

## BIOLOGY AND PATHOGENICITY OF THREE ECTOPARASITIC NEMATODE SPECIES ON CRESTED WHEATGRASSES<sup>†</sup>

G. D. Griffin and K. H. Asay

USDA ARS, Forage and Range Research Laboratory, Utah State University, Logan, UT 84322-6300, U.S.A.

---

### ABSTRACT

Griffin, G. D., and K. H. Asay. 1996. Biology and pathogenicity of three ectoparasitic nematode species on crested wheatgrasses. *Nematopica* 26:15-25.

Greenhouse and growth chamber studies were conducted to determine the pathological relationship of ectoparasitic nematodes on crested wheatgrass (*Agropyron cristatum* and *A. desertorum*) cultivars. Crested wheatgrass cultivars, 'Hycrest', 'Fairway', and 'Nordan', were parasitized by *Merlinius brevidens*, *Tylenchorhynchus acutus*, and *Xiphinema americanum* under greenhouse conditions. *Merlinius brevidens* and *T. acutus* were more pathogenic than *X. americanum* on all grasses. Dry shoot weights of Fairway and Nordan were reduced ( $P \leq 0.05$ ) at Pi of 1.0 and 2.0 nematodes/cm<sup>3</sup> soil, whereas shoot growth of Hycrest was reduced only at 2.0 nematodes/cm<sup>3</sup> soil. Root growth of all cultivars was reduced by the 3 nematode species at both levels of inoculum with the greatest reductions at 2.0 nematodes/cm<sup>3</sup> soil. The nematode reproductive factors (Rf = final nematode population/initial nematode population) were similar for *M. brevidens* and *T. acutus*, whereas the *X. americanum* population did not reproduce on any cultivar. Fairway and Nordan were better hosts to *M. brevidens* and *T. acutus* than was Hycrest. Temperature affected the nematode-grass relationship. The greatest reductions in both shoot and root growth and greatest nematode reproduction occurred at 20 and 25°C. *Xiphinema americanum* did not reproduce on any cultivar at any temperature.

*Key words:* *Agropyron cristatum*, *A. desertorum*, Fairway, Hycrest, *Merlinius brevidens*, Nordan, *Tylenchorhynchus acutus*, reproduction, susceptible, temperature, tolerant, wheatgrass, *Xiphinema americanum*.

---

### RESUMEN

Griffin, G. D. y K. H. Asay. 1996. Biología y patogenicidad de tres especies de nematodos ectoparasitos de la maleza *Agropyron cristatum*. *Nematrópica* 26:15-25.

Estudios realizados en invernadero y cámaras de crecimiento para determinar la patogenicidad de los nematodos ectoparasitos *Merlinius brevidens*, *Tylenchorhynchus acutus* y *Xiphinema americanum* en variedades de las malezas *Agropyron cristatum* y *A. desertorum*, dieron los siguientes resultados: *M. brevidens* y *T. acutus* fueron mas patogénicos que *X. americanum* en todas las malezas ensayadas. El peso seco de la parte aérea en las variedades "Fairway" y "Nordan" se redujo ( $P \leq 0.05$ ) cuando el Pi fue de 1.0 y 2.0 nematodos/cm<sup>3</sup> de suelo. El crecimiento radical se redujo en todas las plantas inoculadas con cualquiera de las tres especies de nematodos, a ambos niveles de inoculación, siendo las mayores reducciones al nivel de 2.0 nematodos/cm<sup>3</sup> de suelo. La tasa reproductiva del nematodo (Rf = población final/población inicial) fue similar en *M. brevidens* y *T. acutus*; mientras que la población de *X. americanum* no se reprodujo en ningún cultivo. Las variedades "Fairway" y "Nordan" resultaron mejores hospedantes para *M. brevidens* y *T. acutus* que la "Hycrest". La temperatura afectó la relación nematodo-maleza. Las mayores disminuciones de el crecimiento de la planta (follaje y raíz), así como la

---

<sup>†</sup>Cooperative investigation by USDA ARS and the Utah Agricultural Experiment Station. Journal Paper No. 4681. 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.

mayor tasa reproductiva ocurrió a 20 y 25°C. *X. americanum* no se reprodujo en ninguna variedad bajo ninguna de las temperaturas ensayadas.

*Palabras clave:* *Agropyron cristatum*, *A. desertorum*, "Fairway", "Hycrest", *Merlinius brevidens*, "Nordan", *Tylenchorhynchus acutus*, reproducción, susceptible, temperatura, tolerante, "whetgrass", *Xiphinema americanum*.

