Etiology

Crown Rot of Alfalfa in Utah

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ABSTRACT

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Alfalfa crowns in Utah are universally affected by a dark, dry necrosis. The isolations and pathogenicity reported here indicated that the cause is a complex of pathogens. Organisms confirmed as pathogens in field plot inoculations were: *Fusarium solani, F. roseum* 'Acuminatum,' and *F. tricinctum, Serratia marcescens*, and *Pseudomonas marginalis* var. *alfalfae*. These organisms were all weakly virulent, and no evidence of synergism was detected. The low virulence of the pathogens was reflected in the slow development of disease symptoms. The average extent of necrosis within naturally infected crowns progressed from about 30% in 2-yr-old alfalfa to about 50% in an 11-yr-old stand. The number of crowns in the 11-yr-old field was sevenfold less than in the 2-yr-old field. The disease thus was associated with a slow reduction of alfalfa stand density. The remaining crowns compensated for the reduction in crown density, however, by increasing their numbers of stems per crown. Thus, no significant decrease in stems per unit area occurred during the study period.

Additional key words: *Medicago sativa*.

Crown rot of alfalfa (*Medicago sativa* L.) is extensive in Utah both in number of cultivars affected and in geographical distribution. The dark, dry necrosis that characterizes crown rot appears to be initiated through wounds and takes a number of years to spread throughout the crown and upper part of the tap root. Similar crown and root rots have been reported elsewhere. A rapidly developing depletion of forage stands in the northeastern United States has been attributed to *Fusarium* spp. (9). In other areas, stand depletion apparently requires in excess of 3 yr (5,7). Most studies of alfalfa crown rot have been directed toward determining its etiology rather than its impact on crop persistence and yield.

Results of pathogenicity studies of organisms implicated in dark-crown necrosis have been variable (5,9). Dark-crown necrosis was by far the most prevalent crown disease studied by Erwin (5) in California; however, *Fusarium* spp., the most commonly isolated fungi, were not pathogenic when inoculated. In Canada, *Fusarium* spp. were found to be causal agents of alfalfa crown and root rot (3,11,12). Workers in the northeastern USA reported variable results when seedlings and older plants were inoculated with the isolates of fungal species considered to be a problem in Canada (9). Potential pathogens most frequently isolated by Minnesota workers were *Phoma medicaginis* Malb. and Roum., *Fusarium solani* (Mart.) Appel. and Wr., and *Rhizoctonia solani* Kuhn (18).

Bacteria have also been implicated in crown rot of alfalfa. Shinde

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and Lukezic (14) reported the association with alfalfa crown rot of two bacteria that they named *Pseudomonas marginalis* var. *alfalfae* and *Erwinia amylovora* var. *alfalfa*. Lukezic et al (10) recently reported that the *E. amylovora* isolate was better classified as *Serratia marcescens* Bizio. Gaudet et al (6) reported the same two bacterial species to be involved in the crown rot of irrigated sainfoin (1,13).

