Etiology and Epidemiology of Seedling Rot of Soybean by *Pythium ultimum*

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ABSTRACT

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Pythium ultimum and *Fusarium* spp. were regularly isolated from soybean seedlings with preemergence seedling rot. Seedling emergence was reduced from 93% in the control to 57, 29, and 0% in propylene oxide-treated soil artificially infested with 5, 10, and 25 sporangia of *P. ultimum*, respectively, per gram of soil. In soil infested with *P. ultimum* at seven propagules per gram increasing soil moisture from −1.8 to −0.018 bars matric potential at 28 C reduced soybean emergence from 66 to 15%, respectively. The influence of temperature on disease development varied with the soil used. In propylene oxide-treated soil infested with seven propagules of *P. ultimum* per gram, emergence at 16, 20, 24, and 28 C was 9, 44, 43, and 60%, respectively. In one of two different naturally infested soil samples, greater emergence was observed at 16 C (23%) than at 28 C (10%), while in the other, there was no significant difference between 16 C (28%) and 28 C (31%). Isolates of *Fusarium* spp. failed to inhibit emergence of soybean seedlings at matric potentials from −0.013 to −0.4 bar. None of three different *Fusarium* spp. increased the severity of *Pythium* damping-off of soybean under conditions suitable for rapid germination. Multiple regression analysis of field data taken from an area with preemergence seedling rot indicated that the number of days of continually wet soil (>−0.5 bar) from the time of planting plus the number of days of low soil moisture (<−3 bars) were positively correlated with disease incidence. Rain in the first 3 days was predicted to reduce emergence further if the soil matric potential was 0 to −3 bars. Weekly average soil temperatures ranging from 20.3 to 28.2 C had no significant effect on emergence.

For at least the past 10 yr, a preemergence rot of soybean (*Glycine max* [L.] Merr.) seedlings was observed in the sandy soils of southwest Michigan. Infected seedlings usually had swollen hypocotyls and lesions at the junction of the hypocotyl and primary root. Other symptoms include a curling growth habit and reddish to brown lesions on the hypocotyls and cotyledons. The disease occurs in small or large (several acres) areas and location is not obviously related to topography. Disease loci may shift in position from year to year and may not occur every year in such loci; a second planting in a disease-affected area frequently results in a full stand without evidence of disease.

Until this work, we attributed the disease to *Fusarium oxysporum* (Schl.) emend Snyd. and Hans. since this fungus was frequently isolated from lesions on diseased seedlings, and *Fusarium* root rot characteristically occurred on surviving plants in diseased areas. However, it has not been possible to induce preemergence seedling rot with *Fusarium* isolates. *F. oxysporum* caused poor germination and stunting of soybean plants (3), but generally is not considered to be a seedling pathogen of soybean. *Pythium ultimum* Trow. is known to cause seed and seedling rot of soybean (21,23) but, to our knowledge, has not been described as being associated with this syndrome.

The objectives of this study were to reexamine the etiology of the disease, particularly the role of *P. ultimum*, to study the influence of inoculum density, soil moisture, and soil temperature on *P. ultimum* preemergence seedling rot under controlled conditions, and to develop a multiple regression equation to predict seedling emergence in soil naturally infested with *P. ultimum* based on soil matric potential, rainfall and temperature data.

MATERIALS AND METHODS

Laboratory experiments. Isolations were made from soybean seedling pieces washed under running tap water for approximately 30 min, split in half, and plated on water agar and on a *Fusarium*-selective medium (11). Selected isolates of *Fusarium* spp. were identified by P. E. Nelson, Department of Plant Pathology, Pennsylvania State University, University Park 16802. Cultures were maintained on potato-dextrose agar. The isolate of *P. ultimum* used was identified by F. F. Hendrix, Department of Plant Pathology and Genetics, University of Georgia, Athens 30601, and was maintained on V-8 juice agar. Inoculum density of *P. ultimum* in soil was estimated by applying five, 0.04-ml drops of soil dilutions made in dilute water agar (0.075%) to each of five petri dishes of water agar by the method of Stanghellini and Hancock (22). Population density of *Fusarium* spp. was determined by plating soil dilutions on *Fusarium*-selective agar. Plates were incubated on the laboratory bench (23 ± 2 C) in ambient light (600–800 lux during the daytime) unless otherwise specified.

