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The Role of Nematodes in a South Dakota Grassland Ecosystem

James D. Smolik

THE ROLE OF NEMATODES
IN A SOUTH DAKOTA GRASSLAND ECOSYSTEM

BY

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This thesis is approved as a creditable and independent investigation by a candidate for the degree, Doctor of Philosophy, and is acceptable as meeting the thesis requirements for this degree, but without implying that the conclusions reached by the candidate are necessarily the conclusions of the major department.

THE ROLE OF NEMATODES

IN A SOUTH DAKOTA GRASSLAND ECOSYSTEM

Abstract

JAMES D. SMOLIK

Under the supervision of Dr. W. S. Gardner and Professor Gerald Thorne

In an attempt to elucidate the role of nematodes in a grassland ecosystem nematode taxa, number and biomass data was gathered over a three year period at the Cottonwood International Biological Program Grassland Biome site in western South Dakota. The effects of grazing intensity, sampling date and sampling depth were studied. Nematicide treatment of range grasses in field and greenhouse studies was also used to evaluate the role of nematodes. Biomass data was used to estimate the intake of plant feeding nematodes.

Results obtained demonstrate that soil inhabiting nematodes constitute a significant proportion of the consumer biomass at the Cottonwood site. Biomass of plant feeding forms was significantly greater in the ungrazed treatment due mainly to the high numbers of dagger nematode, _Xiphinema americanum._ Biomass of predacious forms was also greater in the ungrazed treatment and overall nearly equaled that of the plant feeding forms, thus indicating their potential as agents of biological control. Biomass of saprophagous forms was considerably less than that of the other trophic levels and also showed little treatment response.

An inverse relationship between numbers of _Tylenchorhynchus_ spp. and _Helicotylenchus_ spp. was noted in the grazed treatment. _Tylenchorhynchus_ spp. appeared nearly limited to the upper 10 cm of soil with

Helicotylenchus spp. predominating with increasing depth, indicating a possible antagonistic relationship between these taxa.

The diversity of taxa was found to decrease with increasing sampling depth, a response attributed to a decrease in variety of food sources. Total number of nematodes also decreased with increasing sampling depth and approximately 70% of the nematodes occurred above 20 cm.

Nematicide treatment of range grasses in field and greenhouse studies significantly reduced nematode populations, increased aboveground herbage weight, and further, provided a demonstration of the importance of nematodes as controllers of productivity in range.

A formula was used to estimate nematode intake at the Cottonwood site and, surprisingly, plant feeding nematodes were found to consume more range grass than cattle. In addition, comparisons of nematode intake with that of several other consumer populations indicated that nematodes are major consumers at the Cottonwood site. The large biomass, high metabolic rate and indigenous nature of the nematode populations were suggested as probable reasons for the high intake.

Overall, it is apparent that soil inhabiting nematodes constitute a significant pathway of energy flow in a grassland ecosystem. They also are probably responsible for a significant proportion of the belowground nutrient recycling.

ACKNOWLEDGEMENT

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I am also indebted to J. K. "Tex" Lewis and other members of the Grassland Biome staff for their aid in obtaining much of the material used in this study; and also to Ms. Marilyn Campion, N.R.E.L. statistician, Ft. Collins, Colorado, who provided the statistical analysis for all data except that of nematicide experiments.

I also wish to thank Ms. Cheryl Shjegstad for her very capable technical assistance.

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INTRODUCTION

Range and pasture constitute a considerable portion of the land area in the Great Plains states. Range and pasture alone occupy 60% of the land in South Dakota, and thus are two of the states most important natural resources. Much of western South Dakota is used primarily for grazing and, due to climatic, topographic and edaphic factors rendering it unsuitable for cultivation, will continue to be so used for the forseeable future. Currently the livestock industry of western South Dakota is a $500 million business annually and research devoted to improving range productivity is amply justified.

The role of soil inhabiting nematodes in grasslands of the Northern Great Plains has received comparatively little investigation. A taxonomic study by Thorne and Malek (31) revealed the presence of many known and other potentially important species of plant parasitic nematodes in grasslands of this region. In addition, Smolik (23) has shown growth increases of 35 to 67% of *Agropyron smithii* Rydb. and *Bouteloua gracilis* (H.B.K.) Lag. ex. Steud. following fumigation of naturally infested range soil.

Much of the present study was conducted in cooperation with the Grassland Biome portion of the U.S. International Biological Program. A primary objective of the Grassland Biome Program is improvement of management recommendations through an improved understanding of grassland ecosystems.

The objective of the present study was to determine the role of nematodes in a grassland ecosystem, in particular the Grassland Biome site located at Cottonwood, South Dakota. Concurrent with this objective nematode taxa, numbers and biomass were determined. The effects of sampling depth and grazing intensity on the above were also studied. Nematicide treatment of range grasses in field and greenhouse studies was used to further evaluate the role of nematodes. In addition, using biomass data, an attempt was made to calculate the amount of plant material consumed by plant feeding nematodes.

MATERIALS AND METHODS

A major portion of this study was conducted at the Cottonwood Range Experiment Station in west central South Dakota. A thorough description of the Cottonwood site has been given by Lewis (13). Nematodes were extracted from soil by the method of Christie and Perry (4). With the exception of nematicide experiments, all nematode numbers were corrected for extraction efficiency in an attempt to estimate the actual population. The efficiency of the wet screening portion of the method using a 325 mesh screen was approximately 73%. Ambient temperature influences the efficiency of the Baermann funnels and this efficiency will vary with sampling date, generally from 70 to 95%. Dorylaims tended to remain in the screen residues more frequently than other taxa and consequently their numbers were corrected independently.

The number of nematodes in each of nine taxa groups was determined by counting the number present in each of three 1 ml aliquots of a 50 ml suspension in a Scott slide hookworm larvae counter. Specific identification and values for biomass determinations were obtained from permanent mounts (28) of individuals selected at random from among samples massed by treatment, depth and date. Approximately 1,000 mounts containing from two to twelve nemas per slide were prepared. Biomass was calculated by the formula of Andrassy (1). Lyophilization was used to determine a nematode moisture content of 75%. Trophic levels for the various forms were based on published reports (7, 8, 9, 10, 12, 21, 27, 28, 29, 30, 32) and, for certain of the dorylaims, on the work of J. Ferris (personal communication).

Soil samples were obtained on dates selected by the biome personnel in 1970, 1971 and 1972. Soil cores, 4.2 cm diameter, were removed to a depth of 60 cm from grazed and ungrazed treatments. The cores were subdivided into 0-5, 5-10, 10-20, 20-30, 30-40, 40-50 and 50-60 cm depth increments, placed in plastic bags, and stored at 4 C until processed. Six to eight cores were taken from each treatment on each of three sampling dates in 1970 and 1971 and on four dates in 1972. Generally the sampling dates corresponded to initiation of growth in the spring, period of peak vegetative standing crop (July) and just prior to frost in the fall.

The grazed treatment areas were fenced from a pasture in the spring of each sampling year. This pasture has been heavily grazed since 1942 and is now dominated by Buchloe dactyloides (Nutt.) Engelm. and Bouteloua gracilis (H.B.K.) Lag. ex. Steud. The ungrazed treatment area is located in a pasture that has been fenced to exclude large herbivores since 1963. Prior to this time it had been lightly grazed and vegetation, dominated by Agropyron smithii Rydb., appears to have reached stability. Both treatment areas are located on gentle northeasterly slopes with silty clay soils (13).

The effects of nematicide treatment were evaluated in field and greenhouse experiments. Vydate®, S-methyl 1-(dimethylcarbamoyl)-N-[(methylcarbamoyl) oxy] thioformimidate, a systemic nematicide, was applied as a foliar spray at 20 kg active ingredient/ha four times at two week intervals in all experiments. Nematicide treatments were initiated in 0.5 m^2 field plots in heavily grazed range at the Cottonwood site in June, 1971. Ten replications each of nematicide treated and non-treated plots were arranged in a randomized complete block design. At the same time, twelve 15 cm diameter soil cores were removed from an area adjacent to the field plots and placed in 15 cm clay pots. The pots were placed in an air-conditioned greenhouse (25 ± 3 C) and half were treated with nematicide to determine the effect on nematode populations. The experiment was terminated seven months later and effect of nematicide treatment determined. An additional twelve cores were removed in a similar manner June, 1972, for further evaluation of the effect of nematicide treatment on nematode populations and on growth of range grasses in a second greenhouse experiment. Clipping was initiated one month after the final nematicide application and the grass was clipped at three week intervals to a height of 5 cm until conclusion of the experiment 6 months later.

Evaluation of field plots was initiated 7 July, 1972. One-half of the plots within each treatment were clipped to soil level with hand-operated clippers and a 4.2 cm diameter soil core was removed to a depth of 10 cm and subdivided into 0-5 and 5-10 cm increments. The remaining plots were clipped 21 July, 1972, with an electrically-powered clipper and a 4.2 cm diameter core was removed to a depth of 60 cm and subdivided as previously described. Nematode species present in the treated and non-treated plots were determined by preparing permanent mounts of randomly selected individuals from massed samples. In addition, aboveground arthropods[1] were extracted with Berlese funnels from

[1]Arthropod identification provided by Dr. Burruss McDaniel, Entomology Department, South Dakota State University, Brookings, South Dakota.

herbage obtained on 21 July. Regrowth in all plots was clipped 28 September, 1972. On 5 April, 1973, blocks of soil 6 x 6 cm to a depth of 10 cm were removed from all plots for final evaluation of nematode populations.

All pots in greenhouse experiments received regular applications of water and fertilizer, and insecticide was applied when necessary. Clippings obtained in all experiments were oven dried at 60 C for five days prior to weighing.

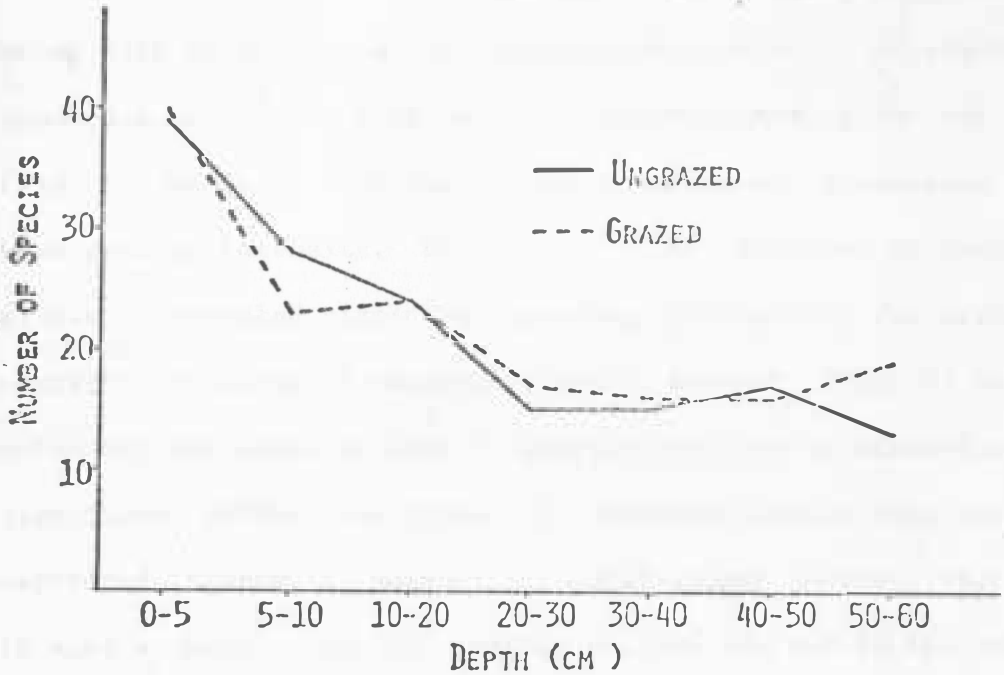
RESULTS AND DISCUSSION

Taxa, number and biomass studies

The following nematodes were identified from samples obtained from the Cottonwood Grassland Biome site: Acrobeles complexus Thorne, 1925; A. ctenocephalus Thorne, 1925; Acrobeloides minor (Thorne, 1925) Thorne, 1937; Akrotonus vigor Thorne, 1973; Aphelenchoides centralis Thorne and Malek, 1968; Aphelenchus avenae Bastian, 1865; Aporcelaimellus clamus Thorne, 1973; A. conoides Thorne, 1973; A. obscuroides Altheer, 1967; A. obscurus (T and S, 1953) Heyns, 1965; A. porcus Thorne, 1973; Axonchium micans Thorne, 1939; A. solitare Thorne, 1939; Basiria graminophila Siddiqi, 1959; Basiroides conurus Thorne and Malek; 1968; Bastiania sp.; Belondira apitica Thorne, 1939; Boleodorus acutus Thorne and Malek; 1968; B. thylactus Thorne, 1941; Cephalobus persegnis Bastian, 1865; Cervidellus serricephalus (Thorne 1925) Thorne, 1937; Chiloplacus contractus Thorne, 1937; Discolaimus texanus Cobb, 1913; Ditylenchus caudatus Thorne and Malek, 1968; D. microdens Thorne and Malek, 1968; Dorylaimellus nodochordus Thorne, 1939; D. tenuidens Thorne, 1939; Dorylaimoides teres Thorne and Swanger, 1936; Ecumenicus monohystera (deMan, 1880, And. 1959) Thorne, 1973; Eucephalobus oxyuroides (deMan, 1876) Steiner, 1936; Eudorylaimus acuticauda (deMan, 1880) Andrassy, 1959; E. conicaudatus Thorne, 1973; E. dubius Thorne, 1973; E. longicardius Thorne, 1973; E. miser (T and S, 1936) Andrassy, 1959; E. modestus (Altheer, 1952) Andrassy, 1959; E. sodakus Thorne, 1973; Helicotylenchus glissus Thorne and Malek, 1968; H. leiocephalus Sher, 1966; Heterodera sp. Labronema rapax Thorne, 1973; Laimydorus flexus (T and S, 1936) Andrassy 1959; Leptonchus obtusus Thorne, 1939; Longidorus crassus Thorne, 1973; Mesodorylaimus pseudobastiani Loof, 1969; Monhystera sp. Mononchus papillatus Bastian, 1865; Nothanquina sp., Nothotylenchus sp. Nygolaimus macrobrachyurus Heyns, 1968; N. papilloides Thorne, 1973; N. parabrachyurus Heyns, 1968; N. paratenuis Thorne, 1973; Paratylenchus brevihastatus Wu, 1962; P. pesticus Thorne and Malek, 1968; P. vexans Thorne and Malek, 1968; Plectus parietinus Bastian, 1865; Pratylenchus scribneri Steiner, 1943; P. tenuis Thorne and Malek, 1968; Prismatolaimus sp.; Psilenchus elegans Thorne and Malek, 1968; P. hilarulus deMan, 1921; Pungentus monohystera Thorne and Swanger, 1936; Solidens vulgaris (Thorne 1930) Thorne, 1973; Thonus major Thorne, 1973; T. nothus (T and S, 1936) Thorne, 1973; Tripyla arenicola deMan, 1880; Trophurus minnesotensis (Caveness, 1958) Caveness, 1959; Tylencholaimellus grandis Thorne, 1973; T. striatus Thorne, 1939; Tylencholaimus proximus Thorne, 1939; Tylenchorhynchus acutus Allen, 1955; T. maximus Allen, 1955; T. nudus Allen, 1955; T. robustoides Thorne and Malek, 1968; Tylenchus exiguus deMan, 1876; T. fusiformis Thorne and Malek, 1968; T. parvissimus Thorne and Malek, 1968; Wilsonema sp.; Xiphinema americanum Cobb, 1913; X. vuittenezi Luc et. al., 1964.

The large variety of nematodes in the above list is apparently due to the mixed prairie nature of the sampling area and the large number of samples collected. Species encountered by treatment and depth for indicated sampling dates are presented in the appendix in Table A1. Appendix tables are designated by the letter A. Figure 1 compares the effects of grazing intensity and sampling depth on species diversity.

Fig. 1. Effect of grazing intensity and sampling depth on number of species encountered at the Cottonwood site.