---

## INTRODUCTION

Of approximately 153 million ha of rangelands in the Intermountain Region of the western United States, nearly 86% are considered in less than good condition and are currently producing only 60% of their natural potential (Schmauty *et al.*, 1980). Some species of plant-parasitic nematodes in rangeland soils reduce the establishment, growth, and productivity of rangeland grasses (Freckman *et al.*, 1979; Griffin, 1984, 1992; Norton and Schmitt, 1978; Orr and Dickerson, 1967; Thorne, 1974; Thorne and Malek, 1968). Nematodes extract energy needed for plant growth (Smolik, 1974) and can reduce the resistance of plants to stress including drought and diseases (Griffin, 1984). The plant-nematode relationship is influenced by biological differences in the reproductive potential of the nematode on the plant and environmental factors that affect the biological activity of the nematode and growth of plant tissue. Nematodes such as *Meloidogyne* spp. and *Heterodera* spp. may produce several generations per year (Griffin, 1985, 1988), whereas *Xiphinema americanum* Cobb produces only one generation per year (Griffin and Darling, 1964; Malek, 1969; Norton, 1963). These differences in reproductive potential and nematode reactions to climatic and edaphic conditions may affect population trends and pathogenicity (Griffin, 1996).

Wheatgrasses are important forage grasses in western North America, especially during the spring and early summer (Asay and Knowles, 1985; Asay *et al.*, 1985).

However, information is lacking on the relationships between many plant-parasitic nematodes commonly associated with rangeland vegetation and the growth and persistence of crested wheatgrass in the western United States. We conducted studies in the greenhouse and growth chamber to determine if 3 native ectoparasitic nematodes, *Merlinius brevidens* (Allen) Siddiqi, *Tylenchorhynchus acutus* Allen, and *X. americanum*, parasitize and reproduce on *Agropyron* crested wheatgrass species and how temperature affected nematode parasitism.

## MATERIALS AND METHODS

*Nematode inocula:* Due to the difficulty in culturing ectoparasitic nematodes, inocula used in greenhouse studies were extracted from a western wheatgrass planting in northern Utah with elutriation (Byrd *et al.*, 1976) and sugar flotation (Jenkins, 1964). Nematode species were extracted from the washings with a micropipette, surface sterilized with solutions of streptomycin and gentamycin aretan and rinsed several times with distilled water (Griffin, 1992). The inoculum was 98-100% pure and free from any other plant-parasitic nematode.

*Greenhouse experiment:* Seedlings (3-6 mm radicle) of crested wheatgrass cultivars Fairway (*Agropyron cristatum* (L.) Gaertner), Nordan (*A. desertorum* Fisch. ex. Link, Schult) or Hycrest (*A. cristatum* × *A. desertorum*) were planted into individual 6-cm-diam plastic pots containing 540 cm<sup>3</sup> steam sterilized Kidman fine sandy loam soil [coarse-loamy mixed mesic Calcic

Haploxeroll (84% sand, 8% silt, 8% clay; pH 7.4, 1.0% OM)]. After 34 days, plants were inoculated with mixed stages of either *M. brevidens*, *T. acutus*, or *X. americanum* at initial nematode populations (Pi) of 0, 1, or 2 per cm<sup>3</sup> soil. A preliminary study showed Pi of 1.0-2.0 are maximum levels of the 3 nematode species encountered under western rangelands. Nematodes in an aqueous suspension of deionized water were poured into holes at a soil depth of 3 cm around the hypocotyl. Control plants were inoculated with filtrate from nematode extraction. Containers were maintained in a muslin-shaded greenhouse at an ambient temperature of 26 ± 3°C.

The experiment was arranged as a 3 × 3 × 3 factorial (3 nematode species, 3 plant species and 3 inoculum densities) in a randomized complete block design with 10 replications. Supplemental light for a 19-hr daylength was provided by high-output fluorescent lamps. A shading canopy was introduced immediately above the plants after inoculation to reduce evaporation, and plants received their first irrigation 3 days after inoculation to minimize irrigating inocula away from plant roots. The canopy was removed 14 days after inoculation. Thereafter, plants were carefully watered daily to avoid runoff. Plants were fertilized monthly with a general purpose N-P-K fertilizer (20-20-20). Shoots were clipped at 60, 120, and 180 days after inoculation to a cutting height of 10 cm. The experiment was terminated 180 days after inoculation and plant persistence, cumulative shoot weights, root weights, and the nematode reproductive factor (Rf = final nematode population divided by initial nematode population) were determined. Nematodes were extracted from the soil by elutriation (Byrd *et al.*, 1976) and sugar flotation (Jenkins, 1964). Data were analyzed using standard analysis of

variance procedures and regression analysis. Means were separated by Duncan's new multiple range test. Plant survival data were arcsine transformed.

