Effect of Soil Water Matric Potential on Resistance to *Fusarium oxysporum* f. sp. *medicaginis* in Alfalfa

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ABSTRACT

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Yields of uninoculated alfalfa cultivars Moapa (resistant) and Narragansett (susceptible) and Moapa inoculated with *Fusarium oxysporum* f. sp. *medicaginis* increased with increased soil moisture. Yield of inoculated Narragansett plants was less than that of uninoculated plants and did not increase in response to increased soil moisture. Severity of Fusarium wilt was not increased for either cultivar by increased soil moisture in greenhouse experiments. During the first 4 wk following inoculation in an outdoor experiment, the number of dead plants of Narragansett alfalfa was significantly larger in wet soil than in moist soil. However, by 8 wk, this difference was no longer observed. Although increased soil moisture may have an effect on the initial rate of Fusarium wilt development, no evidence was found that it altered the basic characterization of Moapa and Narragansett as cultivars resistant and susceptible, respectively, to Fusarium wilt.

Additional key words: disease resistance, disease screening, *Medicago sativa*.

Fusarium wilt of alfalfa, *Medicago sativa* L., was first reported in Mississippi in 1927 (16,17). The disease has been subsequently reported elsewhere in the United States (1,9,11) and abroad (1,8,13) and is considered more severe in warmer areas (7,11).

Shoots of infected plants wilt, die, and become bleached in appearance (7). Often only one or two shoots wilt at first, but eventually the entire plant wilts and dies. A distinctive dark brown discoloration of the root xylem is characteristic of the disease, and the degree of root xylem discoloration, seen in cross section, closely corresponds to the severity of external symptoms.

The organism that usually induces the disease is *Fusarium oxysporum* Schlecht f. sp. *medicaginis* (Weimer) Snyd. & Hans., but *F. oxysporum* f. sp. *vasinfectum* (Atk.) Snyd. & Hans. and *F. oxysporum* f. sp. *cassia* Armst. & Armst. are also reported as pathogens of alfalfa (1).

Fusarium wilt of many crops, including Fusarium wilt of alfalfa, is favored by warm soil temperatures (7) and is reported to be more severe when associated with nematode feeding (12). Increased soil moisture has been reported to increase the severity of Fusarium wilt of alfalfa (18) and other plants (2). Weimer reported an increase from 50 to 80% in infected plants when alfalfa was grown in soil at 35 and 55% water-holding capacity, respectively (18).

The use of resistant cultivars is currently the most economically feasible means of control for Fusarium wilt. To screen alfalfa populations for Fusarium wilt resistance, the effects, if any, that environmental factors may have on the measured levels of resistance should be known. Because the possibility exists that measured levels of resistance could vary as a result of soil moisture conditions during the test period, this work was done to determine the role of soil moisture in Fusarium wilt of alfalfa.

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MATERIALS AND METHODS

Isolates, inoculum preparation, and inoculation. Highly virulent isolates (5) of *F. oxysporum* f. sp. *medicaginis* were obtained from wilting alfalfa plants in North Carolina. An equally proportioned mixture of isolates was used for inoculum. Inoculum was prepared by growing single-spore cultures of each isolate on potato-dextrose agar for 2 wk under fluorescent lights (a daily 12-hr off/on cycle) at 21–23 C (15). Conidia were harvested by flooding the agar surface with distilled water and scraping the conidia into suspension. Mycelium was removed by filtering through two layers of cheesecloth. The suspension contained macroconidia and microconidia and was adjusted to a concentration of 1×10^6 conidia per milliliter as estimated by hemacytometer counts. Moapa and Narragansett (alfalfa cultivars resistant and susceptible, respectively, to Fusarium wilt) were inoculated at seeding with *Rhizobium meliloti* Dangeard and grown in the greenhouse. After 8–11 wk of growth, the plants were lifted. The roots were washed and clipped 7 cm below the crown and soaked in the conidial suspension for approximately 45 min. After inoculation, tops were clipped 7 cm above the crown and the plants replanted. Isolates used in this study (designated 0-979, 0-981, 0-982, 0-984) are being maintained as lyophilized cultures at the USDA Tobacco Research Station at Oxford, NC, the Fusarium Research Center at Pennsylvania State University, and the American Type Culture Collection (Rockville, MD 20852) as ATCC #46584, ATCC #46585, ATCC #46586, and ATCC #46587, respectively. Uninoculated plants were soaked in distilled water.

