Effect of Soil Saturation Duration and Soil Water Content on Root Rot of Maize Caused by *Pythium arrhenomanes*

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ABSTRACT

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Three aggressive isolates of *P. arrhenomanes* (201-25, 7E, and 5E) were used to evaluate the effect of soil saturation duration and soil water content on maize root rot. Maize seedlings grown in infested and noninfested soil:sand mixtures were subjected to saturation durations of 0, 6, 12, 24, or 40 h. Four silty-clay loam soil:sand mixtures (100:0, 80:20, 50:50, and 0:100) were used to evaluate the effect of soil water content on disease development. Matric water potential was maintained at -1 J/kg during the experiment except for the saturation period. Multiple regression analysis was used to evaluate the effect of saturation duration and soil water content on root and shoot dry weight. Negative slope values were obtained for increasing saturation duration and reduced water content (increased proportion of sand to soil). Intercepts of regression lines for shoot and root dry weights were lower for the infested soil:sand treatments than the noninfested treatments. These results indicated that growth of maize plants was negatively affected by increased flooding duration, lower soil water content, and presence of the pathogen. Growth of maize was significantly ($P = 0.05$) less in the presence of the pathogen than in noninoculated control treatments at each soil water content and flooding duration.

Pythium arrhenomanes Drechsler is a common pathogen of maize (*Zea mays* L.), particularly in soils that retain water (9,17,24,29,30). Research to determine the significance of *Pythium* root rot in the production of maize has been hampered by the inability to isolate *P. arrhenomanes* directly from soil and root tissues throughout the growing season. *P. arrhenomanes* could be isolated from maize root tissues for only a few days after rain events that saturated soil (7). Isolation of *P. graminicola* from maize roots also was inconsistent throughout the growing season (14). The association of high soil moisture and the ability to isolate *Pythium* spp. after rain events suggests a relationship between periods of soil saturation and the level of *Pythium* root rot.

Few studies have determined the relationship between soil water and severity of diseases caused by *Pythium* spp. However, as early as 1919, interactions of soil water

and disease severity were observed (18). In general, near-saturated soil conditions increased the incidence of root rot caused by various *Pythium* spp. (4,6,11,12). High soil moisture directly favors *Pythium* spp. by providing a continuous water film necessary for zoospore production and motility (20,33,34). In addition, high soil water may indirectly favor infection and colonization of the host tissues by the fungus by decreasing host vigor and increasing the release of host exudates that may stimulate germination of dormant propagules (1,4,33). The effect of soil water on zoospore release by *Phytophthora* spp. is well documented (13,15,22,28,32). Duniway (10,11) demonstrated that protracted periods of saturated conditions favor zoospore formation, release, dispersal, and attachment to root surfaces. Soil pore size distribution, as it relates to soil texture, limits the movement of zoospores by determining the number of pores large enough to accommodate motile spores (10,28).

The duration and number of periods of soil saturation increases the level of root rot incited by several *Phytophthora* spp. (3,5,19,23,32,36,37). For example, Bowers et al. (3) demonstrated that when soil infested with oospores of *Phytophthora capsici* was held at constant -2.5 J/kg matric potential for 37 to 40 days, a low level of disease occurred. In contrast, when the infested soil was periodically saturated, 20% of the pepper plants died after a single 24-h saturation period. When the saturation period was repeated two and three times,

53 and 100% of the plants died, respectively. Similarly, Wilcox et al. (36,37) reported that *Phytophthora* root and crown rot of cherry trees occurred most frequently in orchards with poorly drained or periodically saturated soil and that longer periods of saturation (24 to 48 h) increased disease incidence.

Reduced tillage is an increasingly popular method for managing soil and crop residues in Ohio (2). However, in poorly drained clay soils, lower yields were obtained with reduced tillage and continuous maize than with fall plowing and a maize-soybean rotation (8,35). These results suggest that reduced yield may have been associated with greater water-retaining properties of soil and the use of reduced tillage or continuous corn (8,13,30). Our study was undertaken to determine the influence of soil saturation duration and soil water content on root rot of young maize plants caused by *P. arrhenomanes*.