Number of Species
40
30
20
10
Ungrazed
Grazed
0-5
5-10
10-20
20-30
30-40
40-50
50-60
Depth (cm)

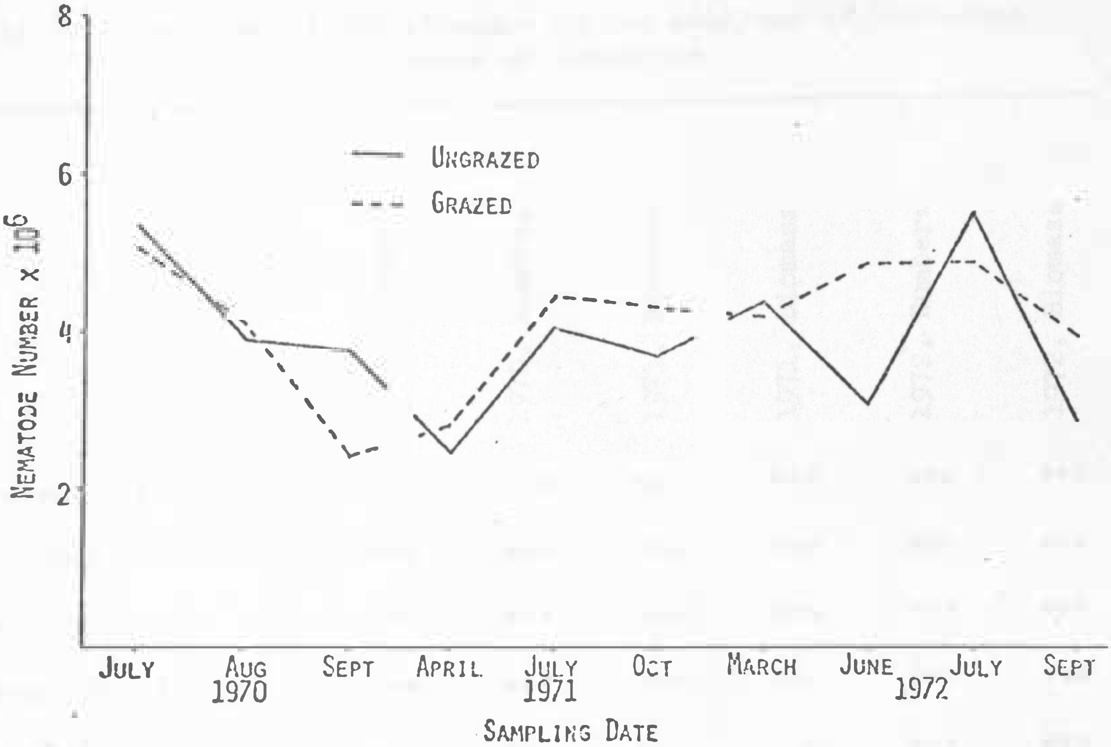
Grazing intensity had little effect on species diversity whereas the reverse is true for sampling depth. The 0-5 cm samples had more than twice the number of species encountered in the 50-60 cm samples (Fig. 1). This greater diversity apparently reflects the greater variety of food sources available in the upper soil layers.

Figures 2 and 3 compare the effects of grazing intensity and sampling date on the number and biomass, respectively, of plant feeding nematodes per m^2 to 60 cm depth at the Cottonwood site. As indicated (Fig. 2), sampling date had a greater influence on nematode numbers than grazing intensity. The summary of the analyses of variances (Table 1) revealed significant grazing effects only for certain 1972 samples. In terms of nematode biomass, however, (Fig. 3) both grazing intensity and sampling date frequently resulted in statistically significant differences (Table 1). Nematode populations are usually expressed in terms of numbers; it would appear however, that biomass is also a useful means for judging populations and in the case of ecological studies is probably superior.

Effects of grazing intensity and sampling depth on number and biomass of plant feeding nematodes for the July, 1970 sampling are shown in Figs. 4, 5. The same general trends are again apparent, i.e., little difference in terms of numbers and greater differences in biomass between grazed and ungrazed treatments. The reason for the highly significant effects of depth (Table 1) are obvious in both Figs. 4 and 5 since well over half of the nematodes occurred above the 20 cm sampling depth. The majority of roots also occur above 20 cm (15) which would

Fig. 2. Effect of grazing intensity and sampling date on number of plant feeding nematodes/m^2 to 60 cm depth at the Cottonwood site.

Fig. 3. Effect of grazing intensity and sampling date on biomass of plant feeding nematodes/m^2 to 60 cm depth at the Cottonwood site.


8
6
4
2
Ungrazed
Grazed
Nematode Number x 10^6
July
Aug
1970
Sept
April
July
1971
Oct
March
June
1972
July
Sept
Sampling Date

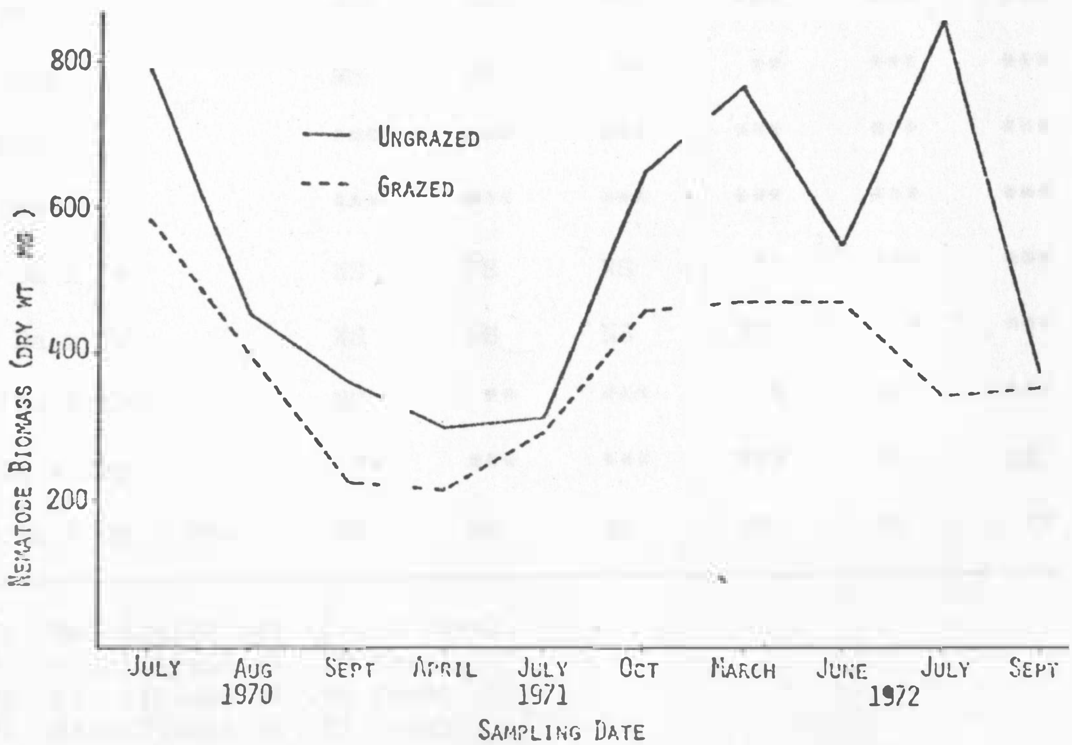

800
600
400
200
Ungrazed
Grazed
Nematode Biomass (dry wt mg)
July
Aug
1970
Sept
April
July
1971
Oct
March
June
1972
July
Sept
Sampling Date

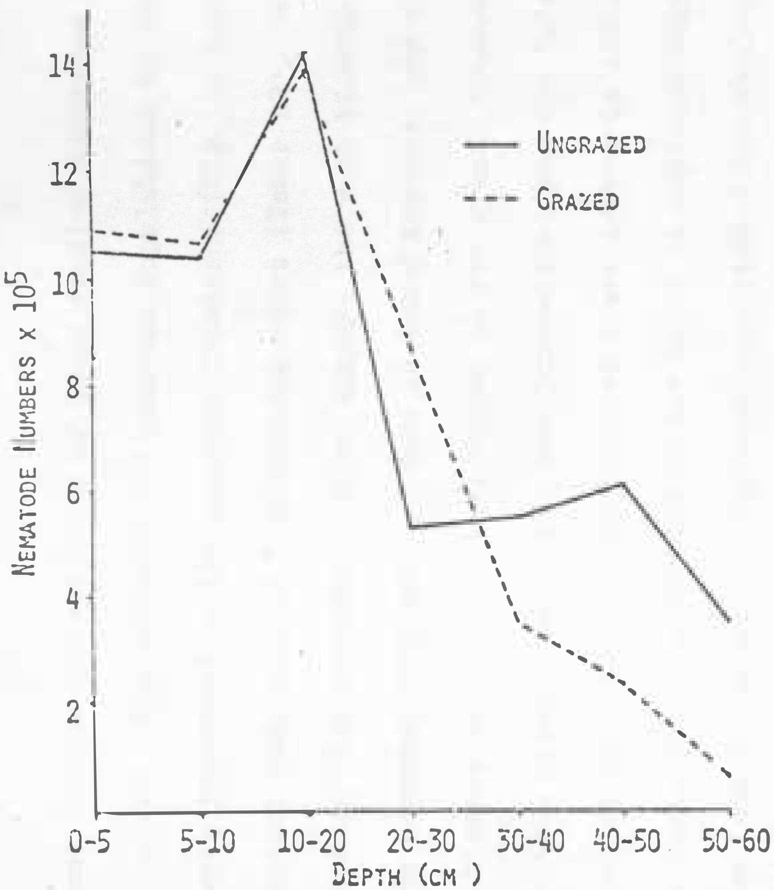
Table 1. Summaries of significance in the analyses of variances of numbers and biomass of nematodes.

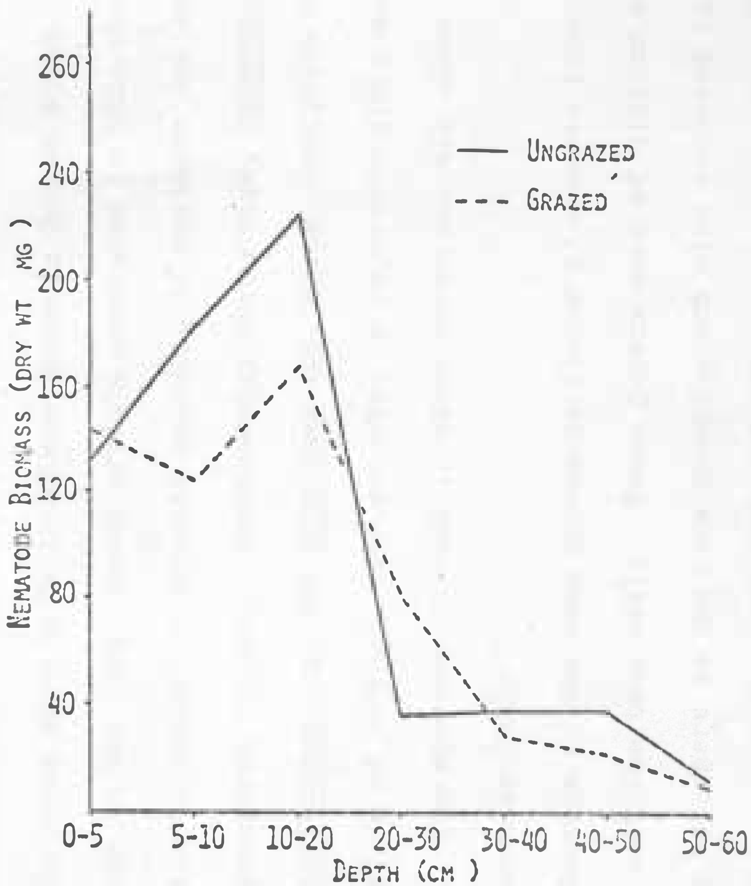
	1970, Numbers	1970, Biomass	1971, Numbers	1971, Biomass	1972, Numbers	1972, Biomass
Treatment (Trt)	NS	*	NS	***	***	***
Date (Da)	***	***	***	***	***	***
Depth (De)	***	***	***	***	***	***
Trophic (Trp)	***	***	***	***	***	***
Trt x Da	NS	NS	NS	*	***	***
Trt x De	**	***	***	**	***	***
Da x De	***	***	***	***	***	***
Trt x Trp	NS	NS	**	**	***	***
Da x Trp	***	***	***	***	***	***
De x Trp	***	***	***	***	***	***
Trt x Da x De	NS	NS	NS	**	***	***
Trt x Da x Trp	NS	NS	NS	NS	*	***
Trt x De x Trp	NS	**	***	*	***	***
Da x De x Trp	**	***	***	***	NS	NS
Trt x Da x De x Trp	NS	NS	NS	NS	NS	**

NS: Nonsignificant at .10 level.
*: Significant at .10 level.
**: Significant at .05 level.
***: Significant at .01 level.

Fig. 4. Effect of grazing intensity and sampling depth on numbers of plant feeding nematodes/m^2 at the Cottonwood site, July, 1970.

Fig. 5. Effect of grazing intensity and sampling depth on biomass of plant feeding nematodes/m^2 at the Cottonwood site, July, 1970.


UNGRAZED
GRAZED
NEMATODE NUMBERS x 10^5
14
12
10
8
6
4
2
0-5
5-10
10-20
20-30
30-40
40-50
50-60
DEPTH (CM)


UNGRAZED
GRAZED
NEMATODE BIOMASS (DRY WT MG)
260
240
200
160
120
80
40
0-5
5-10
10-20
20-30
30-40
40-50
50-60
DEPTH (CM)

account for the concentration of plant feeding nematodes in the upper soil layers. The tendency for nematode populations to remain higher as depth increased in the ungrazed treatment (Fig. 4) appeared to be consistent over most of the sampling dates (Table A2). A logical means to explain this difference is to compare the root biomass in the grazed versus ungrazed treatments. Upon so doing however, one finds that the root biomass is nearly always higher in the grazed treatment (15). It would thus appear that the higher populations are due to a greater proportion of suitable feeding sites at lower depths in the ungrazed treatment, that, in turn, are due to the shift in dominant vegetation that occurs from the grazed to ungrazed condition. The observed population differences also aid in explaining the significant treatment by depth interactions that frequently occurred. The analyses of variance for trophic level data in Table A2 are shown in Tables A3-A5.

Due to the large amount of data generated in this study it was not feasible to conduct a separate analysis of variance for each of the nine taxa groupings counted. Consequently three taxa, *Tylenchorhynchus* spp., *Helicotylenchus* spp. and *Xiphinema* spp. which constitute the greatest proportion of biomass, were selected to represent the plant feeding forms. The species included in these three and all other taxa groupings are shown in Table 2.

Certain of the taxa groupings (Table 2) contain genera that do not agree with the taxa title. These genera were of similar size and food habits to others in the taxa grouping and also occurred infrequently and in low numbers. The values for the predacious forms were based on

Table 2. Taxa groupings used in comparisons of nematode number, biomass and trophic level data obtained at the Cottonwood site.

Taxa grouping	Trophic level	Taxa contained within grouping
Tylenchorhynchus	Plant feeding	Tylenchorhynchus robustoides (90)[a]; T. nudus (6); T. maximus (2); T. acutus (1); Trophurus minnesotensis (1).
Helicotylenchus	Plant feeding	Helicotylenchus leiocephalus (87); H. glissus (12); Heterodera larvae (2).
Xiphinema	Plant feeding	Xiphinema americanum (97); X. vuittenezi (2); Longidorus crassus (1).
Paratylenchus	Plant feeding	Paratylenchus vexans (64); P. brevihastatus (33); P. pesticus (2).
Tylenchinae-Psilenchinae	Plant feeding	Tylenchus exiguus (49); T. parvissimus T. plattensis (1); Ditylenchus caudatus (6); D. microdens (2); Basiroides conurus (13); Basiria graminophila (2); Psilenchus elegans (2); P. hilarulus (1).
Pratylenchus	Plant feeding	Pratylenchus tenuis (85); P. scribneri (15).
Dorylaim	Plant feeding (40)	Pungentus (23); Dorylaimellus (19); Tylencholaimellus (19); Axonchium (16); Belondira (10); Dorylaimoides (6); Tylencholaimus (4); Leptonchus (2).
Dorylaim	Predacious (60)	Eudorylaimus (45); Aporcelaimellus (41); Nygolaimus (10); Akrotonus (1); Mesodorylaimus (1); Laimydorus (1) Solidens (1); Discolaimium (1).
Mononchus	Predacious	Mononchus papillatus (80); Tripyla arenicola (20).
Rhabditida	Saprophagous	Acrobeles (39); Cephalobus (27); Chiloplacus (15); Eucephalobus (10); Plectus (3); Cervidellus (3); Acrobeloides (2); Aphelenchus (2); Wilsonema (1).

[a]Figure in parenthesis indicates the percentage composition of each based on occurrences in permanent mounts of randomly selected individuals.

two taxa groupings and the saprophagous on one (Table 2). Thus, the analyses of variance (Tables A3-A5) are directly applicable to the saprophagous forms and, since the predacious dorylaims comprised about 90% of the predacious taxa, are also applicable to these forms.

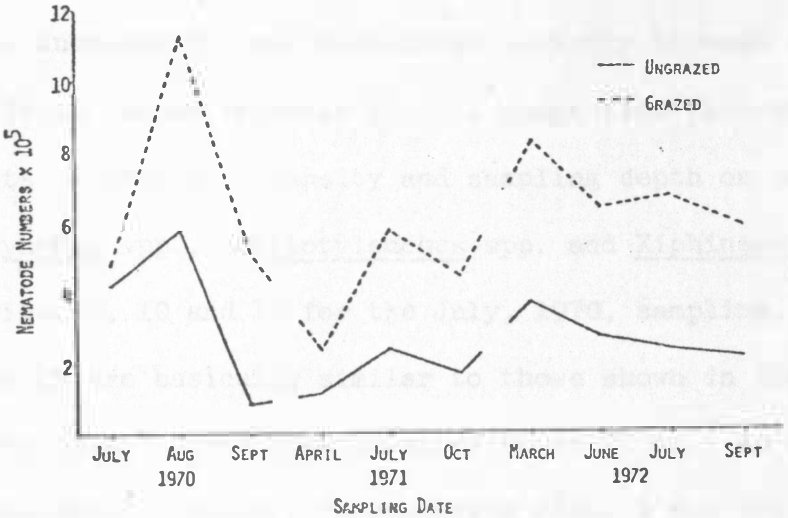
Effects of grazing intensity, sampling depth and sampling date on numbers of all taxa groupings are shown in Table A6. Effects of grazing intensity and sampling date on the number of *Tylenchorhynchus* spp., *Helicotylenchus* spp. and *Xiphinema* spp. are compared in Figs. 6, 7 and 8 respectively. Analyses of variance for these taxa groupings are presented in Tables A7-A9. The number of *Tylenchorhynchus* spp. was significantly higher in the grazed treatment on nearly all sampling dates (Fig. 6), indicating a preference for grasses dominant in the treatment or a shift in other environmental conditions favorable to this group. There was little obvious correlation between grazing intensity and number of *Helicotylenchus* spp. (Fig. 7), although significant treatment differences existed for some dates. It appears that this group is well adapted to both grazing treatments.

