils. Note that in the natural soil, the fungus made only limited growth and caused root rot only at the site of root-inoculum contact. In contrast, the fungus made extensive growth in the heat-treated soil, including along the root for 2 cm or more away from the oat inoculum, and killed the seedling. **E)** Influence of some soil saprophytes added to heat-treated (60 C/30 min) soil on the pathogenicity of *F. roseum* 'Avenaceum' (present in oat inoculum at 0.1%, w/w) to lentils. Top row, from left to right: natural soil (Ck), soil treated with moist heat at 60 C/30 min (Ck), *Trichoderma viride*, *Mucor* spp., *Penicillium verrucosum* var. *cyclopium*, *Penicillium decumbens*, and *Pseudomonas* spp. Bottom row, from left to right: untreated soil (Ck), heat-treated soil (Ck), nontreated soil, and a mixture of the above-named fungi.

per treatment, planted with 8-10 lentil seeds per pot and the number of surviving seedlings was determined after 21 days.

Influence of the soil microflora on saprophytic growth and pathogenicity of Avenaceum. Autoclaved oat kernels or lentil stems colonized by Avenaceum were placed in the bottoms of square petri dishes (9 × 9 × 1.3 cm) and covered with 125 g of either nontreated soil or heat-treated soil. The moisture was adjusted to about −0.5 bars with sterile water. The dishes were incubated at 10, 15, 20, 25, or 30 C. The saprophytic growth of Avenaceum was observed microscopically every other day through the clear bottom of each dish. In another test, lentil seeds were planted in the dishes and whole oat kernels infested with Avenaceum were placed at various distances from the lentil seeds to observe the effects of the soil on the attack of lentils by Avenaceum. The dishes were incubated on edge (vertically) so that downward growth of the root would enable it to make contact with the inoculum.

Isolation of candidate antagonists. Dilution plates were made with treated and nontreated soils on different media for bacteria and fungi as follows: Difco tryptic soy agar at 1/10 strength (15) for total numbers of bacteria; King's B Medium plus antibiotics (16) for *Pseudomonas* spp.; tryptone-glucose-yeast extract agar (18) for *Arthrobacter* spp.; Littman's oxgall agar (14) plus streptomycin for sporulating fungi; and Czapek-Dox agar for *Penicillium* spp. Isolations also were made to determine the organisms present in and near the oat inoculum after a brief burial in nontreated soil. Oat inoculum (whole kernel) was buried in nontreated soil for 3 days, then removed and washed with sterile water. The pieces of inoculum either were placed on potato-dextrose agar (PDA) immediately or surface sterilized for 30 sec in a 1:1 solution of sodium hypochlorite (5.25% active) and ethanol (95%) before being placed on PDA. To study bacteria associated with lysis of Avenaceum hyphae, a layer of nontreated soil was placed 1 cm deep in a petri dish over fragments of oat inoculum of Avenaceum on water agar (2%). After 1 wk the soil was shaken from the dish to expose hyphae that had grown into the soil near the organic fragments. A section of hypha, ascertained by microscopic examination to be undergoing lysis, was cut with a sharp scalpel and shaken in 10 ml of sterile water. Then serial dilutions were plated on tryptic soy agar, and the plates were incubated at room temperature.

