Roles of *Fusarium oxysporum* and *F. solani* in Essex Disease of Soybean in Virginia

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ABSTRACT

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Fusarium oxysporum and *F. solani* were isolated with high frequency from hypocotyl lesions on soybean cultivar Essex seedlings grown in naturally infested soil at −0.01 MPa water potential and 15, 20, or 25 C. *F. oxysporum* was isolated at high frequency from cotyledon lesions at 20 C, and *Rhizoctonia solani* was isolated at high frequency from hypocotyl lesions at 25 C. Thirteen days after planting, disease severity ratings were greatest at 20 C. In incubator trials using artificially infested soil, 41% of 102 representative *F. oxysporum, F. solani*, and *R. solani* isolates gave disease severity ratings on Essex soybean that were significantly higher than those for the pasteurized soil control at 20 C and −0.01 MPa water potential. In soil-temperature tank tests, all *F. oxysporum* and *F. solani* isolates tested delayed seedling emergence and caused significant reductions in stem length and plant fresh weight at 20 C and −0.01 MPa water potential. *F. oxysporum* and *F. solani* appear to be part of a complex that may cause Essex disease in Virginia.

Additional keywords: *Pythium* spp.

In the sandy soils of the King and Queen County area of eastern Virginia, delayed seedling emergence, damping-off, and stunting of the soybean (*Glycine max* (L.) Merr.) cultivar Essex have been observed for several years. In some years, the damping-off and/or delayed emergence phases are not prevalent and, when present, are not always found in the same areas of fields. In a low-rainfall year, chlorosis and early plant death are observed. Because Essex soybean is severely affected, the disease has been termed "Essex disease" or "Essex syndrome." Other cultivars are also affected, however. Grant (4) showed that *Fusarium oxysporum* (Schlecht.) emend Snyd. & Hans. and *F. solani* (Mart.) Appel & Wr. emend. Snyd. & Hans. were associated with the seedling disease phase. In Essex disease, discrete lesions are common on cotyledons, hypocotyls, and roots of seedlings but uncommon on roots of older, stunted plants. This investigation was undertaken to determine the effect of *F. oxysporum* and *F. solani* on the emergence, disease severity, and growth of Essex soybean. For comparison, some experiments also included evaluations of *Rhizoctonia solani* Kühn. Evaluation of *Pythium* spp. is the subject of a separate investigation (G. J. Griffin, *unpublished*).

MATERIALS AND METHODS

Field soil sampling. Soil from a field in King and Queen County, Virginia, with a history of Essex disease was used primarily for evaluation of disease severity and isolation of pathogens from lesions. Soil samples were collected from the field 6 days after planting on 30 May 1986 in areas where Essex seedling emergence and subsequent soybean growth were poor. In some instances, experiments were also conducted with soil from a field in Holland, Virginia, that had no recognized history of soybean seedling disease or plant stunting.

Soils were assayed for pH, soil texture, organic matter, and mineral nutrients. Soil matric potential properties were determined by means of a ceramic plant extractor (Soilmoisture Corp., Santa Barbara, CA) with −0.01 and −1.5 MPa plates; for −0.001 MPa, a tension table was used. Plant-parasitic nematodes were assayed in the Virginia Tech Plant Clinic Nematology Laboratory. Chemical and physical assays indicated that the King and Queen County soil contained 516 μg CaO/g, 120 μg MgO/g, 35 μg P_2O_5/g, 72 μg K_2O/g, 33 μg NO_3-N/g, 1.6% organic matter, 86.5% sand, 13.5% silt, 0.0% clay (= loamy sand texture), 16.2% water at −0.001 MPa, 9.7% water at −0.01 MPa, 6.7% water at −0.03 MPa, and 2.2% water at −1.5 MPa matric potential; pH was 6.0. The Holland soil contained 1,152 μg CaO/g, 120 μg MgO/g, 32 μg P_2O_5/g, 111 μg K_2O/g, 50 μg NO_3-N/g, 2.6% organic matter, 58.5% sand, 41.5% silt, 0.0% clay (= sandy loam texture), 16.3% water at −0.01 MPa, 9.6% water at −0.03 MPa, and 5.1% water at −1.5 MPa matric potential; pH was 5.6. King and Queen County soil contained 0 and 90, and Holland soil 80 and 90, *Tylenchorhynchus* spp. and *Helicotylenchus* spp. of nematodes per 500 cm^3 of soil, respectively.