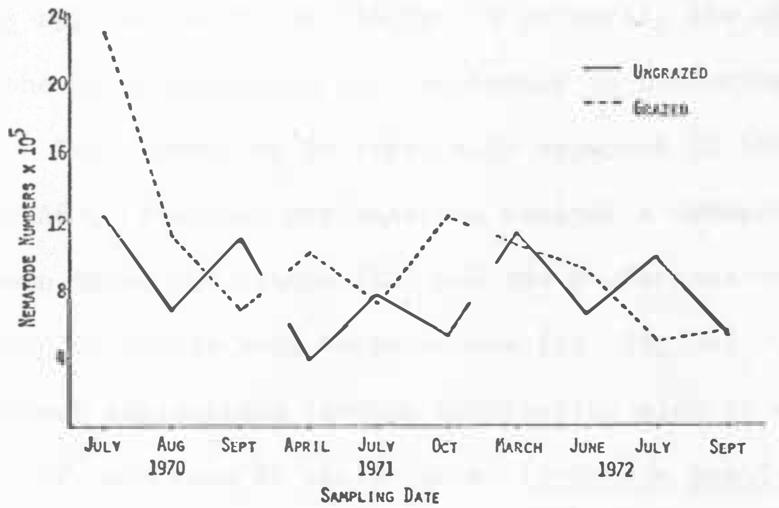
Xiphinema spp. displayed a definite preference for the ungrazed treatment (Fig. 8). Members of this group are much larger than the preceding two and it is probable that they find the coarser-rooted *A. smithii* easier to feed upon than the finer-rooted grasses dominant in the grazed treatment. *Xiphinema* spp., particularly *X. americanum*, are sensitive to perturbations in the environment (20) and thus, environmental changes, beyond those of host that occur under heavy grazing, may also account for the population differences. Two obvious changes

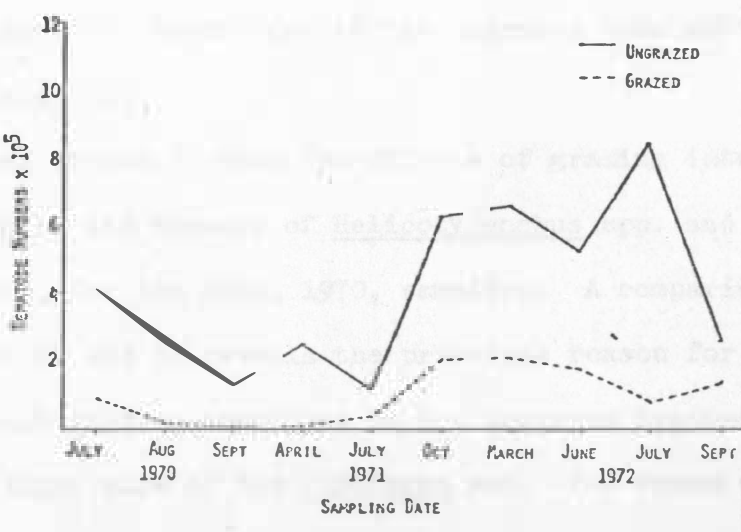
Fig. 6. Effect of grazing intensity and sampling date on number of *Tylenchorhynchus* spp./m^2 to 60 cm depth at the Cottonwood site.

Fig. 7. Effect of grazing intensity and sampling date on number of *Helicotylenchus* spp./m^2 to 60 cm depth at the Cottonwood site.

Fig. 8. Effect of grazing intensity and sampling date on number of *Xiphinema* spp./m^2 to 60 cm depth at the Cottonwood site.


Ungrazed
Grazed
Nematode Numbers x 10^5
12
10
8
6
2
July
Aug
1970
Sept
April
July
1971
Oct
March
June
1972
July
Sept
Sampling Date


Ungrazed
Grazed
Nematode Numbers x 10^5
24
20
16
12
8
4
July
Aug
1970
Sept
April
July
1971
Oct
March
June
1972
July
Sept
Sampling Date


Ungrazed
Grazed
Nematode Numbers x 10^5
12
10
8
6
2
July
Aug
1970
Sept
April
July
1971
Oct
March
June
1972
July
Sept
Sampling Date

would be an increase in soil biological activity through the addition of cattle feces and an increase in soil compaction through trampling.

Effects of grazing intensity and sampling depth on numbers of Tylenchorhynchus spp., Helicotylenchus spp. and Xiphinema spp. are shown in Figs. 9, 10 and 11 for the July, 1970, sampling. Effects of sampling depth are basically similar to those shown in Fig. 4, since the majority of all three taxa occurred above 20 cm. An interesting contrast was noted, however, in comparing Figs. 9 and 10. The Tylenchorhynchus spp. appear to be limited to primarily the upper 10 cm of soil with the Helicotylenchus spp. beginning to predominate at or below this level. This condition is especially apparent in the grazed treatment (Table A6). Possible explanations include a demonstrated antagonism between these two genera (22) and the preference of Tylenchorhynchus spp. for higher soil temperatures (19, 24, 34). Disruption of this natural segregation through cultivation aids in explaining the low numbers of both taxa in winter wheat (Triticum aestivum L.) fields adjacent to the Cottonwood site (unpublished data). Preference of Xiphinema spp. for conditions in the ungrazed treatment were again apparent (Fig. 11).

Figures 12 and 13 show the effects of grazing intensity and sampling depth on the biomass of Helicotylenchus spp. and Xiphinema spp., respectively, for the July, 1970, sampling. A comparison of Figs. 10 and 11 with 12 and 13 reveals the principal reason for the higher biomass of plant feeding nematodes in the ungrazed treatment (Fig. 3) to be the much larger size of the Xiphinema spp. For example, on the above

Fig. 9. Effect of grazing intensity and sampling depth on number of *Tylenchorhynchus* spp./m^2 at the Cottonwood site, July, 1970.

Fig. 10. Effect of grazing intensity and sampling depth on number of *Helicotylenchus* spp./m^2 at the Cottonwood site, July, 1970.

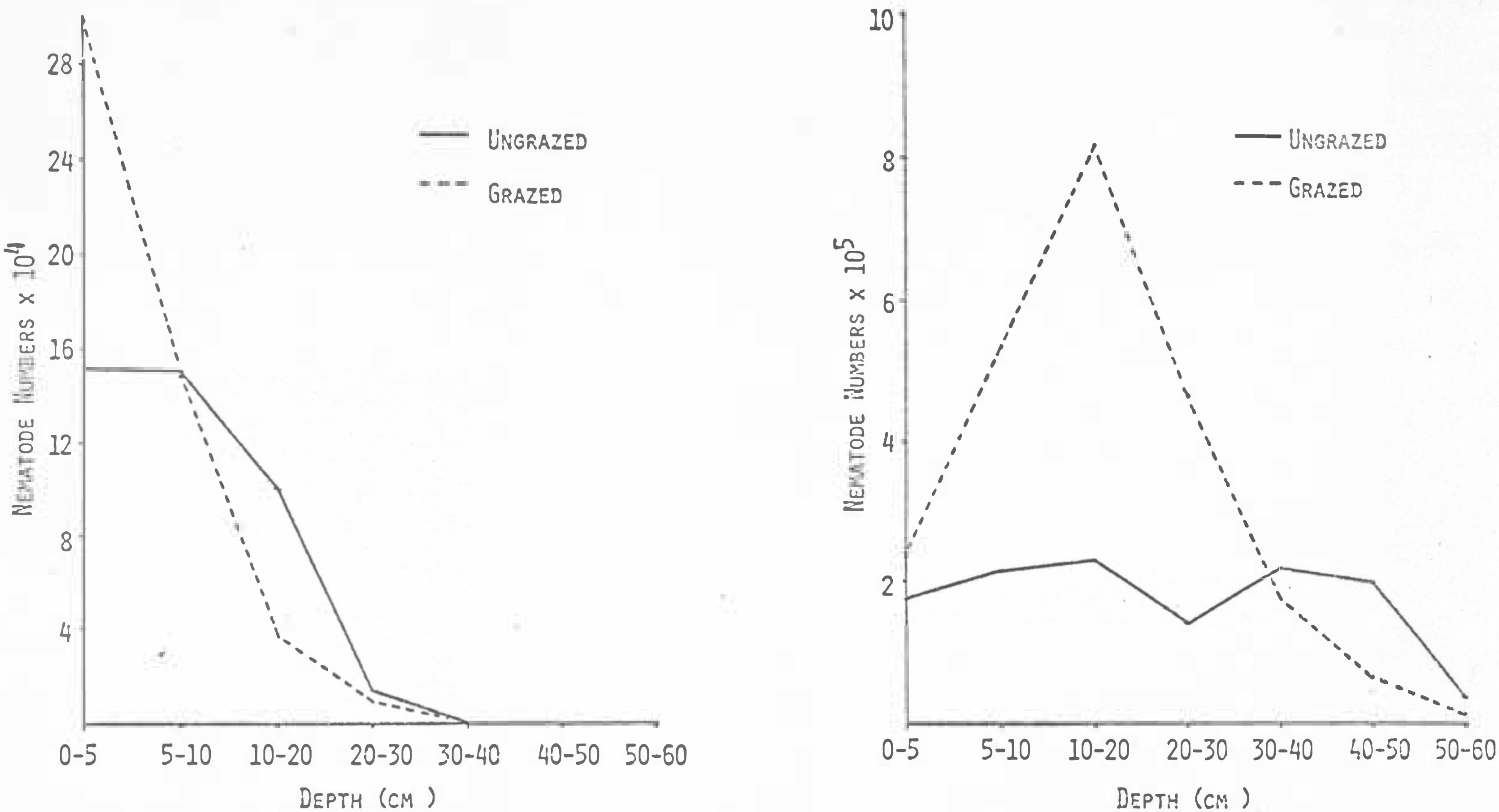
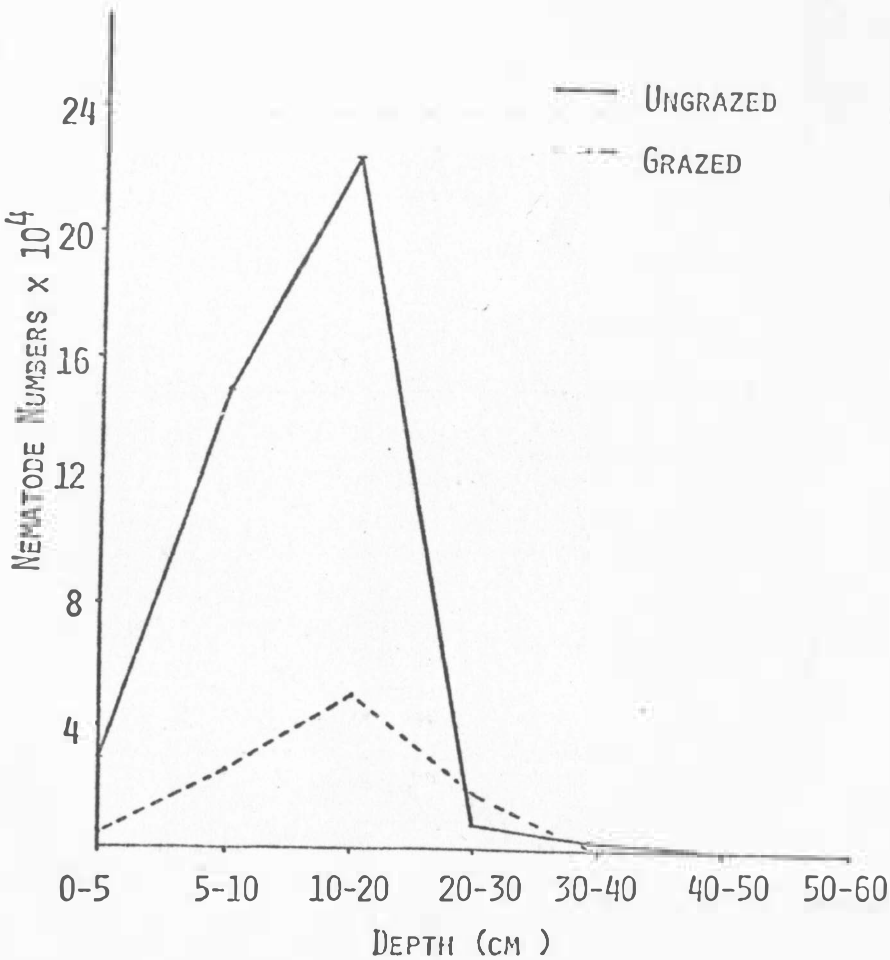

28
24
20
16
12
8
4
Nematode Numbers x 10^4
Ungrazed
Grazed
0-5
5-10
10-20
20-30
30-40
40-50
50-60
Depth (cm)
10
8
6
4
2
Nematode Numbers x 10^5
Ungrazed
Grazed
0-5
5-10
10-20
20-30
30-40
40-50
50-60
Depth (cm)

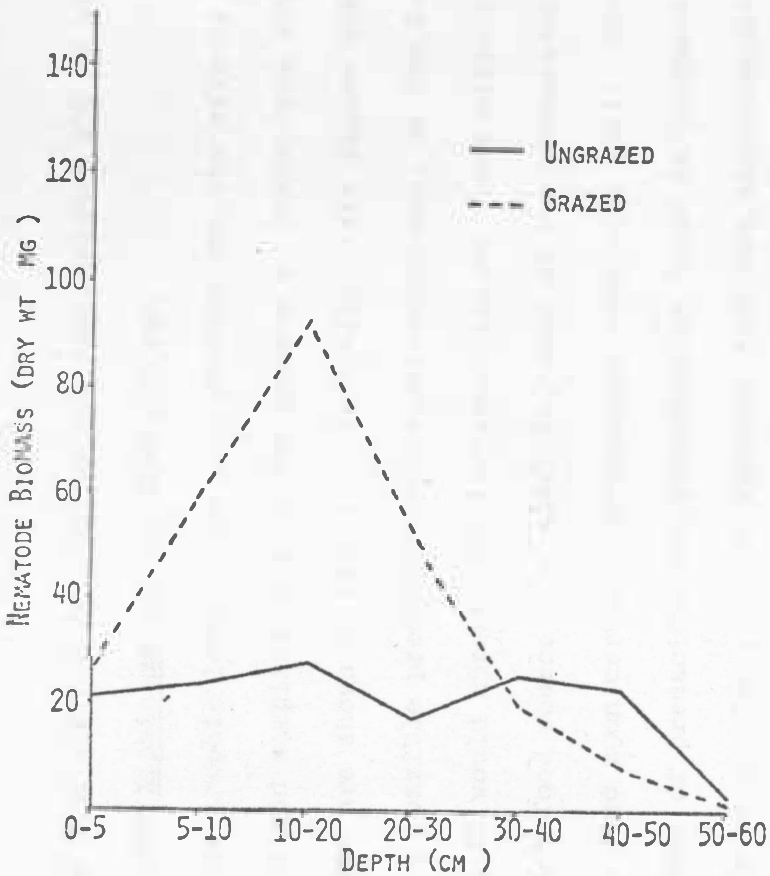
Fig. 11. Effect of grazing intensity and sampling depth on number of *Xiphinema* spp./m^2 at the Cottonwood site, July, 1970.



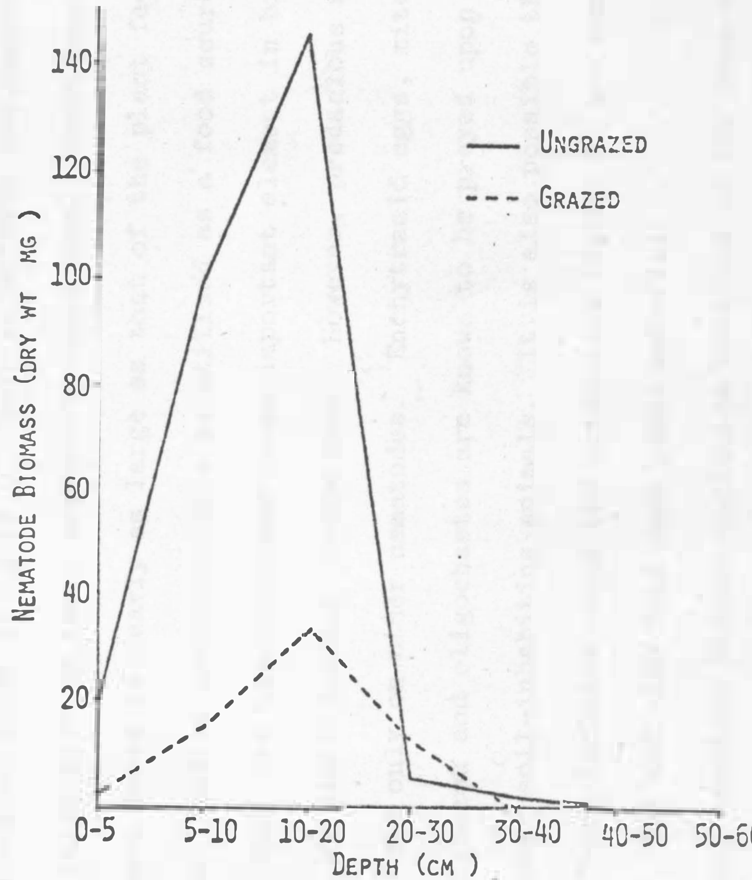
Ungrazed
Grazed
Nematode Numbers x 10^4
24
20
16
12
8
4
0-5
5-10
10-20
20-30
30-40
40-50
50-60
Depth (cm)

Fig. 12. Effect of grazing intensity and sampling depth on biomass of *Helicotylenchus* spp./m^2 at the Cottonwood site, July, 1970.