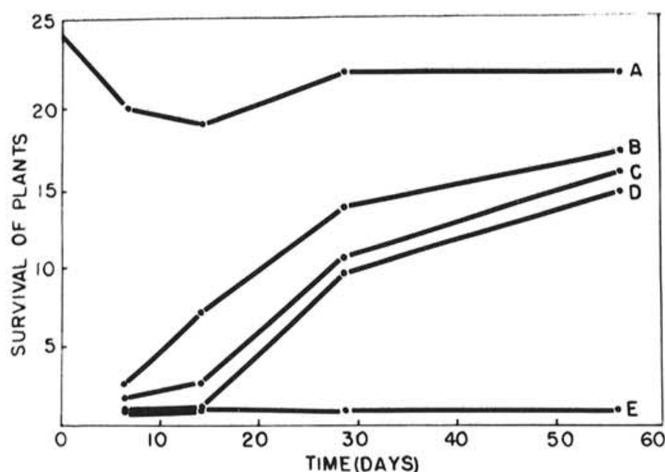

Fig. 2. Effect of airborne microorganisms on return of suppressiveness of soil to root rot of lentil caused by *Fusarium roseum* 'Avenaceum'. One sample of soil (A) was nontreated and the others (B, C, D, and E) were treated with steam-air at 60 C/30 min and then cooled (zero time). The soil was amended at zero time with 0.1% sterile oats (B), oat-inoculum containing the pathogen (C and E), or no amendment (D). A-D were exposed to greenhouse air, while E was kept moist but protected from greenhouse air in a closed Plexiglas cylinder without additional watering. Fresh oat inoculum containing the pathogen was added (0.1%, w/w) to all soils and 24 lentil seeds planted at 1, 2, 4, and 8 wk after treatment. The number of surviving plants was counted 21 days after planting.

Tests for the effect of antagonists on Avenaceum. In tests for the effect of antagonists on saprophytic growth of Avenaceum, whole-kernel oat inoculum was immersed in a spore or cell suspension of the candidate antagonist for 30 min, and the subsequent saprophytic growth of Avenaceum from the kernels was then checked by observing the "contaminated" kernels in heat-treated (60 C for 30 min) soil. In another test, Avenaceum was seeded and allowed to grow for 1 wk at the edge of a petri dish containing PDA; a candidate antagonist was seeded at the opposite edge of the petri dish as a test for inhibition of growth of Avenaceum. In tests for inhibition of Avenaceum, each candidate antagonist was grown in autoclaved soil for 1 wk, and this soil inoculum together with ground oat inoculum of Avenaceum were mixed with treated (60 C for 30 min) soil at 1% (w/w) and 0.1% (w/w), respectively. Lentil seeds were planted immediately, and the pots were incubated in a growth chamber at 10–15 C.

RESULTS

Suppressive effect of nontreated soil. Disease was suppressed in lentil plants in nontreated soil when oat inoculum of the pathogen was used at 0.1% (w/w) or less. The use of higher concentrations (0.25 and 0.5%, w/w) of oat inoculum in nontreated soil resulted in some disease. In contrast, most plants grown in treated (60 C for 30 min) soil amended with 0.1% oat inoculum were killed in the seedling stage. Use of colonized lentil stems with Avenaceum as inoculum produced results like those obtained with oat-kernel inoculum.

Elimination and restoration of suppressive effect in soil. None of the chemicals tested altered the suppressive effect of the soil. When soil was treated with steam-air for 30 min, the suppressive effect was eliminated at 60 C and above, was reduced by 55 C, but was not affected by 45 or 50 C (Fig. 1A).

The addition of only 1% (w/w) of nontreated soil restored suppressiveness to the heat-treated soil (Fig. 1A). Moreover, the suppressive effect of treated (60 C for 30 min) soil gradually returned within 56 days when the soil was incubated in the open air (Fig. 2), although the suppressive effect was not as strong as that of the original nontreated soil. In contrast, the suppressive effect of treated soil stored in closed containers never returned during the 56 days of the study (Fig. 2).

Effect of the microflora acting through the host or directly on inoculum of the pathogen. Lentil seedlings were grown in natural soil, heat-treated soil (60 C for 30 min), or vermiculite for 3–5 days, removed, washed with sterile water, and transplanted into either treated or nontreated soil amended with 0.1% oat inoculum. All seedlings transplanted to nontreated soil survived. In contrast, all seedlings transplanted to treated (60 C for 30 min) soil were killed, regardless of whether they were grown first in treated or nontreated soil.

In an otherwise similar experiment, whole-kernel oat inoculum was substituted for lentil plants. Inoculum buried first in nontreated soil for 3 days, then washed with tap water and transferred to treated soil caused no disease. In contrast, inoculum buried first in treated soil for 3 days then transferred to other treated soil killed all 24 test plants.

Avenaceum grew from a fresh oat or lentil-stem substrate into treated soil, but not into nontreated soil (Fig. 1B). In the nontreated soil, the fungus at first made only sparse growth and only at 10–20 C. Not only was Avenaceum inhibited in growth from the substrate, but the few hyphae that were produced lysed subsequently. Of infested oat kernels incubated in natural soil for 48 hr and subsequently buried in freshly treated soil, growth occurred only from those that were surface sterilized before reburial in treated soil; washing the kernels without surface sterilization did not remove contaminating organisms and did not facilitate recovery of Avenaceum. However, when either washed or surface-sterilized kernels were plated on PDA, Avenaceum was recovered easily (Fig. 1C).

