Predisposing Effect of Water Stress on the Severity of Phytophthora Root Rot in Safflower

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ABSTRACT

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Safflower plants were grown in crocks of steamed soil and were inoculated with zoospores of *Phytophthora cryptogea* when they were 3-5 wk old. Water stress was induced in some of the plants by withholding water from the soil and the remaining plants were watered daily to maintain leaf water potentials between −4 and −6 bars. Symptoms of root rot always developed in the susceptible cultivar Nebraska 10 following inoculation. However, withholding water from Nebraska 10 plants to decrease leaf water potential to −13 or −17 bars before inoculation increased root rot caused by *P. cryptogea*, as measured by the severity of visible symptoms or as a decrease in the fresh weight of roots. Root rot did not develop in well-watered plants of the resistant cultivar Biggs following inoculation, but *P. cryptogea* did cause visible symptoms of root rot and significant reductions in fresh weight of roots in cultivar Biggs when leaf water potential was depressed to −9 or −12 bars before inoculation. With the exception of saturated soil, a variety of soil water regimes under which Nebraska 10 plants were maintained after inoculation were almost equally suitable for the development of severe root rot. The suitable water regimes included soil water potentials that gradually declined from −0.4 bar to −4, −8, or −12 bars and constant soil matric potentials between −0.05 and −0.37 bar. Depending on the methods used, saturated soil was either more or less suitable than the drier soils for disease development.

Additional key words: water relations, *Phytophthora drechsleri*, *Carthamus tinctorius*.

Root and crown rots caused by *Phytophthora* spp. are usually associated with wet soil (2, 3, 12, 22, 25, 27). For example, the severity of Phytophthora root rot in safflower increases with both the frequency and intensity of irrigation (11, 28). Irrigation trials in the field, however, indicate that the occurrence of drought prior to irrigation may also increase the severity of Phytophthora root rot in safflower (17, 28). Conceivably, drought could enhance disease development following irrigation because water stress predisposes the host and/or because water deficiency in the soil increases the subsequent production of effective inoculum by the pathogen. Even though water stress is known to be a predisposing factor for some plant diseases, there are only a few studies in plant pathology in which predisposition by water stress has been quantitatively demonstrated (3, 5, 13, 20). Furthermore, no previous studies have clearly isolated predisposition by water stress as a variable in Phytophthora root rot. The present study examines the influence of controlled water stress, induced either prior to or following inoculation, on the development of Phytopthora root rot in safflower.

MATERIALS AND METHODS

Biological materials.—Two cultivars of safflower (*Carthamus tinctorius* L.) were used. The first, Nebraska 10, is highly susceptible to Phytophthora root rot, and the second, Biggs, is a selection released under the designation USB (23) as a source of resistance to Phytophthora root rot. Plants were grown in 2-liter crocks that contained steamed and sieved U.C.-type soil mix (10). Seedlings were thinned 1 wk after planting to give 10 uniform plants in each crock. Except when soil water was a variable, the soil was watered daily and allowed to drain through holes at the bottoms of the crocks. Plants were usually grown in a controlled environment chamber having 14-hr periods with 85 $W \cdot m^{-2}$ (300-700 nm) of fluorescent and incandescent light at 27 ± 0.1 C and 70 ± 3% relative humidity. The temperature and relative humidity were 21 ± 0.1 C and 80 ± 3% during the 10-hr dark periods.

Plants were inoculated with *Phytophthora cryptogea* Pethyb. and Laff. when they were 3-5 wk old. The isolate of *P. cryptogea* used in all experiments was the A^2 mating type originally isolated from safflower. The same isolate (P201) has been used in previous studies, sometimes under the name *P. drechsleri* Tucker (7, 8, 9, 10). Zoospores were obtained by flooding petri plate cultures with autoclaved water extract of soil (10). Inoculations were made by pipetting 10 ml of soil extract containing 2×10^5 to 1×10^6 motile zoospores onto the soil in each crock. The inoculum was distributed evenly on the soil surface and was not pipetted onto the stems. After the inoculum had penetrated the soil, water was applied to the soil surface and allowed to drain from the bottoms of the crocks.

