Colonization of Soybean Seeds and Plant Tissue by *Fusarium* Species in Soil

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ABSTRACT

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Emergence of soybean (*Glycine max*) seedlings was greatly reduced in a sandy loam soil naturally infested with $5-10 \times 10^3$ propagules of *Fusarium* per gram and kept at −15 bars matric potential for 4–6 days before it was watered to a level sufficient for seed germination. Treatment of the soil with both benomyl and fenaminosulf restored seedling emergence to 80%, whereas fenaminosulf alone did not. Emergence of seedlings was significantly reduced in fumigated soil infested with *Fusarium solani*, *F. tricinctum*, *F. moniliforme* 'Subglutinans,' or *F. oxysporum* and when seeds were incubated in the soil at −15 bars for 6 days before watering. Incubation of sterilized and unsterilized dead plant tissue pieces in field soil at −0.01 to −0.02 and −1.8 bars resulted in a twofold to 32-fold increase in the number of Fusarium propagules in the soil. The increase in propagules was confined to within 3 mm of the tissue surface, after 16 days. Incorporating soybean plant residues into the upper 3 cm of soil in a field in October increased the number of propagules of *Fusarium* in the bulk soil over a 5- to 6-mo period, but after 7–8 mo the population did not differ from that in unamended soil.

During investigation of the causes of a preemergence seedling rot of soybean (*Glycine max* (L.) Merr.) in sandy soils of southwest Michigan, *Fusarium* spp. were among the fungi implicated. One or more *Fusarium* spp. were always isolated from lesions on diseased seedlings (23) and Fusarium root rot occurred on surviving plants in areas where diseased plants had died. Isolates of *F. oxysporum* that produce root rot symptoms also cause poor seed germination and stunted seedlings (6). Seeds infected with *Fusarium* also may have poor emergence (15). Although *Pythium ultimum* Trow was subsequently found to be mainly responsible for the seedling disease (23), it was worthwhile to study the ability of *Fusarium* to cause decay in soybean seedlings and to colonize dead plant debris.

Fusarium root rot of soybean, which is caused by *F. oxysporum* (Schlect.) emend. Snyd. & Hans., is widespread in Michigan and is manifested primarily under hot and dry conditions (J. L. Lockwood, *unpublished*). In this respect, it may be similar to foot, root, stem, and seedling diseases caused by *F. roseum* Lk. emend. Snyd. & Hans. and *F. solani* (Mart.) Appl. & Wr. emend. Snyd. & Hans., which are associated with dry soils (20).

Various species of *Fusarium* also colonize dead plant tissue in soil (2,8,9,27). However, there have been few reports dealing with the influence of such colonization on the inoculum density of *Fusarium* in the soil and none to our knowledge on the influence of such colonization on the population density of Fusarium isolates pathogenic to soybean.

Since *Fusarium* spp. colonize dead plant tissue and are often seedborne in soybean (13,15,19), we tested the ability of different *Fusarium* spp. to colonize and decay seed and to saprophytically colonize plant tissue.

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MATERIALS AND METHODS

Estimation of population of *Fusarium*. Komada's Fusarium-selective medium (14) was used to enumerate population densities of *Fusarium* in bulk soil associated with plant tissue by using standard dilution plate techniques. The number of Fusarium propagules per square centimeter of surface area of plant tissue pieces was determined by mincing premeasured stem pieces in water agar (0.075%) with a Waring Blendor and plating the slurry onto the selective medium. The plates were incubated in plastic bags on a laboratory bench at 23 ± 2 C under ambient light (600–800 lux during the day). After 5–7 days, colonies were tentatively identified on the plates (25). Specific isolates were identified by either Paul E. Nelson (Department of Plant Pathology, Pennsylvania State University, University Park 16802) or Lester W. Burgess (Department of Plant Pathology, University of Sydney, Sydney, N.S.W. 2006, Australia).

Isolates were maintained on potato-dextrose agar (PDA) at 5 C in screw-capped vials or on sterile, propylene oxide-treated (10), soybean pods at 23 ± 2 C. Pathogenicity of isolates was evaluated in 2.5 × 12-cm polystyrene tubes (22). Tukey's *w* procedure ($P = 0.05$) was used to determine significance between means unless otherwise indicated.

Propylene oxide treatment of soil, seeds, and dry plant tissue. One liter of moist soil (moisture approximately −0.4 bar) was disinfested by incubation for 2 days in a 1.9-L glass jar containing 2

ml of propylene oxide. The jar was opened, aired under a fume hood overnight, and the soil was dried in a forced-air oven at 35 C.