*Growth chamber experiment:* A study similar to the greenhouse bench experiment was conducted in temperature-controlled growth chambers except plants were inoculated 28 days after planting with Pi of 0, 1.0, or 2.0 nematodes/cm<sup>3</sup> soil. Temperatures were maintained at 15, 20, 25, or 30°C (±1°C) and a 19-hr daylength was provided by high-output fluorescent lamps. The experiment was arranged as a 4 × 3 × 3 × 3 factorial (4 temperatures, 3 nematode species, 3 cultivars, and 3 inoculum densities) in a randomized complete block design with 5 replications. The experiment was terminated 120 days after inoculation and plant persistence, cumulative shoot weights, root weights, and the nematode Rf were determined. Data were recovered and analyzed as described previously.

## RESULTS AND DISCUSSION

*Greenhouse bench experiment:* The growth of Hycrest crested wheatgrass was reduced only at Pi 2.0 nematode/cm<sup>3</sup> soil, whereas shoot growth of Fairway and Nordan were reduced (P ≤ 0.05) at both 1.0 and 2.0 nematodes/cm<sup>3</sup> soil (Table 1). Average shoot weights of Nordan, which was the most susceptible of the 3 grasses, were reduced 34, 31, and 23% by *M. brevidens*, *T. acutus*, and *X. americanum*, respectively at Pi of 2.0 nematodes/cm<sup>3</sup> soil. Comparable reductions were 27, 28, and 21% for Fairway, and 23, 19, and 11% for Hycrest by *M. brevidens*, *T. acutus*, and *X. americanum*. Reductions in root growth paralleled the reductions in dry shoot weights. Root growth reductions ranged from 16% for Hycrest at Pi of 1.0 *X. americanum* to 58% for Nordan at Pi of 2.0 *M. brevidens*/cm<sup>3</sup> soil. Shoot and root growth decreased linearly to increases in Pi (Tables 2, 3).

Table 1. Nematode reproductive factors and effects of 3 ectoparasitic nematodes on shoot and root weights of 3 crested wheatgrasses 180 days after inoculation at a greenhouse temperature maintained at  $26 \pm 3^\circ\text{C}$ .<sup>v</sup>

Nematode species	Inoculum density (no./cm <sup>3</sup> soil)	Wheatgrass cultivar		
		Hycrest	Fairway	Nordan
		Dry shoot weight (g) <sup>w,x</sup>		
<i>M. brevidens</i>	1	1.67 abA	1.42 bB	1.25 bC
	2	1.37 cA	1.11 dB	0.99 cB
<i>T. acutus</i>	1	1.71 aA	1.39 bB	1.25 bB
	2	1.44 cA	1.10 dB	1.03 cB
<i>X. americanum</i>	1	1.73 aA	1.39 bB	1.29 bB
	2	1.58 bA	1.20 cB	1.16 cC
Uninoculated Control	—	1.77 aA	1.52 aB	1.50 aB
		Dry root weight (g) <sup>y</sup>		
<i>M. brevidens</i>	1	0.79 bA	0.72 bA	0.58 cB
	2	0.62 dA	0.43 cB	0.35 dB
<i>T. acutus</i>	1	0.78 bA	0.72 bA	0.61 cB
	2	0.59 dA	0.47 cB	0.41 dB
<i>X. americanum</i>	1	0.81 bA	0.67 bB	0.70 bB
	2	0.69 cA	0.49 cB	0.51 cB
Uninoculated Control	—	0.94 aA	0.91 aA	0.83 aA
		Reproductive factor (Pf/Pi ratio) <sup>z</sup>		
<i>M. brevidens</i>	1	2.9 aA	3.5 aA	3.4 aA
	2	1.8 bA	2.3 bA	2.1 bA
<i>T. acutus</i>	1	2.4 aA	3.3 aA	3.3 aA
	2	1.4 bA	2.3 bA	2.2 bA
<i>X. americanum</i>	1	0.7 cA	0.7 cA	0.8 cA
	2	0.4 cA	0.5 cA	0.8 cA

<sup>v</sup>Plants were inoculated at 34 days growth with Pi 0, 1, or 2 nematodes/cm<sup>3</sup> soil.

<sup>w</sup>Values are the means of 10 replicates (1 plant/replicate). Cultivar means for shoot dry weight or root dry weight within nematode-density combination followed by same letter are not significantly different ( $P \leq 0.05$ ) according to Duncan's new multiple range test. Lower case letters refer to columns, capital letters refer to rows.

<sup>x</sup>Cumulative total weight of shoots clipped at 60, 120, and 180 days after inoculation.

<sup>y</sup>Root weight determined after 180 days.

<sup>z</sup>Pf/Pi ratio = final nematode population/initial nematode population determined after 180 days.