Disease severity and pathogenicity studies. Two systems (soil-temperature tank and incubator) were used to evaluate disease severity and/or pathogenicity. Soil-temperature tanks in a greenhouse were used to study soybean seedling disease development in naturally infested soil at 15, 20, and 25 C; these temperatures are representative of soil temperatures (5 cm depth) at planting time in eastern Virginia for full-season soybeans (Virginia Agroenvironmental Monitoring System, *unpublished*). Seeds of Essex soybean, used for all experiments, were tested for germinability in moist chambers before all experiments and for seedborne fungi by plating on Komada's *Fusarium*-selective medium (6) and acidified potato-dextrose agar (APDA). Four seeds per pot were planted to a depth of 3.8 cm in 11-cm-diameter plastic containers filled with soil from the field in King and Queen County. Soil was mixed thoroughly for at least 15 min in a cement mixer before use. Inoculum densities of *F. oxysporum* and *F. solani* in the soil were determined by dilution plating on Komada's medium, as indicated below.

Twenty pots were placed in each of the three temperature tanks. Soil moisture level was adjusted daily to approximately −0.01 MPa matric potential by weighing pots and adding the required amount of distilled water. A second experiment was conducted at −0.03 MPa water potential. After 6 and 13 days, 10 pots were harvested from each temperature regime. Plants were removed gently and shaken to loosen surrounding soil, and the roots were washed free from remaining soil. Disease severity on cotyledons, hypocotyls, and roots was determined separately using the following scale for each plant part: 0 = none, 1 = slight (about 10% or less of the plant part with lesions), 2 = moderate (lesions on about 10–25% of the plant part), 3 = extensive (lesions on about 25–50% of the plant part), 4 = severe disease (lesions on more than 50% of the plant part), and 5 = dead plant. Sections of necrotic tissues were cut into two pieces; one was placed on Komada's *Fusarium*-selective medium and the other, on water agar (WA). Plates were incubated at room temperature (25–28 C).

For pathogenicity trials in temperature

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tanks, steam-pasteurized King and Queen County field soil was artificially infested with each test isolate at an inoculum density representative of naturally infested field soil. Four isolates each of *F. solani* and *F. oxysporum* were used. Three pots per isolate, each containing four seeds, were randomized between two temperature tanks. A noninfested control was included, and the experiment was conducted twice. *R. solani* was included in the second experiment and in a separate third experiment. Soil was maintained at 20 C and −0.01 MPa matric potential. After 13 days, plants were harvested and fresh weight, stem length, and disease severity were determined for each plant. Seedling emergence was counted daily. Test fungi were reisolated as indicated above.

Inoculum of *F. oxysporum and F. solani* was prepared by growing each isolate on a PDA slant under room conditions for 7–10 days. A conidial suspension was prepared by washing the inoculum from a slant with sterile distilled water and blending for 2 min in a Waring Blendor. The suspension was filtered through cheesecloth, and conidial density (microconidia plus macroconidia) was determined with a hemacytometer. *R. solani* inoculum was prepared using radish (*Raphanus sativus* L.) seeds. Seeds were moistened to full imbibition (3 hr) and autoclaved in 9-cm-diameter petri dishes (100 seeds per dish). A 2-cm agar disk from a 3-day-old PDA culture of *R. solani* was placed in each dish and incubated at 18 C for 30 days. Sclerotia of *R. solani* from these dishes were mixed with soil at a rate of 120 per kilogram of oven-dried soil (9).

An incubator test was used to evaluate disease severity and pathogenicity over short intervals (6 days) and for a large number of fungal isolates. Naturally or artificially infested soil (300 g) moistened to −0.01 MPa matric potential was spread on a 30 × 40 cm polyethylene plastic sheet. Ten seeds were distributed evenly in the soil. Another plastic sheet was laid over the soil and seeds, and the whole was rolled into a cylinder. The cylinders were incubated at 20 C, and the seedlings were removed after 6 days. Disease severity was rated according to the previously described scale, and the test fungi were reisolated.