Soil moisture regulation. A 1:1 (v/v) mixture of pasteurized (aerated steam at 82 C for 30 min) coarse sand and soil (sandy loam) was used as a growing medium in all experiments. If experiments were to be repeated, enough soil for both studies was prepared and stored in plastic trash cans. A soil moisture release curve (Fig. 1) was determined for this soil and sand mixture. Moisture determinations from −0.001 to −0.1 bar were made, using 9-cm Buchner funnels with fritted glass plates of fine porosity as tension plates (4,10); determinations from −0.1 to −15 bars were made

using a pressure membrane apparatus (10,14).

Three fluctuating soil moistures were established by varying the intervals between irrigations (3). Soil moisture was monitored gravimetrically or with tensiometers 16 cm in length (Irrometer Co., Riverside, CA) placed in the soil to a depth of 10 cm. In terms of soil moisture status, wet soil was defined as that fluctuating from 0 to −0.01 or −0.02 bar, moist soil from 0 to −0.8 or −0.1 bar, and dry soil from 0 to approximately −10 bars. Following each irrigation, plants were allowed to extract soil moisture to the predetermined matric potentials, at which point the soil was once again irrigated to saturation.

Greenhouse tensiometer experiments. Forty wooden flats (51 × 35 × 14 cm deep) were filled to a uniform depth with the soil-sand mixture. Twelve 9-wk-old seedlings of either Moapa or Narragansett were transplanted into each flat. All plants in a flat were either inoculated or uninoculated and were irrigated for 4 days as needed to promote vigorous growth and seedling establishment. Differential irrigation was started on day 5 to establish soil moisture levels. Flats receiving the wet soil treatment were irrigated daily to saturation. Moisture determinations of soil samples from these flats were used in conjunction with the soil moisture release curve to determine matric potentials existing between irrigations. Depending on plant size and environmental conditions, matric potential in these flats varied from 0 bars after irrigating to −0.01 to −0.02 bar before irrigating. Moisture extraction was monitored with tensiometers, and soil was irrigated when tensiometers read −0.8 bar in the flats receiving the moist-soil treatment.

The experimental design was a split-split plot with five replications. Main plots were the inoculation treatments, split plots were the cultivars, and split-split plots were the soil water treatments. The experiment was repeated. Each experiment was terminated when the regrowth flowered (9 wk after inoculation in the first experiment and 5 wk after in the second).

Outdoor tensiometer experiment. A second experiment was conducted outdoors to subject inoculated plants to environmental stresses greater than those existing in the greenhouse. Sixty wooden flats were filled with the soil-sand mixture and placed outdoors. Eight-week-old plants of Moapa and Narragansett were inoculated with *F. oxysporum* f. sp. *medicaginis* as previously described and transplanted at 12 per flat. Only one uninoculated flat of each treatment combination was included because the primary emphasis was on the reaction of inoculated cultivars to differing soil moisture treatments. Plants were irrigated for 5 days as needed to promote vigorous growth and establishment. Wet and moist soil levels were subsequently maintained as previously described. Soil receiving the wet soil treatment was often watered twice daily. Matric potentials existing between irrigations for the wet soil treatments were similar to those determined in the greenhouse tensiometer experiment. Soil was watered when tensiometers read −0.8 bar in the moist soil treatment.

The design was completely random, with 15 flats per treatment. Plants flowered and were clipped 31 (21 August), 56 (15 September), and 90 (19 October) days after inoculation. At each flowering date, 20 flats (comprising five flats per treatment) were randomly sampled and the plants rated for disease severity. In this manner, plant yield data and disease severity ratings were obtained for plants after one and then two clipping and regrowth periods. Rainfall occurring during the experiment was recorded.