Disease severity was evaluated 5-11 days after inoculation. Symptoms in the tops of the plants were rated on an arbitrary scale in which zero represented the

absence of symptoms and five represented severe wilting of all plants. In order to measure the final fresh weight of roots in each crock, stems were cut at the soil surface and the soil was washed from the roots. The finer roots were recovered from the wash water by filtration through paper or a fine sieve. Roots were weighed after the excess water was blotted from them in a standardized manner. In some experiments, so that they would attain their highest turgor, the leaves and stems were cut into segments and floated on water for 12 hr at 25 C. The surface water was blotted from them before weighing. After fresh weights were determined, tissues were dried to a constant weight at 98 C.

Water status.—In experiments in which plant water stress was induced before inoculation, water was withheld from the soil for 2-4 days. At midday of the final day water was to be withheld, 8-10 representative leaves were sampled from each treatment and promptly placed in thermocouple psychrometers (8, 9) to determine their water potentials (ψ). The plants were watered within 1 hr after leaves were sampled and inoculations were made about 1 hr after the stressed plants were watered.

In some experiments, water was withheld from plants for various periods immediately after the inoculation procedures were completed. When this was done, representative leaves were periodically placed in thermocouple psychrometers to determine their ψ values, or soil ψ was measured once every 6-14 hr with thermocouple psychrometers (Type PT51, Wescor, Inc., Logan, UT 84321) buried at the center of the volume of soil in some of the crocks at the time of planting (9). The bulk of the soil in some crocks was maintained at ψ values of approximately 0 and −0.01 bar by standing crocks in reservoirs of water so that the soil surface was 1 or 10 cm above the water surface. Daily watering of soil in crocks that drained water freely maintained soil ψ at nearly −0.4 bar.

The influence of more constant levels of soil moisture on disease development was examined by using Büchner funnels with porous plates as tension plates to control soil matric potential (ψ_m). The conditions and methods described (10) were used to grow safflower seedlings in soil mix at $\psi_m = -0.03$ bar, except that funnels were exposed to 7-10 $W \cdot m^{-2}$ (300-700 nm) of indirect sun and fluorescent light for 10-14 hr per day. Six days after planting, seedlings were thinned to 10 in each funnel, the soil was adjusted to the final ψ_m values, and 2×10^5 zoospores were pipetted onto the soil in half of the funnels. Disease severity was evaluated 6 days after inoculation. The range of ψ_m values used gave soil water contents (7, 10) between saturation and field capacity.

RESULTS

Symptoms of root rot always developed in the cultivar Nebraska 10 following inoculation with *P. cryptogea*. However, withholding water from Nebraska 10 plants before inoculation, to the extent that leaf ψ was depressed to −13.2 or −17.2 bars, increased the severity of visible symptoms and decreased the fresh weight of roots on infected plants (Table 1, Fig. 1-A). In the resistant cultivar Biggs, *P. cryptogea* did not induce visible symptoms or reduce root fresh weight when leaf ψ was maintained at −4 bars (Table 1, Fig. 1-B). If, however, leaf ψ was depressed to −8.8 bars and Biggs plants then were inoculated, symptoms of root rot developed and the

TABLE 1. Influence of preinoculation water stress on the severity of root rot caused by *Phytophthora cryptogea* in safflower[a]

Cultivar	Experiment	Leaf water potential before inoculation (bars)	Number of zoospores used as inoculum (no./crock)	Relative top symptoms (0-5)	Root fresh weight (g/crock)
Nebraska 10	1[b]	− 5.9[d]	0	0[e]	62[e] A[f]
			2×10^5	1.6	61 A
		−13.2	0	0	41 B
			2×10^5	3.8	21 C
	2[c]	− 4.5	0	0	83 A
			2×10^5	3.6	64 B
		−17.2	0	0	58 B
			2×10^5	4.4	28 C
Biggs	3[b]	− 4.0	0	0	55 A
			4×10^5	0	45 A B
		− 8.8	0	0	41 A B
			4×10^5	0.4	32 B
	4[c]	− 4.2	0	0	53 A
			5×10^5	0	57 A
		−12.4	0	0	46 A
			5×10^5	1.2	27 B