MATERIALS AND METHODS

Media. The *Pythium*-selective PY-medium developed by Schmitthenner (31) was used throughout this study. The medium contained 2.5 g sucrose, 0.27 g asparagine, 0.15 g KH_2PO_4 , 0.15 g K_2HPO_4 , 0.10 g $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 0.08 g CaCl_2 , 0.01 g cholesterol, 0.01 g ascorbic acid, 0.002 g thiamine, 0.01 g chloroamphenicol, 0.027 g pentachloronitrobenzene (PCNB), 0.02 g benomyl, 0.10 g neomycin sulfate, 19 g bacto agar, and 1,000 ml water. The antibiotics were added aseptically after the medium was autoclaved. The medium was modified for maintaining *P. arrhenomanes* cultures by leaving out the fungicides, PCNB, and benomyl.

Soil. Hoytville silty-clay loam (Mollic ochraqualf, sand 21%, silt 39%, clay 40%) obtained from rotation-tillage plots located at the Ohio Agricultural Research and Development Center Northwest Branch (OARDC-NW Branch) near Hoytville was used in all experiments (21,35).

Inoculum. A soil-potato medium was prepared by mixing 400 g Hoytville silty-clay loam, 100 g river sand, and 50 g chopped potato. The ingredients were mixed by hand with enough water to obtain a friable, moist medium. The 550 g of medium was placed in a one liter flask closed with a cotton plug, covered with aluminum foil, and then autoclaved on two consecutive days at 121°C for 90 min each

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day. Sterile distilled water was added to maintain adequate moisture for fungal growth as needed. *P. arrhenomanes* isolates were grown on modified PY-medium for 3 days in 9-cm-diameter petri dishes, then half the volume of a dish was transferred to each flask of soil-potato medium. After inoculation, flasks were maintained at 22 to 25°C for 6 days and periodically shaken by hand. Microscopic examination indicated that inoculum consisted mostly of mycelium and sporangia, but the proportion of sporangia capable of producing zoospores was unknown.

Aggressiveness tests. Fifteen *P. arrhenomanes* isolates previously obtained from maize roots collected from field plots at the OARDC-NW Branch were tested for aggressiveness on maize. Tests were conducted three times with four replications using a completely randomized-block, factorial design. The factors were isolate,

soil mixture, and maize hybrid. The two soil mixtures were Hoytville silty-clay loam and a 50:50 (wt/wt) mixture of Hoytville silty-clay loam and river sand. The two soil mixtures were used to obtain different water contents in the soil matrix. The soil mixtures were sterilized by autoclaving at 121°C for 24 h prior to use. The two hybrids were Terra 1060 and French's 250. Soil-potato inoculum (550 g) was mixed with sterile soil or the soil:sand mixture (5080 g) and divided equally into eight 11.5-cm-diameter plastic pots. Non-infested soil-potato medium was mixed with sterile soil or the soil:sand mixture for control treatments. Four seeds were planted in each pot (four pots/isolate/soil/hybrid). Pots were watered to saturation daily and 50 ml of nutrient solution was added every 2 days. The nutrient solution was prepared by mixing a stock solution of a commercial 20-20-20 fertilizer (Peters Professional, Scotts-Sierra Horticultural Products Co., Marysville, OH) to obtain 400 ppm N-P-K. Plants were maintained in a greenhouse in sunlight with an air temperature ranging from 22 to 25°C. Thirty days after planting, shoots were cut at the soil surface and placed in paper bags. Roots were washed free of soil under running tap water and examined for root rot. Several small discolored root pieces were selected for reisolation of the fungus on PY-medium and the remainder placed in paper bags. Plant tissues were dried in an oven at 51°C until no further weight was lost, and dry weights of roots and shoots recorded.

Effect of saturation duration and soil water content. Three aggressive isolates (7E, 5E, and 201-25) were chosen to evaluate the effect of saturation duration and soil water content on severity of maize root rot using the hybrid Terra 1060. The

experiment was conducted three times with four replications using a split-split plot design in which the whole plot was isolate, subplot was soil:sand mixture, and sub-subplot was saturation duration. In order to obtain soils of different water content based on soil texture, Hoytville silty-clay loam and river sand were mixed on a dry weight basis to obtain four soil:sand mixtures (100:0, 80:20, 50:50, and 0:100). After mixing, soil:sand mixtures were autoclaved at 121°C for 24 hr. Five periods of saturation duration (0, 6, 12, 24, and 40 h) were tested.

