

Factors Affecting Population Trends of Plant-Parasitic Nematodes on Rangeland Grasses¹

G. D. GRIFFIN, K. H. ASAY, AND W. H. HORTON²

Abstract: The effects of environmental conditions on population trends of plant-parasitic nematodes were studied in experimental plots of five wheatgrasses in the western Utah desert. In a 3-year (1984-86) field study, soil water and temperature affected the population trends of the ectoparasites, *Tylenchorhynchus acutoides* and *Xiphinema americanum*, and the migratory endoparasite, *Pratylenchus neglectus*, on Fairway crested wheatgrass, *Agropyron cristatum*; 'Hycrest' crested wheatgrass, *A. cristatum* X *A. desertorum*; 'Rosana' western wheatgrass, *Pascopyrum smithii*; 'Oahe' intermediate wheatgrass, *Thinopyrum intermedium*; and RS-1 hybrid (*Elytrigia repens* X *Pseudoroegneria spicata*). The largest soil populations of these nematode species were collected in 1984 under good plant-growth conditions. A reduction in nematode populations occurred in 1985 and 1986, possibly because of low soil-water conditions. There was a positive relationship between high soil water and maximum population densities of *T. acutoides* in the spring and fall of 1984, and between low soil water and minimum population densities of the nematode in 1985 and 1986. *Pratylenchus neglectus* populations were affected by soil water, although to a lesser degree than the ectoparasitic nematodes. Population densities of the three nematode species were significantly lower in the drier years of 1985 and 1986 than in 1984. Nematode populations were greater at the lower soil depths in the fall than in the spring or summer.

Key words: *Agropyron cristatum*, ecology, *Elytrigia repens* X *Pseudoroegneria spicata*, nematode, *Pascopyrum smithii*, population dynamics, *Pratylenchus neglectus*, *Tylenchorhynchus acutoides*, RS-1 hybrid, soil temperature, soil water, *Thinopyrum intermedium*, wheatgrasses, *Xiphinema americanum*.

There are approximately 153 million ha of rangelands in the Intermountain Region of the western United States. It is estimated that more than 86% of the rangelands are in poor condition, and productivity is less than 60% of their natural potential (24).

Plant-parasitic nematodes are associated with rangeland grasses (3,6,31,32). Several genera, including *Pratylenchus* Filipjev and *Xiphinema* Cobb, reduce the establishment, growth, and productivity of grasses (7,10,14,28). Nematodes extract significant amounts of energy from plants (25,26) and reduce plant resistance to drought, plant stress, and diseases by interfering with plant metabolic activity (7).

Plant-nematode relationships are influenced by genetic and environmental fac-

tors. Genetic differences can be found, for example, in the feeding habits of the different nematode genera. *Meloidogyne* spp., *Heterodera* spp., and *Pratylenchus* spp. produce several generations annually (8,9,13,29), whereas *X. americanum* produces one generation per year (12,15,18,19).

Wheatgrasses are important forage range grasses in western North America, particularly during the spring and early summer (2). Minimal data have been obtained regarding environmental effects on seasonal population densities of individual species of plant-parasitic nematodes on rangeland vegetation (14,20,21,27).

This study was initiated to determine climatic effects on population trends of the ectoparasitic nematodes, *Tylenchorhynchus acutoides* Thorne and Malek and *Xiphinema americanum* Cobb, and the migratory endoparasite, *Pratylenchus neglectus* (Rensch) Filipjev & Schuurmans Stekhoven on five wheatgrasses, and how nematode population densities are affected by soil water and temperature.

MATERIALS AND METHODS

Perennial grasses used in the study were 'Hycrest' crested wheatgrass, *Agropyron*

Received for publication 1 August 1995.

¹ Cooperative investigation by USDA Agricultural Research Service and the Utah Agricultural Experiment Station. Journal Paper No. 4800. Mention of a trademark, proprietary product, or vendor does not constitute a guarantee or warranty of the product by the U.S. Department of Agriculture or Utah State University.

² Nematologist, Plant Geneticist, and Range Scientist, USDA ARS, Forage and Range Research, Utah State University, Logan, UT 84322-6300.

