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Predispositional Effect of Soil Water Saturation on Infection of Chile Pepper by *Phytophthora capsici*

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Abstract. Phytophthora capsici* is a serious soilborne pathogen in chile pepper [*Capsicum annuum* L.] in New Mexico, and has been shown to spread under high soil moisture conditions and cause losses in a wide array of crops worldwide. This study was conducted to assess whether soil water saturation predisposes chile pepper to infection by *P. capsici*. Potted chile pepper plants of 'Criollo de Morelos 334' ('CM334') and 'New Mexico 6-4' ('NM6-4'), resistant and susceptible to *P. capsici*, respectively, were subjected to soil water saturation conditions (saturated and nonsaturated) for 3 and 6 days at two growth stages (six- to eight-leaf stage and one- to four-flower bud stage) prior to being inoculated or noninoculated with zoospores of *P. capsici*. Regardless of growth stage, no disease symptoms developed in 'CM334' grown either under saturated or nonsaturated soil conditions at any of the two periods (3 or 6 days) of soil water saturation. In 'NM6-4', disease symptoms consisting of stem necrosis, defoliation, and wilting were expressed. Plant growth stage at inoculation had a significant effect on disease severity ($P < 0.0001$). However, the response of 'NM6-4' to *P. capsici* at each growth stage under saturated soil conditions was similar to that under nonsaturated conditions regardless of the period of saturation ($P = 0.09$). These results indicate that soil water saturation does not exert a significant predispositional effect on infection of chile pepper by *P. capsici*.

Phytophthora blight, caused by *Phytophthora capsici*, was first described by Leonian (1922) as a disease affecting roots, stems, and fruit of chile pepper (*Capsicum annuum* L.). Infection of roots results in root rot and plant wilting. Brown to black lesions may develop on stems, and brown water-soaked lesions may be found on leaves and fruit. Since the publication of Leonian's work, the disease has been reported in a wide array of crops in plant families such as solanaceae and cucurbitaceae (Erwin and Ribeiro, 1996). Phytophthora blight is a serious disease on chile pepper, and was shown to decrease yield of green chile pepper by 55% and combined yield of green and red chile pepper by 36% (Xie et al., 1999).

Development of Phytophthora blight in pepper has been invariably associated with high soil moisture conditions as generated from irrigation or rainfall (Biles et al., 1992; Bowers and Mitchell, 1990; Bowers et al., 1990; Café-Filho and Duniway, 1995; Ristaino, 1991; Xie et al., 1999). The relationship between soil moisture and ecology of *P. capsici* in pepper has been extensively researched and knowledge accumulated in this area has been reviewed (Erwin and Ribeiro, 1996; Ristaino and Johnston, 1999). Bowers and Mitchell (1990) showed that plant mortality increased in pepper seedlings growing in soil infested with oospores of *P. capsici* and exposed to 24-h periodic flooding after three flooding events temporally spaced 10 d apart. Survival of potted chile pepper plants, grown in soil infested with *P. capsici* and flooded for 48 h every 2 weeks over a period of about 60 d, was 8 to 13 d less than plants irrigated daily over a period of about 60 d (Matheron and Porchas, 2002). Drip irrigation was demonstrated to reduce incidence of *P. capsici* in pepper (Xie et al., 1999). However, effectiveness of drip irrigation depends on the frequency of utilization. Higher drip irrigation frequencies may increase disease incidence (Ristaino, 1991). Alternate-furrow irrigation decreased incidence of disease compared to irrigation of every furrow (Biles et al., 1992). Lower frequencies of furrow irrigation may also reduce disease incidence (Café-Filho and Duniway, 1995).

Outbreaks of diseases caused by *P. capsici* under high soil moisture conditions could be explained from at least two perspectives. First, under saturated conditions, abundant swimming zoospores are produced by the pathogen and enable it to spread rapidly to target plants. Second, saturated conditions may induce stress in plants and increase their proneness to attacks by *P. capsici*. Whereas there is a mammoth amount of literature supporting the first perspective (Bowers and Mitchell, 1990; Ristaino, 1991), there is virtually no report on predispositional effects of soil water saturation on the response of chile pepper to *P. capsici*. Water saturation of soil has been shown to predispose alfalfa (*Medicago sativa* L.) to Phytophthora root rot, caused by *P. megasperma* f. sp. *medicaginis*, by inducing cracks in the roots and increasing leakage of nutrients from roots (Kuan and Erwin, 1980). Average root rot severity index was 4.8 (on a scale of 0 to 5) on alfalfa plants grown in saturated soil for 5 d before inoculation, whereas average root rot severity index was 2.5 on plants grown in unsaturated soil.