Soil-potato inoculum was mixed with each soil:sand mixture and placed into 14-cm-diameter Styrofoam cups. Each cup contained 55 g of soil-potato inoculum and 1000 g of a soil:sand mixture, based on dry weight. Noninfested soil-potato medium mixed with each soil:sand mixture served as the control treatments. Four seeds were planted in each cup, then cups were arranged on the greenhouse bench and maintained at 22 to 25°C in sunlight. Four days after planting, cups with seedlings were placed in 14-cm-diameter, 3-cm-deep plastic saucers. The height of water in the saucers was maintained at 10 cm below the soil surface in each cup so that all soils would be maintained at a matric water potential above -1 J/kg. Water was added to saucers each day to maintain this specific water level. Every other day, 50 ml of a 400 ppm N-P-K nutrient solution, prepared as described earlier, was added to the soil surface of each cup. Ten days after planting, pots were placed in large containers so water could be added to bring the water surface level with the soil surface in each cup. This level was maintained until cups were removed at the end of each saturation duration period. Each saturation treatment was repeated 10 days later.

Fig. 1. Effect of *Pythium arrhenomanes* isolate on shoot dry weight of maize hybrid Terra 1060 and French's 250 thirty days after planting in infested Hoytville silty-clay loam or a 50:50 (wt/wt) mixture of Hoytville silty-clay loam: river sand. Least significant difference = 0.04g ($P = 0.05$).

Fig. 2. Effect of *Pythium arrhenomanes* isolate on root dry weight of maize hybrid Terra 1060 and French's 250 thirty days after planting in infested Hoytville silty-clay loam or a 50:50 (wt/wt) mixture of Hoytville silty-clay loam:river sand. Least significant difference = 0.02g ($P = 0.05$).

Table 1. Analysis of variance for main effects of *Pythium arrhenomanes* isolates (isolate), water content in soil (water), saturation duration (saturation), and interaction of these factors on shoot and root dry weights of maize plants grown in the greenhouse

Source of variation	df ^a	Shoot weight	Root weight
		MS ^b	MS
Experiment	2	57.57***c	25.77***
Experimental error	9	0.246	0.063
Isolate	3	92.10***	13.56***
Isolate error	27	0.046*	0.013***
Water	3	22.11***	3.27***
Water error	27	0.053	0.011*
Isolate* water	9	3.53***	0.429***
Isolate* water error	81	0.055***	0.022***
Saturation	4	9.30***	2.76***
Saturation* isolate	12	0.391***	0.063***
Saturation* water	12	0.09***	0.02**
Saturation* isolate* water	36	0.042*	0.01*
Error	396	0.025	0.006
R ²		0.98	0.98

^a df = degrees of freedom.

^b MS = mean squares were obtained from analysis of variance table.

^c Three asterisks indicate significance at $P = 0.0001$, two asterisks indicate significance at $P = 0.001$, and one asterisk indicates significance at $P = 0.05$.

Thirty-five days after planting, plants were cut at the soil surface and tops placed into paper bags. Roots were washed free of soil under running tap water and placed into paper bags. All tissues were dried in an oven at 51°C until no further weight was lost, and then dry weights were recorded.

Statistical analyses. Shoot and root dry weight data (an observation was the mean of four plants per pot) were analyzed by analysis of variance (ANOVA) procedures (SAS Institute, Cary, NC). Means were compared using Fisher's least significant difference. Relationships among saturation durations, soil water content, and plant shoot and root dry weights were examined by regression analysis using the general linear models (GLM) procedures of SAS. The multiple regression equation used was: $Y = b_0 + b_1(\text{FD}) + b_2(\text{PS})$ in which Y was shoot or root dry weight (dependent variable), FD was flooding duration, PS was percentage of sand in soil:sand mixtures, and b_0 , b_1 , and b_2 were parameters. Simple correlations were calculated to determine the relationships between shoot and root dry weights.

RESULTS

Isolate aggressiveness test. The experiment was conducted three times, each time during a different month of the year. Actual mean values for shoot and root dry weight for isolates were different for each experiment, but the rank order of isolate means did not change appreciably across experiments (data not presented). Combined analysis of the three experiments indicated that the main effect of the two soil:sand mixtures was not significant ($P = 0.05$) and the interactions of soil:sand mixture by isolate, hybrid by soil:sand mixture, and hybrid by isolate by soil:sand mixture also were not significant for shoot and root dry weight.

The main effect of isolate and the hybrid by isolate interaction were significant for both shoot and root dry weight ($P < 0.05$). Thus, data for the two hybrids are presented separately (Figs. 1 and 2). The significant interaction was due to a wide range in reduction (5 to 75%) of plant shoot dry weight caused by the 15 isolates tested, with the more aggressive isolates causing greater reduction in shoot dry weight on Terra 1060 than on French's 250

compared to less aggressive isolates (Fig. 1). Reduction in root dry weight followed a similar trend (0 to 72% reduction) (Fig. 2). All isolations from discolored root tissues collected from test plants yielded cultures of *P. arrhenomanes*. Highly aggressive isolates 201-25, 7E, and 5E were selected for use in additional tests.