Greenhouse gravimetric experiment. Tensiometers cannot monitor soil water matric potentials more negative than approximately −0.8 bar (10). To study the effect of drier soil on disease severity, a study was done using a gravimetric soil moisture regulation technique. Plastic pots 20 cm in diameter and 10 cm high were filled with the soil-sand mixture. Five 11-wk-old seedlings of Narragansett were inoculated or left uninoculated and transplanted into each pot. All plants were watered for 3 days as needed to promote vigorous growth and seedling establishment, and wet, moist, and dry soil moisture regimes were begun on day 4. Plants were allowed to extract soil moisture to predetermined weights for the entire soil-plant-pot system. Using the soil moisture release curve (Fig. 1), weights were chosen that corresponded to matric potentials of −0.01 bar (wet), −0.1 bar (moist), and approximately −10 bars (dry). Pots were weighed twice a day and watered as needed. Matric potentials for the wet soil moisture treatment before irrigating varied from −0.01 to −0.02 bar depending on plant size and environmental factors.

The experimental design was a randomized complete block with five blocks. In each block were two inoculated treatments for each uninoculated treatment at each water level. The experiment was repeated. Each experiment was terminated when plants flowered, which occurred 32 days after inoculation in the first experiment and 34 days after in the second.

Evaluation of plant growth and disease severity. During the course of each experiment, plants were rated weekly for symptom expression. At the termination of each experiment, plant height and dry matter (dried in a forced-air oven at 60 C) were recorded. In addition, all plants were rated for disease severity using a 1–6 scale for xylem discoloration in the taproot (6), in which 1 = no discoloration, 2 = one to three small dark areas of discoloration, 3 = more than three small isolated areas of discoloration, 4 = a partial ring of discoloration, 5 = a complete ring of discoloration, and 6 = complete discoloration of the xylem or death of plant. The average rating for a given treatment comprised the disease severity index (DSI). DSI ratings of 4.0 or above were characteristic of susceptible populations of alfalfa. Individual plants scored as 1 or 2 were considered resistant. Isolations from plant materials were made to confirm the presence of *F. oxysporum*. Soil temperatures were measured and recorded daily at 0800 and 1600 hr at a depth of 8–10 cm in flats or pots receiving the wet soil moisture treatment.

RESULTS

Greenhouse tensiometer experiments. Plant growth and disease severity data for all treatments (Table 1) indicated that increased soil moisture resulted in increased plant growth. Analysis of variance indicated highly significant differences ($P = 0.01$) for soil moisture and inoculation treatment and for soil moisture and both cultivars. Growth of inoculated plants of Narragansett was considerably less at both soil moisture contents than the growth of uninoculated plants. In contrast, growth of Moapa plants was only slightly affected by inoculation.

Wet and moist soil conditions had no effect ($P = 0.05$) on the DSI and seedling mortality (Fig. 2). No difference in rate of mortality was noted at either soil moisture level (slopes were not significantly different). The correlation between the number of dead plants and the weeks after inoculation was significant ($P = 0.01$) for each soil moisture treatment (Fig. 2).

Soil temperatures during the course of the experiment ranged

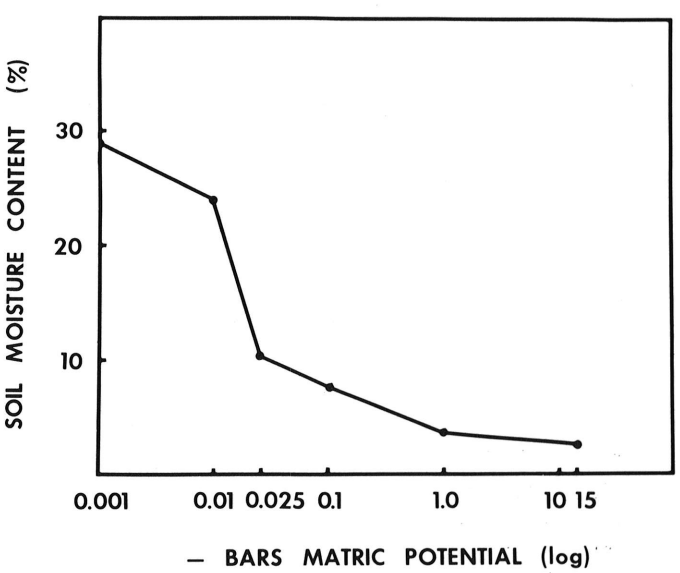

Fig. 1. Soil moisture release curve for a 1:1 mix of sandy loam and coarse sand.