Soybean seeds of cultivar Hark, disinfested with propylene oxide (24), were used throughout this study. After treatment, 3% of the seeds yielded *Fusarium* spp. when plated on Komada's selective medium.

Mature soybean stem pieces ($3.0 \pm 0.5 \times 0.4 \pm 0.2$ cm) were treated twice with propylene oxide (10) with a 24-hr airing period between treatments. No fungal contaminants were found when samples of the treated stem pieces were plated on Komada's medium and on PDA.

Soil characteristics and matric potential determinations. Unless otherwise indicated, the soil was a sandy loam that has been previously described (23). Soil matric potential values were estimated based on a drying soil moisture-matric potential curve by using a −15 bar ceramic plate extractor (Soilmoisture Corp., Santa Barbara, CA 93105). After determination of a soil moisture-matric potential curve, a given soil matric potential was established by atomizing water onto the dry soil in a plastic bag with frequent shaking until a predetermined soil moisture percentage was reached. Since the soil was calibrated by using a drying curve, soil hysteresis will cause an error in relating these values to percent moisture when dry soil is moistened from −0.2 to −0.01 bar; therefore, only a range of values will be given where appropriate (17).

Preemergence rotting of soybean seeds by *Fusarium*. Twenty disinfected seeds were planted 2.5 cm deep in soil at specified matric potentials in a plastic tray ($19.6 \times 9.7 \times 5.5$ cm), double-bagged in plastic and incubated at 24 C. At intervals of 0 to 6 days, the seeds were removed, the soil was moistened to −0.24 bar and the seeds were replanted in the same soil. There were three replications over time per experiment unless indicated otherwise.

Benomyl (methyl 1-[butylcarbamoyl]-2-benzimidazolcarbamate) was used to control *Fusarium* spp. in soil (11). Fenaminosulf (sodium [4-(dimethylamino)phenyl]diazene sulfonate) (11) was used routinely to control Pythiaceous fungi that frequently interfered with soybean seed germination in moist soil. Aqueous suspensions of the chemicals were atomized into the soil, which was allowed to dry on paper toweling. Final concentrations were 30 mg fenaminosulf or 300 mg benomyl (active ingredient) or both per kilogram of soil.

Soil used in pathogenicity tests was prepared by adding 5 ml of water to 1- to 2-wk-old cultures of *Fusarium* on PDA and sprinkling the conidial suspension onto dry, disinfested soil until the moisture was approximately −0.5 bar matric potential. This soil was stored at 23 ± 2 C in a plastic bag for at least 1 wk before it was allowed to air-dry. The population density of *Fusarium* was determined after drying. Soil was then diluted with disinfested soil so that a population density of 3,000 propagules per gram (ppg) of soil was established.

Survival in nonsterile tissue in the field. Survival of *Fusarium* in infected host tissue was studied by burying six mature soybean root tissue pieces ($\sim 2.5 \times 0.5$ cm) with Fusarium root rot symptoms in 250 ml of soil (naturally infested with *Fusarium*) in nylon mesh bags (320-μm meshes). The bags were placed on the soil surface or at depths of 8 or 15 cm. Three small plots within the field were used as blocks. Separate bags of soil containing tissue pieces (~2.5 cm long) of either mature corn stalks, wheat stems, soybean pods or soybean stems without Fusarium rot symptoms were buried 15 cm deep.

Influence of soybean residues on population density of *Fusarium* in field soil. In September, 2 wk after a soybean crop had been harvested and the soil disked, small portions of the soil were sieved (4-mm mesh) to remove plant residues. This sieved soil constituted the low-residue treatment. The residues that were retained on the sieve were added to the unsieved field soil and buried in nylon bags (800 g/bag) 15 cm deep in the field, constituting the high-residue treatment. Unsieved field soil was used as the medium residue soil. After 7 and 9 mo, the residue pieces were removed by sieving (4-mm mesh), and populations of *Fusarium* in the soil were determined. In another set of experiments the same partitioning of residues was followed but the residues were incorporated into the top soil (~3 cm deep) by hand raking. The plots were established on October 29 and soil samples were taken 5.5, 6, 7, and 8 mo later.