Population densities of *F. oxysporum* and *F. solani* in soil. Population densities of *F. oxysporum* and *F. solani* in the two test soils were determined using the dilution-plate technique in combination with Komada's medium. Soil samples were thoroughly mixed by hand in plastic bags, and the 10^{-1} soil suspensions were shaken on a wrist-action shaker for 15 min. Colony counts of *F. oxysporum* and *F. solani* were made on five petri plates prepared from the 10^{-3} dilution. Representative colonies were subcultured for use in pathogenicity trials.

RESULTS

Influence of soil temperature on disease development. The percentage emergence of soybean seedlings at 15, 20, and 25 C after 6 and 13 days in King and Queen County soil at −0.01 MPa water potential is shown in Table 1. Emergence was least at 15 C after 6 days; after 13 days, emergence was high at all temperatures. Moist chamber trials showed the seeds were 100% germinable. At 13 days, disease severity was significantly ($P \leq 0.05$) greatest at 20 C, whereas no differences were observed among temperatures at 6 days. In a second trial, at −0.03 MPa water potential, disease severity ratings were equally high at 15 and 20 C after 13 days and highest at 15 C after 6 days.

The lesions on Essex soybean plants grown in naturally infested soil in temperature tanks were the same type as those observed in this soil in the field. Both *F. oxysporum* and *F. solani* were isolated from brown or reddish brown, small, discrete lesions on cotyledons and from brown, elongated, often quite severe lesions on the hypocotyl-root transition zone. *F. solani* was isolated along with *Pythium* spp. from dark brown, sunken cotyledon lesions. *F. oxysporum* was found in association with *Pythium* spp. from brown, elongated hypocotyl lesions. On roots, *F. oxysporum* was isolated from small, light brown lesions and *F. solani*, from dark brown lesions, especially on the lateral roots. *R. solani* was isolated from red to reddish brown, sunken hypocotyl lesions. A few lesions of this type also yielded *F. oxysporum*. *R. solani* was not found in association with *Pythium* spp. Anastomosis studies showed that four of 10 *R. solani* isolates belonged to group AG-4.

At 20 C and −0.01 MPa matric potential, *F. oxysporum* was isolated at high frequency from lesions on cotyledons, whereas at 20 and 25 C, *F. solani* was the most frequently isolated fungus from root lesions (Table 2). Both species were isolated at high frequency from hypocotyl lesions at all temperatures. At 15 C, none of the three fungi were isolated from roots and *F. oxysporum* and *F. solani* were isolated from cotyledon lesions. At 25 C, *R. solani* was isolated from hypocotyl lesions at high frequency; this value was significantly ($P \leq 0.05$) greater than that of isolation at 15 or 20 C in a test of independent proportions. In the second temperature trial, conducted at −0.03 MPa water potential, isolation frequency trends among the three fungi were generally similar except that *F. oxysporum* was not isolated from root lesions. In both tests, lesions on the root-hypocotyl transition zone were included in the hypocotyl category. *Pythium* spp. were isolated mostly from large water-soaked, brown lesions on cotyledons and from elongated brown lesions on hypocotyls; at 6 days, 30% of the lesions on cotyledons of plants growing at 20 C and −0.01 MPa matric potential yielded *Pythium* spp. Other tissue samplings yielded lower percentages of *Pythium* spp. *P. ultimum* was the predominant species found in separate

Table 1. Influence of soil temperature on soybean cultivar Essex seedling emergence and disease severity at 6 and 13 days after planting in naturally infested King and Queen County, Virginia, field soil maintained near −0.01 MPa water potential

Soil temperature (C)	Seedling emergence[a] (%)		Disease severity[b]	
	6 Days	13 Days	6 Days	13 Days
15	17.5	85.0	1.14	0.74
20	87.5	92.5	1.38	1.16
25	80.0	90.0	1.36	0.80
LSD[c]	7.7	8.2	0.35	0.24

[a] Data are the means of 10 replications (pots) with four plants per replicate.
[b] Rated on a 0–5 scale, with 0 = none, 1 = slight, 2 = moderate, 3 = extensive, 4 = severe disease, and 5 = dead plant.
[c] LSD = least significant difference ($P \leq 0.05$).

Table 2. Frequency of isolation of *Fusarium oxysporum*, *F. solani*, and *Rhizoctonia solani* from lesions on cotyledons, hypocotyls, and roots of soybean cultivar Essex plants grown in naturally infested King and Queen County, Virginia, field soil at three temperatures and −0.01 MPa water potential in the greenhouse[a]

	Isolation frequency (%)								
	Cotyledons[c]			Hypocotyls[d]			Roots[e]		
Fungus[b]	15 C	20 C	25 C	15 C	20 C	25 C	15 C	20 C	25 C
Fusarium oxysporum	13.3	30.0	16.6	25.0	31.2	43.5	0.0	12.5	12.5
F. solani	3.3	6.6	6.6	32.0	31.2	37.5	0.0	18.7	18.7
Rhizoctonia solani	0.0	10.0	5.0	12.5	12.5	25.0	0.0	0.0	0.0

[a] Isolations at 6 and 13 days were combined to calculate isolation frequency.
[b] Komada's selective medium was used for *Fusarium* isolations and water agar for *Rhizoctonia*; most lesions were cut into two pieces and assayed on each medium.
[c] Total tissue pieces plated = 180.
[d] Included tissues from hypocotyl-root transition zone; total tissue pieces plated = 100.
[e] Included taproot and lateral roots; total tissue pieces plated = 50.

trials (*unpublished*).

Population densities of *F. oxysporum* and *F. solani* in naturally infested soils. The population densities of *F. oxysporum* and *F. solani* in the King and Queen County soil were 1.6×10^4 and 1.1×10^4 propagules per gram of soil, respectively. The population densities of *F. oxysporum* and *F. solani* were both significantly less ($P \leq 0.05$), by Student's *t* test, in the Holland soil than in the King and Queen County soil and were 6.2×10^3 and 5.5×10^3 propagules per gram of soil, respectively. Similar values were obtained in several trials. In incubator tests at 20 C and −0.01 MPa water potential, disease severity after 6 days in King and Queen County soil was 3.46 and significantly greater ($P \leq 0.05$) by Student's *t* test than in Holland soil, which had a value of 2.78. Many of the seedling symptoms in both soils in these tests were of the water-soaked *Pythium* type.

Pathogenicity of *F. oxysporum* and *F. solani* on Essex soybean. In incubator tests, 42 (41%) of 102 isolates of *F. oxysporum, F. solani*, and *R. solani* from lesions or soil tested gave disease severity ratings that differed significantly ($P \leq 0.05$) from the control according to Duncan's multiple range test. Many of the remaining isolates produced symptoms, but statistical differences were not observed. Disease severity ratings for pathogenic isolates of *F. oxysporum* ranged from 2.89 (King and Queen County soil, hypocotyl lesion isolate) to 1.72 (King and Queen County soil, hypocotyl lesion isolate). Disease severity ratings for *F. solani* ranged from 2.33 (King and Queen County soil, root lesion isolate) to 1.74 (King and Queen County soil, root lesion isolate). *F. oxysporum* accounted for 60% of the 42 pathogenic isolates, *F. solani* for 38%, and *R. solani* for 2%; 10 *R. solani* isolates (all from hypocotyl lesions), 54 *F. oxysporum*, and 38 *F. solani* isolates were tested. Pathogenic isolates were found in both the King and Queen County (32 of 85) and the Holland (10 of 16) plant-lesion or soil isolates.

Ten pathogenic and representative isolates of *F. oxysporum, F. solani*, and *R. solani* from the incubator tests were used in pathogenicity trials conducted in greenhouse soil-temperature tanks. All *F. oxysporum* and *F. solani* isolates examined caused a significant ($P \leq 0.05$) reduction in stem length and plant fresh weight compared with the noninfested control (Table 3). Disease severity ratings were also significantly higher for plants grown in soil artificially infested with *F. oxysporum* and *F. solani* isolates than for plants grown in noninfested soil. Also, disease severity ratings for all isolates were as great as or greater than those for naturally infested soil at 20 C and −0.01 MPa matric potentials (Table 1). *F. solani* 91 (King and Queen County soil, root lesion isolate) caused the highest disease severity rating, the shortest stem length, and the second-lowest plant fresh weight. *F. oxysporum* 64 (King and Queen County soil, hypocotyl lesion isolate) gave results similar to those of *F. oxysporum* 10, a reference pathogenic isolate from Delaware. All *F. oxysporum* and *F. solani* isolates caused lesions that were located mainly on hypocotyls and cotyledons and were similar in appearance to those observed in naturally infested soils. All *F. oxysporum* and *F. solani* isolates significantly ($P \leq 0.05$) reduced the rate of seedling emergence by 6 days, but final stands at 13 days were affected only a little (Figs. 1 and 2). Similar results were obtained in a second trial.

Three of four *R. solani* (AG-4) isolates gave disease severity ratings significantly ($P \leq 0.05$) different from the control. One of the four, *R. solani* 34, gave a disease severity rating (3.5) that was slightly higher than that for *F. solani* 91. The other *R. solani* AG-4 isolates gave disease severity ratings ranging from 0.5 to 1.6. Two of these isolates reduced stem length, plant fresh weight, and rate of seedling emergence. Final stands at 13 days, however, were not significantly different from those of the control. All species of fungi that were used to artificially infest soils were reisolated from lesions on seedlings.

Table 3. Mean stem length, plant fresh weight, and disease severity of soybean cultivar Essex plants grown in pasteurized King and Queen County, Virginia, field soil artificially infested with *Fusarium oxysporum* and *F. solani* isolates, at 20 C and −0.01 MPa water potential

Isolate code[w]	Stem length (cm)[x]	Plant fresh weight (g)[x]	Disease severity[y]
Control (noninfested)	18.4 a[z]	7.2 a	0.0 f
F. solani 21	17.0 b	6.0 b	1.7 e
F. oxysporum 71	16.2 b	5.8 b	1.8 de
F. solani 110	16.3 b	5.8 b	2.1 cde
F. oxysporum 66	16.4 b	5.8 b	2.1 cde
F. solani 100	16.0 c	5.6 b	2.4 bc
F. oxysporum 10	16.1 c	5.2 c	2.6 bc
F. oxysporum 64	16.0 d	4.8 c	2.7 ab
F. solani 91	15.5 e	5.0 c	3.1 a

[w] Inoculum density for *F. oxysporum* was 2.0×10^4 conidia per gram of soil and for *F. solani*, 5.0×10^3 conidia per gram of soil.

[x] Values are average of three replications with four plants per replicate.

[y] Rated 13 days after planting on a 0–5 scale, with 0 = none, 1 = slight, 2 = moderate, 3 = extensive, 4 = severe disease, and 5 = dead plant.

[z] Values followed by the same letter are not significantly ($P \leq 0.05$) different according to Duncan's multiple range test.

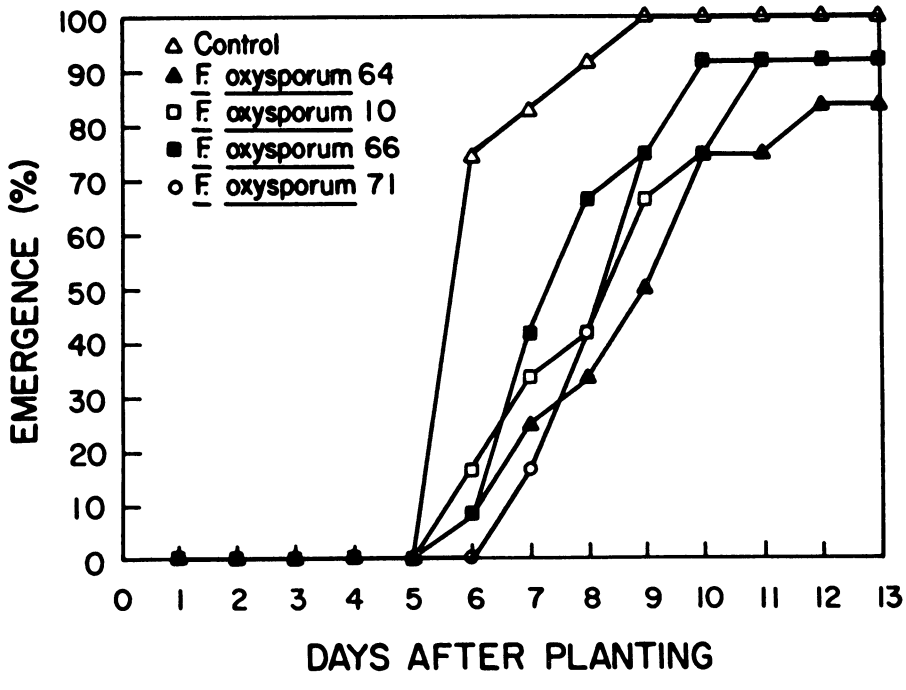

Fig. 1. Speed of emergence at 20 C and −0.01 MPa water potential of soybean cultivar Essex in pasteurized King and Queen County, Virginia, field soil artificially infested with four isolates of *Fusarium oxysporum*.

DISCUSSION

Results of isolations from diseased Essex soybean plants grown in naturally infested soil at three temperatures coupled with pathogenicity tests suggest that *F. oxysporum* and *F. solani* are both involved in Essex disease. These species produced symptoms on Essex soybean plants that were observed in the field and in soil-temperature tank tests with naturally infested soil. Reductions in Essex seedling emergence rate, stem length, and plant fresh weight were found for both *F. oxysporum* and *F. solani*. Only the seed and seedling rot disease phase, with water-soaked lesions, found in some areas of fields (and characteristic of *Pythium* spp.), was not observed in these pathogenicity trials.

Grant (4) found *F. oxysporum* and *F. solani* were associated with seedling disease of Essex, Lee 60, and McNair soybean. He suggested that *F. oxysporum* was more pathogenic than *F. solani* in tests conducted at ambient greenhouse temperatures. Other studies have also emphasized the pathogenicity of *F. oxysporum* on soybean (1–3,7). In the present study, strains of *F. solani* and *F. oxysporum* appeared to be equally pathogenic at 20 C and −0.01 MPa water potential. However, *F. oxysporum* may be more important on cotyledons and *F. solani* may be more important on roots. The two species appeared to be equally important on hypocotyls, including the hypocotyl-root transition zone. In the Delaware portion of the Delmarva region (Delaware, Maryland, and Virginia), *F. oxysporum* is believed to be an important root pathogen in sandy soybean field soils (2,7); *F. oxysporum* 10, a pathogenic Delaware isolate, behaved similarly in the present study to pathogenic *F. oxysporum* isolates from the King and Queen County soil. Ferrant and Carroll (2), however, isolated two cultural types of *F. solani* from diseased soybean plants in Delaware. In Florida, *F. solani* reduced root weight, shoot weight, and plant height of soybean without lesion development (11).

Klag et al (5) indicated that *Fusarium* spp. isolated from soybean plants with root rot in Maryland were not pathogenic. However, the temperature (30 C) used by these workers for incubation may have been too high. According to French (3), Fusarium root rot was not present on soybean at 29 and 32 C, but disease severity was high at lower temperatures. Dunleavy (1) found Fusarium blight of soybean was more severe at 21 C than at 27 C when the soil moisture level was maintained at 100% of field capacity. In the present study, disease severity was generally higher at 20 C than at 25 C in soil maintained near field capacity (−0.01 MPa water potential). Soil temperature data collected in the area of the experimental King and Queen County field (at Warsaw, Virginia) indicated that soil temperatures near 30 C are uncommon in the upper 10 cm of soil during the planting months of May and June (Virginia Agroenvironmental Monitoring System, *unpublished*).

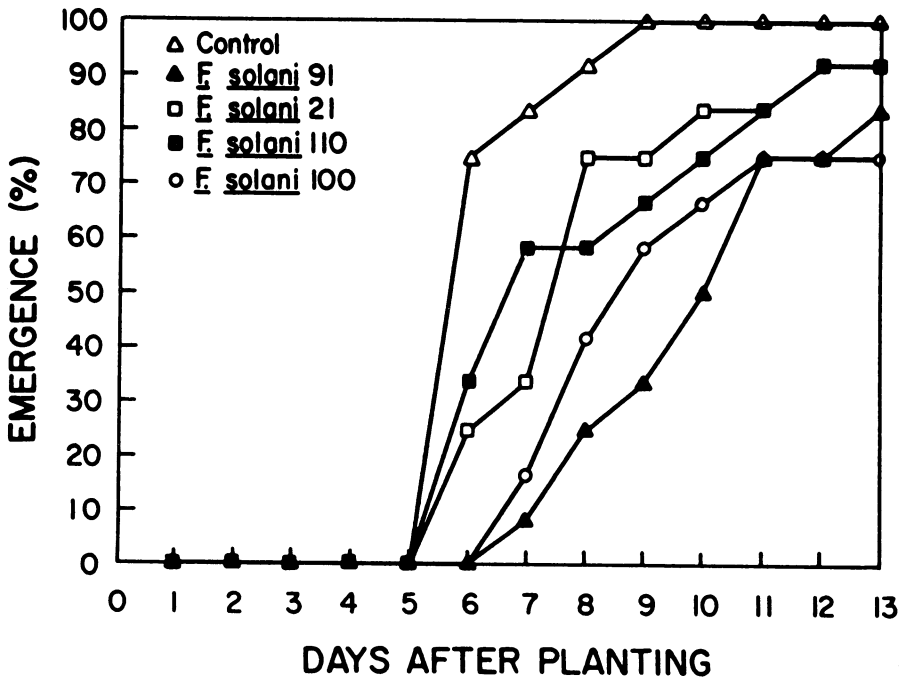

Fig. 2. Speed of emergence at 20 C and −0.01 MPa water potential of soybean cultivar Essex in pasteurized King and Queen County, Virginia, field soil artificially infested with four isolates of *Fusarium solani*.

Two pathogenic isolates (*F. oxysporum* 66 and *F. solani* 100) in the temperature tank tests were obtained from the Holland soil. This finding, along with results of the incubator test assays of naturally infested soil and the fact that the percentage of pathogenic isolates from the Holland soil was high, suggests that this soil has the potential for soybean seedling disease. The lower population densities of *F. oxysporum* and *F. solani* in the Holland soil, together with the higher temperatures at planting time in the Holland field, vs. the King and Queen County field, may explain in part the apparent absence of disease in the Holland field. Data of the Virginia Agroenvironmental Monitoring System (*unpublished*) show that the median soil temperature for the Holland soil area (5 cm depth) during the average day of planting (27 May) for 2 yr was 25 C. In the King and Queen County field area (Warsaw), the median soil temperature for the average day of planting (24 May) for the 2 yr was 21 C.

R. solani was isolated with moderate frequency from symptomatic cotyledons and with higher frequency from symptomatic hypocotyls, especially at 25 C. In most instances, the *R. solani* AG-4 isolates tested were pathogenic to hypocotyls but not to roots in temperature tank trials. Similar results were reported by Ploetz et al (8), and symptoms found by these workers were the same as found here. Klag et al (5) found that all pathogenic isolates of *R. solani* in Maryland were AG-4. *R. solani* isolates tested here delayed seedling emergence, as found by van Bruggen et al (10), but, with one exception, were not highly pathogenic. However, along with *Pythium* spp. (*unpublished*), *F. oxysporum*, and *F. solani*, *R. solani* may be part of a disease complex that may be the cause of Essex disease in the King and Queen County area of Virginia. *R. solani* may be more important in years when the soil temperature is relatively higher and the soil moisture lower at planting time. For the King and Queen County field, the stunting or reduced growth of soybean appears to be the most important phase of Essex disease, as damping-off and reduced rate of seedling emergence are not always observed.

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