Seeds of the soybean cultivar Hark used in pathogenicity tests were disinfested with propylene oxide (20). The soil used was a sandy loam with the following characteristics: sand:silt:clay = 81:4:15%, pH 5.5–6.5, 1.8% organic matter, and exchangeable bases (K:Ca:Mg) in the ratio 4:81:15%. The soil moisture-matric potential curve was determined using a 15-bar ceramic plate extractor (Soilmoisture Equipment Corp., Santa Barbara, CA 93105). Seven seeds were planted on the surface of a 5-cm-deep base layer of soil (440 g soil, dry weight) in plastic cups (14 cm × 11.5 cm) and covered with approximately 3.8 cm of soil (400 g soil, dry weight). Cups were incubated in the dark and emergence was recorded 10 days after 50% of the seedlings in the disinfested soil had emerged. In some experiments a soil moisture differential was established by watering the bottom soil layer, on which the seeds were placed, to −0.013 bar matric potential and then covering the seeds with air-dry soil. After 2 days the soil moisture at seed placement was −0.18 bar. Pots were watered daily from the bottom until the weight of the pot at planting was reached. A given matric potential was established in a soil sample by atomizing water onto dry soil in a plastic bag with frequent shaking until a predetermined percent soil moisture level was reached. In experiments in which a constant soil moisture was desired, the pots were covered with polyethylene film and placed in a sealed polyethylene bag. In some experiments 20 seeds were sown 2.5 cm deep in plastic trays 19.5 × 19.5 × 6 cm deep.

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To control pythiaceous fungi in naturally infested soil, Lesan (formerly known as Dexon (sodium [4-(dimethylamino)phenyl] diazene sulfonate))(6,7) was added to the soil with an atomizer at a concentration of 30 mg a.i. per kg soil. The soil was air-dried on paper toweling before use. To disinfest soil, 1 L of moist soil (−0.4 ± 0.2 bar) was placed in a 1.9-L glass jar. Two milliliters of propylene oxide were added to each jar before it was sealed for 2 days. The jar was opened, aired under a fume hood overnight, and soil was dried in a forced air oven at 35 C. Soil was reinfested by sprinkling an aqueous suspension of *P. ultimum* sporangia from hemp seed broth culture (21) on the soil contained in a plastic bag. The bag was sealed and allowed to incubate at 23 ± 2 C for 1 wk after which soil was air-dried, sieved (4-mm meshes), and stored at 5 C. Inoculum density in the soil was determined before each set of experiments. Disinfested soil was added to infested soil to obtain the desired inoculum concentration.

Except where indicated otherwise, all experiments were replicated four or more times, and data were analyzed by analysis of variance. Differences between means were detected by Tukey's *w* procedure ($P = 0.05$).

Collection and analysis of field data. Environmental and soybean seed emergence data, which were obtained from a field containing a high population of *P. ultimum* (100–300 propagules per gram of soil). were analyzed by multiple regression. A treatment mean was the average of two 3-m rows, each planted with 100 seeds. Nontreated Hark soybean seeds were sown at a depth of 6.5 cm unless otherwise indicated. During each experiment soil matric potential, soil temperature, and rainfall were continually recorded. Rainfall was measured with a tipping bucket rain gauge (Weather Measure Corporation, Sacramento, CA 95841) and recorded by an event-marker on the Esterline Angus temperature recorder, −20 to 130 F (Esterline Angus Instrument Corporation, Indianapolis, IN 46224) which also recorded soil temperature at 6.5 cm with a thermistor probe. Soil moisture was measured with cylindrical gypsum soil moisture resistance blocks (2.5 × 2.5 cm) with 4.57-M (15-foot) leads obtained from Soilmoisture Equipment Corp., Santa Barbara, CA 93105. Changes in resistance of the blocks were continuously monitored with a portable recorder (19). The data used for analysis were those recorded during the first week after planting. Emergence was recorded 2–3 wk after planting. Since postemergence damping-off symptoms were rarely seen, percent emergence was used as the measure of disease. To create different soil moisture levels, some rows were watered at the rate of 6.7–13.4 L per row with a sprinkling can (roughly 1–2 cm of water) or with 21.1–27.8 L/row (3–4cm).

The multiple regression analysis was done by the stepwise deletion of variables method with addition capabilities which is on the Michigan State University statistical computer package. Criterium for deleting or adding a variable was set at $P = 10\%$. The dependent variable was seedling emergence, and no more than five independent variables were analyzed at one time.