E-mail: Griffin@cc.usu.edu

cristatum (L.) Gaertner X *A. desertorum* Fisch ex. Link; 'Fairway' crested wheatgrass, *A. cristatum*; 'Oahe' intermediate wheatgrass, *Thinopyrum intermedium* (Host) Barkworth & D. R. Dewey; 'Rosana' western wheatgrass, *Pascopyrum smithii* (Rydb.) Löve; and the 'RS-1' hybrid quackgrass, *Elytrigia repens* (L.) Nevski X bluebunch wheatgrass, *Pseudoroegneria spicata* (Pursh) Löve.

The study site was located in the lower foothills of the western desert in northwestern Utah at an elevation of 1,390 m. Average annual precipitation is 30–35 cm, of which approximately 70% falls between October and May. The soil was a Thiokol fine silty loam (mixed mesic Xerollic Calciorthids [19% sand, 65% silt, 16% clay; pH 7.9, OM 3.2%]).

Each cultivar was planted in a plot consisting of 10 drilled rows 30 cm apart and 40 m long. A firm, plant-free seedbed was prepared with a cultipacker, and seeds were planted 1.5–2.0 cm deep and 1.0 cm apart within a row with a modified John Deere Flexiplanter minimum-till drill equipped with double disc openers and depth-band regulators. A 70-kg weight was placed on each timing wheel to improve consistency of seedling depth. Plots were seeded on 26 April 1982. Approximately 6 cm of rain was received within a week after planting, which contributed to excellent seedling establishment. Livestock were not allowed on the site. Soil water and soil temperature was monitored with a Field Unit Recording System (EL824-MS WITH EPRON pack, thermistor probes with soil moisture blocks - Omnidata International, Logan, UT) at a soil depth of 20 cm.

Beginning in 1984, plots were divided into five equal subplots, and soil and root samples were collected monthly from April through October. Fifteen composite soil samples were collected from each subplot with a 9-cm bucket auger at 25-cm intervals from the center of each row at depths of 0–10, 11–20, and 21–30 cm. Auger samples from each cultivar and soil depth were composited and transported to

the laboratory in portable coolers and then refrigerated at 5 C until processed within 10 days. Samples were thoroughly mixed and screened, and root tissue was removed. Four 250-cm³ aliquants from each sample were processed by elutriation (4) and the nematodes concentrated using centrifugal flotation (16). Nematodes from the four aliquants were combined and the number of nematodes per liter of soil determined by microscopic examination.

Because the lesion nematode, *P. neglectus*, is a migratory endoparasite, counts were made in both roots and soil. Root tissues collected from the soil samples were misted with deionized water in 500-ml glass containers at room temperature (24 ± 4 C); liquid was decanted daily, nematodes were counted over a 10-day period, and this number was added to the soil population.

The study was conducted over a 3-year (1984–86) period. Data were subjected to standard analyses of variance. Means were separated on the basis of Duncan's Multiple-Range Test, and nematode population trends were determined.

RESULTS

Rainfall differed from year to year, but there was little yearly deviation in soil temperature (Fig. 1). In 1984, the site received 48 cm of precipitation, of which 23 cm was received between May and October. Annual precipitation in 1985 was 22 cm, with little or no precipitation during the summer months; 6.3 cm was recorded during November and December as rain and snow. Annual precipitation during 1986 was 26 cm, with 9.6 cm of the rain recorded from September to December. Spring and summer soil temperatures were similar during 1984–86.

Pratylenchus neglectus and *T. acutooides* were collected in the greatest numbers from all grass selections in 1984 (Table 1). There was a reduction in *P. neglectus* and *T. acutooides* population densities ($P < 0.05$) and, to a lesser extent, in the *X. americanum* population density between 1984–86. Den-

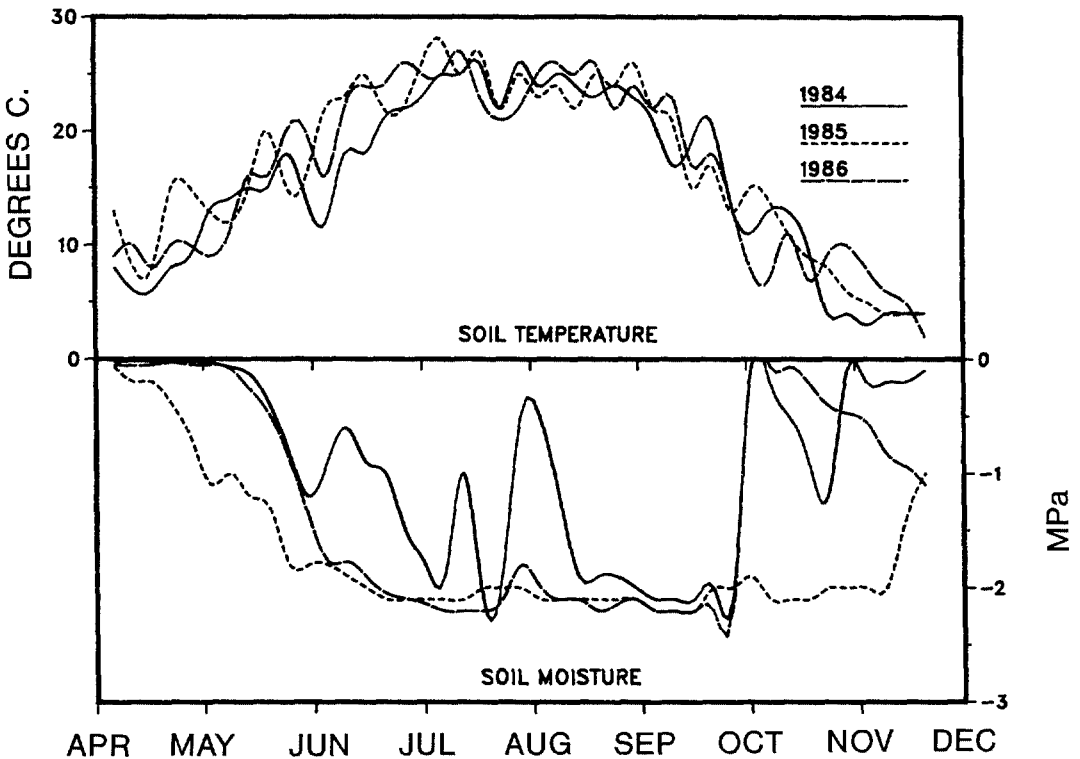


FIG. 1. Soil water (mega pascals 'MPa') and soil temperature (C) monitored with a Field Unit Recording System (EL824-MS with EPRON pack, thermistor probes with soil moisture blocks - Omnidata International, Logan, UT) at a soil depth of 20 cm.

sities of *P. neglectus* and *T. acutoides*, were positively correlated ($r = 0.89$) with soil water. Soil temperature did not affect nematode population density, and there were no differences between soil temperatures ($P > 0.05$) during the three-year study (Fig. 1). Although soil water did not significantly increase, there was a slight increase in the population density of *X. americanum* during the fall of 1985. This was associated with a decrease in soil temperature. Soil population densities of *T. acutoides* were approximately six-fold greater than that of *X. americanum* on all grasses, but population densities were greater in 1984 than in 1985–86 ($P < 0.05$).

In most instances, the greatest nematode population densities were found in the spring and in the fall. This was more noticeable with *P. neglectus* and *T. acutoides* than with *X. americanum*. *Pratylenchus neglectus* was not affected as severely by low soil-water conditions as was *T. acutoides* and

X. americanum, but the mean *P. neglectus* population densities were lower in 1985–86 than in 1984 ($P < 0.05$). The greatest nematode population density of any of the three nematode species was 2,184 *T. acutoides* per liter of soil during June 1984; the greatest numbers of *P. neglectus*, 1,733 and 1,675 per liter of soil, were found on Fairway during April and October of 1984. This corresponded to a maximum of 255 *X. americanum* per liter of soil on Hycrest during May 1984. As observed with *X. americanum* and *T. acutoides*, low population densities of *P. neglectus* were observed during the summer months.

There was no direct relationship between soil depth and nematode population densities of any of the three nematode species on any of the plant species. The numerically highest *X. americanum* population densities were generally found during 1984 at 21–30 cm on Fairway and Hycrest, whereas *T. acutoides* population densities

TABLE 1. Seasonal population means of *Pratylenchus neglectus*, *Tylenchorhynchus acutooides*, and *Xiphinema americanum* on Rosana western wheatgrass, Fairway and Hycrest crested wheatgrass, Oahe intermediate wheatgrass, and the RS-1 wheatgrass hybrid during a 3-year period.

Cultivar	Date	<i>P. neglectus</i>			<i>T. acutooides</i>			<i>X. americanum</i>		
		1984	1985	1986	1984	1985	1986	1984	1985	1986
Rosana	April	1,210 a A	367 a B	138 a B	209 d A	33 bc B	84 b B	1 b B	37 b A	49 a A
	May	661 ab A	313 a B	90 ab B	255 cd A	9 c C	88 b B	33 ab A	32 bc A	5 b A
	June	1,083 a A	63 b B	52 b B	809 a A	149 a B	35 bc B	43 ab A	5 d A	41 a A
	July	387 b A	126 b B	37 b B	453 bc A	136 a B	13 bc C	51 ab A	31 bc A	0 b B
	August	231 b A	15 b B	19 b B	519 b A	59 bc B	0 c B	12 b B	60 a A	8 b B
	September	380 b A	24 b B	22 b B	287 bcd A	52 bc A	16 bc B	8 b A	12 cd A	4 b A
	October	725 ab A	75 b B	34 b B	293 bcd A	69 b B	323 a A	68 a A	23 bcd A	17 b A
	April	1,733 a A	558 ab B	669 a B	224 b A	36 c B	188 b A	19 b B	49 abc B	209 a A
Fairway	May	642 b A	469 a AB	281 bc B	69 b A	96 c A	112 bc A	27 b A	15 c A	0 b A
	June	415 b A	345 bc A	224 bc A	2,184 a A	65 c B	40 cd B	84 b A	20 bc B	43 b AB
	July	505 b A	141 c B	107 bc B	504 b A	528 a A	7 d B	21 b B	52 ab A	0 b B
	August	335 b A	68 c A	306 bc A	273 b A	63 c B	15 d B	16 b B	59 a A	15 b B
	September	582 b A	637 a A	36 c B	88 b A	49 c A	8 d B	252 a A	76 a AB	4 b B
	October	1,675 a A	113 c B	346 b B	245 b B	251 b B	475 a A	13 b B	73 a A	5 b B
	April	362 b A	169 b A	307 ab A	115 b B	13 c C	204 b A	36 bc B	44 b B	247 a A
	May	907 a A	721 a A	420 a A	96 b AB	12 c B	140 bc A	255 a A	56 b B	20 b B
Hycrest	June	367 b A	189 b B	211 bc AB	707 a A	32 c B	111 bc B	100 b A	35 b B	9 b B
	July	316 b A	64 b B	171 cd AB	257 b B	441 a A	25 c C	19 bc B	56 b A	29 b B
	August	199 b A	43 b B	93 cd B	199 b A	149 b A	7 c B	84 bc B	209 a A	13 b C
	September	282 b A	287 b A	37 d B	60 b B	141 b A	9 c C	1 c B	67 b A	11 b B
	October	980 a A	43 b B	101 cd B	156 b B	56 c B	535 a A	255 a A	37 b B	11 b B
	April	315 b A	448 a A	71 a B	172 a A	35 cd B	63 bc B	13 b A	37 cd A	37 b A
	May	632 a A	272 b B	53 ab C	415 cd A	4 d B	111 b B	161 a A	36 cd B	203 a A
	June	196 bc A	116 cd A	15 c B	636 bcd A	63 bc B	35 c B	23 b B	1 d B	65 b A
Oahe	July	95 c B	219 bc A	16 c B	269 d A	288 a A	3 c B	33 b A	121 ab A	25 b A
	August	76 c A	30 d B	34 bc D	409 cd A	104 b B	9 c B	11 b B	163 a A	15 b B
	September	141 bc A	26 d B	60 ab B	707 bc A	53 bcd B	9 c B	104 a A	31 cd B	13 b B
	October	164 bc A	98 cd B	31 bc C	849 ab A	104 b B	225 a B	117 a A	81 bc A	8 b B
	April	967 ab A	742 a A	700 a A	743 c A	8 c B	172 b B	4 c B	21 c B	293 a A
	May	1,090 a A	709 a AB	270 bc B	325 c A	9 c B	84 bc B	1 c B	33 bc B	160 b A
	June	628 abc A	359 b B	130 c B	2,016 a A	40 c B	65 bc B	88 ab A	9 c B	1 c B
	July	725 abc A	187 bc B	352 abc AB	297 c A	383 a A	21 c B	32 bc A	32 bc A	16 c A
RS-1	August	332 c AB	41 c B	605 ab A	1,443 b A	112 b B	15 c B	19 bc B	124 a A	20 c B
	September	484 bc A	60 c B	111 c B	315 c A	105 b AB	12 c B	136 a A	124 a A	8 c A
	October	867 ab A	180 bc B	152 c B	407 c A	113 b B	459 a A	0 c B	91 ab A	3 c B