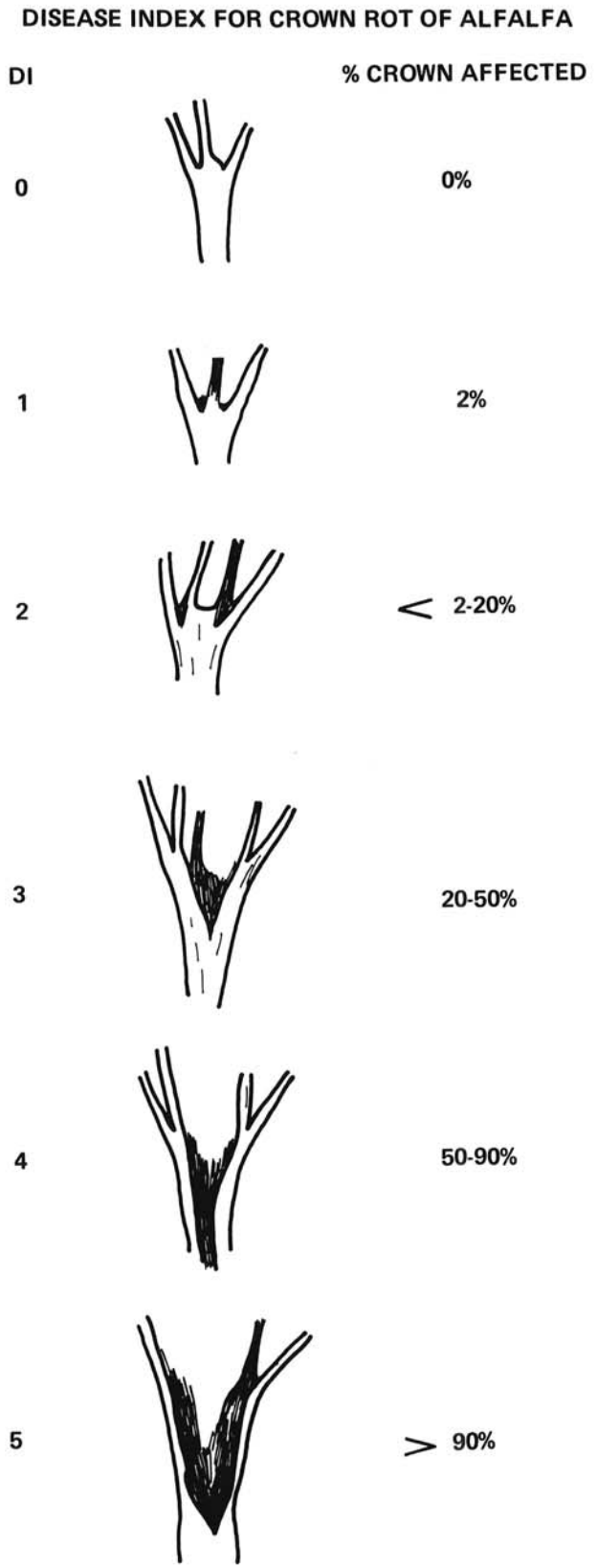

Fig. 1. Extent of crown necrosis for each disease index (DI) class.

The objectives of this study were to determine the occurrence and severity of dark-crown necrosis in Utah, to identify the pathogens involved in disease development, and to assess the potential of this disease to reduce stand longevity and vigor.

MATERIALS AND METHODS

Disease index. To facilitate assessment of disease severity in naturally infected and inoculated alfalfa crowns, a disease index (DI) was devised. The DI represents an estimate of the percentage crown necrosis. The following DI classes were established: 0 = 0%; 1 = >0 to <2%; 2 = 2 to 20%; 3 = >20 to 50%; 4 = >50 to 90%; 5 = >90% crown necrosis (Fig. 1). Crowns were dug, split in half, and rated for DI.

DI data were collected in five cultivar test plots; each plot being located in a different county. Plots ranged from 1 to 4 yr old. A total of 20 cultivars were planted in a random, complete-block design, with four or six replicates, depending upon the location of the test plot. Plots were 0.6 × 2.4 m and contained four drill rows. Two plants per cultivar were sampled and indexed in each block. Data were subjected to analysis of variance.

Isolation from diseased plants. Plants were selected at random from cultivar test plots and fields for isolation of potential pathogens. Potato-dextrose agar (Inolex Corp., Glenwood, IL 60425) supplemented with 100 ppm streptomycin (Sigma Chemical Co., St. Louis, MO 63178) and 50 ppm vancomycin (Sigma) to inhibit bacterial growth was used for fungal isolations. Bacteria were isolated by using King's B agar supplemented with 1% cycloheximide. Crown and taproot sections were washed in a dilute (~1 gm/l) Alconox® (Alconox, Inc., New York, NY 10003) detergent solution to remove adhering soil. Sections approximately 2.5 cm long were excised and soaked in 10% Clorox® (Clorox Co., Oakland, CA) solution for 5 min, rinsed in sterile distilled water, dipped in 95% ethanol, and flamed. Four 1 × 2-mm pieces cut from the leading edge of dark necrotic zones were transferred to petri plates containing the above media. The 1 × 2-mm sections included non-necrotic as well as necrotic tissue. Plates were incubated under a regime of varying temperatures and a 12-hr photoperiod. Temperatures varied between 18 and 24 C four times within a 24-hr period. The variations were used to promote sporulation of *Fusarium* spp. (16). Percent isolation of fungal isolates was recorded following identification of all potential pathogens. *Fusarium* spp. were identified according to the procedures outlined by Toussoun and Nelson (16). *Fusarium* spp. were maintained in soil or by lyophilization on carnation leaves.