In treated soil seeded with lentils, the fungus grew from the oat inoculum, grew along the lentil root, eventually made contact with the seed, and killed the plant (Fig. 1D). This sequence occurred even when the oat inoculum was as much as 2 cm below the seed. In

contrast, in nontreated soil the fungus grew no further than the initial contact site on the root and even this contact occurred only when the growing taproot actually reached the inoculum in nontreated soil (Fig. 1D). The root in nontreated soil was decayed at the contact site, but secondary roots from the upper part of the taproot kept the plant alive. Only when the inoculum was placed immediately beneath the seed did Avenaceum kill the plant in natural soil.

Effect of candidate antagonists on saprophytic growth and pathogenicity of Avenaceum. Neither the bacterial isolates tested nor the *Cephalosporium* sp. slowed the saprophytic growth of Avenaceum from oat inoculum (Table 1). In contrast, the pathogen made no saphrophytic growth from the oat substrate when the test antagonists were *Trichoderma viride* Pers. ex Fr. or *Mucor hiemalis* Wehm. and only limited growth when *Mucor plumbeus* Bon was the test antagonist. Two *Penicillium spp.* provided slight inhibition of saprophytic growth.

In the disease severity tests, the *Trichoderma, Mucor,* and *Penicillium* spp. all provided sufficient protection to keep at least some of the seedlings alive for the entire 21-day test (Table 1). *Trichoderma viride* gave the best protection. None of the bacteria or the *Cephalosporium* sp. kept the seedlings alive for 21 days. The greatest supression of disease occurred with a mixture of *Trichoderma, Mucor,* and *Penicillium* spp.; this mixture restored as much suppressiveness as did 1% nontreated soil added to treated soil (Table 1, Fig. 1E). Every candidate antagonist [*T. viride, M. plumbeus, M. hiemalis,* and *Penicillium verrucosum* Dierchx. var. *cyclopium* (Westling) Sampson et al] that was tested grew into the target colonies of Avenaceum on PDA, but none produced an antibiotic reaction.

DISCUSSION

The failure of Avenaceum to cause severe root rot in natural soil apparently results from an invasion of the inoculum substrate by common species of fast-growing saprophytic fungi. When these fungi were eliminated by a steam-air treatment (55 C/30 min or greater), and the treated soil subsequently was amended with oat-inoculum of the pathogen, Avenaceum persisted as virtually the sole occupant of the substrate. When the substrate was used as a food-base, Avenaceum was capable of extensive saprophytic growth through soil and over the host surface and of total destruction of the host. Tests for evidence of increased host resistance caused by the soil microbiota, or for an effect of the rhizosphere microbiota on the pathogen all were negative. The suppression of Avenaceum in natural soil operated whether or not the host was present.

The return of suppressiveness to heat-treated soil resulted from airborne invaders and also from addition of 1% nontreated soil, but not from multiplication of organisms that survived the treatment. The suppressive effect thus returned in the absence of and presumably was independent of the pathogen. These findings, and the fact that either methyl bromide fumigation (13) or heat treatment destroyed the suppressive effect of the soil all indicate that the effect is microbial, can be transferred, and is not due to actinomycetes or to spore-forming bacteria (1,17). None of the bacteria tested reduced either saprophytic growth or pathogenicity of Avenaceum. The only positive results were with common, fast-growing fungi, namely *T. viride, M. hiemalis, M. plumbeus,* and possibly *Penicillium* spp. These also are the organisms most likely to reinvade soil from airborne propagules which can account for the gradual return of suppressiveness to soil exposed to air.

The colonization of inoculum substrate by *T. viride, M. hiemalis,* and *M. plumbeus* (and probably other fungi) reduced the effectiveness of Avenacum as a pathogen, but did not kill the pathogen or even replace it in the substrate. Surface sterilization of the inoculum fragments or removal of the outer layers with a scalpel resulted in 100% recovery of Avenaceum on PDA. All tests for an antibiotic effect of the antagonists were negative. Moreover, it seems unlikely that such unrelated fungi as *T. viride,* and *Mucor* species could all accomplish the same antibiotic or hyperparasitic effect. The common features of these fungi are rapid growth and rapid use of sugars and other readily available nutrients. The mechanism of antagonism is thus probably competition for the food base and not antibiosis or hyperparasitism.