Values are the means of nematodes collected from 0–30 cm soil depth from four plots each consisting of five subplots ($n = 20$). Samples were collected monthly with a 9-cm bucket auger at 25-cm intervals from the center of each row. Nematode populations were determined from roots and soil of four 250-cm³ aliquants from each sample. Means in columns not followed by a common lowercase letter are different ($P < 0.05$). Means in rows not followed by a common uppercase letter are different ($P < 0.05$).

were higher in the 0–10 cm of soil ($P < 0.05$) (Table 2). The greatest *P. neglectus* and *X. americanum* population densities were found on Fairway and Hycrest at a soil depth of 21–30 cm during 1984, whereas the greatest *T. acutooides* population densities were found on RS-1 at 0–10 cm during 1984. The smallest density of all nematodes was found on Rosana at 21–30 cm during 1986.

DISCUSSION

Few data have been generated on the root phenology of grasses. Caldwell et al. (5) found that root biomass of *A. desertorum*, one of the parents of Hycrest, increased during the spring and fall. Thorgeirsson (30) reported that *A. desertorum* extracted soil water during the early spring, indicator that roots had initiated growth, and that *A. desertorum* initiated adventitious roots in early spring and fall when soil water was more optimal or abundant. There is a direct relationship between root growth and nematode population densities (7). Hence, the increased nematode density observed in this study could be associated with increased root growth resulting from adequate soil water since nematodes were collected in the greatest numbers from all grass selections during the spring of 1984, when supposedly adequate soil water would favor plant growth. Since there is a lack of data on root phenology, we can only speculate that differences among the three nematode species in relation to maximum population densities may be due to differences in plant root growth, host preference, and nematode fecundity. The low reproductive potential of *X. americanum* may account for the low population densities. Previous studies have shown that *X. americanum* produces only one generation per year on alfalfa, *Medicago sativa* L.; spruce, *Picea pungens* L.; and peach, *Prunus persica* (L.) Batsch; population density peaks usually occurred during the spring or fall (12, 15, 19). The lack of soil water may have delayed the 1985 spring egg hatching,

which would lead to a *X. americanum* population density peak during the late summer and early fall. Previous studies have shown that *X. americanum* population densities decline at high soil temperatures and low soil water (11, 17). Lownsbery and Maggenti (17) reported that the optimum temperature for *X. americanum* was 21 C, and the nematode population density declined at 27 C. Summer temperatures at the Thiokol study site exceeded 21 C from June to September and approached 30 C during July and August. While *X. americanum* cannot survive high soil temperatures, it can survive winter months at low temperatures (12). A possible carryover of the nematode population density from 1985, plus the normal hatch in the following spring, may explain the higher population density levels in April 1986.