Bacteria were isolated by placing tissue pieces prepared as above in 1-ml sterile H_2O blanks and incubating them at 20 C for approximately 18 hr. The H_2O blanks containing the tissue pieces were then agitated, and a loopful of suspension was aseptically removed and streaked onto plates of King's B agar supplemented with 1% cycloheximide (KBC) (6). Tissue pieces were also plated directly onto KBC medium as described for fungal isolations.

The procedures of Dye (4) and Stanier et al (15) were used to identify bacteria. Bacteria were stored in 0.1 M $MgSO_4$ solution at 4 C and were grown on King's B agar for inoculations and other tests.

Pathogenicity tests. Pathogenicity studies were done with single isolates and mixtures of isolates. Ten treatments were replicated five times in a completely randomized design. Five square plots each 900 cm^2 were located at 3-m intervals along each of 10 parallel transects 7.6 m apart established in a 3- to 4-mo-old stand of cultivar Washoe alfalfa that had been cut once. Numbers of spores per milliliter in spore suspensions were determined by using a hemacytometer. Approximately 6×10^4 fungal spores or 10^7 bacterial cells were injected into alfalfa crowns by means of a 1-cc tuberculin-type syringe fitted with a 0.45-mm-diameter (25-gauge) needle. For controls, some crowns were left unwounded and others were injected with sterile water. Nearly 1,000 plants were inoculated. This experiment was repeated with some organisms in common in two different years.

Plants were indexed 3–4 mo after inoculation. Plots were coded so that DI values were recorded without knowledge of the

treatment given. Five plants per plot (a total of 25 per treatment) were selected for isolation onto media. Percent recovery of inoculum was based on total number of tissue pieces exhibiting growth for each treatment. DI data were statistically analyzed to determine significant differences among treatments.

Disease loss. Disease impact upon stand persistence and stem production was assessed in 2-, 4-, 7-, and 11-yr-old 'Ranger' alfalfa fields located near Milford in Beaver County, Utah. The four fields were in close proximity to each other and had been planted and managed by one farmer. All fields were furrow irrigated. Three parallel 15-m transects placed at 15-m intervals were established in each field. Plots of 900 cm^2 were sampled at 3-m intervals along each transect for a total of 15 plots per field. DI values, numbers of crowns and stems, stems per crown, and crown-taproot basal areas were determined for each 900-cm^2 plot. Crown-taproot basal area (CTBA) was determined by measuring the diameter of the interface between the crown and taproot. Analysis of variance was performed to determine significant differences among the fields for each parameter.

RESULTS

Isolation of potential pathogens. *Fusarium* spp. were the fungal isolates most frequently obtained from plants throughout the state. However, differences in occurrence of certain *Fusarium* species were noted. *Fusarium* spp. composed 90.9% of the isolates obtained from plots in Wasatch and Tooele counties, *F. solani* being the most frequently isolated. *Fusarium* spp. composed 86% of the fungal isolates taken from Juab County. None of these included *F. solani* or *F. oxysporum* Schlecht. ex. Fr. In Beaver County, 69% of the isolates were *F. roseum* Lk. ex. Fr. emend. Snyder and Hans. and *F. tricinctum* (Cda.) emend. Snyder and Hans. Again, *F. oxysporum* and *F. solani* were not isolated. Isolations from control plants, ie, plants with no disease symptoms, yielded very few organisms.

Bacteria were commonly isolated from infected tissue. The frequency of bacterial isolation ranged from 9 to 78% of the tissue pieces. The bacteria that were predominant in the isolations resembled those described from alfalfa by Shinde and Lukezic (14) and Gaudet et al (6).

Identification of isolates. Isolates of *P. marginalis* var. *alfalfa* and *S. marcescens* from sainfoin were obtained from D. Mathre of Montana State University for comparison with our isolates. Comparative biochemical and physiological tests (Tables 1–3) indicated that our alfalfa isolates were probably the same species as those isolated from sainfoin. Our identification test results agreed with those of Gaudet et al (6) with the exception of our positive NO_3 reduction for the group characterized by *P. marginalis* var. *alfalfa*. The identification of the isolates of *Fusarium* was confirmed by Thor Komendahl, University of Minnesota and Paul Nelson, The Pennsylvania State University.