Influence of saturation duration and soil water content. The experiment was conducted three times, each time during a different month of the year. Therefore, the experiment was analyzed as replicated over time (Table 1). The main effect of experiment was significant ($P = 0.0001$), indicating that environmental conditions affected growth of plants differently during repetitions of the experiment. The main effect of isolate also was significant ($P = 0.0001$). For most treatments, isolate 201-25 caused less reduction in shoot and root dry weight than isolates 5E or 7E (Figs. 3 and 4). All two-way and the three-way interactions were significant ($P = 0.01$) for shoot and root dry weight (Table 1).

Negative slope values were obtained for the relationships between soil saturation duration and soil water content for shoot

Fig. 3. Effect of soil saturation duration and soil water content (percent river sand in Hoytville silty-clay loam) on shoot dry weight of maize hybrid Terra 1060 infested with three isolates of *Pythium arrhenomanes* (7E, 201-25, and 5E) and a noninfested control 35 days after planting. Least significant difference = 0.13g ($P = 0.05$).

Fig. 4. Effect of soil saturation duration and soil water content (percent river sand in Hoytville silty-clay loam) on root dry weight of maize hybrid Terra 1060 infested with three isolates of *Pythium arrhenomanes* (7E, 210-25, and 5E) and a noninfested control 35 days after planting. Least significant difference = 0.13g ($P = 0.05$).

and root dry weights (Table 2). Reduction in shoot and root dry weights of plants grown in noninfested soil:sand mixtures occurred, but no root discoloration was observed. Longer periods of saturation duration caused lower shoot and root dry weights, as did lower soil water content (increased sand content of soil:sand mixtures) (Figs. 3 and 4). The one exception to this trend was that isolate 201-25 caused significantly lower shoot and root weights in the soil:sand mixture containing 20% sand than in 100% sand (Figs. 3 and 4). Intercepts of regression lines were lower for all inoculated treatments than for the controls (Table 2).

Slope values for saturation duration and soil water content were less negative for isolates than for the noninfested control. The lower slope values (b_1 and b_2) obtained in inoculated treatments indicated that longer saturation durations and lower soil water content caused less change in shoot and root dry weight in comparison with the non-inoculated controls. Additionally, the lower intercepts in inoculated treatments than in the non-inoculated controls indicated that the presence of the

pathogen reduced root/shoot weights for all saturation durations and soil water contents (Figs. 3 and 4). In general, R^2 values were higher for regression equations for individual experiments than for data combined across experiments (Table 2). There was a significant ($P = 0.001$) positive correlation between shoot and root dry weight, but the correlation coefficient was low ($r = 0.19$).

DISCUSSION

A range in aggressiveness was detected among 15 field isolates of *P. arrhenomanes* from maize. Deep and Lipps (7) reported similar differences among isolates from maize; Hoy et al. (16) reported differences among isolates from sugarcane; and Rands (29) reported differences among isolates from both maize and sugarcane.

Several isolates capable of inciting high levels of disease under the conditions of these tests were used to evaluate the effect of flooding duration and soil water content on maize root rot. Maize growth was proportional to the duration of soil saturation and soil water content without the presence of *P. arrhenomanes* and with each of the three isolates tested. Root and shoot

weights were significantly lower in infested soil:sand mixtures than in the noninfested controls for each of the five saturation durations. When soil matric potential was maintained at/or above -1 J/kg, maize plants grown in infested soil:sand mixtures had significantly lower shoot and root dry weights than plants grown in noninfested controls. Apparently, soil saturation was not necessary for infection and disease development, but plants were more negatively affected when saturated conditions existed for an extended period of time because of the additive effect of the pathogen and soil water on plant growth.