[a]The soil was maintained in a well-watered state after inoculation.
[b]Symptoms and root fresh weights determined 7 days after inoculation.
[c]Symptoms and root fresh weights determined 10 or 11 days after inoculation.
[d]Average values for eight to 10 leaves measured by thermocouple psychrometry (8).
[e]Average values for five crocks containing 10 plants each.
[f]Weights within the same experiment that are followed by different letters are significantly different by Duncan's multiple range test, $P = 0.05$.

combined influence of water stress and *P. cryptogea* on root fresh weight was significant (Table 1, Fig. 1-B). When leaf ψ of the cultivar Biggs was depressed to −12.4 bars before inoculation, *P. cryptogea* caused many plants to wilt and caused a large and significant reduction in root fresh weight (Table 1). Decreases in the dry weight of roots and in the dry and fresh weights of aboveground parts of plants caused by *P. cryptogea* also were increased significantly in both cultivars when leaf ψ was depressed to values lower than −12 bars before inoculation.

The influence of water stress induced either before or after inoculation on disease severity was examined further in a greenhouse at 20-26 C. Crocks containing Nebraska 10 plants were inoculated with 2×10^5 zoospores and those containing Biggs plants were inoculated with 10^6 zoospores. Water was withheld from some of the plants so that leaf ψ averaged −12 bars just before inoculation. The remaining plants were watered regularly and had leaf ψ values higher than −5 bars. Starting immediately after inoculation, water was withheld from some of the plants that had previously been watered regularly so that their leaf ψ values dropped to between −10 and −12 bars in 2-4 days. The regular watering schedule was then resumed. Unfortunately, there were large differences in light, temperature, humidity, and air turbulence among locations of replicate crocks in the greenhouse. These differences gave rise to variation in leaf ψ and plant growth such that water stress did not change significantly the influence of *P. cryptogea* on the weights of roots or tops of plants in the greenhouse. Nevertheless, water stress before, but not after, inoculation had a visible effect on the severity of root rot in both Nebraska 10 and Biggs plants. For example, darkening of infected roots was greatest in those plants that were stressed before inoculation (Fig. 2). Ratings of top symptoms caused by *P. cryptogea* in plants that were watered regularly or that were stressed before or after inoculation, respectively, averaged 2.5, 4.8, and 2.8 [LSD ($P = 0.01$) = 1.1] in the cultivar Nebraska 10 and 1.8, 3.0, and 2.1 (not significantly different, $P = 0.05$) in the cultivar Biggs.

Four additional experiments in which Nebraska 10 plants were subjected to various soil water regimes after inoculation were done in a controlled-environment chamber. All the plants were watered regularly before the soil in half of the crocks was inoculated with 4×10^5 zoospores. Soil ψ in some crocks then was maintained at nearly 0, −0.01, or −0.4 bar whereas the remaining crocks were watered only once if soil ψ decreased to −4, −8, or −12 bars before the experiment was terminated 5 days after inoculation [Fig. 3-(A, B)]. Infected roots from representative crocks that were sampled from all treatments 2 days after inoculation were only slightly discolored and had fresh weights only 3-8% less than the