Pathogenicity studies. Frequently occurring fungal isolates were used in our first pathogenicity study (Table 4). All of the *Fusarium* spp. were significantly pathogenic as compared with the unwounded controls. Some, however, were not pathogenic when compared with wounded controls. The *Phoma* sp. isolate was not pathogenic. Combinations of the pathogens did not increase or decrease DI values. In all cases, upon reisolation the isolate inoculated was most often obtained (frequency 51–92%). Reisolation from mixed inoculations resulted in recovery of all components in about equal frequency. *F. solani* and bacteria were isolated from wounded control plants.

A second pathogenicity study involving bacterial isolates and three of the fungi tested previously was conducted by using the same procedures. *P. marginalis* var. *alfalfa*, inoculated singly and in combination with *S. marcescens*, produced the highest DI values among all treatments with ratings of 2.68 and 2.67, respectively (Table 5). The combination of all bacteria and fungi resulted in a slightly lower DI of 2.37. With the exception of *Phoma* sp., all bacterial and fungal treatments resulted in significantly higher disease indices than were noted in H_2O-inoculated and

TABLE 1. Biochemical and physiological tests of *Serratia marcescens* isolates from Utah alfalfa and Montana sainfoin

	Isolates			
	Alfalfa		Sainfoin[a]	
Test	3R3[b]	1R3	E-5	E15-3
Catalase	+	+	+	+
Motility	+	+	+	+
Growth factors	−	−	−	−
Gelatin hydrolysis	−	−	−	−
Lipase	+	+	+	+
Levan	+	+	+	+
Pectate liquifaction	−	−	−	−
Urease	−	−	−	−
Gas from glucose	−	−	−	−
Anerobic growth	+	+	+	+
Acetoin production	+	+	+	+
H_2S production from cysteine	−	−	−	−
Gluconate utilization	+	+	+	+
1) Medium 0[c] + bromthymol blue	+	+	+	+
2) Medium 0	+	+	+	+
Growth at 37 C	+	+	+	+
Nitrate reduction	+	+	+	+
Oxidase	−	−	−	−

[a] Obtained from D. Mathre, Montana State University, Bozeman.
[b] Each test was done with three replicates.
[c] Medium 0 (4).

TABLE 2. Acid production from organic compounds by alfalfa and sainfoin isolates of *Serratia marcescens*

	Isolates							
	Alfalfa				Sainfoin[a]			
	3R3[b]		1R3		E-5		E15-3	
Organic substrate	C[c]	P/W[d]	C	P/W	C	P/W	C	P/W
Methyl glucoside	−	−	−	−	−	−	−	−
Arabinose	+	−	+	−	+	−	+	−
Glycerol	−	−	−	−	−	−	−	−
Lactose	−	−	−	−	−	−	−	−
Maltose	−	−	−	−[e]	−	+	−	−
Mannitol	−	−	−	−	−	−	−	−
Raffinose	−	+	−	−	−	+	−	−
Rhamnose	−	−	−	−	−	+	−	−
Salicin	−	−	−	−	−	−[e]	−	−
Xylose	−	+	−	−[e]	−	+	−	−
Cellobiose	+	+	+	+	+	+	+	+

[a] Obtained from D. Mathre, Montana State University, Bozeman.
[b] Each test done with three replicates.
[c] Medium C (4).
[d] Peptone-water.
[e] One of the three replicates tested was +.

TABLE 3. Biochemical and physiological tests of *Pseudomonas* spp. isolates from Utah alfalfa and Montana sainfoin

	Alfalfa	Sainfoin[a]	
	P. marginalis[b]	*P. marginalis*	*P. syringae*
Oxidase	+	+	−
Gelatin hydrolysis	+	+	+
Lipase	+	+	+
Levan	+	+	+
Pectate liquification	−	−	−
Nitrate reduction	+	+	−
Arginine dihydrolase	+	+	−
Carbon substrate:			
Sucrose	+	+	+
Sorbitol	+	+	+
Alanine	+	+	+
Motility	+	+	+

[a] Obtained from D. Mathre, Montana State University, Bozeman.
[b] Data represent two isolates: Ut 3RUC and UT 3R4a.

uninoculated controls.

These data confirm those obtained in the previous field inoculation study. In both studies, *Phoma* sp. produced results that were not significantly different from those of the H_2O-inoculated control, and the two fusaria performed identically in terms of their rankings relative to each other. Overall, the DI values were higher in the first study than in the second one (eg, DI values for the uninoculated control were 0.21 and 1.59, respectively, in the 2 yr).