Soil moisture block calibration and field use. The blocks were calibrated by using the pressure plate apparatus. A piece of nylon mesh (320 μm) was placed over the plate, then 0.5-cm layer of sieved (4-mm meshes) soil was added. Blocks were placed laterally on the plate and covered with additional soil. Electrical connection with the blocks inside the pressure plate apparatus was made through an electrical lead-through accessory. Soil and blocks were saturated overnight before the pressure was applied.

In the field, two moisture blocks were placed in one of the two rows at depths of 5.1 and 12.7 cm as measured from the top of the blocks, unless otherwise indicated. The sandy loam soil did not shrink and swell enough to influence contact of the blocks with the soil.

RESULTS

Pathogenicity of *Pythium ultimum* and the influence of matric potential on disease. Both *P. ultimum* and *Fusarium* spp. were isolated from soybean seeds and seedlings collected from natural soil (Table 1). Both fungi were easily isolated from the seed coats within 24 hr of planting. *Pythium* was not isolated from the tip of the primary root until 6 days after planting, when it was recovered from 30% of the pieces. *Fusarium* was isolated from 10% of the root tips after 3 and 6 days. *Pythium* was isolated from 21% of the cotyledon pieces within 1 day and with high frequency thereafter. *Fusarium* was obtained from only 7% of the cotyledon pieces after 1 day, but at high frequency thereafter. Both fungi were isolated from hypocotyls at moderate frequencies (20–33%) after 3 days and at high frequencies (60–70%) at 6 days.

Of some 200 *Fusarium* isolates screened for pathogenicity by a laboratory method (18), 11 isolates of *F. oxysporum* and seven of *F. solani* (Mart.) Appel. and Wr. emend Snyd. and Hans. were tested in soil. None reduced seedling emergence at water potentials suitable for good soybean seed germination (−0.013 to −0.4 bar). Some isolates caused seed rot at water potentials substantially lower than those normally occurring in the field (R. L. Schlub and J. L. Lockwood, *unpublished*). These results will be discussed in another report. By contrast, most isolates of *P. ultimum* reduced seedling emergence, and produced symptoms similar to those characteristically seen in the field, except that the curling growth habit was less evident than in field conditions.

As few as 25 propagules per gram (ppg) of *P. ultimum* completely prevented emergence of soybean seedlings in artificially infested soil at −0.18 bar at 28 C, whereas percent seedling emergence at inoculum densities of 0, 5, and 10 ppg were 93±7, 57±16 and 29±17, respectively. The influence of matric potential was tested by using soil infested with 7 ppg *P. ultimum*. At −1.8 bars percent emergence in soil containing *P. ultimum* was 66±13, as compared to soil without *P. ultimum*, 73±13. At −0.18 bar matric potential, percent emergence was reduced to 29±14 as compared with 65±17 in the control. However, due to the large amount of variability the difference was only significant at $P = 0.10$. At −0.018 bar, percent emergence in infested soil was 15±11, which was significantly less than that in disinfested soil, 45±8. Similar results were obtained with a naturally infested soil containing 500 ppg at 28 C. Percent emergence was significantly less at −0.018 bar matric potential (23±14) than at −0.18 (83±3) or −1.8 bars (57±21). The same trend also was seen with other soil samples taken from the same farm.

Three *Fusarium* species, *F. oxysporum, F. moniliforme* 'Subglutinans' Wollew. and Reink., and *F. tricinctum* (Cda.) emend Snyd. and Hans., which caused soybean seed rot in dry soils

TABLE 1. Percentages of seedling tissue pieces from which *Pythium* and *Fusarium* spp. were isolated 1, 3, and 6 days after soybean seeds were planted in natural soil containing 300 propagules of *Pythium* and 5,000 propagules of *Fusarium* per gram of soil, at 28 C

Tissue[b]	Day 1		Day 3		Day 6	
	Pythium[c]	*Fusarium*[d]	*Pythium*	*Fusarium*	*Pythium*	*Fusarium*
Seed coats	84[a]	95	...	...	...	...
Root tips	0	0	0	10	30	10
Cotyledons	21	7	60	40	60	60
Hypocotyls	...	...	33	20	70	60

[a] Percentages are based on 10–15 tissue pieces.
[b] Tissue pieces were from nonemerged plants and were approximately 4 mm^2 in size. Lesioned tissue was plated when present. Seeds were planted in wet soil (−0.013 bar) and were covered (3.8 cm deep) with air-dry soil.
[c] All *Pythium* isolates grew at 10 C, but none grew at 37 C.
[d] *F. oxysporum* comprised 85% of the *Fusarium* spp. isolated.