Saprophytic colonization of disinfected tissue. Two disinfected soybean stem pieces (2.5×0.5 cm) were placed in 200 g of soil at −0.01 to −0.02 and −1.8 bar matric potential in plastic cups (530 ml), which were placed in plastic bags in an incubator at 20 C. The stem pieces were removed after 8, 16, and 32 days. Population densities of *Fusarium* associated with the tissue pieces and the adhering soil (~10 g soil) were then determined as described before. Each stem constituted a subsample, and the experiment was repeated twice for a total of three blocks.

To determine the sphere of influence of the tissue pieces on the population of *Fusarium*, disinfected soybean stem pieces were placed horizontally in a pan of soil (−1.8 bars) at 20 C, and covered to a depth of 1 mm. The pan was placed in a plastic bag to reduce evaporation. After 16 days, the soil was moistened with an atomizer, and sections were removed with a razor blade at marked distances from the stem pieces for population determinations.

RESULTS

Preemergence rotting of soybean seeds. Soybean seeds were placed in nonsterile soil at −15 bars for 0–6 days before watering to a level sufficient for germination. Emergence was reduced from 82% in the control to 24 and 4% when exposed to dry soil for 4 and 6 days, respectively (Fig. 1). Two days of incubation in dry soil before watering did not reduce emergence. Isolates of *Fusarium oxysporum* accounted for 86% of the *Fusarium* spp. isolated from seed buried 6 days.

The same sample of soil was treated with fenaminosulf or with fenaminosulf and benomyl in another experiment. The seeds were again left in soil at −15 bars for 4 and 6 days before watering. Germination in the fenaminosulf-treated soil after 4 days (32%) and 6 days (17%) was significantly less than that in soil treated with fenaminosulf + benomyl after 4 days (80%) and 6 days (83%).

In another experiment, fresh nonsterile soil was used for each replication at soil moistures of 4.8, 4.2, 3.5, 3.0 and 2.5% (−2, −4, −8, −16 and <−16 bars, respectively). Use of fresh soil eliminated any influence on populations of *Fusarium* due to continuous plantings. After 6 days the seeds held at 2.5% soil moisture in fenaminosulf-treated soil had 42% emergence compared to the mean of 89% for seeds in soil at the other soil moisture treatments. At moisture levels of 4.8, 4.2, 3.5, and 3.0%, emergence in soil treated with fenaminosulf + benomyl was not significantly greater (range, 90–97%) than that in soil treated with fenaminosulf alone (range, 83–93%).

A sandy-loam soil collected from another farm, and which had a Fusarium population density of 2.1×10^3 ppg, was treated with fenaminosulf or fenaminosulf + benomyl before the soil moisture was adjusted to 2.5% and seeds were planted. Seeds were left in the soil for 8 days before watering. Those planted in soil treated with benomyl + fenaminosulf germinated significantly better (95%) than those in soil treated with fenaminosulf alone (71%).

Seven isolates of *Fusarium* were tested singly for ability to rot soybean seeds planted in soil at −15 bars for 6 days. All the isolates produced seedling disease indices of greater than 2.0 in a possible range of 0–5, with 5 indicating a dead plant (22). Emergence of seed planted in propylene oxide-treated soil at −15 bars was 93%. Emergence in soil infested with one isolate of *F. oxysporum* and two isolates of *F. solani* (Mart.) Appel & Wr. emend. Snyd. & Hans. was 85%, which did not differ significantly from 93%. One isolate of each of the following fungi significantly reduced germination to the indicated levels: *F. solani*, 40%; *F. tricinctum* (Cda.) emend. Snyd. & Hans., 53%; *F. moniliforme* 'Subglutinans' Sheldon, 72%; *F. oxysporum*, 80%.

Survival of *Fusarium* associated with nonsterile tissue. The number of propagules of *Fusarium* in the surface soil (0–3 cm) of a soybean field did not change significantly over a 9-mo sampling period. Counts were as follows: September, 4.8×10^3; October, 6.0×10^3; April, 7.6×10^3; June, 3.9×10^3 ppg. There were no significant differences in the proportions of different *Fusarium* spp. recovered over the same period; ie, *F. oxysporum* accounted for a

mean 80.8% of the Fusarium colonies; *F. solani*, 15.5%, and other *Fusarium* spp., 3.7%. However, the number of propagules in Fusarium-infested mature soybean root pieces that were placed on the soil surface increased significantly ($P = 0.10$) in October. Values were as follows: September, 5.2×10^3; October, 7.9×10^4; April, 1.0×10^4; June, 9.4×10^3 per cm^2 of root surface. The proportion of different *Fusarium* species recovered from the root tissue pieces did not change over the sampling periods; ie, *F. oxysporum* accounted for a mean of 92% of the colonies, which is similar to the 84% reported by Ferrant and Carroll (7). *Fusarium solani* accounted for 6.2% and other *Fusarium* spp., 1.8%. No differences were detected in the pathogenicity to soybean seedlings of 40 isolates of *F. oxysporum* obtained from buried root tissues and 40 isolates from soil (disease indices of 2.0 and 2.4, respectively, on a scale of 0–5).