Each bacteria, when inoculated singly into alfalfa, was reisolated from 50% of plants sampled. Inoculation of the two bacteria together resulted in recovery from 37 and 32% of the crowns, respectively, of *S. marcescens* and *P. marginalis*. Other fluorescent bacteria were recovered occasionally from plants of all treatments but were not identified.

TABLE 4. Pathogenicity of fungi inoculated singly or in combination into Washoe alfalfa crowns in the field and indexed 3 mo later

Treatment[w]	Mean disease index[x]
Fusarium solani	1.82 ± 0.48 a[y]
F. roseum 'Acuminatum' (Tooele)[z] + *F. oxysporum* + *F. solani* + *F. tricinctum*	1.82 ± 0.59 a
F. roseum 'Acuminatum' (Tooele)	1.78 ± 0.51 a
F. tricinctum	1.72 ± 0.51 a
Phoma sp. + *F. roseum* 'Acuminatum' (Tooele) + *F. oxysporum* + *F. solani* + *F. tricinctum*	1.69 ± 0.57 a
F. oxysporum	1.66 ± 0.52 ab
F. roseum 'Acuminatum' (Milford)[z]	1.62 ± 0.58 abcd
Control (inoculated with H_2O)	1.37 ± 0.47 bcd
Phoma sp.	1.35 ± 0.53 cd
Phoma sp. + *F. roseum* 'Acuminatum' (Milford)	1.33 ± 0.52 d
Control (uninoculated)	0.21 ± 0.57 e

[w] Total plants sampled was 936; average number per treatment was 85.
[x] Means followed by the same letter are not significantly different (± LSD, $P = 0.05$).
[y] Disease index: 0 = 0%; 1 = >0 to <2%; and 2 = 2 to 20% rot.
[z] Isolated from Tooele and Milford areas, respectively.

TABLE 5. Pathogenicity of fungi and bacteria inoculated singly or in combination into Washoe alfalfa crowns in the field and indexed 3 mo later

Treatment[x]	Mean disease index[y]
Pseudomonas marginalis	2.68 ± 0.70 a[z]
P. marginalis + *E. amylovora*	2.67 ± 0.97 a
E. amylovora	2.53 ± 0.85 ab
Fusarium solani	2.48 ± 0.87 ab
Three Fungi	2.38 ± 1.22 b
Three Fungi + two Bacteria	2.37 ± 0.59 b
F. roseum 'Acuminatum'	2.32 ± 0.71 bc
Phoma sp.	2.06 ± 0.69 cd
Control (H_2O inoculated)	1.92 ± 0.85 de
Control (uninoculated)	1.59 ± 1.15 e

[x] Total plants sampled was 756, average number per treatment was 75.6.
[y] Disease index: 0 = 0%; 1 = >0 to <2%; 2 = 2 to 20%; and 3 = >20 to 50% rot.
[z] Means followed by the same letter are not significantly different (LSD, $P = 0.05$). F test was significant at $P > 0.005$.

TABLE 6. Mean disease index[x] (DI) determined for each alfalfa cultivar test plot located in five counties in Utah

	County				
	Juab	Millard	Tooele	Morgan	Wasatch
Plot age (yr)	1.0	1.3	2.4	3.0	4.0
DI[y]	0.76 a[z]	1.34 b	2.19 c	2.50 d	2.64 d

[x] Mean DI based on nine cultivars common to each test plot in each of the five counties.
[y] DI is disease index: 0 = 0%; 1 = >0 to <2%; 2 = >2 to 20%; and 3 = >20 to 50% rot.
[z] Means followed by different letters are significantly different (LSD, $P = 0.05$). F-test computed from ANOVA was significant ($P = 0.001$).

Percent recovery of fungi was based upon the total number of tissue pieces (four per plant) exhibiting growth. A single sample per plant was used for recovery data in bacterial isolations. *F. solani* had the greatest percent of recovery, 49%, among the fungi inoculated singly. *F. roseum* 'Acuminatum'; was recovered from only 17% of the tissue pieces. The greatest recovery of *Phoma* sp., 10%, was from *Phoma* sp. inoculated crowns. Another pycnidial fungus resembling *Phoma* was recovered more frequently. In culture, it had lighter, more diffuse aerial hyphae and larger, more irregularly-shaped pycnidiospores than the *Phoma* sp. used for inoculation. *Fusarium* spp. were recovered from all treatments, *F. solani* being the most prevalent species.