Table 2. Regression models for effects of nematodes on shoot weight of crested wheatgrass across inoculum densities of 0, 1, and 2 nematodes/cm<sup>3</sup> soil.<sup>v,z</sup>

Cultivar	Intercept	r <sup>2</sup>	P
<i>Mertinius brevidens</i>			
Hycrest	1.88	0.61	**
Fairway	1.58	0.42	**
Nordan	1.65	0.51	**
<i>Tylenchorhynchus acutus</i>			
Hycrest	1.93	0.53	**
Fairway	1.55	0.42	**
Nordan	1.50	0.47	**
<i>Xiphinema americanum</i>			
Hycrest	1.89	0.39	**
Fairway	1.54	0.33	**
Nordan	1.51	0.45	**
Combined			
Hycrest	1.94	0.55	**
Fairway	1.59	0.43	**
Nordan	1.50	0.48	**

<sup>v</sup>Plants were inoculated after 34 days growth and grown for 180 days.

<sup>z</sup>Values are the means of 10 replicates (1 plant/replicate).

Nematode recovery was similar on all 3 cultivars, and Rf were similar for like inoculum densities of *M. brevidens* and *T. acutus*. *Xiphinema americanum* populations failed to increase (Rf < 1) on any cultivar (Table 1). At Pi 1.0, the reproductive factor ranged from 0.7 for *X. americanum* on Hycrest to 3.5 for *M. brevidens* on Fairway. At Pi of 2.0, Rf ranged from 0.4 for *X. americanum* on Hycrest to 2.5 for *M. brevidens* on Fairway. Final nematode densities varied with root weights; densities were greatest ( $P \leq 0.05$ ) on Fairway and Nordan with *M. brevidens* and *T. acutus* (Table 4). Nematode reproduction was less on Hycrest, and Rf was less ( $P \leq 0.05$ ) on Hycrest across all nematode populations.

*Growth chamber experiment:* Temperature significantly affected the nematode-grass relationships. The greatest reduction in shoot growth occurred at 20-25°C (Fig. 1). As observed in the greenhouse experiment, Hycrest was more tolerant to the 3 nematodes than were Fairway and Nordan, and *X. americanum* was the least pathogenic of the 3 nematode species. The reduction in dry shoot weights of Fairway at Pi of 2.0 nematodes/cm<sup>3</sup> soil were 28, 34, 37, and 17% by *M. brevidens*, 23, 31, 33, and 13% by *T. acutus*, and 14, 26, 28, and 13% by *X. americanum* at 15, 20, 25, and 30°C, respectively. Shoot weight reductions for Nordan at similar temperatures were 29, 41, 43, and 19% by *M. brevidens*, 27, 30, 40, and

Table 3. Regression models for effects of nematodes on root weight of crested wheatgrass across inoculum densities of 0, 1, and 2 nematodes/cm<sup>3</sup> soil.<sup>v,z</sup>

Cultivar	Intercept	r <sup>2</sup>	P
<i>Merlinius brevidens</i>			
Hycrest	0.95	0.52	**
Fairway	0.93	0.48	**
Nordan	0.83	0.48	**
<i>Tylenchorhynchus acutus</i>			
Hycrest	0.94	0.36	**
Fairway	0.92	0.44	**
Nordan	0.86	0.42	**
<i>Xiphinema americanum</i>			
Hycrest	0.95	0.45	**
Fairway	0.90	0.32	**
Nordan	0.81	0.33	**
Combined			
Hycrest	0.95	0.41	**
Fairway	0.92	0.45	**
Nordan	0.83	0.41	**

<sup>v</sup>Plants were inoculated after 34 days growth and grown for 180 days.

<sup>z</sup>Values are the means of 10 replicates (1 plant/replicate).

19% by *T. acutus*, and 17, 30, 31, and 13% by *X. americanum*, respectively. Reductions in dry shoot weight of Hycrest at Pi of 2.0 nematodes/cm<sup>3</sup> soil at the same temperatures were 9, 16, 22, and 11% by *M. brevidens*, 9, 17, 22, and 11% by *T. acutus*, and 4, 6, 15, and 10% by *X. americanum*.

Temperature had a similar effect on root growth. The reduction in root growth was particularly evident in Fairway and Nordan and at 20-30°C (Fig. 2). Dry root weight reductions by *M. brevidens* at 2.0 nematodes/cm<sup>3</sup> soil were 29, 41, 46, and 42% for Fairway, 41, 46, 51, and 49% for Nordan, and 23, 40, 39, and 36% for Hycrest at 15, 20, 25, and 30°C, respectively. Dry root

weight reductions by *T. acutus* at 2.0 nematodes/cm<sup>3</sup> soil were 28, 42, 45, and 37% for Fairway, 31, 46, 44, and 44% for Nordan, and 22, 34, 38, and 30% for Hycrest at 15, 20, 25, and 30°C, respectively. Dry root weight reductions by *X. americanum* at 2.0 nematodes/cm<sup>3</sup> soil were 33, 37, 41 and 34% for Fairway, 29, 31, 41, and 38% for Nordan, and 25, 35, 35, and 31% for Hycrest at 15, 20, 25, and 30°C, respectively.