After 9 mo, the population density of *Fusarium* in soil adhering to soybean root pieces incubated 0–3 cm deep was four to five times greater than that of similar pieces incubated at the 8- and 15-cm depths (Table 1). The population densities in the soil that adhered to the root pieces were 6–23 times higher than those in soil apart from the root pieces. Pieces of mature corn stalks, wheat stems, soybean stems and pods, and soybean roots with Fusarium root rot were buried 15 cm deep in the field. The population density of *Fusarium* in the soil adhering to these tissue pieces, after 9 mo of burial, was 6–27 times higher than that of soil not associated with the tissue pieces (Table 2). Twenty isolates of *F. oxysporum* were obtained from soil adhering to each tissue type and their pathogenicities were compared with isolates from field soil. No significant differences in pathogenicity were detected among the isolates as reflected by their seedling disease indices (soybean pods, 2.0; soybean stems, 1.5; corn, 2.1; wheat, 1.9; and field soil, 1.7).

When soybean residues were raked into the soil surface in late October, the Fusarium population at the first sampling 5.5 mo later was significantly higher in the medium (8.5×10^3 ppg) and high-residue soils (9.5×10^3 ppg) than in the low-residue soil (4.3×10^3 ppg). After an additional 3 wk the population density of *Fusarium* in the high-residue soil (4.9×10^3 ppg) was significantly higher than that in the low (2.6×10^3 ppg) and medium (2.7×10^3 ppg) residue soils. Treatment means did not differ significantly in samples taken 4 and 7 wk later. By contrast, when soybean residues were buried 15 cm deep, the populations of *Fusarium* in sieved soil were not changed after 7 or 9 mo. Low-residue soil had a Fusarium population density of 5.6×10^3 ppg; unaltered field soil, 6.2×10^3 ppg; and high-residue soil, 4.4×10^3 ppg.

Saprophytic colonization of disinfested tissue. To determine whether *Fusarium* spp. could colonize tissue pieces that did not contain *Fusarium* or other fungi, disinfested soybean stem pieces were added to field soil in the laboratory and incubated for 8, 16, and 32 days at −0.01 to −0.02 and −1.8 bars matric potential (Table