Evaluation of symptom severity in cultivar test plots. DI values did not differ significantly among cultivars in the 1- and 1.3-yr-old test plots. Significant differences in DI values were observed, however, among cultivars in 2.4-, 3-, and 4-yr-old test plots. A combined analysis of nine cultivars common to all five locations indicated no significant differences among cultivars overall; however, the location × cultivar interaction was significant.

The five location means based on the nine common cultivars differed significantly among all locations except Morgan and Wasatch counties (Table 6). DI values increased with age of the test plot (Fig. 2). Since age was confounded with location, however, one cannot conclude from these data that age influenced DI.

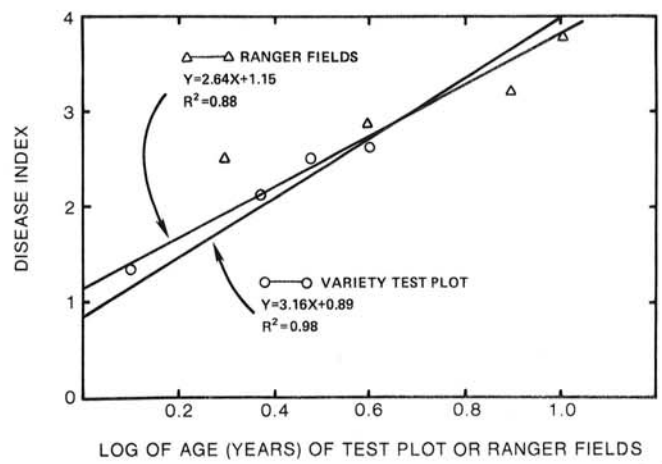

Fig. 2. Disease index versus $\log_{10}$ of stand age of cultivar Ranger alfalfa fields (——) and cultivar test plots (-o-o-).

TABLE 7. Numbers of stems and crowns and area of the crown-taproot basal area (CTBA) in 2, 4, 7, and 11-yr-old cultivar Ranger alfalfa fields near Milford, UT.

	Age[t] (yr)				
Parameters	2	4	7	11	LSD[u] ($P = 0.05$)
Stems	64.6 a[v]	62.0 a	50.9 a	44.7 a	NS[w]
Crowns	15.1 a	8.3 b	6.5 b	2.3 c	3.13
Stems/Crown[x]	5.3 a	11.4 a	7.8 a	20.0 b	7.28
CTBA[y]/Plant[x]	51.4 a	95.3 ab	171.6 b	344.8 c	114.39
Total CTBA[y]	666.1 a	757.6 a	1,086.0 a	879.9 a	NS
DI[z]	2.55 a	2.87 ab	3.24 b	3.78 c	0.47

[t] Means for each age are based on a sample size of 15 900-cm² plots.
[u] LSD = least significant difference test.
[v] Row means followed by the same letter are not significantly different (LSD, $P = 0.05$).
[w] Results of ANOVA were not significant; therefore, an LSD test was not done.
[x] These are measured, not calculated, values; thus, they may not agree with values determined if means are divided (eg, 64.6/15.1 = 4.3 compared to a not measured value of 5.3).
[y] CTBA = crown-taproot basal area (mm²).
[z] DI is disease index: 0 = 0%; 1 = >0 to <2%; 2 = >2 to 20%; 3 = >20 to 50%; and 4 = >50 to 90% rot.

Assessment of disease impact. Mean number of stems and total crown-taproot basal area (CTBA) per 900 cm^2, as determined for each of the four 'Ranger' alfalfa fields of various ages near Milford, were not significantly different (Table 7). Number of crowns per 900 cm^2 decreased from 15.1 in the 2-yr-old field to 2.3 in the 11-yr-old field. The 11-yr-old crowns produced approximately four times as many stems per crown, however, as did the 2-yr-old crowns. CTBA values of 11-yr-old plants differed significantly from those of 2-, 4-, and 7-yr-old plants. DI values ranged from 2.55 in the 2-yr-old field to 3.78 in the 11-yr-old field. The regression lines of DI values vs $\log_{10}$ of age of both the cultivar test plots and the different aged Ranger fields were closely similar (Fig. 2).