The soil:sand mixtures used in these tests provided a range of soil water contents. At saturation the 0:100 soil:sand mix had only half the amount of water of the 100:0 mix (19.4 g and 38.3 g water per 100 g soil:sand mix, respectively). Maize plants were more adversely affected by root rot when grown in soil:sand mixtures with less water content. The influence of 100% sand may have been due to the greater number of large pore spaces suitable to accommodate zoospore movement (10,28) or to more root surface in direct

Table 2. Multiple regression statistics describing the relationship between flooding duration and soil water content, as percentage of sand in soil:sand mixtures, and their effect on shoot and root dry weight of maize inoculated with three isolates of *Pythium arrhenomanes*

Isolate	Experiment	Partial regression coefficients			R ²	df ^a	Error MS
		Intercept	Flooding duration	Percent sand			
Shoot dry weight (g)							
7E	1	0.43(0.014) ^b	−0.004(0.0005)	−0.077(0.019)	0.52	77	0.004
	2	1.26(0.028)	−0.012(0.0010)	−0.350(0.039)	0.74	77	0.017
	3	1.48(0.041)	−0.014(0.0015)	−0.675(0.057)	0.74	77	0.037
	Combined	1.06(0.042)	−0.011(0.0016)	−0.367(0.059)	0.25	237	0.118
201-25	1	0.49(0.023)	−0.006(0.0009)	−0.043(0.032)	0.38	77	0.118
	2	1.55(0.080)	−0.012(0.0030)	−0.804(0.112)	0.47	77	0.143
	3	1.80(0.108)	−0.019(0.0040)	−0.695(0.151)	0.36	77	0.258
	Combined	1.28(0.065)	−0.012(0.0024)	−0.514(0.090)	0.20	237	0.278
5E	1	0.29(0.013)	−0.003(0.0005)	−0.045(0.018)	0.33	77	0.004
	2	1.75(0.035)	−0.012(0.0013)	−0.856(0.050)	0.83	77	0.028
	3	1.28(0.051)	−0.015(0.0019)	−0.284(0.071)	0.52	77	0.057
	Combined	1.11(0.058)	−0.010(0.0021)	−0.340(0.081)	0.16	237	0.221
Control	1	2.05(0.050)	−0.015(0.0019)	−0.622(0.070)	0.65	77	0.056
	2	3.05(0.080)	−0.025(0.0029)	−1.639(0.111)	0.79	77	0.140
	3	3.67(0.067)	−0.024(0.0025)	−1.634(0.094)	0.84	77	0.101
	Combined	2.93(0.069)	−0.021(0.0026)	−1.298(0.097)	0.51	237	0.319
Root dry weight (g)							
7E	1	0.19(0.007)	−0.002(0.0003)	−0.001(0.011)	0.39	77	0.001
	2	0.68(0.018)	−0.007(0.0007)	−0.221(0.026)	0.68	77	0.008
	3	0.89(0.027)	−0.009(0.0010)	−0.359(0.037)	0.69	77	0.016
	Combined	0.58(0.027)	−0.006(0.0010)	−0.194(0.038)	0.20	237	0.048
201-25	1	0.20(0.010)	−0.003(0.0004)	−0.009(0.014)	0.47	77	0.002
	2	0.76(0.036)	−0.007(0.0013)	−0.283(0.051)	0.43	77	0.029
	3	0.95(0.058)	−0.010(0.0021)	−0.311(0.081)	0.32	77	0.074
	Combined	0.63(0.035)	−0.007(0.0013)	−0.201(0.050)	0.15	237	0.084
5E	1	0.22(0.008)	−0.002(0.0003)	−0.051(0.011)	0.48	77	0.001
	2	0.88(0.021)	−0.008(0.0008)	−0.350(0.029)	0.76	77	0.009
	3	0.70(0.028)	−0.008(0.0011)	−0.104(0.040)	0.43	77	0.018
	Combined	0.60(0.028)	−0.006(0.0010)	−0.168(0.040)	0.18	237	0.051
Control	1	0.55(0.016)	−0.004(0.0006)	−0.082(0.023)	0.44	77	0.006
	2	1.31(0.036)	−0.010(0.0013)	−0.445(0.051)	0.63	77	0.029
	3	1.83(0.040)	−0.016(0.0015)	−0.624(0.056)	0.75	77	0.036
	Combined	1.23(0.049)	−0.010(0.0018)	−0.384(0.069)	0.20	237	0.163

^a df = degrees of freedom.

^b The value in parentheses represents the standard deviation of the estimate.

contact with water films. In any case, the effect of soil water content on maize root rot could be due to conditions that favor pathogen activity as well as factors that predispose the plant to infection (1,5,6, 25,26,27).

In northwest Ohio, where maize is grown in heavy clay soils like the Hoytville silty-clay loam used in this study, water drains more slowly from the soil profile following a heavy rain than locations with more sandy soil textures. Maize growth is adversely affected under these conditions as a result of root rot caused by *P. arrhenomanes* and protracted periods of soil saturation in heavy clay soils (7). It may be possible to increase the growth of maize in heavy clay soil by managing soil water through improved drainage by tiling, tillage, or a combination of both.

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