(Schlub and Lockwood, *unpublished*) and root rot in other tests (18), were individually combined with *Pythium*-infested soil (7 ppg) and adjusted to 3,000 ppg *Fusarium*. Seeds were placed on wet soil −0.013 and covered with air-dry soil at 28 C. None of the Fusarium isolates decreased emergence below that induced by *Pythium* alone.

Influence of temperature and Lesan on emergence. To investigate the influence of temperature on disease development, seeds were planted on wet soil and covered with dry soil. Under such conditions seed germination in disinfested soil was consistently higher and less variable than in moist soil (−0.18 bars). Seeds covered with dry soil also germinated poorly in soil infested with *P. ultimum*. When *P. ultimum* (7 ppg) was added to propylene oxide-disinfested soil, a significant reduction in emergence occurred over a range of temperatures. Emergence at 16 C (9%) was significantly less than that at 20 C (44%), 24 C (43%), and 28 C (60%). In natural soil with a *P. ultimum* concentration of 500 ppg, emergence was significantly higher at 16 C (23%) than at 20 C (15%), 24 C (13%), or 28 C (10%), and all values were less than the mean of the disinfested soil control over the four temperatures (96%). With another soil sample collected 1 yr later, having a *P. ultimum* population of 300 ppg, there was no significant difference between 16 and 28 C in soybean emergence (28 and 31%, respectively). However, at 16 C, soil treatment with Lesan increased emergence to 89%.

Natural soil repeatedly planted to soybean and which had a *P. ultimum* inoculum density of ~1,000 ppg, was also treated with Lesan. In three replicate plantings of 20 seeds each in plastic trays at 24 C, mean emergence in untreated soil was 47%, whereas emergence in Lesan-treated soil was 88%.

TABLE 2. A partial list of independent variables that were eliminated from the regression equation due to their low level of significance (> 0.10)

1. Weekly average soil temperature.
2. Number of days maximum soil moisture was >−0.5 bar plus number of days minimum soil moisture was <−3 bars plus number of days average temperature was <25 C.
3. Total rainfall.
4. Rainfall the first day.
5. Rainfall in the first 3 days.
6. Average weekly soil moisture.
7. Number of days soil moisture was >−0.5 bar.
8. Number of hours of rain in the first week.
9. Total rain in the first week.

Multiple regression analysis of field data. Rainfall, soil moisture (matric potential), soil temperature, and emergence data are shown in Fig. 1. Since the most complete set of environmental data had been collected from the soybean rows which were not artificially watered, these were used to form the regression equation.

$$\hat{y} = 87.6 - 5.32(SM) - 17.76(Rain)$$

The soil moisture variable (SM) was the number of days continuously after planting that the maximum soil moisture at planting depth was >−0.5 bar matric potential plus the number of days in the first 3 days after planting that the minimum soil moisture at planting depth was <−3 bars matric potential.

The rain variable (Rain) was the total rainfall in centimeters within the first 3 days after planting plus the number of days in the first 3 days after planting that the minimum soil moisture at planting depth was < −3 bars matric potential.

The coefficient of determination (R^2) based on 10 plantings made in the natural rainfall-watered rows from 17 May to 16 September

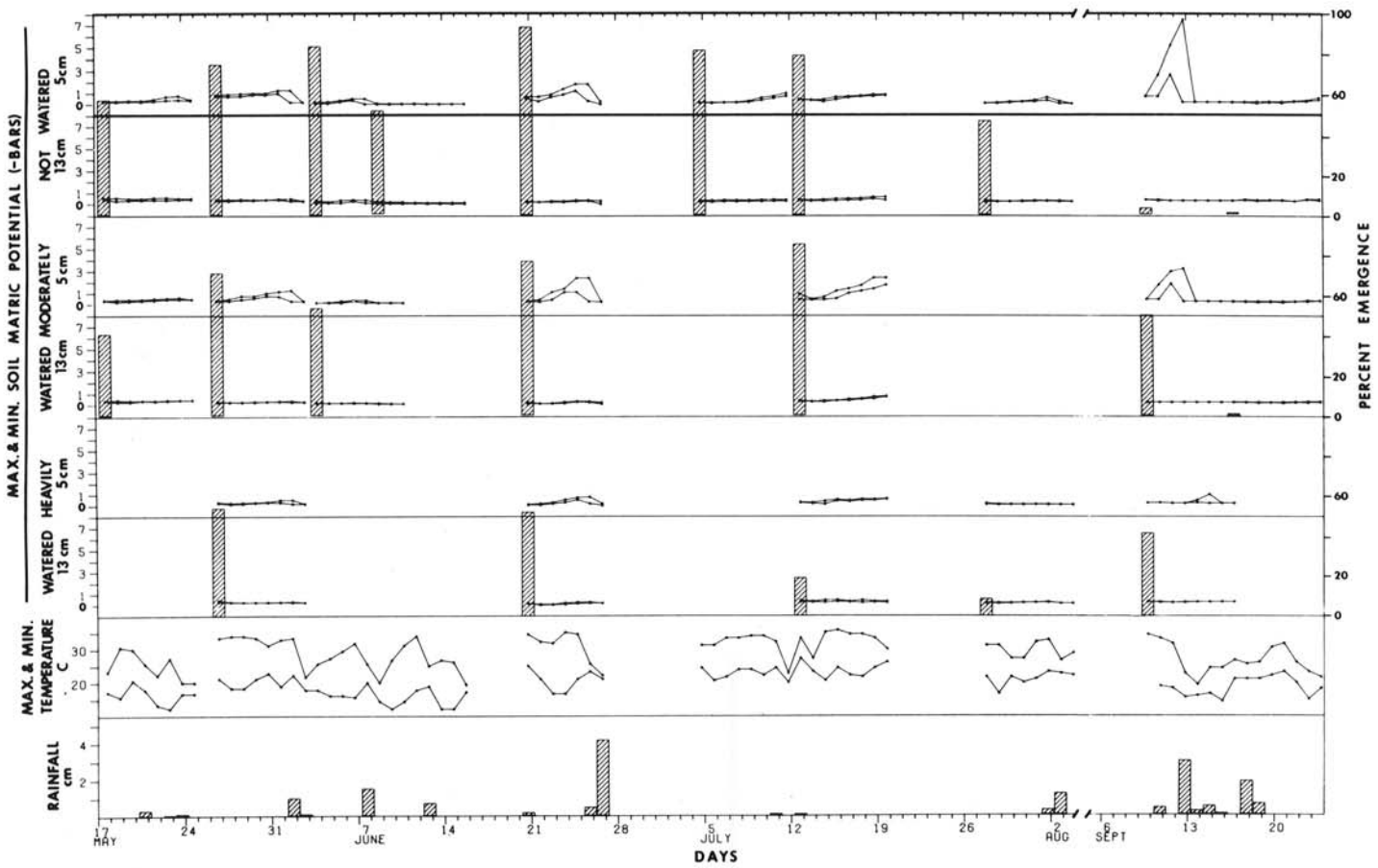

Fig. 1. Emergence of soybean seeds planted during the summer, 1978, with corresponding data on rainfall, soil temperature at 6.5 cm, and soil matric potential at soil depths of 5 and 13 cm. The soil, a sandy loam, was naturally infested with *Pythium ultimum*. The emergence data were recorded 2–3 wk after planting, but in the figure these data are shown by bars over the planting date.

was 0.84, and the simple correlation between actual and predicted emergence was $r = 0.91$ ($P = 0.01$). Data from four plantings of seeds 3.5 cm deep, which had corresponding moisture blocks with their tops positioned at 2 cm depth had an $r = 0.74$ ($P = 0.05$). Some of the 23 factors which were eliminated from the regression equation due to low level of significance ($P > 0.10$) are listed in Table 2. If the rainfall data are omitted from the regression equation a new prediction equation is formed:

$$\hat{y} = 79.03 - 6.64(SM)$$

The R^2 for this equation = 0.21. The emergence data obtained from the watered rows correlated well with values from this single-value equation ($r = 0.72$) ($P = 0.05$).

The multiple regression analysis indicates that if a naturally infested soil is continuously wet (>0.5 bar) or is dry (<−3 bars) within the first 3 days, then emergence of soybeans is reduced.