DISCUSSION

Initial isolation studies of potential pathogens from necrotic crowns consistently yielded *Fusarium* spp. and bacteria. These results were comparable to those of other researchers (2,5,9,11,18). White, mucoid, Gram-negative bacteria and Gram-negative, fluorescent bacteria were generally present at the leading edge of necrotic zones in crown tissue. In some of our studies, *Fusarium* spp. were either relatively inactive during certain seasons and stages of the disease and were easily masked by other organisms, or they simply were not there. When *F. solani* and other *Fusarium* spp. were inoculated into crowns, these organisms were always recovered. When we combined them with bacteria, however, fusaria were infrequently recovered.

Most *Fusarium* spp. inoculated into alfalfa crowns resulted in significantly higher DI values than were found in the water-inoculated controls. Percent recovery of these organisms from crowns was high, thus confirming pathogenicity. *F. roseum* 'Acuminatum' and *F. solani* have previously been shown to be pathogenic in crowns and roots of alfalfa (8,11). Recovery of *Fusarium* spp. and *Phoma* spp. from water-inoculated crowns and naturally infected crowns indicated the presence of natural inoculum in the soil. The significantly lower DI values of the uninoculated controls suggested the importance of injury to the progress of crown rot.

Our alfalfa bacteria isolates responded identically in characterization studies to the sainfoin isolates which Gaudet et al (6) had reported to be *P. marginalis* var. *alfalfa* and *E. amylovora* var. *alfalfa*. Recently, Lukezic et al (10) demonstrated that *E. amylovora* var. *alfalfa* was better classified as *S. marcescens*. Unlike the situation described for these bacteria in Pennsylvania alfalfa (14), the bacteria we isolated were found to be associated with typically dark, necrotic crowns of plants that exhibited healthy top growth. These same bacteria were able to reproduce the reddish-brown streaking disease symptom commonly observed in the leading edges of dark crown necrosis. Results of pathogenicity tests showed that *P. marginalis* var. *alfalfa*, *S. marcescens*, and *F. solani* were equally capable of inciting disease symptoms. The results of inoculating different combinations of suspected pathogens during pathogenicity tests showed no evidence of synergism.

All alfalfa cultivars examined in Utah, growing under both irrigation or dry-land conditions, exhibited typical symptoms of crown rot. Differences in DI among cultivars were noted for varieties in test plots 2.4 yr old and older. Overall, varietal differences were not significant when a combined analysis of variance of cultivars common to the five locations was performed. However, the location × cultivar interaction was significant. These results implied that no particular cultivar had done well everywhere, but that DI in a particular cultivar depended upon where that cultivar had been grown. In a study of winter injury, survival and vigor of alfalfa, similar results were recorded by Wallen and Jackson (17). Location differences were much larger than those due to variety. Workers in the northeastern USA (9) defined the crown and root rot complex as being a product of an interaction among physical and biological factors. Unique edaphic and climatic factors at each location may be reflected in the differential responses of the cultivars to location. Biological factors such as nematodes, the clover root curculio (*Sitona* spp.), or other pathogens may contribute to the interaction.

Evaluations of stem production in four differently aged stands of cultivar Ranger alfalfa did not identify any significant differences among the stands despite an approximately sevenfold decrease in number of crowns per 900 cm^2 in the 11-yr-old stand as compared to the 2-yr-old stand. Despite a greater percent necrosis in older crowns, plants in the older stand apparently compensated by producing stems in numbers comparable to those counted in younger stands. Increases in DI values strongly correlated with increases in the ages of the stands studied. Trends were similar in both the cultivar test plot study and the study of cultivar Ranger alfalfa fields (Fig. 2).

In conclusion, *Fusarium* spp. and two bacteria appeared to be able to incite the symptoms of crown rot that were observed in the field. These organisms may act together or in succession as the disease progresses from cut stems or other wounds to the crowns. Their actual impact on yield appeared to be insignificant in Utah. At some point, however, the stand thinning observed in our studies must affect yield despite compensation by older crowns. Each successive yearly loss of individuals could lead to a significant decline in stem production, since the loss of a single crown in older fields would have a much greater impact on stem count than it would in younger fields. Further study is necessary, however, to clarify the effects of crown-rot disease organisms on long-term stand vigor and yield.

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