Only 0.1% (w/w) ground oat inoculum of the pathogen added to treated soil resulted in total destruction of lentils in the seedling stage. This is not an extraordinary amount of inoculum, but shows the value of a food-base to production of disease by a soilborne pathogen (10). The inability of Avenaceum to produce disease of lentils when it is in the substrate as a coinhabitant with other fungi

TABLE 1. Effect of various candidate antagonists on the pathogenicity to lentils and saprophytic growth of *Fusarium roseum* 'Avenaceum' in soil previously treated at 60 C/30 min with steam-air mixture

Candidate antagonists	Source of isolations	Pathogenicity tests[a] survival of plants at days after planting			Mycelial growth[b] after 6 days at 20 C (mm)[c]
		7 days (no.)	14 days (no.)	21 days (no.)	
Control (treated soil only)		23	3	0	6.0
Mixture of *Pseudomonas* spp.	Rhizosphere area of lentils and soil	19	5	0	5.6
Mixture of *Arthrobacter* spp.	Soil	21	7	0	6.1
Isolate BOI-1 of bacterium	Lysed hypha	22	11	0	5.8
Isolate BOI-2 of bacterium	Lysed hypha	22	5	0	5.5
Cephalosporium sp.	Soil	21	4	0	6.0
Mucor plumbeus plus *Mucor hiemalis*	Oat inoculum in nontreated soil	20	12	8	...
Mucor plumbeus		...	...	...	2.0
Mucor hiemalis		...	...	...	0.0
Penicillium verucosum var. *cyclopium*	Soil	19	4	3	3.2
Penicillium decumbens	Heat-treated soil	20	9	9	5.2
Trichoderma viride	Contaminated heat-treated soil	22	18	14	0.0
Mixture of fungi[d]		23	17	15	...
Nontreated soil (1%,w/w)		24	20	18	...
Nontreated soil (100%)		23	22	22	0.0

[a] Each antagonist was grown in autoclaved soil, and then this colonized soil was added to heat-treated soil together with oat inoculum of the pathogen at 1% and 0.1% (w/w), respectively. Number of surviving plants are out of 24 plants at time zero.
[b] Oat inoculum coated with spore or cell suspension of candidate antagonists.
[c] Each number is the average radial growth of 20 oat inoculum of Avenaceum.
[d] *Mucor plumbeus, Mucor hiemalis, Penicillium* spp., and *Trichoderma viride* were mixed together in "soil inoculum".

can be explained in terms of the inoculum potential concept of Garrett (10). In essence, the coinhabiting fungi reduced "the energy of growth available for infection of at the surface of the host organ to be infected" (10).

Bruehl (6) reviewed some of the mechanisms used by pioneer colonists of a substrate to defend their substrate (a crop residue) against would-be colonists from the outside. Apparently Avenaceum is a weak defender of lentil roots and oat-kernel fragments against *T. viride* and *Mucor* species. On the other hand, under different soil conditions or on a different substrate, Avenaceum might be more successful in keeping possession of its substrate. The severe losses of lentil seedlings following blue grass (13) may be related not only to an abundance of Avenaceum in the blue grass residue but also to a greater capacity of Avenaceum to persist as sole occupant in such residue. More work on the mechanisms of possession of residue by Avenaceum, or by soilborne pathogens generally, and on means to weaken the possession could lead to more success in biological control of soilborne plant pathogens.

Toussoun (20) indicated that the examples of *Fusarium*-suppressive soils known to date are of the type in which *Fusarium* will not become established. He indicated further that the suppressiveness probably is due to the biological factors associated with the soil on formation or persistence of the chlamydospores. Avenaceum produces chlamydospores in the cortical tissue of lentil roots (Lin and Cook, *unpublished*) and presumably they become scattered in soil after the complete decomposition of lentil roots. Whether the longevity of these chlamydospores varies with the soil as described by Toussoun (20) for certain other *Fusarium* species is not known. Regardless of this, the persistence or longevity of chlamydospores is not the relevant consideration in explaining the suppressive effect of natural soil on root rot of lentils caused by Avenaceum. We believe instead that Avenaceum is unable to tolerate competition for the food base by the common, fast-growing, saprophytic fungi which are present in most if not all soil. This difference may explain why, with the examples reviewed by Toussoun (20), both conducive and suppressive soils are known, but with root rot of lentil caused by Avenaceum, only suppressive soils are known to date.

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