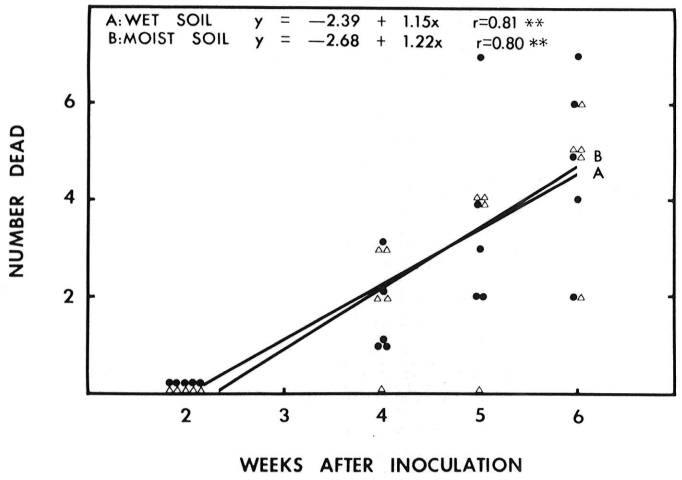

Fig. 2. Number of dead Narragansett alfalfa seedlings in wet (Δ = 0 to −0.02 bar) or moist (• = 0 to −0.8 bar) soil in the greenhouse following inoculation with *Fusarium oxysporum* f. sp. *medicaginis* over time. Each data point is the number dead per flat of 12 plants. Correlations were significant at $P = 0.01$.

from a morning (0800 hr) average of 18 C to an afternoon (1600 hr) average of 23 C. *F. oxysporum* was consistently isolated from roots of inoculated plants. Some uninoculated plants developed a few small areas of discoloration, enough to be scored 2, but *F. oxysporum* was not isolated from these areas. The cause of this discoloration is not known.

Outdoor tensiometer experiment. Plant growth and disease severity (Table 2) were measured for each of the three groups of 20 flats. Growth of the Moapa plants at all three sampling dates was greater ($P = 0.05$) with the increased soil moisture. Except for the last sampling, Narragansett plants showed no increase in growth in response to increased soil moisture. For Narragansett plants sampled 31 days after inoculation and for Moapa plants sampled 56 days after inoculation, plants provided increased soil moisture showed increased ($P = 0.05$) disease severity. Soil moisture did not affect DSI in any other samples. The correlation between the number of dead plants and weeks after inoculation was significant ($P = 0.01$) for each soil moisture treatment (Fig. 3). The relationship between the number of Narragansett plants that died between inoculation and the first sample period (31 days) at the two soil moisture levels is plotted in Fig. 3. Slopes of the two lines are signficantly different at $P = 0.01$, indicating a relationship with soil moisture. However, this effect was not apparent after 31 days, and

TABLE 1. Plant growth and disease severity of seedlings of alfalfa resistant (Moapa) and susceptible (Narragansett) to Fusarium wilt in soil with matric potential of 0 to −0.02 bar (wet) and 0 to −0.8 bar (moist) in the greenhouse following inoculation with *Fusarium oxysporum* f. sp. *medicaginis*

			Plant growth[a]		Disease severity[a]	
Treatment	Cultivar	Soil moisture status	Dry matter (g)	Height (cm)	DSI[b] (1–6)	Mortality[c] (%)
Inoculated	Moapa	Wet	19.8	52	2.03	1.6
		Moist	13.6	40	2.09	1.6
	Narragansett	Wet	11.6	39	4.53	38.6
		Moist	7.2	31	4.46	40.0
Uninoculated	Moapa	Wet	22.0	51	1.44	0.0
		Moist	12.0	38	1.36	0.0
	Narragansett	Wet	24.8	44	1.61	0.0
		Moist	15.6	34	1.36	0.0

[a] Mean of 12 plants per flat. Analysis of variance for the effect of soil moisture over inoculation and cultivar was high significant ($P = 0.01$). Individual mean comparisons were not made.
[b] Disease severity index, based on degree of root xylem discoloration where 1 = no disease and 6 = highest disease rating.
[c] Average percentage dead of 12 plants per flat.