Fig. 13. Effect of grazing intensity and sampling depth on biomass of *Xiphinema* spp./m^2 at the Cottonwood site, July, 1970.



Nematode Biomass (dry wt mg)
140
120
100
80
60
40
20
Ungrazed
Grazed
0-5
5-10
10-20
20-30
30-40
40-50
50-60
Depth (cm)



Nematode Biomass (dry wt mg)
140
120
100
80
60
40
20
Ungrazed
Grazed
0-5
5-10
10-20
20-30
30-40
40-50
50-60
Depth (cm)

sampling date 234,000 Helicotylenchus spp. weighed 256 mg whereas only 41,000 Xiphinema spp. weighed 273 mg.

Other trophic levels were also studied and the effects of grazing intensity and sampling date on the numbers of predacious and saprophagous forms are shown in Fig. 14. Initially, this figure was prepared to show a possible predator-prey relationship and, on the basis of numbers, it would appear that the saprophagous forms might provide a sufficient food source. In addition, some of the predacious forms are known to feed upon certain saprophagous nematodes (32). However, when the biomass of predacious and saprophagous forms is compared, (Figs. 15 and 16 respectively) it is apparent that the saprophagous forms are not the sole food source of the predators. The large biomass of the predacious forms in spite of their relatively low numbers is due to the large size of these aggressive nematodes. The biomass of the predacious forms is nearly as large as that of the plant feeding (Fig. 3) and plant feeders are probably also utilized as a food source. It thus appears that the predators may be an important element in biological control of plant feeding populations. However, predacious nematodes do not feed only on other nematodes. Enchytraeid eggs, mites, mite eggs, protozoa and oligochaetes are known to be preyed upon and no doubt other soil-inhabiting animals. It is also possible that certain of the forms included among the predacious (Table 2) are omnivorous (10, 27, 30) and also feed upon plant material.

Total nematode biomass estimates obtained in the present study are within the range of those reported in previous work (Table 3) in spite of the wide diversity of habitats and extraction techniques.

Fig. 14. Effect of grazing intensity and sampling date on number of predacious and saprophagous nematodes/m^2 to 60 cm depth at the Cottonwood site.

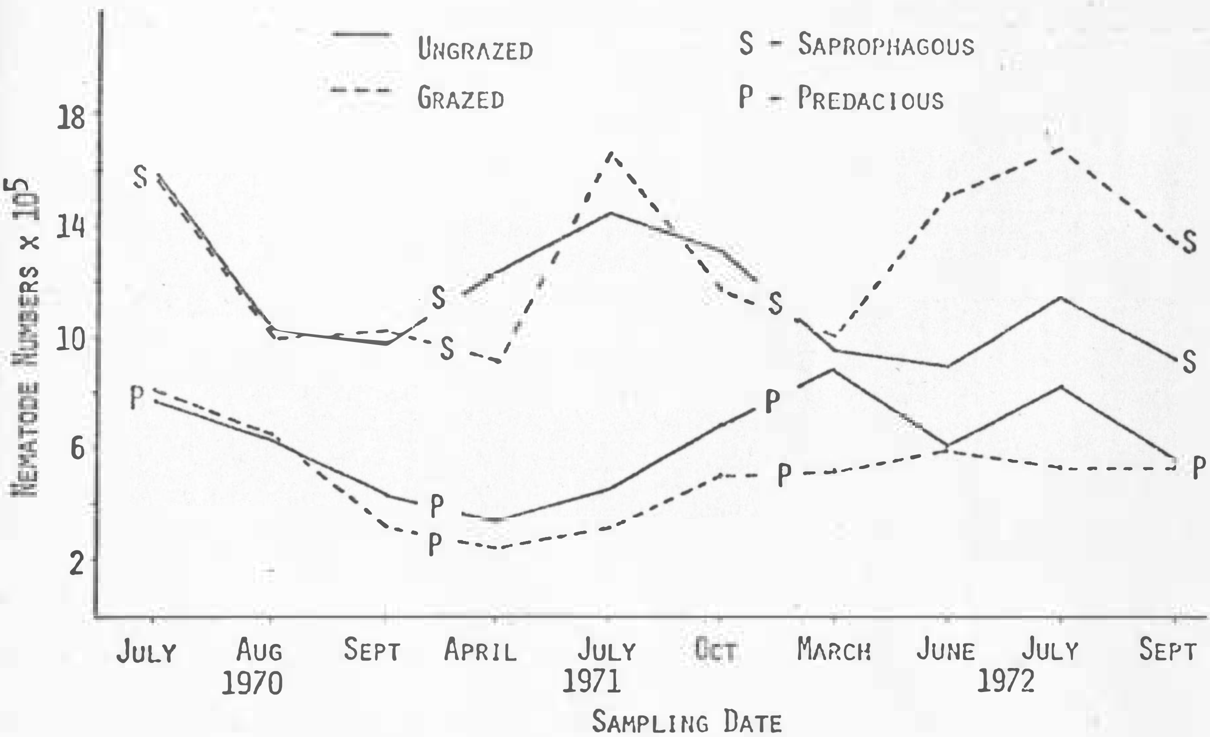
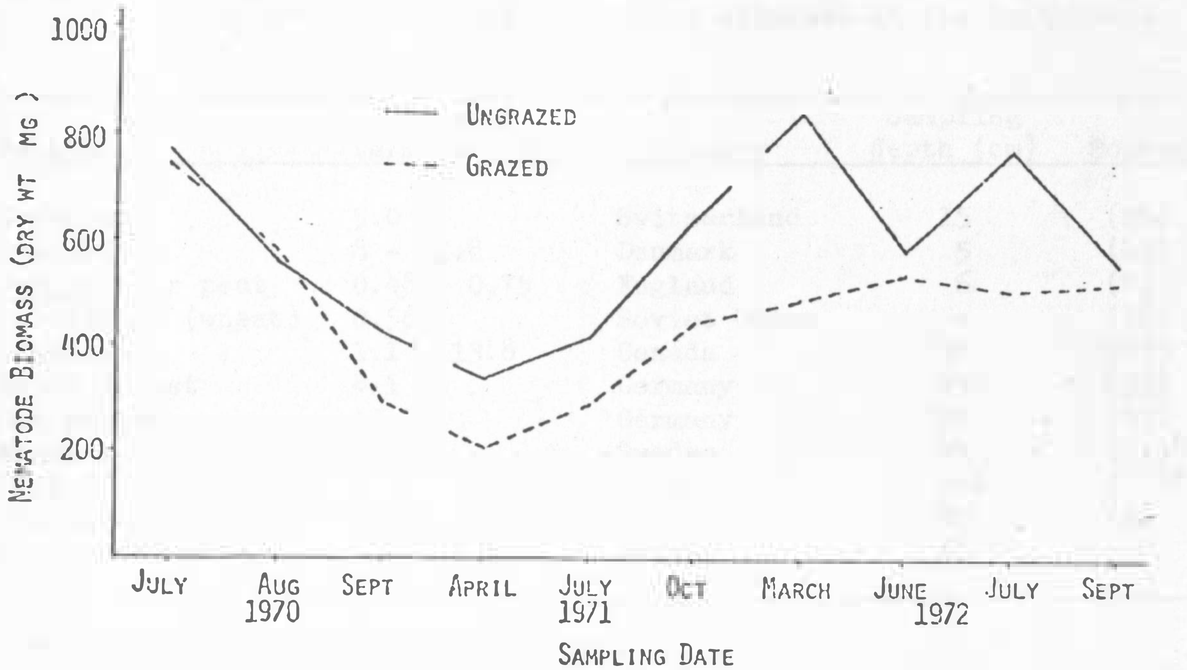

UNGRAZED
GRAZED
S - SAPROPHAGOUS
P - PREDACIOUS
NEMATODE NUMBERS x 10^5
18
14
10
6
2
JULY
AUG
SEPT
APRIL
JULY
OCT
MARCH
JUNE
JULY
SEPT
1970
1971
1972
SAMPLING DATE

Fig. 15. Effect of grazing intensity and sampling date on biomass of predacious nematodes/m^2 to 60 cm depth at the Cottonwood site.

Fig. 16. Effect of grazing intensity and sampling date on biomass of saprophagous nematodes/m^2 to 60 cm depth at the Cottonwood site.


1000
800
600
400
200
NEMATODE BIOMASS (DRY WT MG)
UNGRAZED
GRAZED
JULY
AUG
1970
SEPT
APRIL
JULY
1971
OCT
MARCH
JUNE
1972
JULY
SEPT
SAMPLING DATE

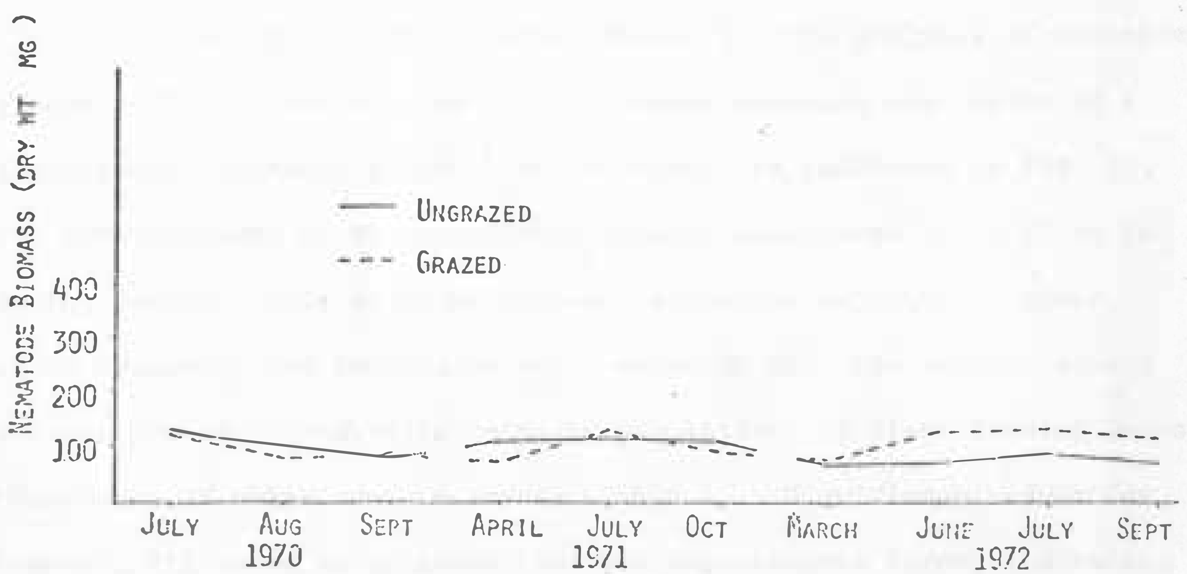

NEMATODE BIOMASS (DRY WT MG)
UNGRAZED
GRAZED
400
300
200
100
JULY
AUG
1970
SEPT
APRIL
JULY
1971
OCT
MARCH
JUNE
1972
JULY
SEPT

Table 3. A comparison of estimates of biomass of nematode populations from several habitats with those obtained at the Cottonwood site.

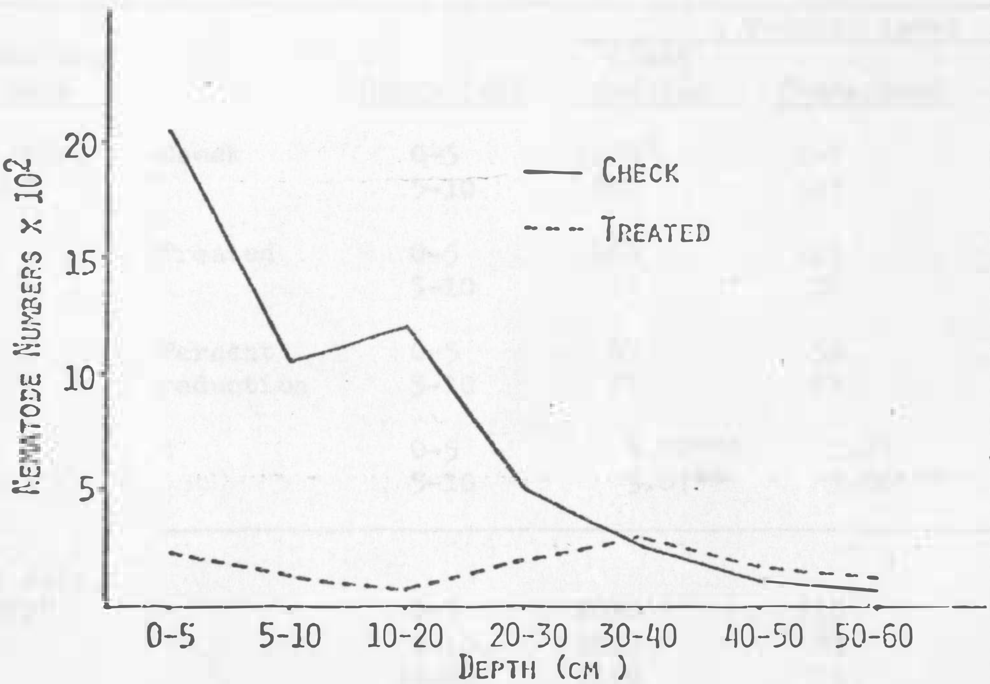
Habitat	Biomass (g/m^2 wet wt)	Country	Sampling depth (cm)	Source
Grassland	5.0	Switzerland	15	(26)
Grassland	8 - 17.8	Denmark	5	(18)
Juncus moor peat	0.48 - 0.75	England	6	(2)
Cultivated (wheat)	0.56	Soviet Union	-	(36)
Grassland	1.1 - 13.8	Canada	30	(35)
Beech forest	4.1	Germany	25	(33)
Oak forest	15.2	Germany	25	(33)
Aspen forest	1.86	Sweden	24	( )[a]
Pine forest	0.3	Sweden	2-4	( )[a]
Old field	0.5 - 3.0	U.S.A.	80	(5)
Cottonwood site	2.0 - 7.1	U.S.A.	60	

[a]Sohlenius (*personal communication*).

Nematicide studies

Nematicide treatment significantly reduced nematode numbers in field plots at the Cottonwood site (Table 4). The analysis of variance (Table A10) for data obtained on the second sampling date revealed a significant treatment by depth interaction. As indicated in Fig. 17, the effectiveness of the nematicide rapidly diminished below 30 cm in depth; however, this might be expected since the majority of roots, which transport the nematicide, occur above 30 cm. The nematicide was generally more effective in reducing populations of plant feeding forms than those of other trophic levels (Table 4). Significant reductions, however, did occur among predacious and saprophagous forms, indicating that the chemical possesses substantial rhizosphere activity. Species diversity was also reduced by nematicide treatment (Table 5). Nematode

Fig. 17. Effect of nematicide treatment and sampling depth on number of plant feeding nematodes at the Cottonwood site.


20
15
10
5
NEMATODE NUMBERS x 10^2
CHECK
TREATED
0-5
5-10
10-20
20-30
30-40
40-50
50-60
DEPTH (CM)

control appeared to be deteriorating on the final sampling date (Table 4), however, significant reductions did occur among all trophic levels.

Table 4. Effect of nematicide treatment on numbers of nematodes in heavily grazed range at the Cottonwood site.

Sampling date		Depth (cm)	Trophic level: Plant feeding	Predacious	Saprophagous
6 July, 1972	Check	0-5	1266[a]	244	707
		5-10	864	123	116
	Treated	0-5	169	123	309
		5-10	74	20	37
	Percent reduction	0-5	87	50	67
		5-10	91	84	68
	t	0-5	4.02***	1.27	2.98**
		5-10	3.07**	3.56***	2.69**
21 July, 1972[b]	Check	0-5	2030	270	1044
		5-10	1013	83	133
		10-20	1169	73	70
		20-30	456	16	39
		30-40	237	11	14
		40-50	78	4	43
		50-60	54	8	44
	Treated	0-5	222	74	246
		5-10	108	24	16
		10-20	49	4	16
		20-30	161	10	17
		30-40	295	10	39
		40-50	214	8	53
		50-60	73	2	16
	Percent reduction	0-5	89	73	76
		5-10	89	71	88
		10-20	96	95	77
		20-30	65	37	56
		30-40	--	9	--
		40-50	--	--	--
		50-60	--	75	64

Table 4. Continued.

Sampling date		Depth (cm)	Trophic level: Plant feeding	Predacious	Saprophagous
5 April, 1973	Check	0-10	4949[c]	551	1808
	Treated	0-10	892	264	868
	Percent reduction		82	52	52
	t		6.97***	6.77***	7.10***

[a]Each value is mean of 5 replications, number/4.2 cm diameter core to indicated depth.

[b]Analysis of variance is shown in Table A12.

[c]Each value is mean of 10 replications, number/6x6x10 cm block.

**Significant at .05 level.

***Significant at .01 level.

Significant growth increases resulted on all clipping dates (Table 6). Figure 18 compares representative amounts of herbage from treated and check plots obtained on the first clipping date.

Clipping weights were increased from 28 to 59% in treated plots (Table 6). Initial clipping of half of the field plots was accomplished with hand-powered clippers and consequently much of the crown material was not removed. Electrically-powered clippers were used for all subsequent clippings and as indicated in Table 6 the overall amount of herbage obtained on the second clipping was substantially greater. A further indication of the increased vigor of plants in treated plots was the 45% increase in weight of regrowth obtained on the final

Table 5. Nematodes identified among randomly selected individuals from check and nematicide treated plots at the Cottonwood site.