Chile pepper is produced predominantly in southern New Mexico where furrow irrigation is the most practiced method of irrigation (Skaggs et al., 2000). Saturated soil conditions are commonly encountered in chile pepper fields under furrow irrigation, and following midseason and late season rainfalls (Biles et al., 1992). However, it is not known whether predispositional effects occur in the interaction of chile pepper with *P. capsici* under saturated soil conditions.

The objective of this study was to assess the effect of soil water saturation on infection of chile pepper by *P. capsici*.

Materials and Methods

Inoculum preparation and plant production. *Phytophthora capsici*, isolate PWB-24 (Bosland and Lindsey, 1991), was used in this study, and inoculum was prepared as follows. Briefly, PWB-24 was grown on V8 juice-agar at 25 °C. After 5 d of growth, six mycelial plugs (1 cm in diameter) were cut from the culture. The plugs were placed in 20 mL sterile distilled water in a petri dish and incubated at 25 °C for 3 d for sporangia formation. The plates were then transferred to 10 °C for 60 min, and returned at 25 °C for 90 min. At this point, zoospores were produced and released into the water. The contents of each petri dish were passed through three layers of cheesecloth to remove agar plugs. The concentration of zoospores was assessed with a hemacytometer and adjusted to 2000 zoospores/mL.

Chile pepper cultivar 'New Mexico 6-4' (NM6-4) and chile pepper line 'Criollo de Morelos #334' (CM334) were used in this study. Cultivar 'NM6-4' is susceptible to *P. capsici,* whereas 'CM334' is resistant (Bosland and Lindsey, 1991). Chile seeds were planted in six-cell plastic trays (with a cell dimension of 6, 4, and 6 cm in length, width, and depth, respectively) filled with sterilized Terra-Lite Metro Mix 360 (W. R. Grace & Co., Memphis, Tenn.). At the fourth fully expanded true leaf stage, seedlings were transplanted into plastic pots (with a diameter of 10 cm on top and 7.5 cm on bottom, and a depth of 9 cm) filled with sterilized Terra-Lite Metro Mix 360 at the rate of one seedling per pot. Seedlings were then fertilized by adding to each pot 150 mL solution of a 20%N–20%P_2O_5–20%K_2O fertilizer (Scotts Co., Marysville, Ohio) containing 3.94% ammoniacal nitrogen, 6.05% nitrate, 10.01% urea, 0.05% Mg, 0.0068% B, 0.0036% Cu (chelated Cu), 0.05% Fe (chelated Fe), 0.025% Mn (chelated Mn), 0.0009% Mo, and 0.0025% Zn (chelated Zn). Planting of seeds and transplanting of seedlings were staggered to produce plants at two phenological stages (six- to eight-leaf stage, and one- to four-flower bud stage).

Effects of soil water saturation on infection of chile pepper by Phytophthora capsici. At the six to eight-leaf stage and at the one- to

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four-flower bud stage, potted plants were subjected to varying levels of nonsaturated and saturated conditions in the greenhouse following procedures described by Kuan and Erwin (1980). Pots maintained under saturated conditions were placed on plant saucers (12.5 cm diameter, and 3.5 cm depth), which were kept full of tap water (electrical conductivity = 0.5 $dS \cdot m^{-1}$) for 3 and 6 d before inoculation with *P. capsici*. No saucers were placed beneath pots maintained under nonsaturated conditions. In order to determine the effect of soil water saturation on plants in absence of the pathogen, a set of potted plants noninoculated with *P. capsici* were included in the experiment. There were 32 treatments generated from the combination of two soil water saturation conditions (saturated and nonsaturated), two periods of soil water saturation (3 and 6 d of saturated and nonsaturated conditions), two inoculum levels (no inoculum added and inoculum added to soil), two chile entries (susceptible and resistant to *P. capsici*), and two growth stages (six- to eight-leaf, and one- to four-flower bud stages). The 32 treatment combinations were evaluated in a split split-plot design, with inoculum levels as whole-plot factor, cultivar by growth stage as subplot factor, and soil water saturation (saturated and nonsaturated) by period (3 and 6 d) of soil water saturation as sub-subplot factor. Each treatment was replicated 5 times, with a pot being a replication. Three additional potted plants were allocated to the 6-d period of soil water conditions (with no inoculum added) and were used for assessment of plant stress as described below. The entire experiment was completed three times.