TABLE 2. Plant growth and disease severity of seedlings of alfalfa resistant (Moapa) and susceptible (Narragansett) to Fusarium wilt in soil with matric potential of 0 to −0.02 bar (wet) and 0 to −0.8 bar (moist) growing outdoors following inoculation with *Fusarium oxysporum* f. sp. *medicaginis*

			Plant growth[b,c]		Disease severity[c,d]	
Cultivar	Sampling time[a]	Soil moisture status	Dry matter (g)	Height (cm)	DSI[e] (1–6)	Mortality[f] (%)
Narragansett	31	Wet	3.43	22	5.05	66.6
		Moist	4.25	18	4.44*	43.4*
	56	Wet	10.66	30	5.08	66.8
		Moist	7.24	33	5.03	64.8
	90	Wet	7.92	37	5.37	76.6
		Moist	4.54*	30	5.33	73.6
Moapa	31	Wet	15.02	36	2.27	1.6[g]
		Moist	8.96*	27**	2.08	3.2
	56	Wet	28.59	44	3.10	16.6
		Moist	19.15*	36	2.35*	4.8
	90	Wet	32.43	50	2.81	13.2
		Moist	18.22**	40*	2.47	6.6

[a] One third of the total experiment was sampled at 31 (21 August), 56 (15 September), and 90 (19 October) days after inoculation.
[b] Mean of 12 plants per flat. Plant growth data for second and third sample times are not cumulative.
[c] * or ** indicates that means for wet and moist soil matric potential within a sample time and cultivar are different at $P = 0.05$ or 0.01, respectively.
[d] Data are cumulative, recorded as the totals from the date of transplanting to the last date of sampling.
[e] Disease severity index, based on degree of root xylem discoloration where 1 = no disease and 6 = highest disease rating.
[f] Average percentage dead of 12 plants per flat.
[g] Mortality information for Moapa was not analyzed due to the large number of zeros in the data.

the different soil moistures had no effect on disease severity for Narragansett plants sampled 56 and 90 days after inoculation. A few plants of Moapa died within 56 days after inoculation but none after this date. Of the Moapa plants that died, most died between 21 August (31 days) and 15 September (56 days).

After 90 days (19 October), uninoculated plants were also sampled and rated for disease severity. No plants had died, and DSI scores were the lowest of any in the experiment.

Rainfall during the experiment measured 0.4 cm from 21 July to 21 August, 5.3 cm from 23 August to 13 September, and 8.4 cm from 22 September to 19 October. Rainfall did not obscure the effect of differential irrigations on plant growth.

Average morning (0800 hr) and afternoon (1600 hr) soil temperatures at a depth of 8–10 cm were 20 and 26 C, respectively, for the first period, 18 and 24 C during the second period, and 12 and 17 C during the third period, which ended 19 October.

F. oxysporum (15) was consistently isolated from roots of inoculated plants that had died during the course of the experiment and from root tissue of surviving plants. The fungus was isolated from a few uninoculated plants at the end of the experiment.

Moisture determinations of soil samples indicated that when tensiometers read −0.8 bar, the actual matric potential of the soil in the upper layers of the flats was as low as −5 to −10 bars. Apparently the tensiometers, which had their porous tips near the bottom of the flats, did not accurately monitor moisture extraction for the entire soil mass in the wooden flats.

Greenhouse gravimetric experiment. As soil moisture increased, the growth of uninoculated Narragansett plants increased (Table 3). Growth of the inoculated plants was reduced, but not differentially, by soil moisture. Numbers of dead inoculated plants and DSI were similar for each of the three soil moisture regimes. None of the uninoculated plants died, and xylem discoloration was slight. Regression of the number of dead plants on time after inoculation at the three soil moisture treatments indicated that the slopes of the three lines were not different from each other (Fig. 4). For each soil moisture level (Fig. 4), the correlation between the number of dead plants and days after inoculation was significant ($P = 0.01$).

Average soil temperatures varied from 17 C in the morning (0800 hr) to 22 C in the afternoon (1600 hr).

F. oxysporum was consistently isolated from roots of inoculated plants but not from roots of uninoculated plants.

DISCUSSION

Greenhouse studies indicate that the severity of Fusarium wilt of alfalfa is not influenced by soil moisture within a fluctuating range of −0.01 to −10 bars. Disease severity for each cultivar was similar at all soil moisture levels. In contrast, an outdoor experiment indicated that a restricted water supply delayed disease development in the susceptible cultivar Narragansett during the first 4 wk after inoculation.