Check	Treated
Acrobeles ctenocephalus	Acrobeles ctenocephalus
Aphelenchus avenae	Acrobeloides minor
Aporcelaimellus obscuroides	Aphelenchoides sp.
Aporcelaimellus obscurus	Aporcelaimellus conoides
Axonchium sp.	Basiroides conurus
Bastiania sp.	Belondira apitica
Belondira apitica	Cephalobus persegnis
Boleodorus similis	Chiloplacus contractus
Cephalobus persegnis	Eucephalobus oxyuroides
Chiloplacus contractus	Eudorylaimus sp.
Discolaimus texanus	Helicotylenchus glissus
Ditylenchus microdens	Helicotylenchus leiocephalus
Dorylaimellus tenuidens	Heterodera larvae
Eucephalobus oxyuroides	Mononchus papillatus
Eudorylaimus longicardius	Paratylenchus brevihastatus
Eudorylaimus miser	Plectus parietinus
Helicotylenchus glissus	Pratylenchus tenuis
Helicotylenchus leiocephalus	Tylencholaimellus sp.
Leptonchus obtusus	Tylenchorhynchus robustoides
Mesodorylaimus sp.	Tylenchus exiguus
Mononchus papillatus	Tylenchus fusiformis
Nygolaimus sp.	Tylenchus parvissimus
Plectus parietinus	
Prismatolaimus sp.	
Tylencholaimellus striatus	
Tylencholaimellus sp.	
Tylenchorhynchus nudus	
Tylenchorhynchus robustoides	
Tylenchus exiguus	
Tylenchus parvissimus	
Wilsonema sp.	
Xiphinema americanum	

Table 6. Effect of nematicide treatment on growth of range grasses in heavily grazed range at the Cottonwood site.

Clipping date		Clipping weight[a]	Percent increase	F
6 July, 1972	Check	52.52[b]		
	Treated	83.24	59	24.07***
21 July, 1972	Check	109.05[b]		
	Treated	139.80	28	10.81**
26 September, 1972	Check	35.98[c]		
	Treated	52.35	45	15.16***

[a]Total dry herbage weight in $g/0.5m^2$.

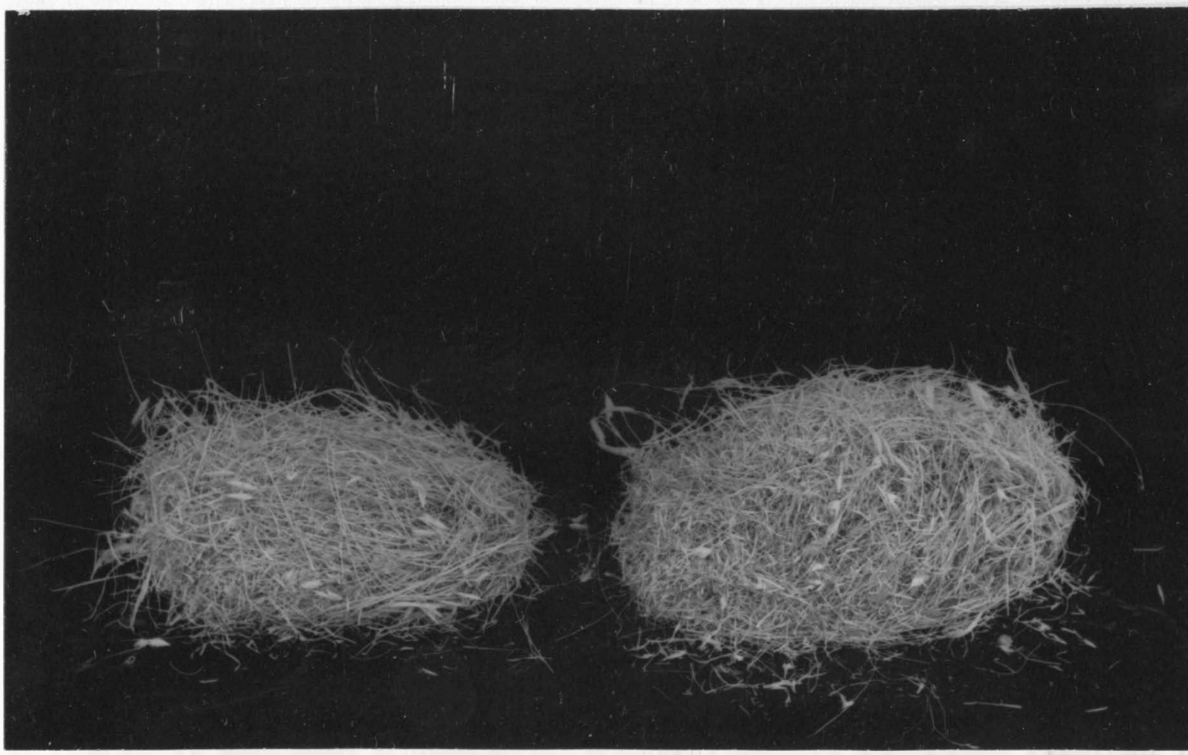
[b]Each value is mean of five replications.

[c]Each value is mean of ten replications.

**Significant at .05 level.

***Significant at .01 level.

Fig. 18. Effect of nematicide treatment on amounts of herbage obtained on the initial clipping of field plots at the Cottonwood site - treated on right.



clipping date. The numbers of selected aboveground arthropods extracted from herbage on the second clipping was generally higher in treated plots (Table 7), although no statistically significant differences existed within taxa.

Results obtained in greenhouse experiments substantiate those obtained in field plots. In the initial greenhouse experiment (Table 8) nematicide treatment significantly reduced nematode numbers among all trophic levels and substantially improved the top and root growth of treated grass (Fig. 19). In the second experiment nematode control was again excellent (Table 9) and clipping weights in treated pots were increased by 31% (Table 10). The confined nature and consequent more thorough nematicide coverage of plants in the greenhouse experiments would explain the greater reduction in nematode numbers. Plants in greenhouse experiments were watered and fertilized regularly and, since it has been demonstrated that stresses in the physical environment increase nematode injury to plants (25), clipping weight increases in treated pots were generally not as great as those obtained in the field study.

It is probable a portion of observed growth increases resulted from insect control since Vydate® is an insecticide as well as a nematicide. However, the peak biomass of aboveground arthropods at Cottonwood in 1970 was 0.385 g/m^2 (17), while in the present study the peak nematode biomass was 1.773 g/m^2, or about 5 times greater than the arthropods. Thus, it is apparent that plant feeding nematodes not only occupy a

Table 7. Effect of nematicide treatment on numbers of selected above-ground arthropods in heavily grazed range at the Cottonwood site.

	Arthropod taxa							
	Pseudococcidae	Arachnida	Phloeothripidae	Thripidae	Formicidae	Aranaea	Entomobryidae	Sminthuridae
Check	9[a]	117	6	4	0.5	0.2	0.6	0.5
Treated	21	126	14	5	0.5	0.2	0.8	0

[a]Extracted from herbage with Berlese funnels, each value is mean of five replications (McDaniel, unpublished data).

Table 8. Effect of nematicide treatment on nematode numbers in soil cores in greenhouse experiment I.

	Trophic level		
	Plant feeding	Predacious	Saprophagous
Initial population	8,448[a]	1,352	9,580
Check	15,462[b]	1,378	12,516
Treated	765	134	1,436
Percent reduction	95	90	89
t	6.14***	6.70***	5.32***

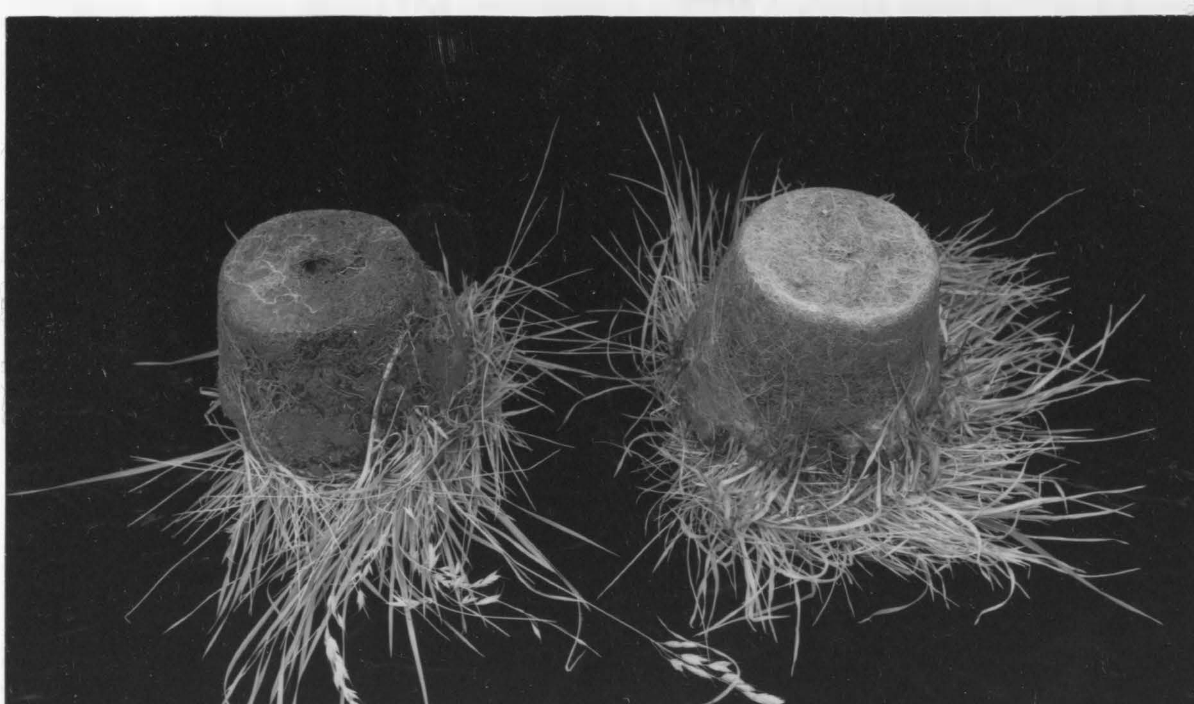
[a]Each value is mean of three replications.

[b]Each value is mean of six replications seven months after treatment.

***Significant at .01 level.

Fig. 19. Effect of nematicide treatment on growth of range grasses in soil cores in greenhouse experiment I. A. Top growth - treated on right. B. Root growth - treated on right.

A



B

Table 9. Effect of nematicide treatment on nematode numbers in soil cores in greenhouse experiment II.

	Trophic level		
	Plant feeding	Predacious	Saprophagous
Check	6,733[a]	611	27,176
Treated	240	96	1,272
Percent reduction	96	84	95
t	5.61***	4.54***	6.13***

[a]Each value is mean of six replications seven months after treatment.

***Significant at .01 level.

Table 10. Effect of nematicide treatment on growth of range grasses in soil cores in greenhouse experiment II.

	Cumulative clipping weight	Root and crown weight
Check	9.27[a]	10.87
Treated	12.15	12.32
Percent increase	31	13
t	2.70**	1.06

[a]Each value is mean of six replications, dry wt in g.

**Significant at .05 level.

significant proportion of the invertebrate biomass at the Cottonwood site, but also function as controllers of productivity in range.

Nematode intake studies

Data thus far presented, while demonstrating the importance of nematodes, is deficient in one respect; it does not allow a direct comparison of nematode consumption with that of other consumers as is necessary to quantify energy flow in an ecosystem study. In an attempt to correct this deficiency a formula for estimating invertebrate intake developed by Lewis (14) was modified to estimate intake for plant feeding nematodes (Table 11). Metabolic rates were obtained from published values (3, 6, 11, 12, 16) and corrected for the mean of soil temperatures at 10 and 20 cm depths based on Cottonwood abiotic data (15). The growing season was divided into three periods; April-June, July-August and September-October, and the average plant feeding nematode biomass for each period was obtained from the three years of data. The next two values (Table 11), cal/ml O_2 and cal/g, were obtained from Lewis (14). Activity requirement was included to compensate for the nearly inactive condition of nematodes in a respirometer as compared to those in soil actively feeding or moving about in search of a host. The assimilation efficiency was based on the work of Sohlenius (personal communication). Calculations, with the omission of constants, are shown in Table 12 for the grazed and ungrazed treatment. Estimates of herbage net primary production at Cottonwood in 1970 (14) for the various components are shown in Table 13.

Table 11. Formula for estimating intake in g/m^2 for plant feeding nematodes at the Cottonwood site. Adapted from Lewis (14).

Temp-corrected		Nematode										
metabolic rate		weight -		Calories/		Calories/		Activity		Assimilation		Hours
at field temp	X	dry wt	X	ml O_2	÷	gram	X	requirement	÷	efficiency	X	in
ml O^2/gr/hr		in g/m^2		(4.8)		(4500)		(2)		(0.35)		period
(dry wt)												

= intake (g/m^2)

Table 12. Calculations for estimation of intake in g/m^2 for plant feeding nematodes at the Cottonwood site.

	Grazed	
Date:		
April - June:	(3.5) x (0.3887) x ( )[a] x (2184) =	18.1
July - August:	(7.4) x (0.4047) x ( )[a] x (1488) =	27.2
Sept. - October:	(3.5) x (0.3529) x ( )[a] x (1464) =	11.0
	Total	56.3
	Ungrazed	
April - June:	(3.5) x (0.5521) x ( )[a] x (2184) =	25.6
July - August:	(7.4) x (0.6130) x ( )[a] x (1488) =	41.2
Sept. - October:	(3.5) x (0.4614) x ( )[a] x (1464) =	14.4
	Total	81.2

[a]Constants: See Table 11.

Table 13. Estimated net primary productivity for grazed and ungrazed treatments at the Cottonwood site, 1970. From Lewis (14).

Component	Treatment Grazed	Treatment Ungrazed
Aboveground herbage	247[a]	450
Aboveground crowns and stolons	33	104
Belowground crowns	113	113
Roots	226	261

[a]Oven dry weight in g/m^2.

Presence of an adequate food base for plant feeding nematodes in terms of net root production is apparent (Table 13). A comparison of estimated intake of primary producers by cattle, small mammal, bird and insect populations with that for nematodes is shown in Table 14.

Table 14. Estimated intake of primary producers by cattle, small mammal, bird, insect and nematode populations at the Cottonwood site.[a]

Treatment	Cattle[b]	Small mammal	Bird	Insect	Nematode
Grazed	22[c]	0.3	0.10	3.9	56
Ungrazed	37	0.3	0.06	1.9	81

[a]All values except those for nematodes were obtained from Lewis (14).

[b]Hypothetical cattle populations - based on moderate stocking rate.

[c]Intake in g/m^2.

The comparatively high intake for plant feeding nematode populations (Table 14) is due in part to their large biomass. The mean nematode biomass for the grazed and ungrazed treatments is 0.38 and 0.54 g/m^2 while that for cattle is 1.69 and 2.85 g/m^2. Although the biomass for cattle is higher, the metabolic rate for nematodes is much higher, as would be expected on the basis of their much smaller size (12), and consequently their intake is greater. It should also be kept in mind when interpreting Table 14 that nematodes are indigenous and cattle are introduced. Thus, it might be expected that nematode populations are more efficient in utilizing the available food sources. A possible deficiency of the formula in Table 11 is the assumption that nematodes were active throughout the entire April-October period. While precipitation was above normal for all of the sampling years (Lewis, personal communication), it is possible that either soil moisture or soil temperature may at times have been at levels that would limit nematode activity. Studies designed to determine the effects of soil moisture and temperature on nematode populations native to the Cottonwood site are currently underway.

CONCLUSIONS

Results presented demonstrate that soil inhabiting nematodes constitute a significant proportion of the consumer biomass at the Cottonwood site. Biomass of plant feeding forms was significantly greater in the ungrazed treatment due mainly to the high numbers of dagger nematode, *Xiphinema americanum.* Biomass of predacious forms was also greater in the ungrazed treatment and overall nearly equaled that of the plant feeding forms, thus indicating their potential as agents of biological control. Biomass of saprophagous forms was considerably less than that of the other trophic levels and also showed little treatment response.

An inverse relationship between numbers of *Tylenchorhynchus* spp. and *Helicotylenchus* spp. was noted in the grazed treatment. *Tylenchorhynchus* spp. appeared nearly limited to the upper 10 cm of soil with *Helicotylenchus* spp. predominating with increasing depth, indicating a possible antagonistic relationship between these taxa.

The diversity of taxa was found to decrease with increasing sampling depth, a response attributed to a decrease in variety of food sources. Total number of nematodes also decreased with increasing sampling depth and approximately 70% of the nematodes occurred above 20 cm.

Nematicide treatment of range grasses in field and greenhouse studies significantly reduced nematode populations, increased aboveground herbage weight, and further, provided a demonstration of the importance of nematodes as controllers of productivity in range.

A formula was used to estimate nematode intake at the Cottonwood site and, surprisingly, plant feeding nematodes were found to consume more range grass than cattle. In addition, comparisons of nematode intake with that of several other consumer populations indicated that nematodes are major consumers at the Cottonwood site. The large biomass, high metabolic rate and indigenous nature of the nematode populations were suggested as probable reasons for the high intake.

Overall, it is apparent that soil inhabiting nematodes constitute a significant pathway of energy flow in a grassland ecosystem. They also are probably responsible for a significant proportion of the belowground nutrient recycling.

Results of the present study are not applicable to Cottonwood alone since numerous surveys (unpublished data) have shown the existence of equally high nematode numbers throughout the range area of western South Dakota. In addition, Thorne (31) has commented on the general distribution of nematode species in prairie sod in the Northern Great Plains. Assuming that nematodes could be controlled, and, further, that what they now consume could be made available to cattle, it appears that the carrying capacity of the range could be doubled. Economic benefits of such a situation are obvious, however, the reverse is true under present conditions and in terms of economic loss plant feeding nematodes in range appear to be a major biotic agent of plant disease in the Northern Great Plains.