For plant inoculation, 5 mL of a zoospore suspension (2000 zoospores/mL) was dispensed onto the surface of the soil in each pot at about 2 cm away from the lower stem of each plant. For seedlings serving as controls (noninoculated), 5 mL of sterile water was dispensed on top of soil in each pot. The 6-d soil water saturation treatment was initiated 3 d before the 3-d soil water saturation treatment to enable plant inoculation to be performed on the same day for all treatments. Plant inoculation was performed 30 min after soil water saturation treatments were terminated. Plants were watered once a day following inoculation.

Assessment of soil conditions, plant stress, and plant infection. Soil water potential was monitored in potted plants placed under both saturated and nonsaturated conditions using Watermark soil moisture sensors (Spectrum Technologies, Inc.). In plants at the six- to eight-leaf stage subjected to 6-d period of saturated and nonsaturated soil water conditions, chlorophyll content index and dry weight of above-ground plant parts were measured to assess whether plant stress was generated under the soil water saturation treatments. The 6-d period was selected to represent the extreme level of plant stress, and the six- to eight-leaf stage was chosen because previous studies, as summarized by Café-Filho and Duniway (1995), have shown that pepper is most susceptible to *P. capsici* at this stage. Leaf chlorophyll content index was measured using a CCM-200 chlorophyll-content meter (Opti-Sciences, Tyngsboro, Mass.). Measurements were performed on the fourth fully expanded leaf from the shoot apex on each of the three additional plants (noninoculated) from saturated and nonsaturated treatments in the 6-d period of soil water condition as indicated previously. Stems from the three plants were cut at the crown, inserted individually in a brown paper bag, and placed in an oven at 65 °C. Dry weights were recorded after 48 h. Plants were monitored for disease symptoms, and disease severity on above-ground plant parts was evaluated at 7 d (six- to eight-leaf stage) and 14 d (one- to four-flower bud stage) after inoculation using a scale modified from Ristaino (1990) as follows: 0 = no visual disease symptoms, 1 = stem necrosis with no girdling, 2 = stem necrosis with girdling, 3 = stem necrosis with <50% defoliation, 4 = stem necrosis with >50% defoliation, 5 = wilted, and 6 = dead.

Statistical analysis. Data consisting of chlorophyll content index and dry weight of above-ground plant parts from each experiment were subjected to analysis of variance using Proc Mixed procedure in SAS (SAS Institute, Cary, N.C.). The data consisting of disease severity ratings were ordinal, therefore these data were analyzed by nonparametric approaches using SAS macros F2_LD_F1 and LD_CI as outlined by Brunner et al. (2002). These macros allow computation of mean rank of treatments, relative treatment effects (RTE), 95% confidence intervals for RTE, and ANOVA-type statistics for gauging the significance of main factors and the interactions among these factors. Data from individual experiments were analyzed separately to determine consistency of results among repetitions of experiments. When results were consistent among experiments and the error variances were homogeneous ($P > 0.05$), results from all repetitions of experiments were combined. Error variances were evaluated for homogeneity using procedures outlined by Gomez and Gomez (1984).

Results and Discussion

No disease symptoms developed in the resistant chile line 'Criollo de Morelos #334' (CM334) grown either under saturated or nonsaturated soil conditions at any of the two periods (3 or 6 d) of soil water saturation. Because no visual disease symptoms were recorded on 'CM334', disease severity ratings were all 0 values. Therefore, data on 'CM334' were not included in the final statistical analysis, which was conducted with inoculum and growth stage as whole plot factors, and the combination of soil saturation conditions by period of saturation as subplot factor. In the chile pepper cultivar 'New Mexico 6-4' (NM 6-4), disease symptoms, consisting of stem necrosis, defoliation, and wilting, were recorded under both saturated and nonsaturated soil conditions. When plants were inoculated at six to eight-leaf growth stage, these symptoms were visible within 5 to 7 d. Relative treatment effects ranged from 0.845 to 0.910 across soil water saturation conditions and duration (Table 1). In plants inoculated at one- to four-flower bud stage, symptoms appeared within 10 to 14 d. Relative treatment effects ranged from 0.621 to 0.629 across soil water saturation conditions and duration (Table 1). The differential response of 'NM6-4' with respect to the appearance and severity of symptoms may reflect age-related reaction as shown by Kim et al. (1989) and Reifschneider et al., (1992). Notwithstanding these differences, the response of 'NM6-4' to *P. capsici* at each growth stage under saturated soil conditions was similar to that under nonsaturated conditions regardless of the period of saturation (Table 2; $P = 0.09$). Except for the interaction of inoculation by growth stage which was significant (Table 2; $P < 0.0001$), all other two-way interactions (inoculation by soil water saturation, and growth stage by soil water saturation) were not significant (Table 2; $P = 0.09$). Similarly, the main effect of soil water saturation was not