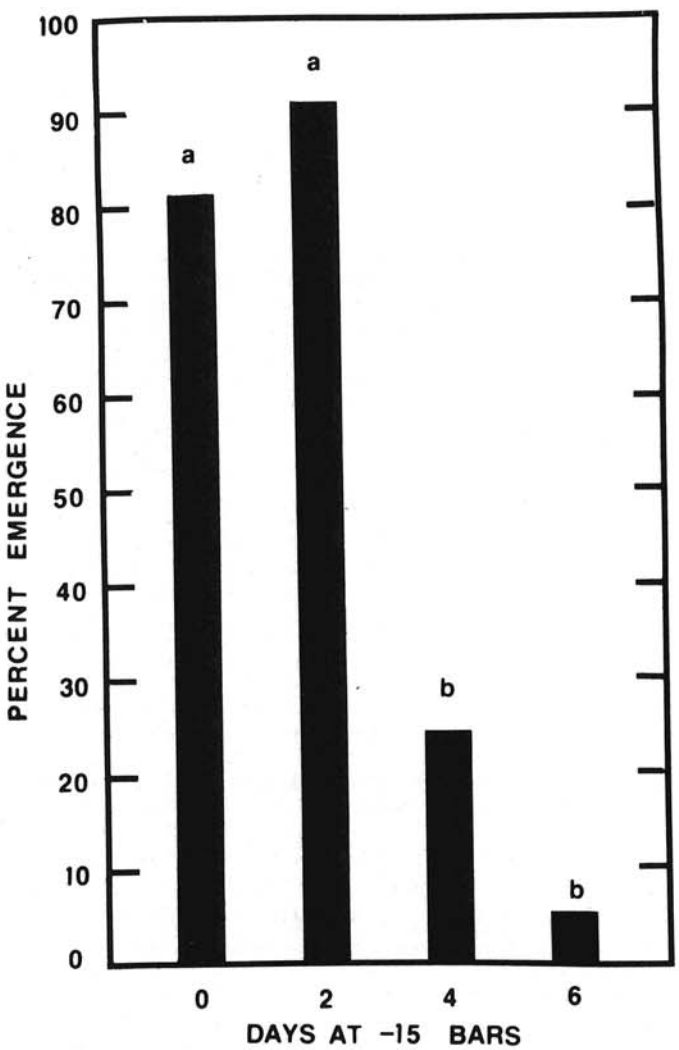

Fig. 1. Emergence of soybean seedlings from seeds sown in a sandy-loam soil held at −15 bars matric potential for 0, 2, 4, and 6 days before watering to −0.24 bar. Values are means of three consecutive plantings of 20 seeds per treatment in the same soil. Means followed by different letters are significantly different from each other using Tukey's *w* procedure ($P = 0.05$) on transformed data: $\sqrt{x + 0.5}$.

TABLE 1. Population densities of *Fusarium* in a sandy-loam soil adhering to and apart from mature soybean root tissue pieces buried at different soil depths for 9 mo[y]

Subtrate	Number of propagules ($\times 10^3$)/g soil[z]		
	0–3 cm	8 cm	15 cm
Soil apart from roots	5.8 a	3.3 a	5.1 a
Soil adhering to root	132.3 b	23.9 a	31.6 a

[y] Mature soybean root pieces with Fusarium root rot symptoms were buried in soil in nylon mesh bags in September. Adhering soil was removed from the root pieces by shaking in water agar.

[z] Means of three blocks combined over two sampling periods (7 and 9 mo). Means for the same subtrate followed by the same letter are not significantly different from each other using Tukey's *w* procedure ($P = 0.05$) on transformed data, $\log_{10}X$.

TABLE 2. Population densities of *Fusarium* in a sandy-loam soil and in soil that adhered to plant tissue pieces after they were buried for 9 mo in the field[y]

Soil samples	Number of propagules ($\times 10^3$)/g soil[z]
Field soil (control)	5.1 a
Corn stalks	127.0 b
Soybean stems	50.3 b
Soybean pods	138.7 b
Wheat straws	58.2 b
Soybean roots with Fusarium root rot	31.6 b

[y] Tissue pieces (~2.5 cm long) were buried in September in nylon mesh bags at a depth of 15 cm.

[z] Means of three blocks combined over two sampling periods (7 and 9 mo). Means followed by the same letter are not significantly different from each other using Tukey's *w* procedure ($P = 0.05$) on transformed data, $\log_{10}X$.

TABLE 3. Population densities of *Fusarium* in soil adhering to disinfested soybean stem pieces buried in soil containing 8,200 propagules of *Fusarium* per gram of soil at two matric potentials over three time periods.

Matric potential (−bars)	Number of propagules ($\times 10^3$)/g soil[z]		
	8 days	16 days	32 days
0.01 to 0.02	25.1a	38.0ab	30.9a
1.8	36.3ab	104.7bc	269.2c

[z] Means of three blocks. Means followed by the same letter are not significantly different ($P = 0.05$) from each other using Tukey's *w* procedure on transformed data, $\log_{10}X$.

3).

Soil adhering to tissue pieces had higher population densities than the soil at the start of the experiment without tissue pieces (Table 3). Increases ranged from twofold to 32-fold and were greatest at −1.8 bars after 32 days. *Fusarium oxysporum* and *F. solani* accounted for 88 and 8% of the Fusarium isolates, respectively. There were no significant differences between the pathogenicities of *F. oxysporum* isolates obtained from field soil and those from soil adhering to soybean stem pieces (disease indices of 2.3 and 2.6, respectively, on a scale of 0–5).

Since *F. oxysporum* was the most prevalent *Fusarium* sp. isolated from soil and buried plant tissue, its population density was measured at distances from disinfected stem pieces after 16 days. The population density of *F. oxysporum* 0–3 mm from the stem pieces (1.0×10^4 ppg) was significantly higher than that in control soil (4.1×10^3). At 3–6 mm and 6–9 mm distances, the densities were 4.4×10^3 and 2.6×10^3 ppg, respectively, which were not significantly different from that of the control.