The obvious response, of course, is what can be done about nematodes in range. One of the first things that might be done is to follow grazing recommendations. Certain of the desirable range grass species rapidly disappear under heavy grazing, probably because they cannot tolerate high populations of cattle grazing on shoots and high numbers of nematodes grazing on roots. Nematicide treatment is not economically feasible and with presently available chemicals is ecologically undesirable. Interseeding resistant or tolerant grasses (providing they could be found) might also provide an answer. At present there is little interseeding of grasses in South Dakota range, apparently because of a previous lack of success. Part of the reason for previous failures may well be due to nematodes. Another possibility is a management regimen that would operate to the advantage of cattle and disadvantage to nematodes. Number, taxa and biomass data of the type presented in this study for a greater variety of range conditions between heavily grazed and ungrazed might provide the basis for such a regimen. Whatever the answer might be, continued research is justified.

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APPENDIX

Table A1. Influence of grazing intensity and sampling depth on species encountered among randomly selected individuals at the Cottonwood site.

Date: July and October 1971, March 1972

Depth: 0-5 cm

Grazed	Ungrazed
Acrobeles complexus	Acrobeles complexus
Acrobeles ctenocephalus	Acrobeles ctenocephalus
Acrobeloides sp.	Aphelenchus avenae
Aphelenchoides centralis	Aporcelaimellus conoides
Aporcelaimellus clamus	Aporcelaimellus obscuroides
Aporcelaimellus conoides	Aporcelaimellus obscurus
Aporcelaimellus obscurus	Aporcelaimellus porcus
Axonchium micans	Axonchium micans
Boleodorus acutus	Axonchium solitare
Cephalobus persegnis	Belondira apitica
Cervidellus sp.	Boleodorus thylactus
Chiloplacus contractus	Cephalobus persegnis
Ditylenchus microdens	Ditylenchus caudatus
Dorylaimellus sp.	Ditylenchus microdens
Eucephalobus oxyuroides	Dorylaimellus tenuidens
Eudorylaimus monohystera	Eucephalobus oxyuroides
Eudorylaimus conicaudatus	Eudorylaimus acuticauda
Eudorylaimus loacuticauda	Eudorylaimus longicardius
Helicotylenchus glissus	Eudorylaimus modestus
Helicotylenchus leiocephalus	Eudorylaimus sodakus
Labronema rapax	Helicotylenchus leiocephalus
Laimydorus flexus	Heterodera sp.
Mesodorylaimus pseudobastiani	Laimydorus flexus
Nygolaimus paratenuis	Leptonchus sp.
Paratylenchus vexans	Longidorus crassus
Plectus parietinus	Monhystera sp.
Pratylenchus tenuis	Mononchus papillatus
Prismatolaimus sp.	Nygolaimus macrobrachyurus
Solidens vulgaris	Paratylenchus vexans
Thonus major	Plectus parietinus
Thonus nothus	Pungentus monohystera
Tripyla arenicola	Tripyla arenicola
Tylencholaimellus sp.	Tylencholaimellus striatus
Tylencholaimus proximus	Tylencholaimellus sp.
Tylenchorhynchus robustoides	Tylenchorhynchus acutus
Tylenchus exiguus	Tylenchorhynchus robustoides
Tylenchus parvissimus	Tylenchus exiguus
Xiphinema americanum	Xiphinema americanum
Xiphinema vuittenezi	Xiphinema vuittenezi
Wilsonema sp.	

Table Al. Continued.

Date: July and October 1971, March 1972

Depth: 5-10 cm

Grazed	Ungrazed
Acrobeles complexus	Acrobeles complexus
Akrotonus vigor	Akrotonus vigor
Aporcelaimellus obscuroides	Aporcelaimellus obscuroides
Aporcelaimellus obscurus	Aporcelaimellus obscurus
Aporcelaimellus porcus	Axonchium micans
Axonchium micans	Cephalobus persegnis
Boleodorus acutus	Dorylaimellus sp.
Cephalobus persegnis	Eucephalobus oxyroides
Ditylenchus microdens	Eudorylaimus sp.
Dorylaimellus sp.	Helicotylenchus glissus
Eudorylaimus miser	Helicotylenchus leiocephalus
Helicotvlenchus glissus	Heterodera sp.
Helicotylenchus leiocephalus	Longidorus crassus
Leptonchus obtusus	Mononchus papillatus
Paratylenchus pesticus	Nygolaimus macrobrachyurus
Paratylenchus vexans	Nygolaimus papilloides
Pratylenchus scribneri	Nygolaimus parabrachyurus
Prismatolaimus sp.	Nygolaimus paratenuis
Tylencholaimellus striatus	Paratylenchus vexans
Tylenchorhynchus maximus	Prismatolaimus sp.
Tylenchorhynchus robustoides	Pungentus monohystera
Tylenchus exiguus	Tylencholaimellus sp.
Xiphinema americanum	Tylenchorhynchus acutus
	Tylenchorhynchus nudus
	Tylenchorhynchus robustoides
	Tylenchus exiguus
	Xiphinema americanum
	Xiphinema vuittenezi

Date: July and October 1971, March 1972

Depth: 10-20 cm

Grazed	Ungrazed
Acrobeles sp.	Acrobeles complexus
Akrotonus vigor	Akrotonus vigor
Aporcelaimellus obscurus	Aporcelaimellus obscurus
Axonchium	Belondira apitica
Bastiania sp.	Boleodorus acutus
Belondira apitica	Cephalobus persegnis

Table A1. Continued.

Grazed	Ungrazed
Cephalobus persegnis	*Ditylenchus caudatus*
Cervidellus sp.	*Dorylaimellus* sp.
Ditylenchus sp.	*Eudorylaimus dubius*
Dorylaimellus nodochordus	*Eudorylaimus miser*
Dorylaimellus tenuidens	*Helicotylenchus glissus*
Eudorylaimus miser	*Helicotylenchus leiocephalus*
Helicotylenchus glissus	*Longidorus crassus*
Helicotylenchus leiocephalus	*Mononchus papillatus*
Paratylenchus vexans	*Nygolaimus macrobrachyurus*
Pratylenchus hexincisus	*Paratylenchus brevihastatus*
Pratylenchus scribneri	*Paratylenchus vexans*
Tylencholaimellus striatus	*Pungentus monohystera*
Tylencholaimus proximus	*Tripyla arenicola*
Tylenchorhynchus robustoides	*Tylencholaimellus striatus*
Tylenchus exiguus	*Tylenchorhynchus nudus*
Tylenchus fusiformis	*Tylenchorhynchus robustoides*
Tylenchus parvissimus	*Tylenchus exiguus*
Xiphinema americanum	*Xiphinema americanum*

Date: July and October 1971

Depth: 20-30 cm

Grazed	Ungrazed
Aporcelaimellus obscurus	*Aporcelaimellus* sp.
Basiroides conurus	*Cephalobus persegnis*
Chiloplacus contractus	*Dorylaimoides* sp.
Dorylaimellus tenuidens	*Helicotylenchus glissus*
Dorylaimellus sp.	*Helicotylenchus leiocephalus*
Eucephalobus oxyuroides	*Longidorus crassus*
Eudorylaimus sp.	*Nygolaimus parabrachyurus*
Helicotylenchus glissus	*Paratylenchus vexans*
Helicotylenchus leiocephalus	*Pungentus monohystera*
Nygolaimus macrobrachyurus	*Pratylenchus scribneri*
Trophurus minnesotensis	*Psilenchus hilarulus*
Tylencholaimellus sp.	*Tylenchorhynchus robustoides*
Tylenchorhynchus acutus	*Tylenchus exiguus*
Tylenchus exiguus	*Tylenchus* sp.
Tylenchus fusiformis	*Xiphinema americanum*
Tylenchus parvissimus	
Xiphinema americanum	

Table A1. Continued.

Date: July and October 1972

Depth: 30-40 cm

Grazed	Ungrazed
Acrobeles complexus	Acrobeles complexus
Aporcelaimellus obscuroides	Aporcelaimellus obscuroides
Aporcelaimellus obscurus	Basiroides conurus
Cephalobus persegnis	Cephalobus persegnis
Chiloplacus sp.	Chiloplacus contractus
Dorylaimellus tenuidens	Ditylenchus caudatus
Eudorylaimus sp.	Helicotylenchus glissus
Helicotylenchus glissus	Helicotylenchus leiocephalus
Helicotylenchus leiocephalus	Longidorus crassus
Paratylenchus brevihastatus	Pratylenchus tenuis
Pratylenchus tenuis	Pungentus monohystera
Trophurus minnesotensis	Tylencholaimellus sp.
Tylenchus exiguus	Tylenchus exiguus
Tylenchus parvissimus	Tylenchus parvissimus
Tylenchus plattensis	Xiphinema americanum
Xiphinema americanum	

Date: July and October 1971

Depth: 40-50 cm

Acrobeles sp.	Acrobeles sp.
Aporcelaimellus obscuroides	Aphelenchus sp.
Basiroides conurus	Aporcelaimellus obscuroides
Cephalobus persegnis	Aporcelaimellus obscurus
Dorylaimellus sp.	Basiroides conurus
Eudorylaimus sp.	Cephalobus persegnis
Helicotylenchus glissus	Chiloplacus contractus
Helicotylenchus leiocephalus	Ditylenchus caudatus
Paratylenchus brevihastatus	Eudorylaimus sp.
Paratylenchus vexans	Helicotylenchus glissus
Pratylenchus scribneri	Helicotylenchus leiocephalus
Trophurus minnesotensis	Paratylenchus vexans
Tylencholaimellus sp.	Psilenchus elegans
Tylenchus exiguus	Pungentus monohystera
Tylenchus parvissimus	Tylenchorhynchus robustoides
Xiphinema americanum	Tylenchus exiguus
	Xiphinema americanum

Table A1. Continued.

Date: July and October 1971

Depth: 50-60 cm

Grazed	Ungrazed
Acrobeles sp.	Aporcelaimellus sp.
Acrobeloides sp.	Basiria graminophila
Aporcelaimellus obscurus	Basiroides conurus
Basiroides conurus	Cephalobus persegnis
Cephalobus persegnis	Ditylenchus caudatus
Cervidellus serricephalus	Eudorylaimus sp.
Chiloplacus contractus	Helicotylenchus glissus
Dorylaimellus tenuidens	Helicotylenchus leiocephalus
Dorylaimoides teres	Plectus sp.
Eudorylaimus sp.	Trophurus minnesotensis
Helicotylenchus leiocephalus	Tylencholaimellus sp.
Nothotylenchus sp.	Tylenchus exiguus
Paratylenchus brevihastatus	Tylenchus parvissimus
Tylenchus exiguus	
Tylenchus parvissimus	
Tylenchus plattensis	
Wilsonema sp.	
Xiphinema americanum	

Table A2. Effect of grazing intensity, sampling date and sampling depth on numbers and biomass of plant feeding, predacious and saprophagous nematodes at the Cottonwood site.

July, 1970

	Grazed					
	Plant Feeding		Predacious		Saprophagous	
Depth (cm)	Number	Biomass	Number	Biomass	Number	Biomass
0-5	1,097,800[a]	0.1429[b]	378,200	0.3468	849,000	0.0675
5-10	1,078,200	0.1238	139,800	0.1282	337,000	0.0268
10-20	1,397,200	0.1692	142,800	0.1306	157,000	0.0125
20-30	876,200	0.0820	34,800	0.0318	92,000	0.0073
30-40	346,800	0.0282	22,200	0.0203	50,000	0.0040
40-50	233,400	0.0219	51,600	0.0472	42,000	0.0033
50-60	68,400	0.0093	33,600	0.0307	66,000	0.0052
Total	5,098,000	0.5773	803,000	0.7356	1,593,000	0.1266
				Grand Total:		7,494,000
						1.4395

	Ungrazed					
	Plant Feeding		Predacious		Saprophagous	
Depth (cm)	Number	Biomass	Number	Biomass	Number	Biomass
0-5	1,055,000	0.1361	332,500	0.3050	830,000	0.0660
5-10	1,049,800	0.1834	173,700	0.1588	273,000	0.0217
10-20	1,427,600	0.2261	148,400	0.1378	284,000	0.0226
20-30	536,400	0.0375	39,600	0.0969	69,000	0.0055
30-40	559,200	0.0389	25,800	0.0236	58,000	0.0046
40-50	610,400	0.0389	36,600	0.0335	48,000	0.0038
50-60	357,400	0.0123	15,600	0.0143	37,000	0.0029
Total	5,595,800	0.7839	772,200	0.7699	1,599,000	0.1271
				Grand Total:		7,967,000
						1.6809

[a]Avg. of six replications - number/m^2.

[b]Dry weight in g/m^2.

Table A2. Continued.

August, 1970

Grazed						
	Plant Feeding		Predacious		Saprophagous	
Depth (cm)	Number	Biomass	Number	Biomass	Number	Biomass
0-5	1,531,200[a]	0.1471[b]	185,300	0.1703	598,500	0.0476
5-10	504,000	0.0558	136,500	0.1248	147,000	0.0117
10-20	747,400	0.0865	175,600	0.1622	100,000	0.0080
20-30	600,200	0.0611	73,800	0.0675	51,000	0.0041
30-40	418,800	0.0349	31,200	0.0285	60,000	0.0048
40-50	181,000	0.0098	15,000	0.0137	23,000	0.0018
50-60	59,000	0.0048	15,000	0.0137	23,000	0.0018
Total	4,041,600	0.4000	632,400	0.5807	1,002,500	0.0798
				Grand Total:		5,676,500
						1.0605

Ungrazed						
	Plant Feeding		Predacious		Saprophagous	
Depth (cm)	Number	Biomass	Number	Biomass	Number	Biomass
0-5	799,800	0.0612	122,200	0.1130	688,000	0.0547
5-10	835,900	0.1124	154,100	0.1417	164,000	0.0130
10-20	923,800	0.1497	122,200	0.1130	101,000	0.0080
20-30	652,200	0.0585	80,800	0.0744	33,000	0.0026
30-40	359,400	0.0405	61,600	0.0569	33,000	0.0026
40-50	241,000	0.0151	15,000	0.0137	36,000	0.0029
50-60	142,600	0.0161	50,400	0.0461	28,000	0.0022
Total	3,954,700	0.4535	606,300	0.5588	1,083,000	0.0860
				Grand Total:		5,644,000
						1.0983

[a]Avg. of six replications - number/m^2.

[b]Dry weight in g/m^2.

Table A2. Continued.

September, 1970

Grazed

	Plant Feeding		Predacious		Saprophagous	
Depth (cm)	Number	Biomass	Number	Biomass	Number	Biomass
0-5	691,100[a]	0.0791[b]	147,400	0.1358	684,500	0.0544
5-10	196,300	0.0452	73,200	0.0673	103,000	0.0082
10-20	830,000	0.0437	52,800	0.0486	100,000	0.0080
20-30	416,200	0.0348	22,800	0.0208	41,000	0.0033
30-40	245,800	0.0246	13,200	0.0121	20,000	0.0016
40-50	71,600	0.0058	11,400	0.0104	38,000	0.0030
50-60	45,600	0.0017	2,400	0.0021	61,000	0.0047
Total	2,496,600	0.2349	323,200	0.2970	1,047,500	0.0832
					Grand Total:	3,867,300 0.6151

Ungrazed

	Plant Feeding		Predacious		Saprophagous	
Depth (cm)	Number	Biomass	Number	Biomass	Number	Biomass
0-5	648,400	0.0453	136,100	0.1273	489,500	0.0389
5-10	541,500	0.0467	117,000	0.1073	94,500	0.0075
10-20	999,600	0.1173	110,400	0.1009	204,000	0.0162
20-30	610,200	0.0716	49,800	0.0455	77,000	0.0061
30-40	646,200	0.0563	28,800	0.0263	46,000	0.0037
40-50	319,800	0.0226	19,200	0.0176	49,000	0.0039
50-60	95,600	0.0047	5,400	0.0049	32,000	0.0025
Total	3,861,300	0.3645	466,700	0.4298	992,000	0.0788
					Grand Total:	5,320,000 0.8731

[a]Avg. of six replications - number/m^2.

[b]Dry weight in g/m^2.

Table A2. Continued.

April, 1971

Grazed

Depth (cm)	Plant Feeding Number	Plant Feeding Biomass	Predacious Number	Predacious Biomass	Saprophagous Number	Saprophagous Biomass
0-10	1,990,000[a]	0.1815[b]	231,200	0.2134	795,000	0.0632
10-20	328,000	0.0276	3,200	0.0029	12,000	0.0010
20-30	163,000	0.0063	0	0.0000	32,000	0.0025
30-40	159,000	0.0063	0	0.0000	47,000	0.0037
40-50	26,000	0.0008	0	0.0000	11,000	0.0009
50-60	35,000	0.0008	0	0.0000	32,000	0.0025
Total	2,701,000	0.2233	234,400	0.2163	929,000	0.0729
					Grand Total:	3,864,400
						0.5125

Ungrazed

Depth (cm)	Plant Feeding Number	Plant Feeding Biomass	Predacious Number	Predacious Biomass	Saprophagous Number	Saprophagous Biomass
0-10	1,127,000	0.2148	329,000	0.3092	1,093,000	0.0869
10-20	569,200	0.0703	32,800	0.0305	58,000	0.0046
20-30	151,000	0.0062	0	0.0000	44,000	0.0035
30-40	358,600	0.0154	2,400	0.0022	38,000	0.0030
40-50	166,000	0.0067	0	0.0000	21,000	0.0017
50-60	85,000	0.0034	0	0.0000	17,000	0.0014
Total	2,456,800	0.3168	364,200	0.3419	1,271,000	0.1011
					Grand Total:	4,092,000
						0.7598

[a]Avg. of six replications - number/m^2.

[b]Dry weight in g/m^2.

Table A2. Continued.

July, 1971

	Grazed					
	Plant Feeding		Predacious		Saprophagous	
Depth (cm)	Number	Biomass	Number	Biomass	Number	Biomass
0-5	1,041,900[a]	0.0734[b]	127,600	0.1180	1,071,000	0.0851
5-10	559,800	0.0365	61,200	0.0560	208,500	0.0166
10-20	1,012,600	0.0553	47,400	0.0433	173,000	0.0138
20-30	919,000	0.0697	27,000	0.0247	75,000	0.0060
30-40	510,200	0.0315	31,800	0.0291	74,000	0.0059
40-50	322,000	0.0196	18,000	0.0161	52,000	0.0041
50-60	169,000	0.0066	9,000	0.0082	30,000	0.0024
Total	4,534,500	0.2926	322,000	0.2954	1,683,500	0.1339
					Grand Total:	6,540,000 0.7219

	Ungrazed					
	Plant Feeding		Predacious		Saprophagous	
Depth (cm)	Number	Biomass	Number	Biomass	Number	Biomass
0-5	696,200	0.0706	205,800	0.1958	847,500	0.0674
5-10	594,700	0.0431	49,300	0.0461	211,500	0.0168
10-20	926,800	0.0911	88,200	0.0829	157,000	0.0125
20-30	584,200	0.0455	37,800	0.0353	57,000	0.0045
30-40	617,400	0.0390	36,600	0.0335	64,000	0.0051
40-50	491,800	0.0288	13,200	0.0121	83,000	0.0066
50-60	191,600	0.0103	14,400	0.0132	33,000	0.0026
Total	4,102,700	0.3284	445,300	0.4189	1,453,000	0.1155
					Grand Total:	6,001,000 0.8628

[a]Avg. of eight replications - number/m^2.

[b]Dry weight in g/m^2.

Table A2. Continued.

October, 1971

	Grazed					
	Plant Feeding		Predacious		Saprophagous	
Depth (cm)	Number	Biomass	Number	Biomass	Number	Biomass
0-5	1,272,500[a]	0.0988[b]	195,000	0.1783	791,000	0.0629
5-10	665,500	0.0746	114,300	0.1045	139,000	0.0111
10-20	1,251,600	0.1766	119,400	0.1092	102,000	0.0081
20-30	691,400	0.0822	45,600	0.0417	69,000	0.0055
30-40	337,000	0.0265	15,000	0.0137	43,000	0.0034
40-50	193,200	0.0096	7,800	0.0071	31,000	0.0025
50-60	58,000	0.0013	0	0	20,000	0.0016
Total	4,469,200	0.4696	497,100	0.4545	1,195,000	0.0951
					Grand Total:	6,161,300
						1.0192

	Ungrazed					
	Plant Feeding		Predacious		Saprophagous	
Depth (cm)	Number	Biomass	Number	Biomass	Number	Biomass
0-5	299,900	0.0592	209,100	0.1988	829,500	0.0659
5-10	695,600	0.1502	168,900	0.1593	184,000	0.0146
10-20	1,283,800	0.2855	197,200	0.1838	185,000	0.0147
20-30	787,400	0.1134	92,600	0.0864	47,000	0.0037
30-40	336,400	0.0278	18,600	0.0170	38,000	0.0030
40-50	179,800	0.0123	7,200	0.0066	27,000	0.0021
50-60	187,800	0.0088	1,200	0.0011	14,000	0.0011
Total	3,770,700	0.6572	694,800	0.6530	1,324,500	0.1051
					Grand Total:	5,790,000
						1.4153

[a]Avg. of eight replications - number/m^2.

[b]Dry weight in g/m^2.

Table A2. Continued.

March, 1972

Grazed						
	Plant Feeding		Predacious		Saprophagous	
Depth (cm)	Number	Biomass	Number	Biomass	Number	Biomass
0-5	1,180,500[a]	0.0933[b]	220,000	0.2091	677,500	0.0539
5-10	785,500	0.1024	123,000	0.1153	125,500	0.0100
10-20	1,290,400	0.1757	125,600	0.1170	116,000	0.0092
20-30	641,000	0.0715	30,000	0.0274	36,000	0.0029
30-40	265,600	0.0170	11,400	0.0104	39,000	0.0031
40-50	149,800	0.0083	13,200	0.0121	28,000	0.0022
50-60	43,600	0.0034	11,400	0.0104	5,000	0.0004
Total	4,356,400	0.4716	534,600	0.5017	1,027,000	0.0817

Grand Total: 5,918,000
1.0550

Ungrazed						
	Plant Feeding		Predacious		Saprophagous	
Depth (cm)	Number	Biomass	Number	Biomass	Number	Biomass
0-5	931,300	0.1205	327,700	0.3173	575,000	0.0457
5-10	910,200	0.2248	214,300	0.2026	190,000	0.0151
10-20	1,035,800	0.2283	198,200	0.1870	73,000	0.0058
20-30	663,600	0.1366	130,400	0.1198	48,000	0.0038
30-40	612,800	0.0463	19,200	0.0176	19,000	0.0015
40-50	308,600	0.0152	5,400	0.0049	34,000	0.0027
50-60	99,200	0.0039	1,800	0.0016	42,000	0.0033
Total	4,561,500	0.7756	897,000	0.8508	981,000	0.0779

Grand Total: 6,439,500
1.7043

[a]Avg. of six replications - number/m^2.

[b]Dry weight in g/m^2.

Table A2. Continued.

June, 1972

Grazed

Depth (cm)	Plant Feeding Number	Plant Feeding Biomass	Predacious Number	Predacious Biomass	Saprophagous Number	Saprophagous Biomass
0-5	1,241,900[a]	0.1123[b]	300,100	0.2792	1,061,000	0.0843
5-10	1,199,700	0.0994	133,800	0.1236	197,500	0.0157
10-20	1,088,000	0.1243	62,000	0.0573	80,000	0.0064
20-30	635,000	0.0732	48,000	0.0439	62,000	0.0049
30-40	461,600	0.0447	38,400	0.0355	50,000	0.0040
40-50	211,600	0.0137	11,400	0.0104	68,000	0.0054
50-60	60,400	0.0036	9,600	0.0088	49,000	0.0039
Total	4,898,200	0.4712	603,300	0.5587	1.567,500	0.1246

Grand Total: 7,069,000
1.1545

Ungrazed

Depth (cm)	Plant Feeding Number	Plant Feeding Biomass	Predacious Number	Predacious Biomass	Saprophagous Number	Saprophagous Biomass
0-5	581,200	0.0716	219,800	0.2068	567,000	0.0451
5-10	527,300	0.1291	83,700	0.0797	140,000	0.0111
10-20	668,400	0.1770	185,600	0.1804	123,000	0.0098
20-30	525,800	0.1102	77,200	0.0737	13,000	0.0010
30-40	321,400	0.0394	24,600	0.0225	36,000	0.0029
40-50	367,800	0.0251	7,200	0.0066	25,000	0.0020
50-60	143,600	0.0114	5,400	0.0049	11,000	0.0009
Total	3,135,500	0.5638	603,500	0.5746	915,000	0.0728

Grand Total: 4,654,000
1.2112

[a]Avg. of six replications - number/m^2.

[b]Dry weight in g/m^2.

Table A2. Continued.

July, 1972

Grazed

Depth (cm)	Plant Feeding Number	Plant Feeding Biomass	Predacious Number	Predacious Biomass	Saprophagous Number	Saprophagous Biomass
0-5	1,785,100[a]	0.1343[b]	268,900	0.2517	1,254,000	0.0997
5-10	768,700	0.0632	125,300	0.1159	205,500	0.0163
10-20	783,000	0.0624	82,000	0.0762	73,000	0.0058
20-30	610,200	0.0374	30,800	0.0284	58,000	0.0046
30-40	394,800	0.0232	24,200	0.0224	32,000	0.0025
40-50	399,000	0.0188	18,000	0.0165	40,000	0.0032
50-60	152,800	0.0095	16,200	0.0148	21,000	0.0017
Total	4,893,600	0.3488	565,400	0.5259	1,683,500	0.1338

Grand Total: 7,142,500
1.0085

Ungrazed

Depth (cm)	Plant Feeding Number	Plant Feeding Biomass	Predacious Number	Predacious Biomass	Saprophagous Number	Saprophagous Biomass
0-5	752,700	0.0917	290,300	0.2728	679,000	0.0540
5-10	986,200	0.3045	178,800	0.1687	179,000	0.0142
10-20	1,123,200	0.2380	158,800	0.1520	158,000	0.0126
20-30	907,200	0.1148	134,800	0.1301	54,000	0.0043
30-40	654,000	0.0736	45,000	0.0419	25,000	0.0020
40-50	744,600	0.0469	23,400	0.0214	13,000	0.0010
50-60	383,200	0.0166	10,800	0.0099	19,000	0.0015
Total	5,551,100	0.8861	841,900	0.7968	1,127,000	0.0896

Grand Total: 7,520,000
1.7725

[a]Avg. of eight replications - number/m^2.

[b]Dry weight in g/m^2.

Table A2. Continued.

September, 1972

Grazed

Depth (cm)	Plant Feeding Number	Plant Feeding Biomass	Predacious Number	Predacious Biomass	Saprophagous Number	Saprophagous Biomass
0-5	1,138,900[a]	0.1023[b]	249,600	0.2343	976,000	0.0776
5-10	648,700	0.0791	123,300	0.1159	113,500	0.0090
10-20	832,800	0.0925	100,200	0.0946	116,000	0.0092
20-30	688,200	0.0468	53,800	0.0508	65,000	0.0052
30-40	329,200	0.0159	34,800	0.0344	36,000	0.0029
40-50	189,600	0.0145	5,400	0.0053	62,000	0.0049
50-60	147,000	0.0030	0	0	16,000	0.0013
Total	3.974,400	0.3541	567,100	0.5353	1,384,500	0.1101

Grand Total: 5,926,000
0.9995

Ungrazed

Depth (cm)	Plant Feeding Number	Plant Feeding Biomass	Predacious Number	Predacious Biomass	Saprophagous Number	Saprophagous Biomass
0-5	363,600	0.0412	165,900	0.1586	575,500	0.0458
5-10	578,100	0.1030	140,400	0.1336	131,500	0.0105
10-20	775,400	0.1314	175,600	0.1718	71,000	0.0056
20-30	543,400	0.0460	49,600	0.0473	46,000	0.0037
30-40	285,200	0.0255	39,800	0.0400	30,000	0.0024
40-50	226,800	0.0107	10,200	0.0097	16,000	0.0013
50-60	100,000	0.0046	0	0	45,000	0.0036
Total	2,872,500	0.3624	581,500	0.5610	915,000	0.0729

Grand Total: 4,369,000
0.9963

[a]Avg. of six replications - number/m^2.

[b]Dry weight in g/m^2.

Table A3. The analysis of variance for 1970 nematode number and biomass data by trophic levels.

Numbers

Source	df	ss	ms	F	Sign.
Treatment (Trt)	1	18773.37	18773.37	0.65	NS
Date (Da)	2	1320343.00	660171.30	22.99	***
Depth (De)	6	19005020.00	3167503.00	110.31	***
Trophic (Trp)	2	10922080.00	5461039.00	190.19	***
Trt x Da	2	78720.78	39360.39	1.37	NS
Trt x De	6	461217.30	76869.55	2.68	**
Da x De	12	1310693.00	109224.40	3.80	***
Trt x Trp	2	57244.78	28622.39	1.00	NS
Da x Trp	4	699868.70	174967.20	6.09	***
De x Trp	12	5681418.00	473451.50	16.49	***
Tri x Da x De	12	258776.60	21564.71	0.75	NS
Trt x Da x Trp	4	178902.20	44725.56	1.56	NS
Trt x De x Trp	12	488479.90	40706.66	1.42	NS
Da x De x Trp	24	1218904.00	50787.68	1.77	**
Trt x Da x De x Trp	24	651484.10	27145.17	0.95	NS
Error	630		28713.52		

Biomass

Source	df	ss	ms	F	Sign.
Treatment (Trt)	1	85281.07	85281.07	3.07	*
Date (Da)	2	2787748.00	1393874.00	50.17	***
Depth (De)	6	18364320.00	3060721.00	110.17	***
Trophic (Trp)	2	9716697.00	4858348.00	174.87	***
Trt x Da	2	100781.60	50390.82	1.81	NS
Trt x De	6	891144.80	148524.10	5.35	***
Da x De	12	2944653.00	245387.70	8.83	***
Trt x Trp	2	104050.60	52025.31	1.87	NS
Da x Trp	4	954603.10	238650.80	8.59	***
De x Trp	12	6812333.00	567694.40	20.43	***
Trt x Da x De	12	307704.00	25642.00	0.92	NS
Trt x Da x Trp	4	78779.44	19694.86	0.71	NS
Trt x De x Trp	12	628679.60	52389.97	1.89	**
Da x De x Trp	24	2922907.00	121787.80	4.38	***
Trt x Da x De x Trp	24	459587.40	19149.48	0.69	NS
Error	630		27782.75		

NS: Nonsignificant at .10 level.
*: Significant at .10 level.
**: Significant at .05 level.
***: Significant at .01 level.

Table A4. The analysis of variance for 1971 nematode number and biomass data by trophic levels.

Numbers

Source	df	ss	ms	F	Sign.
Treatment (Trt)	1	26133.33	26133.33	1.07	NS
Date (Da)	2	1779015.00	889507.70	36.42	***
Depth (De)	5	14139780.00	2827955.00	115.78	***
Trophic (Trp)	2	8096411.00	4048205.00	165.74	***
Trt x Da	2	19303.72	9651.86	0.40	NS
Trt x De	5	431140.80	86228.16	3.53	***
Da x De	10	599547.30	59954.73	2.45	***
Trt x Trp	2	155862.00	77931.00	3.19	**
Da x Trp	4	880354.20	220088.60	9.01	***
De x Trp	10	4155994.00	415599.40	17.02	***
Trt x Da x De	10	60939.17	6093.92	0.25	NS
Trt x Da x Trp	4	56976.11	14244.03	0.58	NS
Trt x De x Trp	10	1081714.00	108171.40	4.43	***
Da x De x Trp	20	997176.10	49858.81	2.04	***
Trt x Da x De x Trp	20	311185.30	15559.27	0.64	NS
Error	678		24424.53		

Biomass

Source	df	ss	ms	F	Sign.
Treatment (Trt)	1	381938.90	381938.90	16.79	***
Date (Da)	2	4208916.00	2104458.00	92.52	***
Depth (De)	5	10597790.00	2119559.00	93.18	***
Trophic (Trp)	2	4274562.00	2137281.00	93.96	***
Trt x Da	2	121497.60	60748.79	2.67	*
Trt x De	5	269237.30	53847.45	2.37	**
Da x De	10	3474480.00	347448.00	15.27	***
Trt x Trp	2	183387.50	91693.77	4.03	**
Da x Trp	4	1582676.00	395668.90	17.39	***
De x Trp	10	3735111.00	373511.10	16.42	***
Trt x Da x De	10	521660.00	52116.00	2.29	**
Trt x Da x Trp	4	65933.56	16483.39	0.72	NS
Trt x De x Trp	10	369844.20	36984.42	1.63	*
Da x De x Trp	20	2655328.00	132766.40	5.84	***
Trt x Da x De x Trp	20	365374.90	18268.75	0.80	NS
Error	678		22746.24		

NS: Nonsignificant at .10 level.
*: Significant at .10 level.
**: Significant at .05 level.
***: Significant at .01 level.

Table A5. The analysis of variance for 1972 nematode number and biomass data by trophic levels.

Numbers

Source	df	ss	ms	F	Sign.
Treatment (Trt)	1	375448.60	375448.60	20.52	***
Date (Da)	3	538693.90	179564.60	9.81	***
Depth (De)	6	30476430.00	5079406.00	277.59	***
Trophic (Trp)	2	1549762.00	7748811.00	423.48	***
Trt x Da	3	299879.00	99959.66	5.46	***
Trt x De	6	2895979.00	482663.20	26.38	***
Da x De	18	758855.70	42158.65	2.30	***
Trt x Trp	2	338510.90	169255.50	9.25	***
Da x Trp	6	565522.90	94253.81	5.15	***
De x Trp	12	9104265.00	758688.70	41.46	***
Trt x Da x De	18	862493.90	47916.33	2.62	***
Trt x Da x Trp	6	208553.80	34758.97	1.90	*
Trt x De x Trp	12	1774756.00	147896.30	8.08	***
Da x De x Trp	36	683006.10	18972.39	1.04	NS
Trt x Da x De x Trp	36	730836.80	20301.02	1.11	NS
Error	923		18298.00		

Biomass

Source	df	ss	ms	F	Sign.
Treatment (Trt)	1	1213514.00	1213514.00	44.03	***
Date (Da)	3	965769.60	321923.20	11.68	***
Depth (De)	6	35608530.00	5934755.00	215.31	***
Trophic (Trp)	2	17312440.00	8656218.00	314.05	***
Trt x Da	3	1049545.00	349848.30	12.69	***
Trt x De	6	2643658.00	440609.70	15.99	***
Da x De	18	1220357.00	66797.61	2.46	***
Trt x Trp	2	1089012.00	544506.00	19.75	***
Da x Trp	6	710785.20	118464.20	4.30	***
De x Trp	12	17660220.00	1471685.00	53.39	***
Trt x Da x De	18	1528674.00	84926.31	3.08	***
Trt x Da x Trp	6	735356.80	122559.50	4.45	***
Trt x De x Trp	12	1390923.00	115910.30	4.21	***
Da x De x Trp	36	1134428.00	31511.89	1.14	NS
Trt x Da x De x Trp	36	1519465.00	42207.36	1.53	**
Error	923		27563.35		

NS: Nonsignificant at .10 level.
*: Significant at .10 level.
**: Significant at .05 level.
***: Significant at .01 level.