These observations are consistent with the available evidence that wet soil generally favors wilt diseases whereas dry soil does not. By restricting transpirational flow in the plant, dry soil might impede the upward movement of the fungus and delay disease symptoms (2). Under greenhouse conditions of low evaporative demand, total transpiration might not have differed significantly among the soil moisture treatments. If so, upward movement of the fungus would be favored and not significantly affected by soil

TABLE 3. Plant growth, disease severity, and mortality of Narragansett plants in soil with matric potential of 0 to −0.02 bar (wet), 0 to −0.8 bar (moist), or 0 to −10 bars (dry) in the greenhouse following inoculation with *Fusarium oxysporum* f. sp. *medicaginis*

Treatment	Soil moisture status	Plant growth[a] Dry matter (g)	Plant growth[a] Height (cm)	Disease severity DSI[b] (1–6)	Disease severity Mortality[c] (%)
Uninoculated	Wet	9.08	49	1.55	0
	Moist	7.14	39	1.45	0
	Dry	5.62	33	1.70	0
	FLSD[d]	1.34	3	0.31	···
Inoculated	Wet	1.12	25	5.42	70
	Moist	2.08	31	5.12	65
	Dry	1.21	20	5.20	75
	FLSD	1.98	20	0.97	33

[a] Mean of five plants per pot.
[b] Disease severity index, based on degree of root xylem discoloration where 1 = no disease and 6 = highest disease rating.
[c] Average percentage dead of five plants per pot.
[d] Fisher's (protected) LSD; $P = 0.05$.

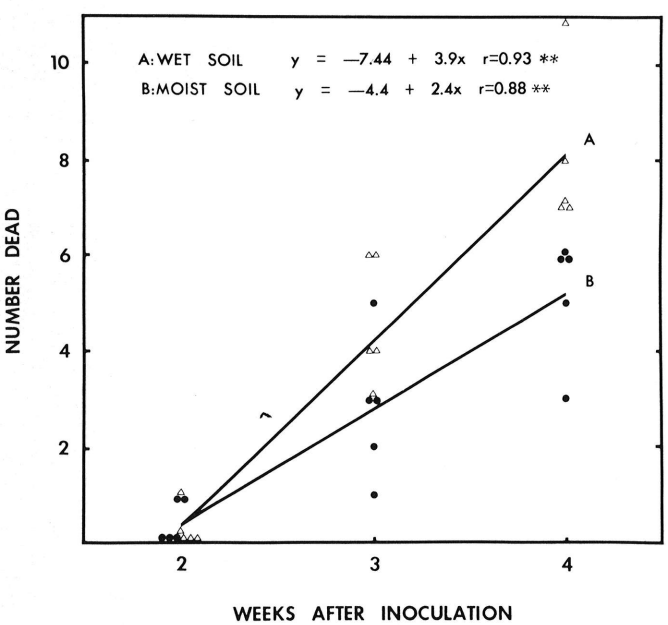

Fig. 3. Number of dead Narragansett alfalfa seedlings in wet (Δ = 0 to −0.02 bar) or moist (• = 0 to −0.8 bar) soil outdoors following inoculation with *Fusarium oxysporum* f. sp. *medicaginis* over time. Each data point is the number dead per flat of 12 plants. Correlations were significant at $P = 0.01$.