Little or no nematode reproduction occurred on any grass at 15°C, whereas reproduction was greatest at 25°C (Fig. 3). The relationship between nematode reproduction and root growth also was similar to that obtained in the greenhouse.

Table 4. Nematodes per g of root tissue of 3 crested wheatgrasses 180 days after inoculation at a greenhouse temperature of  $26 \pm 3^\circ\text{C}$ .<sup>y</sup>

Nematode species	Inoculum density (nemas/cm <sup>3</sup> soil)	Wheatgrass cultivar		
		Hycrest	Fairway	Nordan
<i>M. brevidens</i>	1	3.7 aA <sup>z</sup>	4.9 aB	5.9 aB
	2	2.9 bA	5.4 aB	6.0 aB
<i>T. acutus</i>	1	3.1 bA	4.6 aB	5.4 aB
	2	2.4 bA	4.9 aB	5.4 aB
<i>X. americanum</i>	1	0.9 cA	1.0 bA	1.1 bA
	2	0.6 cA	1.0 bA	1.6 bA

<sup>y</sup>Plants were inoculated after 34 days growth. Values are the means of 10 replicates (1 plant/replicate).

<sup>z</sup>Means followed by the same letter are not significantly different ( $P < 0.05$ ) according to Duncan's new multiple range test. Lower case letters refer to columns, capital letters refer to rows.

Numbers of *Merlinius brevidens* per g of root at 1.0 nematode/cm<sup>3</sup> soil inoculum level ranged from 0.6 to 4.6 for Hycrest, 0.8 to 6.0 for Fairway, and 1.0 to 6.6 for Nordan at 15 and 25°C. Values for *T. acutus* were 0.6 to 3.9 for Hycrest, 0.8 to 8.1 for Fairway, and 1.0 to 6.2 for Nordan. Populations of *Xiphinema americanum* did not increase on any of the grasses, and nematodes per g of root was > 1 only on Fairway at 20°C.

The adverse effects of ectoparasitic nematodes on rangeland wheatgrasses are consistent with the results of field studies involving nematicides (Smolik, 1973) and indicate that these nematodes damage rangeland grasses. The optimum temperature for development and reproduction of *M. brevidens* and *T. acutus* on the wheatgrasses was 25°C; the persistence of *X. americanum* did not differ between 20 and 30°C. Hycrest was more resistant to the 3 species of nematodes than were Fairway or Nordan. The combined density of *M. brevidens* and *T. acutus* populations per g of root weight on Fairway was 39% (Pi 1.0) and 58% (Pi 2.0) higher than on Hycrest.

Similarly, the combined mean final density of *M. brevidens* and *T. acutus* populations per g of root weight was 53% (Pi 1.0) and 59% (Pi 2.0) higher on Nordan than on Hycrest. These data support those of a previous study in which Hycrest was more tolerant of nematode parasitism than other grasses and supported a lower root density of ectoparasitic and lesion nematodes (Griffin, 1992).

Results of this work show that root feeding ectoparasitic plant-parasitic nematodes affect the growth of rangeland grasses (Griffin, 1984, 1992; Ingham and Detling, 1990; Smolik, 1973). Additional cooperative research is needed to evaluate benefits of nematode-tolerant grass cultivars in desert ecosystems and the potential of breeding nematode resistant cultivars.

#### LITERATURE CITED

- 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. Iowa State University Press, Ames, Iowa, U.S.A.