DISCUSSION

Fusarium spp. appear to be weak pathogens of soybean (23,26), requiring environmental conditions either unfavorable for the host or highly favorable to the pathogen for disease development. *Fusarium* spp. were not reported to be a major cause of preemergence seedling rot of soybean; however, we found that *Fusarium* spp. induced substantial losses if the seeds were exposed to dry soil for 6 days at potentials as high as −15 bars before moistening to −0.24 bars. Emergence was not reduced if the soil was treated with fungicides or incubated at −2, −4, or −8 bars even though *Fusarium* spp. colonized the seed coats (23). The failure of soybeans to germinate when placed in dry soil (−9.1 bars) for 8 days as reported by Hunter and Erickson (12) may have been due to soilborne or seedborne fungi such as *Fusarium* that were not controlled. It is possible that exposure of seeds to moisture conditions too low for germination may stress the seed and thereby favor disease. Water stress of mature plants favored crown and root rot of wheat caused by *F. roseum* f. sp. *cerealis* 'Culmorum' (20). This was related to reduced bacterial antagonism and to the ability of the pathogen to extract water for chlamydospore germination and growth at low soil matric potentials (4), and also to its ability to grow well at low osmotic potentials corresponding to those in mature wheat plant tissues (3). Possibly, infection of soybean seeds by *F. oxysporum* is favored by low water potentials for similar reasons.

The evidence that *Fusarium* spp. are causally involved in the soybean seed and seedling rot at low soil matric potential is indirect. Population densities of *Fusarium oxysporum* increased rapidly in and around decaying seeds and seedlings. Emergence of seedlings was reduced with the addition of each of four *Fusarium* spp. to propylene oxide-treated soil but the reduction was less than with natural soil. Other fungi present in the soil and known to colonize seeds under low moisture conditions are *Aspergillus* and *Penicillium*. These fungi are less virulent seedling pathogens than *Fusarium* spp. (15) and should play a lesser role in soil at a matric potential of −15 bars for 6–8 days.

The population density of *Fusarium* in the studied field remained relatively constant over the four sampling periods from September to June. Similar results were found for *F. solani* f. *phaseoli* in bean fields (1,18). Other researchers reported that the population of *F. oxysporum* varied over the season with the lowest population occurring in the beginning of the season (16,21). In our work, *F. oxysporum* was the predominant species isolated. *Fusarium oxysporum* was also the predominant species in a monocultured soybean field in Minnesota (26). The population density of *Fusarium* in soil and in Fusarium-infected root tissues did not vary with soil depth from 0 to 15 cm. The even distribution of Fusarium propagules in the plow layer also has been reported for *F. solani* f. *phaseoli* (1,18).

Several experiments in the field and laboratory indicated that population densities of *Fusarium* increased in and around soybean and other plant residues. In field experiments, populations in infected root tissue pieces increased in the fall, but these were not sustained the following spring. However, soil adhering to root pieces showed large population increases in the spring, which were greater around root pieces incubated on the soil surface than in those buried 15 cm deep. Fusarium population increases in the bulk soil (apart from residues) also occurred in the spring following the incorporation of soybean harvest residues into the top 3 cm of soil in the fall. These increased population levels also did not persist beyond early June, and soil containing residues buried 15 cm deep showed no increases at any time. If the residue pieces had been included with soil samples, greater and more sustained increases might have been demonstrated.

In laboratory experiments, fumigated and nonfumigated stem pieces of soybean and of other plants also supported increases in numbers of propagules of *Fusarium* in soil close to the tissues. Colonization occurred over a wide range of soil matric potentials, indicating that soil moisture conditions in nature should rarely prevent saprophytic increases. Saprophytic increases are favored by moist soil conditions (−1.8 bars) rather than wet (−0.01 to −0.02 bar). This may be due to the direct decrease of the water potential or the increased availability of oxygen. Weakly pathogenic isolates of *F. oxysporum* did not appear to have a competitive advantage over more highly pathogenic ones in colonizing tissue pieces.

Saprophytic colonization by *Fusarium* spp. of infected and uninfected plant tissues is well-known (2,5,9,27), but little quantitative work had been done. Our work indicates that populations of *F. oxysporum* pathogenic on soybean may be increased or maintained by colonization of dead plant residues. The proportion of isolates of *F. oxysporum* to those of *F. solani* from soil and colonized tissue remained nearly the same, indicating that both have similar saprophytic capabilities under field conditions. Either species can rot soybean seeds in dry soil, but single isolates varied greatly in pathogenicity.

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