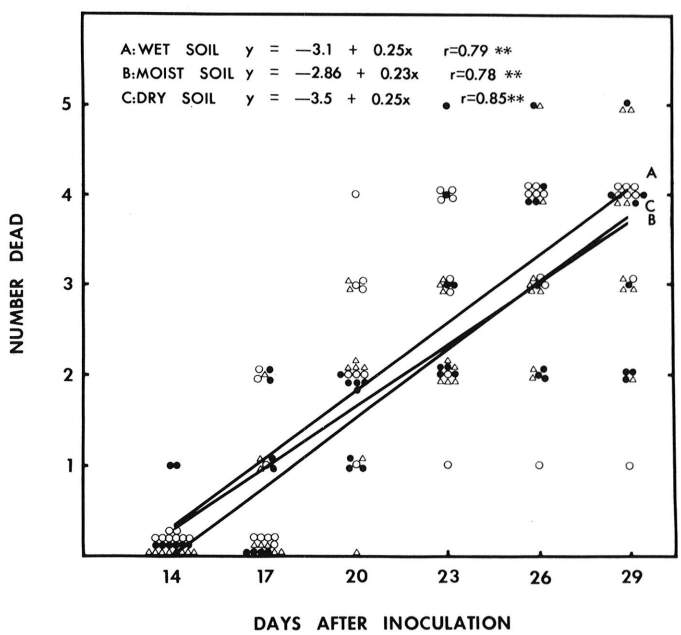

Fig. 4. Number of dead Narragansett alfalfa seedlings grown in wet (o = 0 to −0.02 bar), moist (• = 0 to −0.8 bar), and dry (Δ = 0 to −10 bars) soil in the greenhouse following inoculation with *Fusarium oxysporum* f. sp. *medicaginis* over time. Each data point is the number dead per pot of five plants. Correlations were significant at $P = 0.01$.

moisture treatment. As was observed, disease severity values for the various soil moisture treatments were similar and probably represent the maximum possible for this particular pathogen-host combination. Outdoors, evaporative demand would be higher, and the stomates would be more likely to close in response to a limited water supply, thereby discontinuing transpiration and restricting the upward movement of the fungus. This could explain the delayed symptom development observed for Narragansett. With time, and after repeated watering of the soil to saturation (favoring transpiration), fungal conidia were probably swept upward in the plants to the extent that by 8 wk after inoculation, disease severity was essentially the same as in the wet soil treatment.

In effect, then, restricting water may temporarily suppress wilt symptoms. The suppressive effect was not as apparent with Moapa. The basic characterization of Moapa and Narragansett as resistant and susceptible to Fusarium wilt, respectively, was not altered at any soil moisture level tested in the greenhouse or outdoors.

Within the range of soil moisture from dry (0 to −10 bars) to moist (0 to −0.8 bar) to wet (0 to −0.01 bar), as defined in these studies, growth of uninoculated plants of both cultivars increased as soil moisture increased. Growth was optimal in the wettest soil and progressively reduced in the moist and dry soil moisture conditions. However, infection by *F. oxysporum* f. sp. *medicaginis* altered these soil moisture-growth relationships. The increased growth in response to increased soil moisture was no longer observed in Narragansett when disease severity was high following inoculation in the gravimetric experiment in the greenhouse and the tensiometer experiment outdoors. In fact, yield differences for this cultivar in the presence of *F. oxysporum* were virtually nonexistent in response to soil moisture. Because disease severity in Narragansett was not as severe in the greenhouse experiment employing tensiometers, growth increased with increased soil moisture.

During conditions of severe disease (large DSI and seedling mortality), growth of diseased Narragansett plants was highly variable, with no apparent relation to soil moisture level. This, together with variable levels of mortality in response to inoculation, could explain the lack of response of inoculated Narragansett plants to increased soil moisture level. Moapa responded to increased soil moisture with little difference between yields of inoculated and uninoculated plants.

The results of this study do not agree with the earlier report that the severity of Fusarium wilt of alfalfa is suppressed in drier soil in greenhouse experiments (18). We observed a temporary suppressive effect outdoors, but only for the cultivar susceptible to Fusarium wilt. These studies (18) may not be directly comparable because of differences in soil types, moisture regulation techniques, greenhouse conditions, temperature used in pasteurizing soils, alfalfa cultivars, methods of inoculation, and statistical analysis of data. Also, soil moisture levels (reported as percent of moisture-holding capacity [18]) cannot be equated to matric potentials. We believe the data from the present studies are reliable because the studies were done over a broad range of soil moisture contents in several environments and used moisture regulation techniques that are more widely accepted for their accuracy (3).

Conclusions from the work reported here are limited to the extent that only two cultivars and one soil texture were studied. Nevertheless, soil moisture within the range studied is apparently not an important variable in the development of Furasium wilt when inoculation and transplanting techniques are used as reported. Aside from a small difference in rate of disease development during the first few weeks after inoculation (outdoor experiment), we found no evidence that soil moisture conditions could change the basic characterization of a given alfalfa population as resistant or susceptible to Fusarium wilt.

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