Table 1. Median, mean rank, relative treatment effects (RTE), and 95% confidence intervals (CI) for RTE of severity ratings on 'New Mexico 6-4' in relation to inoculation with *Phytophthora capsici*, growth stage, and soil water saturation.

Inoculation	Growth stage[z]	Soil water saturation[y]	Median[x]	Mean rank	Relative treatment effect	95% CI for RTE
Inoculated	LS68	NS-3D	4	203.37	0.845	(0.822, 0.865)
		NS-6D	5	209.77	0.872	(0.860, 0.883)
		S-3D	5	209.77	0.872	(0.852, 0.888)
		S-6D	5	218.93	0.910	(0.886, 0.928)
	FB14	NS-3D	2	151.6	0.629	(0.602, 0.656)
		NS-6D	2	149.63	0.621	(0.598, 0.645)
		S-3D	2	149.63	0.621	(0.598, 0.645)
		S-6D	2	151.3	0.628	(0.601, 0.654)
Noninoculated	LS68	NS-3D	0	60.5	0.250	(0.250, 0.250)
		NS-6D	0	60.5	0.250	(0.250, 0.250)
		S-3D	0	60.5	0.250	(0.250, 0.250)
		S-6D	0	60.5	0.250	(0.250, 0.250)
	FB14	NS-3D	0	60.5	0.250	(0.250, 0.250)
		NS-6D	0	60.5	0.250	(0.250, 0.250)
		S-3D	0	60.5	0.250	(0.250, 0.250)
		S-6D	0	60.5	0.250	(0.250, 0.250)

[z]LS68 = six- to eight-leaf stage, FB14 = one- to four-flower bud stage.
[y]S = saturated, NS = nonsaturated conditions, 3D = 3 d, and 6D = 6 d.
[x]Disease severity was rated using the following scale: 0 = no visual disease symptoms, 1 = stem necrosis with no girdling, 2 = stem necrosis with girdling, 3 = stem necrosis with <50% defoliation, 4 = stem necrosis with >50% defoliation, 5 = wilted, and 6 = dead.

significant (Table 2; $P = 0.092$).

In plants (noninoculated with *P. capsici*) at six- to eight-leaf stage and subjected to 6-d soil water saturation, dry weight of above-ground plant parts (Table 3) was not significantly affected by soil water condition ($P = 0.5366$). Chlorophyll content index (Table 3) was greater under saturated conditions than under nonsaturated conditions ($P = 0.0173$). There was no discernable difference in plant appearance, such as leaf chlorosis, whether plants were subjected to saturated or nonsaturated soil conditions. Water potential varied from –0.0055 to –0.0065 MPa in pots placed in plant saucers (saturated conditions), and from –0.008 to –0.020 MPa in pots not placed in plant saucers (nonsaturated conditions). These values of water potential are well within those recorded with the same type of sensors in chile pepper fields fluctuating between –0.006 and –0.017 MPa during furrow irrigation events.

The data on dry weight of above-ground plant parts and chlorophyll content index suggest that there is no significant plant stress under excessive soil moisture conditions. However, other studies have reported the existence of plant stress as gauged by leaf chlorosis and reduction in plant growth (Hasnain and Sheikh, 1976; Sundstrom and Pezeshki, 1988). Hasnain and Sheikh (1976) exposed pepper plants to flooded conditions for 6 weeks, and reported leaf chlorosis and decrease in growth in plants under flooded conditions relative to plants under nonflooded conditions. Sundstrom and Pezeshki (1988) observed that leaves of bell pepper plants flooded for 96 h appeared chlorotic compared to nonflooded plants. In both of these studies, however, no quantitative data on chlorophyll content in the different treatments were provided. The difference between this work and other studies (Hasnain and Sheikh, 1979; Sundstrom and Pezeshki, 1988) may be attributable to differences among cultivars used, flooding period, and the growth stage at which flooding was imposed to plants. Research on the effect of excessive soil moisture on pepper is very scanty.