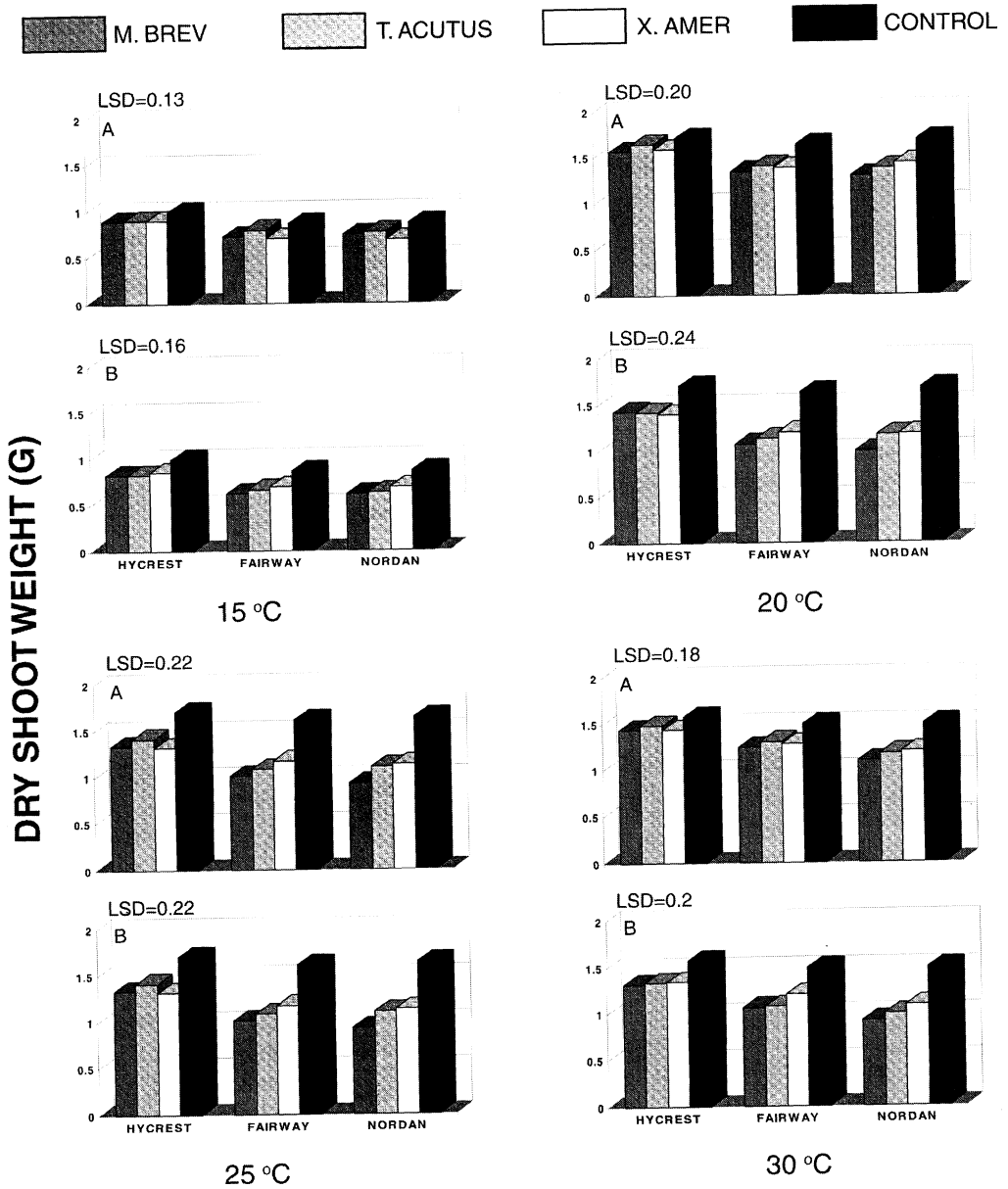


Fig. 1. Effect of *Merlinius brevidens*, *Tylenchorhynchus acutus*, and *Xiphinema americanum* on dry shoot weight of 3 crested wheatgrass cultivars grown for 120 days after inoculation at 4 different temperatures. A) Pi = 1.0 nematode/cm<sup>3</sup> soil. B) Pi = 2.0 nematodes/cm<sup>3</sup> soil. (LSD refers to differences among nematodes within a given cultivar.)