DISCUSSION

As few as 5 ppg *P. ultimum* in disinfested soil were found to significantly reduce seedling emergence. No emergence occurred at 25 ppg; this, plus complete control of the disease afforded by Lesan treatment of natural soil, provides strong evidence for the role of *P. ultimum* in the etiology of the preemergence seedling disease. By contrast, little or no reduction in seedling emergence was obtained with *Fusarium* isolates, principally *F. oxysporum* and *F. solani*, obtained from soybean. Moreover, there appeared to be no interaction between *Fusarium* spp. and *P. ultimum* in causing pre-emergence damping-off of soybean seedlings, at least under moist soil conditions. Dunleavy (3) reported that *F. oxysporum* may cause poor emergence of soybean in moist soil, but we were not able to confirm his findings. Interactions between *P. ultimum* and *Fusarium* spp. have been reported (7,15), and it is possible that these pathogens may interact as soybean root pathogens once the soybean is beyond the seedling stage.

The involvement of *P. ultimum* in the seedling disease was unexpected in view of the disease's apparent restriction to hosts growing in sandy, well-drained soils, and the general association of *Pythium* diseases with high soil moisture (6,8,13,17,21). However, in spite of the soil being light-textured, water potentials in unwatered plots free of emerged plants frequently remained at −1 bar or more for several days at a time 13 cm, or even 5 cm, deep. *P. ultimum* is also considered to be one of the principal pathogens infecting bean roots in sandy soils in Wisconsin (6) and New York (15,16).

Analysis of field data by multiple regression indicated that the number of days of continuously wet soil (maximum >−0.5 bar) from the time of planting plus the number of days of low soil moisture (minimum <−3 bars), and the amount of rainfall in the first 3 days after planting, were positively correlated with disease. Since rainfall during the 3 days immediately after planting reduced emergence, it is very likely that the higher the soil matric potential in the field the more disease will develop. Gypsum soil moisture blocks are not very accurate at potential >−0.5 bar; therefore, this value was used as the upper limit in the analysis. It is not known whether *P. ultimum* causes poor emergence in the field at matric potentials <−3 bars. High soil moisture is not always required for the causation of disease by *Pythium* spp. (2,4) which have been known to colonize plant tissue pieces at moderate water potentials (>−1.4 bar) (12). Soybean seedlings germinate very slowly at −3 bars, and may thereby remain susceptible longer to infection by *P. ultimum* and perhaps by *Fusarium* spp. also.

The emergence of soybean seedlings decreased with increasing soil moisture in propylene oxide-disinfested control soil, but not to the extent that it was decreased in soils artificially and naturally infested with *P. ultimum*. Soybeans appear to be very sensitive to constant wet soil conditions thereby resulting in extreme variability from experiment to experiment. The suspression of soybean emergence by wet soil in the absence of a pathogen has been shown by others (10,21) and was included in a regression equation for hypocotyl elongation by Knittle et al (10). If the seeds were placed on wet soil and covered with air-dry soil, the emergence is much less variable; therefore, this method could be used to determine the disease potential of natural soil samples.

The population in natural soil must be approximately 100 times greater than in artificially infested soil in order to result in the same amount of disease. This is probably due to the existence of nonpathogenic isolates and suppression of *P. ultimum* by biotic and abiotic factors in natural soil.

The influence of temperature on disease development varied depending on whether the soil was artificially or naturally infested, and with different samples of field soil. Inconsistency in the temperature relations of *P. ultimum* diseases of various crops is revealed in the literature. Some diseases were favored by low temperature (17,23), some by high temperatures (1,6,13), and others were more or less unaffected by temperature (5,9). The temperature effect on disease may be more related to its influence on the host than on the pathogen (14). Other factors, as yet unknown, apparently are involed in the temperature optimum for seedling rot of soybean by *P. ultimum*.

We were not able to develop any statistically significant independent variable involving temperature data. This may have been because of the narrow range of weekly average temperatures which were recorded, the low average being 20.3 C and the high average 28.2 C.

Our multiple regression equation is by no means a complete model for the disease because factors such as seed vigor, seed size, soil type, planting depth, soybean cultivar, and inoculum density of the pathogen were not included. The variables used in the equation based on our data are possibly not the only variables or the best ones to use because of their similarities. Both variables (SM and Rain) contained the dry soil (<−3 bars) data. However, through the use of multiple regression techniques the importance of soil moisture in *P. ultimum* seedling rot of soybean was verified in the field. Regression analysis also verified the minor importance of temperature in the range of 20–28 C as being important in disease development, which agrees with laboratory results.

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