Tylenchorhynchus acutooides may not be as sensitive to soil water, soil temperature, and oxygen as has been reported for *X. americanum* (17, 23, 33). The optimum temperature range of *T. acutooides* also may exceed that of *X. americanum*. The fecundity of the nematodes also is apparently different since there was a six-fold greater population density of *T. acutooides* than *X. americanum*. Although there have been no data generated on the biology and fecundity of *T. acutooides*, it appears from its large population density that it may have at least two life cycles per year. Hence, *T. acutooides* could be an important pathogen of rangeland vegetation.

Soil temperature may have less effect on population densities of *P. neglectus* than on the ectoparasitic nematodes. Although reproduction of *P. neglectus* on wheatgrass is greatest at 30 C (9), there was less fluctuation in the nematode population density than with the ectoparasitic nematodes. This is possibly due to the nematode being less affected by environmental conditions since it inhabits both roots and soil. Differences in nematode counts among cultivars at the three soil depths may also be associated with variation in plant phenology and depth of root growth. Soil-depth differences in numbers between the nematode

TABLE 2. Population means of *Pratylenchus neglectus*, *Tylenchorhynchus acutoides*, and *Xiphinema americanum* on Rosana western wheatgrass, Fairway and Hycrest crested wheatgrass, Oahe, intermediate wheatgrass, and the RS-1 hybrid wheatgrass at three soil depths during a 3-year period.

Cultivar	Depth (cm)	<i>P. neglectus</i>			<i>T. acutoides</i>			<i>X. americanum</i>		
		1984	1985	1986	1984	1985	1986	1984	1985	1986
Nematodes per liter										
Rosana	0-10	555 a A	170 a B	92 a B	807 a A	125 a B	148 a B	34 a A	46 a A	24 a A
	11-20	869 a A	142 a B	41 b B	217 b A	42 b B	60 b B	24 a A	21 b A	17 a A
	21-30	580 a A	110 a B	34 b B	187 b A	50 b B	31 b B	35 a A	19 b B	13 a B
Fairway	0-10	347 b A	289 a AB	228 a B	837 a A	206 a B	177 a B	35 a A	53 ab A	52 a A
	11-20	994 a A	347 a B	305 a B	366 b A	147 ab B	96 b B	48 a A	60 a A	36 a A
	21-30	1,183 a A	363 a B	311 a B	335 b A	113 b B	89 b B	102 a A	34 b B	30 a B
Hycrest	0-10	435 a A	305 a AB	171 a B	503 a A	167 a B	255 a B	51 b A	105 a B	66 a A
	11-20	589 a A	190 a B	221 a B	375 a A	94 b B	133 b B	117 a A	57 b B	46 ab B
	21-30	439 a A	154 a B	182 a B	231 a A	102 b B	62 b B	153 a A	54 b B	34 b B
Oahe	0-10	270 a A	161 a AB	51 a B	1,482 a A	150 a B	114 a B	45 a A	60 a A	59 a A
	11-20	299 a A	189 a AB	30 a B	282 b A	70 b B	57 b B	77 a A	70 a B	52 a A
	21-30	125 b A	168 a A	39 a B	146 b A	59 b B	23 b B	77 a A	71 a A	46 a A
RS-1	0-10	521 b A	369 a B	356 a B	1,678 a A	203 a B	201 a B	30 a A	74 a A	33 a A
	11-20	1,121 a A	316 a B	343 a B	423 b A	65 b B	90 b B	45 a A	66 a A	82 a A
	21-30	541 b A	290 a B	295 a B	275 b A	63 b B	63 b B	45 a A	46 a A	101 a A

Values are the means of yearly collections over a 7-month period (April–October). Samples were collected from four plots, each consisting of five subplots. Samples were collected monthly with a 9-cm bucket auger at 25-cm intervals from the center of each row at depths of 0–10, 11–20, and 21–30 cm. Nematode populations were determined from roots and soil of four 250-cm³ aliquants from each sample. Means in columns not followed by a common lowercase letter are different ($P < 0.05$). Means in rows not followed by a common uppercase letter are different ($P < 0.05$).

species may indicate a greater sensitivity of *X. americanum* to the increased soil temperature in the upper soil levels. Nematodes have been found to migrate a distance of more than 1 m (22). Since *X. americanum* population densities decline when summer temperatures are high (17), the nematode might have migrated to the 41–60-cm depth to a more moderate soil temperature. Since nematodes move through a film of moisture, lack of soil water could have inhibited downward movement of the nematode during 1985 and 1986, thus leading to higher numbers of *X. americanum* in the 0–10 cm soil level. *Pratylenchus neglectus* population densities were not consistently associated with particular soil depths, since the nematodes are found where root tissue is most dense (7).

The pathogenicity of *X. americanum*, *P. neglectus*, and *T. acutus* to certain plant species, including wheatgrasses, has been documented (7,9,10). The large numbers of *T. acutoides* found on wheatgrasses suggest that these grasses are good hosts for the nematode. In this study, differences in preference of nematodes on Hycrest and Fairway crested wheatgrass, Oahe intermediate wheatgrass, Rosana western wheatgrass, and RS-1 hybrid, and environmental effects on nematode population trends were observed. A better understanding of climatic effects on nematode population densities is needed. Once data on nematode population plant-growth relationships are generated and understood, they can be utilized to determine nematode species that are the most important parasites to rangeland grasses and plant breeders in development of resistant or tolerant grasses (1).

LITERATURE CITED

- Adkisson, P. L., and V. A. Dyck. 1980. Resistant varieties in pest management systems. Pp. 233–251 in F. G. Maxwell and P. R. Jennings, eds. Breeding plant resistance to insects. New York: John Wiley.
- Asay, K. H., and R. P. Knowles. 1985. The wheatgrasses. Pp. 166–176 in M. E. Heath, R. F. Barnes, and D. S. Metcalfe, eds. Forages, the science of grassland agriculture. Ames: Iowa State University Press.
- Barker, R. E., J. D. Berdahl, J. M. Krupinsky, and E. T. Jacobson. 1981. Collections of western wheatgrass and blue grama associated nematode genera in the western Dakotas. Pp. 237–240 in Proceedings of the XIV International Grassland Congress, Lexington, KY.
- Byrd, D. W., Jr., K. R. Barker, H. Ferris, C. J. Nusbaum, W. E. Griffin, R. H. Small, and Connie A. Stone. 1976. Two semi-automatic elutriators for extracting nematodes and certain fungi from soil. *Journal of Nematology* 8:206–212.
- Caldwell, M. M., J. H. Richards, D. A. Johnson, R. S. Nowak, and R. S. Dzurec. 1981. Coping with herbivory: Photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* 50:14–24.
- Freckman, D. W., D. A. Duncan, and J. R. Larson. 1979. Nematode density and biomass in an annual grassland ecosystem. *Journal of Range Management* 32:418–422.
- Griffin, G. D. 1984. Nematode parasites of alfalfa, cereals, and grasses. Pp. 243–321 in W. R. Nickle, ed. Plant and insect nematodes. New York: Marcel Dekker.
- Griffin, G. D. 1988. Factors affecting the biology and pathogenicity of *Heterodera schachtii* on sugarbeet. *Journal of Nematology* 20:396–404.
- Griffin, G. D. 1992. Pathological effects of *Pratylenchus neglectus* to wheatgrasses. *Journal of Nematology* 24:442–449.
- Griffin, G. D., and K. H. Asay. 1992. Importance of soil texture on the pathogenicity of plant-parasitic nematodes to range grasses. *Phytopathology* 82:1096. (Abstr.).
- Griffin, G. D., and K. R. Barker. 1966. Effect of soil temperature and moisture on the survival and activity of *Xiphinema americanum*. *Proceedings Helminthological Society of Washington* 33:126–130.
- Griffin, G. D., and H. M. Darling. 1964. An ecological study of *Xiphinema americanum* Cobb in an ornamental spruce nursery. *Nematologica* 10:471–479.
- Griffin, G. D., and F. A. Gray. 1990. Biology and pathogenicity of *Pratylenchus neglectus* on alfalfa. *Journal of Nematology* 22:546–551.
- Ingham, R. E., and J. K. Detling. 1984. Plant-herbivore interactions in a North American mixed-grass prairie. III. Soil nematode populations and root biomass on *Cynomys ludovicianus* colonies and adjacent uncolonized areas. *Oecologia* 63:307–313.
- Jaffee, B. A., M. B. Harrison, R. L. Shaffer, and M. B. Strang. 1987. Seasonal population fluctuations of *Xiphinema americanum* in New York and Pennsylvania orchards. *Journal of Nematology* 19:369–378.
- Jenkins, W. R. 1964. A rapid centrifugal-flotation technique for separating nematodes from soil. *Plant Disease Reporter* 48:692.
- Lownsbey, B. F., and A. R. Maggenti. 1963. Some effects of soil temperature and soil moisture on population levels of *Xiphinema americanum*. *Phytopathology* 53:667–668.

18. Malik, Z., and M. S. Jairajpuri. 1983. Population dynamics and life cycle of *Xiphinema americanum* Cobb, 1913. *Indian Journal of Parasitology* 7:21-28.
19. Norton, D. C. 1963. Population fluctuations of *Xiphinema americanum* in Iowa. *Phytopathology* 53:66-68.
20. Norton, D. C., and D. P. Schmitt. 1978. Community analysis of plant-parasitic nematodes in the Kalsow Prairie, Iowa. *Journal of Nematology* 10:171-176.
21. Orr, C. C., and O. J. Dickerson. 1967. Nematodes in true prairie soils of Kansas. *Transactions Kansas Academy of Science* 69:317-334.
22. Pinkerton, J. N., and G. S. Santo. 1986. Control of *Meloidogyne chitwoodi* in commercially grown Russet Burbank potatoes. *Plant Disease* 70:860-863.
23. Ponchillia, P. E. 1972. *Xiphinema americanum* as affected by soil organic matter and porosity. *Journal of Nematology* 4:189-193.
24. Schmautz, J. E., M. D. Belinger, and R. W. Harris. 1980. Range. Pp. 246-315 in *An assessment of the forest and range land situation in the United States*. USDA-Forest Service. FS-345. Washington, D.C.: United States Government Printing Office.
25. Scott, J. A., N. R. French, and J. W. Leetham. 1979. Patterns of consumption in grasslands. Pp. 89-105 in N. R. French, ed. *Perspectives in grassland ecology*. New York: Springer-Verlag.
26. Smolik, J. D. 1974. Nematode studies at the cottonwood site. US/IBP Grassland Biome Technical Report No. 251. Boulder: Colorado State University.
27. Smolik, J. D., and J. K. Lewis. 1982. Effect of range condition on density and biomass of nematodes in a mixed prairie ecosystem. *Journal of Range Management* 35:657-663.
28. Smolik, J. D., and L. E. Rogers. 1976. Effects of cattle grazing and wildfire on soil-dwelling nematodes of the shrub-steppe ecosystem. *Journal of Range Management* 29:304-306.
29. Taylor, A. L., and J. N. Sasser. 1978. *Biology, identification, and control of root-knot nematodes (Meloidogyne species)*. Raleigh: North Carolina State University Graphics.
30. Thorgeirsson, H. 1985. Temporal and spatial partitioning of the soil water resource between two *Agropyron* bunchgrasses and *Artemisia tridentata*. M.S. thesis, Utah State University, Logan.
31. Thorne, G. 1974. Nematodes of the northern great plains. Part II. Dorylaimoidea in part (Nemata: Adenophorea). Technical Bulletin No. 41. South Dakota Agricultural Experiment Station, Brookings.
32. Thorne, G., and R. B. Malek. 1968. Nematodes of the northern great plains. Part I. Tylenchida (Nemata: Secernentea). Technical Bulletin No. 31. South Dakota Agricultural Experiment Station, Brookings.
33. Van Gundy, S. D., L. H. Stolzy, T. E. Szuszkiewicz, and R. L. Rackham. 1962. Influence of oxygen supply on survival of plant-parasitic nematodes in soil. *Phytopathology* 52:628-632.