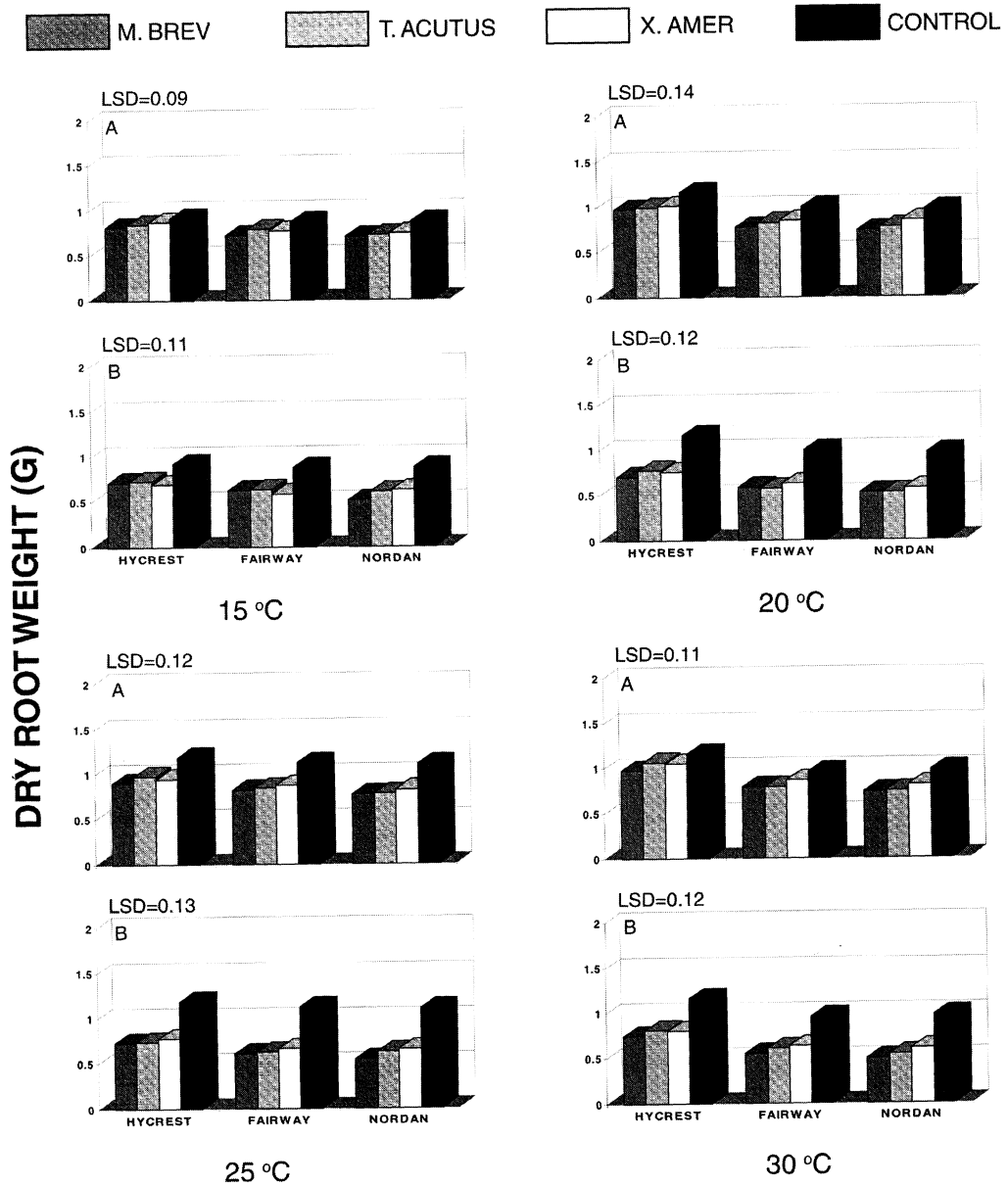


Fig. 2. Effect of *Mertinius brevidens*, *Tylenchorhynchus acutus*, and *Xiphinema americanum* on dry root weight of 3 crested wheatgrass cultivars grown for 120 days after inoculation at 4 different temperatures. A)  $P_i = 1.0$  nematode/ $cm^3$  soil. B)  $P_i = 2.0$  nematodes/ $cm^3$  soil. (LSD refers to differences among nematodes within a given cultivar.)