Table A6. The effects of grazing intensity, sampling date and sampling depth on numbers of nematodes at the Cottonwood site.

		Taxa grouping								
	Depth (cm)	*Tylenchorhynchus*	*Helicotylenchus*	*Paratylenchus*	Tylenchinae-Psilenchinae	*Xiphinema*	*Pratylenchus*	Dorylaimida	*Mononchus*	Rhabditida
July, 1970	0-5	579[a]	462	22	619	10	10	1234	16	1698
	5-10	294	1068	144	345	45	78	456	6	674
	10-20	37	824	120	220	51	50	238	0	157
Grazed	20-30	9	463	84	272	19	6	58	0	92
	30-40	0	177	64	91	0	0	37	0	50
	40-50	0	71	55	73	0	0	86	0	42
	50-60	0	13	19	14	0	0	56	0	66
	0-5	312	368	156	729	62	51	1080	17	1660
	5-10	306	419	290	547	306	0	579	0	546
	10-20	100	245	365	404	223	3	219	17	284
Ungrazed	20-30	14	147	206	137	8	0	61	3	69
	30-40	0	219	161	159	3	0	43	0	58
	40-50	0	201	181	204	0	0	61	0	48
	50-60	0	33	243	71	0	0	26	0	37
August, 1970	0-5	2092	206	87	413	0	26	596	13	1197
	5-10	160	219	167	199	7	74	455	0	294
	10-20	4	317	94	158	13	53	271	13	100
Grazed	20-30	0	362	66	123	0	0	123	0	51
	30-40	0	214	80	104	0	0	52	0	60
	40-50	0	37	97	37	0	0	25	0	23
	50-60	0	6	23	20	0	0	25	0	23
	0-5	287	74	687	362	33	7	374	20	1376
	5-10	567	40	481	241	146	0	492	13	328
	10-20	130	90	328	150	147	4	187	10	101
Ungrazed	20-30	6	237	224	117	13	4	128	4	33
	30-40	4	201	40	66	4	6	96	4	33
	40-50	4	70	56	101	0	0	25	0	36
	50-60	10	20	13	66	0	0	84	0	28

Table A6. Continued.

	Depth (cm)	Tylenchorhynchus	Helicotylenchus	Paratylenchus	Tylenchinae-Psilenchinae	Xiphinema	Pratylenchus	Dorylaimida	Mononchus	Rhabditida
September, 1970 Grazed	0-5	948	17	23	172	14	23	463	17	1369
	5-10	59	71	40	23	0	6	234	6	206
	10-20	3	206	88	188	4	9	83	3	100
	20-30	0	224	35	139	0	3	38	0	41
	30-40	0	180	14	43	0	0	22	0	20
	40-50	0	21	20	23	0	0	19	0	38
	50-60	0	3	17	24	0	0	4	0	61
Ungrazed	0-5	100	6	401	625	14	0	377	46	979
	5-10	71	94	211	541	14	0	380	6	189
	10-20	0	200	371	265	90	0	184	0	204
	20-30	0	324	100	123	30	0	83	0	77
	30-40	0	391	53	183	0	0	48	0	46
	40-50	3	127	82	95	0	0	32	0	49
	50-60	0	14	25	53	0	0	9	0	32
April, 1971 Grazed	0-10	230	808	93	683	4	29	357	17	795
	10-20	12	154	14	140	7	0	4	0	12
	20-30	0	20	12	131	0	0	0	0	32
	30-40	0	23	17	119	0	0	0	0	47
	40-50	0	3	14	9	0	0	0	0	11
	50-60	0	3	25	7	0	0	0	0	32
Ungrazed	0-10	84	166	108	413	184	0	435	68	1093
	10-20	30	103	128	222	64	3	48	4	58
	20-30	0	23	9	119	0	0	0	0	44
	30-40	0	56	14	287	0	0	4	0	38
	40-50	0	35	6	125	0	0	0	0	21
	50-60	0	12	9	64	0	0	0	0	17

Taxa grouping

Table A6. Continued.

	Depth (cm)	Tylenchorhynchus	Helicotylenchus	Paratylenchus	Tylenchinae-Psilenchinae	Xiphinema	Pratylenchus	Dorylaimida	Mononchus	Rhabditida
July, 1971	0-5	859	14	589	440	0	27	387	23	2142
	5-10	238	104	359	333	0	4	204	0	417
	10-20	4	149	339	467	15	7	79	0	173
Grazed	20-30	25	310	95	450	19	2	45	0	75
	30-40	6	99	43	337	4	0	53	0	74
	40-50	2	84	40	182	0	2	30	0	52
	50-60	0	16	88	59	0	0	15	0	30
	0-5	126	95	387	531	57	4	481	123	1695
	5-10	193	104	266	536	32	4	136	17	423
	10-20	83	122	267	342	64	2	117	18	157
Ungrazed	20-30	0	180	95	272	14	2	53	6	57
	30-40	0	184	104	305	0	0	61	0	64
	40-50	0	144	13	326	0	0	22	0	83
	50-60	0	25	9	148	0	0	24	0	33
October, 1971	0-5	784	98	514	872	4	13	650	0	1582
	5-10	111	404	299	303	49	13	381	0	279
	10-20	4	482	197	350	128	11	199	0	102
Grazed	20-30	0	367	70	180	38	6	76	0	69
	30-40	0	91	38	187	11	0	25	0	43
	40-50	0	18	22	146	2	0	13	0	31
	50-60	0	0	27	31	0	0	0	0	20
	0-5	120	0	240	459	43	0	492	123	1659
	5-10	98	67	362	346	328	17	433	78	368
	10-20	58	75	454	219	343	22	282	28	185
Ungrazed	20-30	0	224	232	157	7	25	131	14	47
	30-40	0	133	29	136	6	20	31	0	38
	40-50	0	56	13	100	2	4	12	0	27
	50-60	0	6	2	175	4	0	2	0	14

Table A6. Continued.

	Depth (cm)	Tylenchorhynchus	Helicotylenchus	Paratylenchus	Tylenchinae-Psilenchinae	Xiphinema	Pratylenchus	Dorylaimida	Mononchus	Rhabditida
March, 1972	0-5	835	79	250	967	11	11	520	128	1355
	5-10	467	201	260	362	130	17	335	45	251
	10-20	125	551	152	286	107	0	181	17	116
Grazed	20-30	51	273	66	192	36	3	50	0	36
	30-40	5	69	52	126	3	3	19	0	39
	40-50	0	25	41	75	0	0	22	0	28
	50-60	0	3	11	22	0	0	19	0	5
Ungrazed	0-5	305	274	160	753	123	0	619	284	1150
	5-10	200	250	295	360	496	5	536	107	380
	10-20	98	309	153	150	222	0	252	47	73
	20-30	14	212	93	139	122	0	209	5	48
	30-40	0	255	59	279	7	0	32	0	19
	40-50	3	63	25	214	0	0	9	0	34
	50-60	0	9	8	81	0	0	3	0	42
June, 1972	0-5	528	33	82	1445	30	17	872	77	2122
	5-10	550	200	105	1315	54	11	411	21	395
	10-20	95	256	78	517	90	14	95	5	80
Grazed	20-30	9	298	70	192	34	0	80	0	62
	30-40	3	214	37	175	9	0	59	3	50
	40-50	0	45	17	139	3	0	19	0	68
	50-60	0	5	35	14	0	0	16	0	49
Ungrazed	0-5	139	38	129	568	53	5	576	94	1134
	5-10	250	39	107	277	304	0	194	51	280
	10-20	64	67	97	164	210	0	166	86	123
	20-30	9	161	78	127	116	0	87	25	13
	30-40	0	169	39	78	19	0	41	0	36
	40-50	0	133	115	109	6	0	12	0	25
	50-60	0	56	28	53	3	0	9	0	11

Table A6. Continued.

	Depth (cm)	Tylenchorhynchus	Helicotylenchus	Paratylenchus	Tylenchinae-Psilenchinae	Xiphinema	Pratylenchus	Dorylaimida	Mononchus	Rhabditida
		Taxa grouping								
July, 1972	0-5	1100	13	573	1547	38	4	738	95	2508
	5-10	156	57	714	390	56	12	381	22	411
	10-20	32	150	278	248	25	2	120	10	73
Grazed	20-30	6	159	169	246	5	6	48	2	58
	30-40	2	85	75	216	2	0	37	2	32
	40-50	0	46	94	245	2	0	30	0	40
	50-60	0	28	36	78	0	0	27	0	21
	0-5	150	8	436	524	75	4	771	118	1358
	5-10	195	59	367	383	786	0	456	84	358
	10-20	53	170	366	185	280	0	173	55	158
Ungrazed	20-30	4	232	321	203	94	0	133	25	54
	30-40	2	263	192	126	45	0	65	6	25
	40-50	0	241	237	244	7	0	39	0	13
	50-60	0	58	171	145	2	0	18	0	19
September, 1972	0-5	757	52	150	1028	24	0	667	99	1952
	5-10	309	202	70	479	101	6	326	51	227
	10-20	26	197	81	409	59	10	127	24	116
Grazed	20-30	29	187	75	366	4	0	68	13	65
	30-40	0	52	58	210	0	0	23	21	36
	40-50	3	19	78	75	13	0	4	3	62
	50-60	0	6	114	27	0	0	0	0	16
	0-5	154	67	111	239	9	0	368	111	1151
	5-10	129	142	188	370	190	6	328	84	263
	10-20	39	145	136	267	129	3	141	91	71
Ungrazed	20-30	19	116	168	193	25	0	56	16	46
	30-40	3	100	62	101	12	0	18	29	30
	40-50	0	45	64	113	0	0	12	3	16
	50-60	0	23	16	61	0	0	0	0	45

[a]Number of nematodes/100 cc of soil.

Table A7. The analysis of variance for 1970 nematode number data by taxa.

Tylenchorhynchus spp.

Source	df	ss	ms	F	Sign.
Month (M)	2	168557.5	84278.7	2.39	*
Treatment (T)	1	123771.4	123771.4	3.52	*
Depth (D)	6	2570582.0	428430.3	12.17	***
M x T	2	39902.7	19951.4	.57	NS
M x D	12	602092.9	50174.4	1.43	NS
T x D	6	1326993.0	221165.5	6.28	***
M x T x D	12	617031.0	51419.2	1.46	NS
Error	210	7390047.0	35190.7		

Helicotylenchus spp.

Source	df	ss	ms	F	Sign.
Month (M)	2	387114.4	193557.2	14.59	***
Treatment (T)	1	74845.9	74845.9	5.64	**
Depth (D)	6	510124.6	85020.8	6.41	***
M x T	2	138609.6	69304.8	5.22	***
M x D	12	482702.6	40225.2	3.03	***
T x D	6	184195.2	30699.2	2.31	**
M x T x D	12	134772.8	11231.1	.85	NS
Error	210	2785335.0	13263.5		

Xiphinema spp.

Source	df	ss	ms	F	Sign.
Month (M)	2	11625.3	5812.7	16.18	***
Treatment (T)	1	20152.4	20152.4	56.10	***
Depth (D)	6	56525.7	9420.9	26.23	***
M x T	2	4235.6	2117.8	5.90	***
M x D	12	25969.3	2164.1	6.02	***
T x D	6	35802.6	5967.1	16.61	***
M x T x D	12	13852.4	1154.4	3.21	***
Error	210	75432.0	359.2		

NS: Nonsignificant at .10 level.
*: Significant at .10 level.
**: Significant at .05 level.
***: Significant at .01 level.

Table A8. The analysis of variance for 1971 nematode number data by taxa.

Tylenchorhynchus spp.

Source	df	ss	ms	F	Sign.
Month (M)	2	129603.6	64801.8	3.28	**
Treatment (T)	1	143737.3	143737.3	7.29	**
Depth (D)	5	1390449.0	278089.7	14.11	***
M x T	2	41776.2	20888.1	1.06	NS
M x D	10	266572.4	26657.2	1.35	NS
T x D	5	780489.4	156097.9	7.92	***
M x T x D	10	213672.8	21367.3	1.08	NS
R(MTD)	36	709429.5	19706.4		
P(RMTD)	190	2304282.0	12127.8	1.62	**

Helicotylenchus spp.

Source	df	ss	ms	F	Sign.
Month (M)	2	59138.1	29569.0	1.10	NS
Treatment (T)	1	157641.1	157641.1	5.87	**
Depth (D)	5	184860.8	36972.2	1.38	NS
M x T	2	110010.2	55005.1	2.05	NS
M x D	10	717933.7	71793.4	2.67	**
T x D	5	225113.8	45002.8	1.68	NS
M x T x D	10	501664.6	50166.5	1.87	*
R(MTD)	36	966823.5	26856.2		
P(RMTD)	190	3629817.0	19104.3		

Xiphinema spp.

Source	df	ss	ms	F	Sign.
Month (M)	2	34251.7	17125.9	26.91	***
Treatment (T)	1	22901.8	22901.8	35.99	***
Depth (D)	5	40035.2	8007.0	12.58	***
M x T	2	9535.7	4767.9	7.49	***
M x D	10	70488.3	7048.8	11.08	***
T x D	5	21125.9	4225.2	6.64	***
M x T x D	10	29845.6	2984.6	4.69	***
Error	226	143803.8	636.3		

NS: Nonsignificant at .10 level.
*: Significant at .10 level.
**: Significant at .05 level.
***: Significant at .01 level.

Table A9. The analysis of variance for 1972 nematode number data by taxa.

Tylenchorhynchus spp.

Source	df	ss	ms	F	Sign.
Month (M)	3	15888.6	5296.2	.88	NS
Treatment (T)	1	189778.6	189778.6	31.60	***
Depth (D)	6	1779507.0	296584.5	49.38	***
M x T	3	1208.6	402.9	.07	NS
M x D	18	157350.9	8741.7	1.46	*
T x D	6	638156.9	106359.5	17.71	***
M x T x D	18	121784.9	6765.8	1.13	NS
Error	308	1849940.4	6006.3		

Source	df	ss	ms	F	Sign.
Month (M)	3	37700.3	12566.8	3.16	**
Treatment (T)	1	0.9	0.9	.00	NS
Depth (D)	6	301601.7	50266.9	12.65	***
M x T	3	27678.1	9226.0	2.32	*
M x D	18	138841.3	7713.4	1.94	**
T x D	6	69434.5	11572.4	2.91	***
M x T x D	18	41143.1	2285.7	.58	NS
Error	308	1224053.6	3974.2		

Xiphinema spp.

Source	df	ss	ms	F	Sign.
Month (M)	3	30575.8	10191.9	6.48	***
Treatment (T)	1	104665.0	104665.0	66.51	***
Depth (D)	6	436358.9	72726.5	46.22	***
M x T	3	37493.9	12498.0	7.94	***
M x D	18	80428.9	4468.3	2.84	***
T x D	6	193246.9	32207.8	20.47	***
M x T x D	18	95133.7	5285.2	3.36	***
Error	308	484668.8	1573.6		

NS: Nonsignificant at .10 level.
*: Significant at .10 level.
**: Significant at .05 level.
***: Significant at .01 level.

Table A10. The analysis of variance for data obtained on July 21, 1972 sampling in the nematicide study at the Cottonwood site.

Plant feeding

Source	df	ss	ms	F	Sign.
Total	70	21265.98			
Total reduction	46	20548.97	446.71		
Mu-Ym	1	12327.88	12327.88		
Treatment (T)	1	2054.46	2054.46	50.09	***
Replications (R)	4	70.43	17.60	0.59	NS
Depth (D)	6	2613.87	435.64	21.75	***
T x R	4	164.37	41.09	1.38	NS
T x D	6	2816.10	469.35	15.71	***
R x D	24	501.83	20.90	0.70	NS
Remainder	24	717.01	29.87		

Predacious

Source	df	ss	ms	F	Sign.
Total	70	8275.02			
Total reduction	46	7888.77	171.50		
Mu-Ym	1	3630.46	3630.46		
Treatment (T)	1	194.45	194.45	16.16	***
Replications (R)	4	16.22	4.06	0.25	NS
Depth (D)	6	3395.60	565.93	57.65	***
T x R	4	48.58	12.15	0.76	NS
T x D	6	366.25	61.04	3.79	**
R x D	24	237.20	9.88	0.61	NS
Remainder	24	386.25	16.09		

Saprophagous

Source	df	ss	ms	F	Sign.
Total	70	16144.92			
Total reduction	46	15827.38	344.07		
Mu-Ym	1	6587.83	6587.83		
Treatment (T)	1	648.28	648.28	28.17	***
Replications (R)	4	93.18	23.29	1.76	NS
Depth (D)	6	6852.72	1142.12	86.57	***
T x R	4	94.75	23.69	1.79	NS
T x D	6	1204.22	200.70	15.17	***
R x D	24	346.40	14.43	1.09	NS
Remainder	24	317.54	13.23		

NS: Nonsignificant at .10 level.
*: Significant at .10 level.
**: Significant at .05 level.
***: Significant at .01 level.