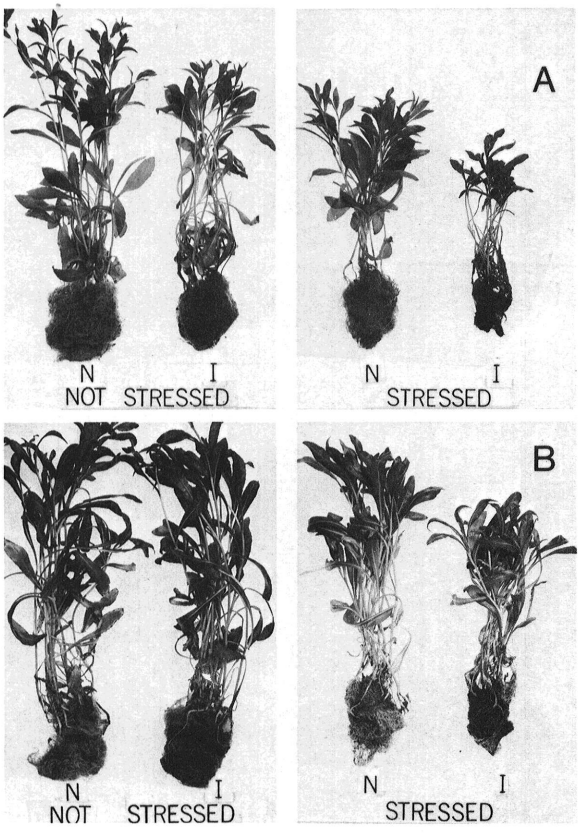

Fig. 1-(A-B). Influence of preinoculation water stress on the severity of root rot caused by *Phytophthora cryptogea* in safflower; **A)** Representative Nebraska 10 plants from experiment 1, Table 1; **B)** Representative Biggs plants from experiment 3, Table 1. The experiments were done in a controlled environment chamber and water stress was induced by withholding water from the soil before inoculation. Legend: N = noninoculated; I = inoculated.

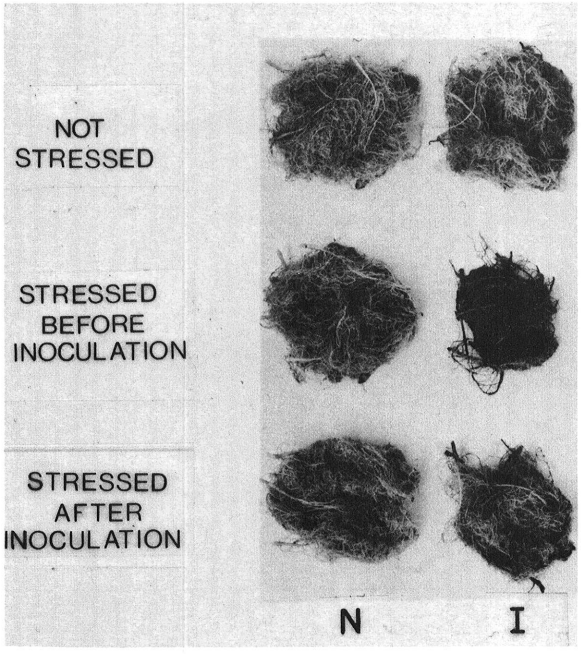

Fig. 2. Influence of water stress induced either before or after inoculation on the severity of root symptoms caused by *Phytophthora cryptogea* in Nebraska 10 safflower. Plants recovered from representative crocks in a greenhouse experiment are shown. Legend: N = noninoculated; I = inoculated.

weights of healthy roots in soil at the same ψ value. Except for the inoculated plants in saturated soil that developed relatively mild symptoms, the severity of root rot at 5 days after inoculation was similar under all the water regimes used. For example, when inoculated plants are compared to the noninoculated plants in soil dried to the same extent [Fig. 3-(A, B)], the comparison shows that infection decreased the final fresh weight of roots by 15% in saturated soil ($\psi = 0$) whereas infection decreased the final fresh weights of roots by 30 to 50% in the drier treatments (Fig. 3-C). Wilt symptoms due to infection were less severe in saturated soil at $\psi = 0$ than in soil at ψ values of -0.01 and -0.4 bar, but it was impossible to compare wilt symptoms in the drier treatments because noninoculated plants wilted in soil at $\psi \leqslant -4$ bars. By the 5th day after inoculation, infection had caused extensive discoloration of the roots under all the water regimes tested. Results similar to those in Fig. 3-C were obtained when the transpiration rate of noninoculated plants was reduced with plastic covers to the extent that the soil in both the noninoculated and inoculated treatments was not watered and gradually dried to approximately -4, -8, or -12 bars after inoculation.

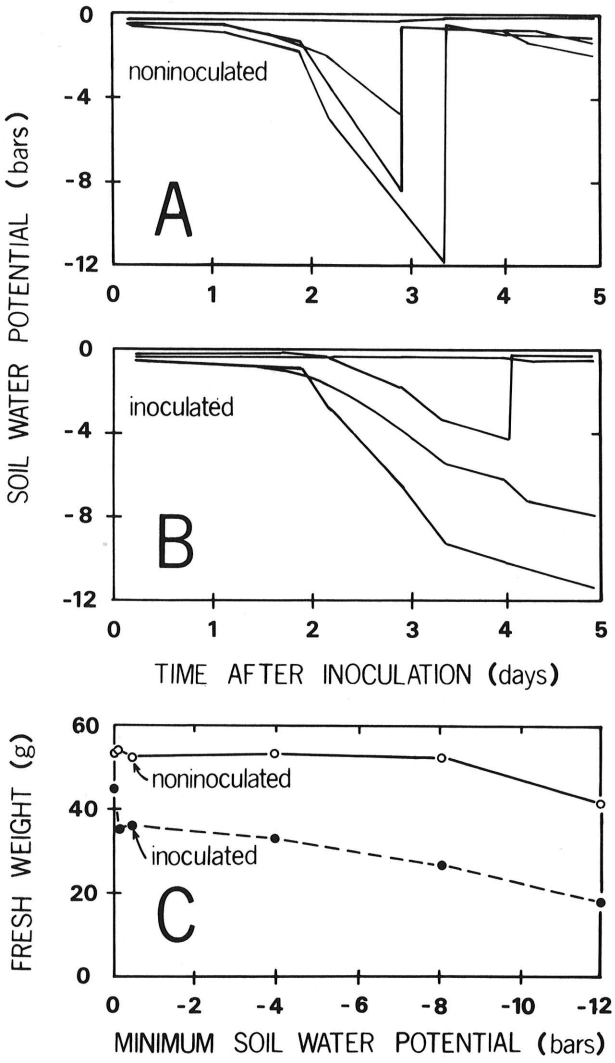

Fig. 3-(A to C). Water potentials of soils in crocks containing **A)** noninoculated and **B)** inoculated plants of Nebraska 10 safflower plotted as functions of time after inoculation with *Phytophthora cryptogea*; **C)** fresh weights of roots recovered from noninoculated and inoculated plants of Nebraska 10 safflower 5 days after inoculation plotted as functions of the minimum soil water potential observed between 0 and 5 days after inoculation with *P. cryptogea*. The data represented in graphs A, B, and C were obtained with the same plants and each line in A and B and each point in C represents one crock containing ten plants. Soil water potentials in C which are higher than those shown in A or B were obtained by standing crocks of soil in reservoirs of water, and the abrupt increases in soil water potential in A and B indicate the times at which soil in the drier treatments was watered.

Although wilting of infected seedlings was somewhat greater at $\psi_m \leqslant -0.2$ bar and root symptoms were greater at $\psi_m \geqslant -0.001$ bar, symptoms of root rot did develop in all of the inoculated seedlings maintained at constant ψ_m values between 0 and -0.37 bar (Fig. 4). Even though infection invariably decreased the final fresh weight of seedling tops by 50 to 60%, reductions in the fresh weights of roots due to infection were 92 and 83% at ψ_m values of 0 and -0.001 bar, but only 41 to 51% at ψ_m values between -0.05 and -0.37 bar. Additional experiments of the type shown in Fig. 4 with both sterilized and nonsterilized soils generally yielded similar results. The only deviations were inoculated seedlings in nonsterilized soil at $\psi_m = -0.2$ bar that developed fewer symptoms of root rot than did the seedlings in other treatments.

DISCUSSION

Plant water stress before inoculation can predispose safflower to root rot caused by *P. cryptogea*. The results fit the definition of predisposition because water stress is a nongenetic factor, acting prior to infection, that increases the severity of a disease (20). In the susceptible cultivar Nebraska 10, severe root rot developed following inoculations of well-watered plants, and significant predisposition by water stress was demonstrated following depressions of leaf ψ to values lower than -13 bars (Table 1, Fig. 1). Under the conditions used, all the leaves of Nebraska 10 plants were visibly wilted at $\psi \leqslant -13$ bars (8). Although comparable depressions of leaf ψ significantly predisposed the resistant cultivar Biggs, a more mild depression of leaf ψ from -4.0 to -8.8 bars also predisposed Biggs plants to Phytophthora root rot (Table 1, Fig. 1). At leaf $\psi = -8.8$ bars, all but the oldest leaves on Biggs plants appeared turgid.

The results do not show the degree to which ψ values of root tissues were depressed by the water stress conditions in these experiments. Measurements with soil psychrometers in some experiments (e.g., Fig. 3), however, indicate that leaf ψ values of -12 to -14 bars generally occurred in healthy plants at soil ψ values between -4 and -7 bars. Soil that was watered daily remained at $\psi \geqslant -0.4$ bar, and drying soil to $\psi = -1.2$ bars depressed the leaf ψ of healthy plants to about -8 bars at midday. While it is obvious that the ψ values of root tissues must fall between those of the soil and leaves, the actual ψ values of the roots cannot be inferred from the data because they depend on complex interactions

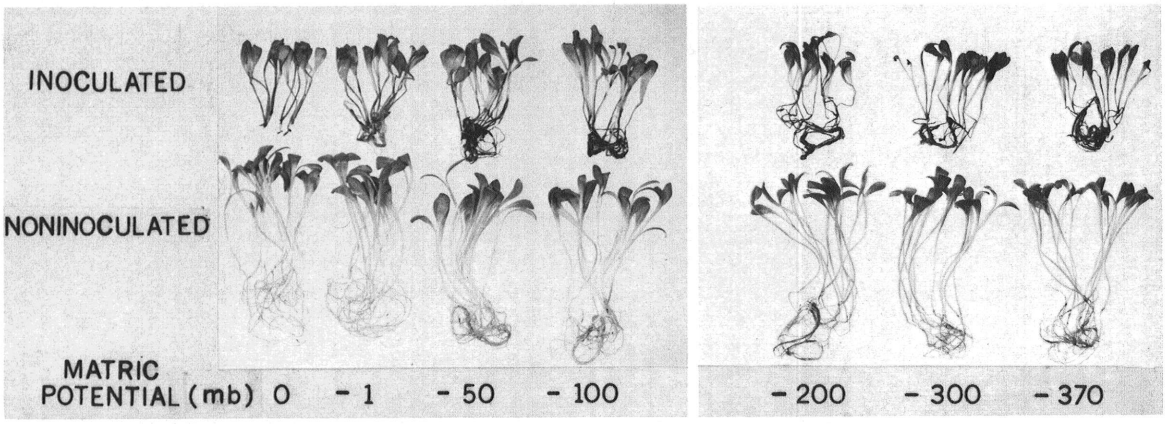

Fig. 4. Influence of constant soil matric potentials (ψ_m) on the severity of root rot caused by *Phytophthora cryptogea* in safflower seedlings of the cultivar Nebraska 10. Soil was adjusted to the ψ_m values given at the time of inoculation and 1,000 millibars (mb) = 1 bar. All 10 inoculated or noninoculated seedlings at each ψ_m value were grouped together and photographed 6 days after inoculation.

between transpiration rate and resistances to water movement in the soil and plant (19). Even though it seems likely that unknown levels of water stress act directly on root tissues when they are predisposed to Phytophthora root rot, there remains a possibility that water stress in other parts of the plant, such as the stress measured in the leaves, may contribute indirectly to the predisposition of root tissues.

Increased root exudation following water stress (15) may enhance the initial establishment of soilborne pathogens in roots. Alternatively, Cook and Papendick (3) suggested that the predisposing effect of water stress generally increases the extent to which established infections develop rather than enhancing the initial establishment of the pathogen. In contrast to water stress before inoculation, induction of water stress after inoculation did not increase the severity of Phytophthora root rot in safflower (Fig. 2, 3). Thus it would appear that the predisposition by water stress involves the early stages of disease development. However, time may be required for the predisposing effect of water stress to be manifested, and the period between the induction of water stress and the termination of the experiment was longer when stress was induced before rather than after inoculation. Furthermore, the results for the resistant cultivar Biggs suggest that water stress may enhance the development of established infections because, in the absence of water stress, the initial development of *Phytophthora* lesions in the cultivar Biggs is similar to that in the cultivar Nebraska 10 (16, 24). Evidently, the resistance of Biggs, which was reduced by water stress (Table 1), is related (at least partly) to the extent to which established infections can develop. Large amounts of inoculum, wounding, prolonged flooding, low light intensities, and high temperatures also have been found to reduce the resistance of Biggs safflower to Phytophthora root rot (14). Reductions in the resistance of safflower by these other factors, however, do not appear to be as great or as likely to occur in the field as does the predisposing influence of water stress.

With the exception of saturated soil, the various water regimes under which Nebraska 10 plants were maintained after inoculation were almost equally suitable for the development of severe Phytophthora root rot (Fig. 3, 4). The results obtained in saturated soil depended on the methods used; i.e., in crocks saturated soil was less suitable (Fig. 3-C) and on tension plates it was more suitable (Fig. 4) than drier soils for the development of root rot. Soil in crocks was inoculated with zoospores, watered, and allowed to drain before it was saturated. Therefore, much of the inoculum was probably deep (10) in the saturated soil where poor aeration may have limited root rot (6). Zoospores were added to the comparatively shallow soil on tension plates after it was adjusted to the final ψ_m values. The soil is sufficiently wet at $\psi_m = 0$ and $\psi_m = -0.001$ bar for active movement of zoospores to the host (10), and perhaps for the formation of sporangia near the surface (7) and subsequent release and movement of zoospores to cause secondary infections. Soil at $\psi_m = -0.05$ bar is too dry for zoospore release or mobility (10), and soil at $\psi = -4$ bars is too dry for sporangia to form (9). Therefore, disease that developed in the drier treatments probably resulted from the development of established primary infections and not to secondary infections. In fact, the results (Fig. 3) suggest that established infections of *P. cryptogea* can continue to develop at all ψ values suitable for the growth of safflower. *Phytophthora* spp. are reported to grow on agar media at ψ values even lower than those recorded here (21).

Although the results show that predisposition can occur and that established infections can develop under relatively dry conditions, the results are not in conflict with reports that wet soil conditions enhance Phytophthora root rot in safflower (11, 28). For example, enhancement by wet conditions may be expected when the production, release, and movement of zoospores are the factors limiting disease development (9, 10, 12, 18). Although most of the literature on Phytophthora root rots other than that caused by *P. cryptogea* in safflower emphasizes the enhancement of disease by saturation of the soil (e.g., 2, 3, 12, 22, 25, 27), there are reports that other Phytophthora root rots can develop under drier conditions (1, 4, 18, 26). Of course, the conditions under which the effects of soil moisture have been observed were

very diverse, and various host-*Phytophthora* spp. combinations may be influenced differently by soil water.

Predisposition of safflower by water stress is probably a major reason why the occurrence of drought prior to irrigation increases the severity of Phytophthora root rot in the field (17, 28). However, temporal variations in plant water status and the pattern of soil water depletion in the field are very different than in container-grown plants, and data on the water relations of plants in small crocks of soil are not expected to apply exactly to the water relations of plants in the field. Therefore, additional research is needed to establish the exact levels of water stress that can predispose safflower to Phytophthora root rot in the field.

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