The relationship between soil moisture and development of plant diseases caused by *P. capsici* has been extensively researched (Erwin and Ribiero, 1996). This relationship may be broadly dissected into two categories. In the first category, studies have demonstrated the effect of soil moisture on the phenology of *P. capsici* including sporangia and oospores formation, and release of zoospores (Bernhardt and Grogan, 1982; Bowers and Mitchell, 1990). In the second category, studies have focused on dispersal of *P. capsici* within plant populations (Ristaino, 1991). The significance of this study lies in the fact that it addressed an unexplored facet of the above-mentioned relationship, the predispositional effect of soil water saturation on plant infection by *P. capsici*.

This work focused on direct effect of soil water saturation on chile pepper and examined subsequent plant response to *P. capsici*. The flooding periods were selected to provide saturation conditions that may exist in furrow-irrigated chile pepper fields in southern New Mexico. Typically, fields are furrow-irrigated for four to 6 h, and saturated conditions may remain for 72 h or more depending on weather conditions. It appears that high soil moisture conditions do not exert a significant predispositional effect on chile pepper plant regardless of resistance to *P. capsici*. The supportive evidence emanates from the fact that the resistant line 'CM334' did not display any disease symptom even though saturated conditions, equivalent to those encountered under field conditions, were imposed. Experimentally, it was expected that the presence of any substantial predispositional effect would be manifested by the presence of disease symptoms in the resistant chile pepper line 'CM334'. But, the fact that the resistant line 'CM334' did not display any disease symptom indicates that high soil moisture conditions do not exert a significant predispositional effect on chile plants. In addition, the response of the susceptible 'NM6-4' to *P. capsici* was not differentially substantial between saturated and nonsaturated conditions at each growth stage.

Several inoculation methods are conceptually applicable to studies such as the one described herein. One method consists of burying mycelium plugs from pathogenic cultures in soil (Bernhardt and Grogan, 1982). This method is easy to perform, but may lead to nonuniform level of inoculum among pots because sporangia formation and zoospore release from these sporangia may be differentially affected by variation in soil conditions (Bernhardt and Grogan, 1982). A sound remedial methodological approach is to inoculate plants with known level of pathogenic propagules which are readily germinable. Such approach, which was used in this study and adopted by others (Kuan and Erwin, 1980), has the benefit of disentangling pathogenic factor from predispositional effect of soil water saturation on chile pepper infection by *P. capsici.* The level of inoculum used mirrored those used in other studies (Bosland and Lindsey, 1991).

In summary, findings from this work provide new information on the relationship between soil moisture and development of plant diseases caused by *P. capsici.* Data obtained suggest that soil water saturation does not impose a significant predispositional effect on chile pepper leading to increased infection by *P. capsici.* An outcome of this study is that it provides further understanding of the behavior of *P. capsici* under saturated soil conditions.

Table 2. Analysis of disease severity ratings on 'New Mexico 6-4' in relation to inoculation with *Phytophthora capsici*, growth stage, and soil water saturation.

	ANOVA-type statistics[z]			
Factor	Fn	df1	df2	*P* value
Inoculation (I)	4410.7	1	22.23	<0.0001
Growth stage (G)	274.90	1	22.23	<0.0001
Saturation (S)	2.710	2.7	∞	0.09
I × G	274.90	1	22.23	<0.0001
I × S	2.710	2.7	∞	0.09
G × S	2.710	2.7	∞	0.092
I × G × S	2.710	2.7	∞	0.092

[z]Fn is an ANOVA-type statistic equivalent to an F value with estimated degrees of freedom df1 (numerator) and df2 (denominator). The significance of main factors and interactions among these factors is gauged by the *P* values.

Table 3. Effect of soil water saturation on mean dry weight of above-ground plant parts and mean chlorophyll content index of chile pepper cultivars 'CM334' and 'NM6-4' noninoculated with *Phytophthora capsici*.

Cultivar	Soil water saturation[z]	Mean dry wt (SE)[y]	Mean chlorophyll content index (SE)[x]
CM334	S	0.22 (0.01)	32.96 (0.91)
	NS	0.21 (0.01)	26.1 (0.46)
NM6-4	S	0.60 (0.07)	28.05 (0.64)
	NS	0.63 (0.03)	26.28 (0.56)

[z]S = saturated, NS = nonsaturated, for 6 d.
[y]Numbers in parentheses are standard error (SE) of the means.
[x]Numbers in parentheses are standard error (SE) of the means.

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