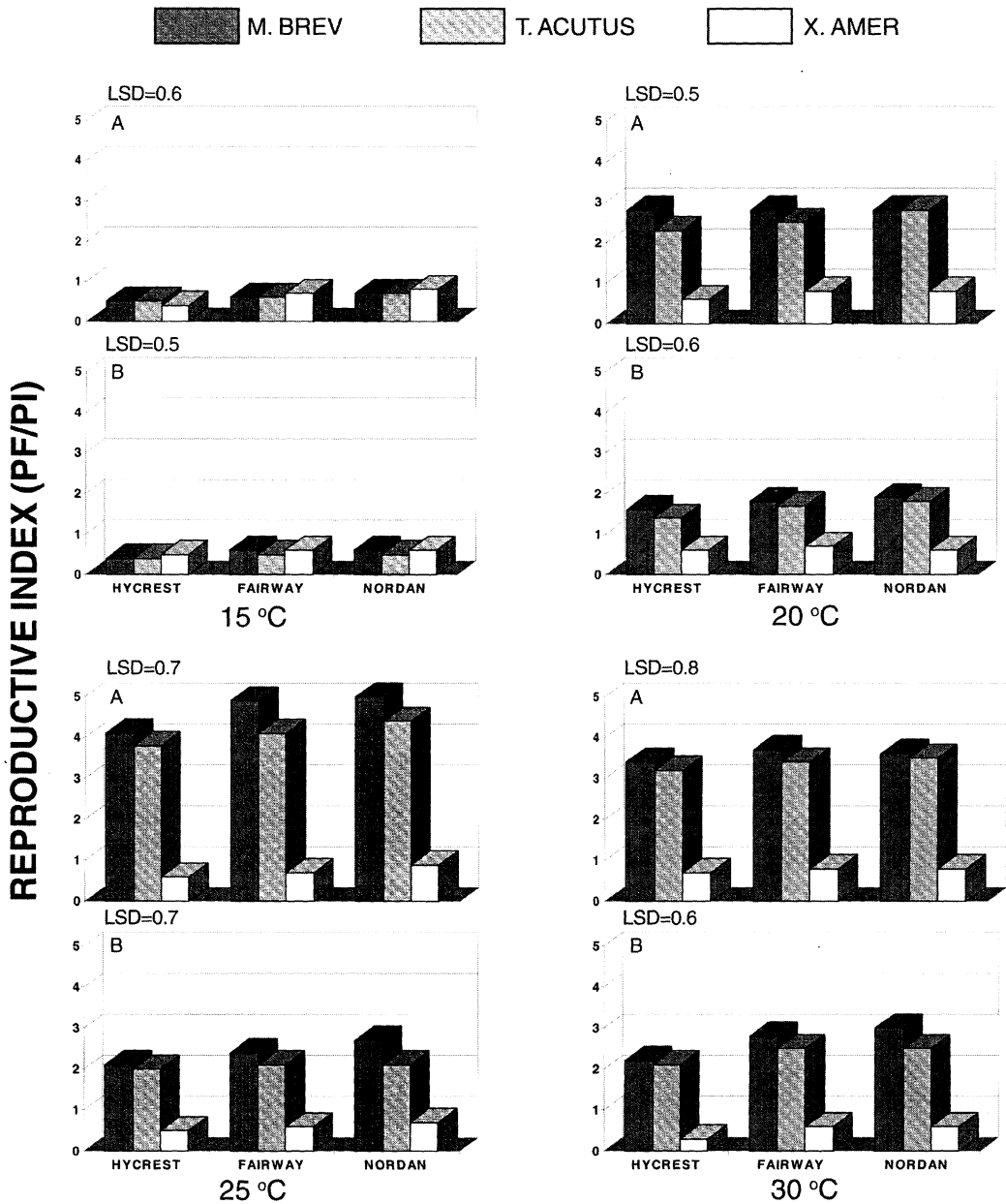


Fig. 3. Reproduction factor (Pf/Pi) of *Merlinius brevidens*, *Tylenchorhynchus acutus*, and *Xiphinema americanum* on 3 crested wheatgrass cultivars grown for 120 days after inoculation at 4 different temperatures. A) Pi = 1.0 nematode/cm<sup>3</sup> soil. B) Pi = 2.0 nematodes/cm<sup>3</sup> soil. (LSD refers to differences among nematodes within a given cultivar.)

- ASAY, K. H., W. H. HORTON, and W. T. HANSEN II. 1985. New grasses for Intermountain rangelands. *Utah Science* 46:119-123.
- 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.
- 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*. Marcel Dekker Inc., New York, NY, U.S.A.
- GRIFFIN, G. D. 1985. Host-parasite relationship of *Meloidogyne chitwoodi* on potato. *Journal of Nematology* 17:395-399.
- 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. 1996. Importance of soil texture on the relationship of plant-parasitic nematodes to range grasses. *Nematropica* 26:27-37.
- GRIFFIN, G. D., and H. M. DARLING. 1964. An ecological study of *Xiphinema americanum* Cobb in an ornamental spruce nursery. *Nematologica* 10:471-479.
- INGHAM, R. E., and J. K. DETLING. 1990. Effect of root-feeding nematodes on aboveground net primary production in a North American grassland. *Plant and Soil* 121:279-281.
- JENKINS, W. R. 1964. A rapid centrifugal-flotation technique for separating nematodes from soil. *Plant Disease Reporter* 48:692.
- MALEK, R. B. 1969. Population fluctuations and observations of the life cycle of *Xiphinema americanum* associated with cottonwood (*Populus deltoides*) in South Dakota. *The Helminthological Society of Washington* 36:270-274.
- NORTON, D. C. 1963. Population fluctuations of *Xiphinema americanum* in Iowa. *Phytopathology* 53:66-68.
- 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.
- ORR, C. C., and O. J. DICKERSON. 1967. Nematodes in true prairie soils of Kansas. *Transactions Kansas Academy of Science* 69:317-334.
- SCHMAUTY, J. E., M. D. BELINGER, and R. W. HARRIS. 1980. Range. Pp. 246-315 in *An Assessment of the Forest and Rangeland Situation in the United States*. United States Department of Agriculture, Forest Service. FS-345. United States Government Printing Office, Washington D.C., U.S.A.
- SMOLIK, J. D. 1973. Effect of soil fumigation and clipping intensity on growth of bluegrass and western wheatgrass. *Proceedings South Dakota Academy of Science* 52:267-268.
- SMOLIK, J. D. 1974. Nematode studies at the cottonwood site. US/IBP Grassland Biome Technical Report. No. 251. Colorado State University, Ft. Collins, Colorado, U.S.A.
- THORNE, G. 1974. Nematodes of the northern great plains. Part 11. Dorylaimoidea in part (Nemata:Adenophorea). Technical Bulletin No. 41. Agricultural Experiment Station, South Dakota State University, Brookings, South Dakota, U.S.A.
- THORNE, G., and R. B. MALEK. 1968. Nematodes of the northern great plains. Part I. Tylenchida (Nemata:Secernentea). Technical Bulletin No. 31. Agricultural Experiment Station, South Dakota State University, Brookings, South Dakota, U.S.A.

---

Received:

15.IX.1994

Accepted for publication:

5.II.1996

Recibido:

Aceptado para publicación: