Nematode Density and Biomass in an Annual Grassland Ecosystem

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Abstract

The nematode community structure was examined in grazed and ungrazed annual-plant rangeland on the US/IBP Grassland Biome San Joaquin Site located in the foothill-grasslands of central California. Nematode numbers and biomass were estimated from early growth to mature stages of the annual-plant vegetation. Nematode density was greater on the grazed area, predominately forbs, than on the ungrazed, mainly grass, area. A lower than normal precipitation appeared to be a limiting factor of nematode population density. The nematode trophic structure differed between the two sites, fungivores and microbivores predominating on the grazed and ungrazed sites, respectively. Indications are that the critical factors controlling nematode density and community structure on this annual grassland are not grazing but soil moisture and temperature.

Yuen (1966), Schmitt and Norton (1972), Schmitt (1973), Stanton (1974), Yeates (1974), and Smolik and Rogers (1976) have studied the function of nematodes in belowground grassland ecosystems; however, knowledge of nematodes from the California annual grassland ecosystem is almost non-existent. Recent investigations in the mixed-grass prairie of South Dakota (Smolik 1974) provided evidence that nematodes constituted a significant pathway of energy flow, and that the application of nematicides significantly reduced nematode populations resulting in large increases in herbage production. Also, phytophagic nematode biomass was significantly higher in an ungrazed pasture than in a grazed pasture. A preliminary study in the shrub-steppe area of south-central Washington (Smolik and Rogers 1976) revealed large numbers of soil-dwelling nematodes but no consistent differences in nematode density or biomass between grazed, ungrazed, and burned areas.

In 1972, the annual grassland site of the United States International Biological Program (US/IBP), Grassland Biome, was established at the U.S. Forest Service's San Joaquin Experimental Range, 40 km northeast of Fresno, California. For a 3-year period, data were collected on abiotic, producer, consumer, and decomposer components of the ecosystem (Duncan 1975). A preliminary soil sampling program was undertaken in 1974 to estimate the importance of nematodes at the San Joaquin site. Soil samples were taken on two dates (March 13 and May 1, 1974) in the grazed and ungrazed portions of the US/IBP site, refrigerated and air-freighted to Dr. J.D. Smolik, Plant Science Department, South Dakota State University, Brookings. Nematodes were extracted by the Christie-Perry (1951) method, and a correction of 73% for extraction efficiency was used. Results of this preliminary effort indicated nematodes could be important components in the functioning of the annual grassland ecosystem. Numbers of nematodes were considerably higher in the May sample than in March on the ungrazed area, with an average of 5 to 12 $\times$ $10^6/m^2$ to a depth of 60 cm for the two dates.[1] Biomass varied from about 623 to 1,309 mg/m^2 (dry weight).

This limited study was conducted in 1976 to further investigate the importance of nematodes in a grazed and ungrazed annual grassland ecosystem. Importance in an ecosystem is often determined by measuring parameters such as nematode density and biomass at different seasons and making estimates of nematode metabolism and productivity.

Study Area

The San Joaquin Experimental Range is representative of the granitic soil area in lower foothill annual grasslands in central California. The area is the annual plant-oak woodland type, with scattered trees and brush. The herbaceous vegetation is made up almost entirely of annual plants. The nematode study area was within the US/IBP site, which is an open grassland area. The study area for nematode investigations was a uniform area of Ahwahnee coarse, sandy loam soil, moderately deep, on a 10% slope with northern exposure. The site was the open rolling slope described by Bentley and Talbot (1951), which is intermediate in herbage production between the swale or gentle slope sites and the rocky, steep slope sites comprising most of the area on the Experimental Range. Yearlong grazing by cows and calves constituted the grazed treatment, which was separated from the ungrazed area by a barbed wire fence (Fig. 1). The ungrazed area had not been grazed since 1971.

Methods

Two plots of 1 square foot (30.48 cm^2) each in the grazed and the ungrazed areas were selected at random for each of five sampling dates from January 21 to May 24, 1976. The annual vegetation in these plots during this period ranged from early vegetative in January to mature stages in May. Aboveground biomass was determined by clipping the vegetation to ground level for both grazed and ungrazed plots inside a square-foot frame at each sampling period. Current year vegetation was placed in a labeled paper bag, oven dried at 60°C, and total dry weight determined. The vegetation was then sorted into species and groups: *Bromus mollis, B. diandrus, Vulpia megalura, Erodium* spp. *Trifolium* spp., *Lotus purshianus* miscellaneous legumes, and miscellaneous forbs other than legumes. Litter from the prior years' growth

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[1] Smolik, J.D. 1975. Unpublished results.

Fig. 1. *Nematode study area, San Joaquin Experimental Range, 1976. Grazed area on left, ungrazed on right.*

was collected with a heavy duty field vacuum, oven dried, weighed, and ashed.

After the current year's vegetation and litter from previous years were removed, three soil cores were taken from each plot. The soil tubes, 5 cm in diameter, were driven into the soil to a depth of 60 cm with a power driver. Two soil cores were used for nematode analysis and the other for determination of soil gravimetric water. Each core was divided into 10-cm segments, and soil temperatures were measured in the center of each soil core segment with calibrated thermometers. Then each segment was placed in a labeled plastic bag and sealed. All soil core samples were collected between 9:00 a.m. and noon.

Each 10-cm soil core segment for nematode analysis was mixed and a 50-cm^3 subsample was placed on a Baermann funnel for 48 h. The extracted nematodes were counted and identified as one of four trophic groups based on feeding habits or relationship to known trophic group: microbivores, mainly Cephalobidae and Rhabditida; omnivore-predators, Dorylamida, excluding *Xiphinema* spp, *Longidorus* spp., and *Trichodorus* spp.; phytophagic nematodes, Tylenchida; and fungivores, *Aphelenchus, Aphelenchoides,* and *Ditylenchus* spp. (Table 1). A fifth group was composed of nematodes which were damaged or unidentifiable. Numbers of nematodes were corrected for extraction efficiency of 26% and density of nematodes was calculated as number/m^2. Body weights of the nematode population were determined by length and width measurements of 250-300 randomly selected nematodes and calculations were according to Andrassy (1956). Biomass was expressed as mg/m^2. Results are based on analysis of four of the five samples, February to May. Extracted nematodes from January samples were destroyed accidentally.

Table 1. Taxonomic list of nematodes at the San Joaquin Experimental Range.

Plant Feeders:	Microbivores:
Hemicycliophora sp.	*Acrobeles* sp.
Heterodera sp.	*Acrobeloides* sp.
Meloidogyne sp.	*Anaplectus* sp.
Paratylenchus sp.	*Cephalobus* sp.
Pratylenchus sp.	*Cervidellus* sp.
Trichodorus sp.	*Elaphonema* sp.
Tylenchorhynchus sp.	*Eucephalobus* sp.
	Plectus spp.
	Rhabditis spp.
Fungivores:	Omnivore-Predators:
Aphelenchus sp.	*Aporcelaimus* sp.
Aphelenchoides sp.	*Aporcelaimellus* spp.
Pseudhalenchus sp.	*Discolaimus* sp.
Ditylenchus sp.	*Dorylaimus* spp.
Tylenchus sp.	*Eudorylaimus* sp.

Results and Discussion

Precipitation during the study period was below normal, with exception of the month of February (Table 2), and the monthly mean air temperatures followed the long-term means.

Herbage yield was considerably less than for the prior 3 years on the same area. The herbage yield was highest, 359 g/m^2, on the ungrazed area in April (Table 2). In terms of plant growth stages, the January and February sampling dates represent early slow growth; the March date was at the beginning of rapid growth, and the April date was near peak production. Virtually all the annual plants were mature and dry on the May date. The effects of prior grazing plus the unfavorable weather conditions during the growing season probably combined to result in yields at all sampling dates on the grazed area which were lower than on the ungrazed area.

Table 2. Herbage yield, composition, litter, and monthly precipitation at five sampling dates in a grazed and ungrazed grassland at the San Joaquin Experimental Range, 1976.

	January	February	March	April	May	Total
Herbage yield						
Grazed (g/m^2)	47.0	115.0	157.0	198.0	216.0	
Grasses (%)	53.3	34.4	19.5	35.8	37.2	
Forbs (%)	46.7	65.6	80.5	64.2	62.8	
Ungrazed (g/m^2)	106.0	163.0	211.0	359.0	326.0	
Grasses (%)	99.8	100.0	100.0	99.6	100.0	
Forbs (%)	0.2	0.0	0.0	0.4	0.0	
Litter						
Grazed (g/m^2)	326.0	162.0	205.0	219.0	344.0	
Ungrazed (g/m^2)	964.0	1182.0	679.0	500.0	477.0	
Precipitation						
1975-1976 (cm)	0.41	13.64	4.17	2.84	0.05	20.70
1934-1975 mean (cm)	8.53	8.76	7.42	4.90	1.40	22.48

The combination of prior use and abnormally low rainfall resulted in an unusual difference in botanical composition during the study and may have been responsible for differences in nematode density and biomass data obtained from 1974 to 1976. Vegetation on the ungrazed areas was almost entirely grasses (mainly *Bromus diandrus* and *B. mollis*), while on the grazed area it was mostly forbs (*Erodium* was the most abundant) for all but the first sample date (Table 2). Dry conditions resulted in very little legume growth in either treatment. Litter accumulation was much greater on the ungrazed area at all times.

Gravimetric soil water never reached field capacity (approximately 16%) on the sampling dates and was unusually low in both grazed and ungrazed areas in January, usually a month of relatively high precipitation. Soil moisture was highest in

February, when it was over 12% at the 0–10 cm depth and approximately 10% at lower depths. The soil was relatively dry on all subsequent dates (Fig. 2) and was less than 1% water at the 0–10 cm depth on the final sampling date in May.

Soil temperatures, expressed as a mean of temperatures at all depth increments, were always 1 to 2°C higher on grazed area (Fig. 2). Seldom was there more than 1° difference between the 0–10 and 50–60 cm core segments in either treatment during the morning sampling periods. The largest difference between the top and bottom segments was on May 25, when the soil temperatures in the ungrazed area were 26.5°C, respectively in the grazed area.

Table 3. Nematode density and biomass in grazed and ungrazed grassland at 0–60 cm depth at San Joaquin Experimental Range, 1976.[1]

Sample date	Nematode density ($\times 10^6/m^2$)		Biomass (mg/m^2)	
	Grazed	Ungrazed	Grazed	Ungrazed
February	0.94	1.82	38.3	72.0
March	4.19	3.13	175.4	125.9
April	4.81	3.85	193.4	152.9
May	2.82	1.99	112.8	79.3
Mean	3.19	2.69	130.0	107.5

[1] Corrected for extraction efficiency.

Total nematode density and biomass were highest on the grazed plot (Table 3, Fig. 2) at all sampling periods but February. The mean number of nematodes for the four sampling periods, corrected for extraction efficiency, was $3.2 \times 10^6/m^2$ at 0–60 cm depth in the grazed plot and $2.7 \times 10^6/m^2$ at 0–60 cm depth in the ungrazed plot. Nematode biomass was 130 mg/m^2 and 108 mg/m^2 at 0–60 cm on the grazed and ungrazed plots, respectively, and was at maximum in April on both plots. Nematode density was closely related to soil temperature and moisture and decreased with depth (Fig. 3). In February, when soil temperatures were low and soil moisture high, nematode density on both plots was low. As soil temperatures became

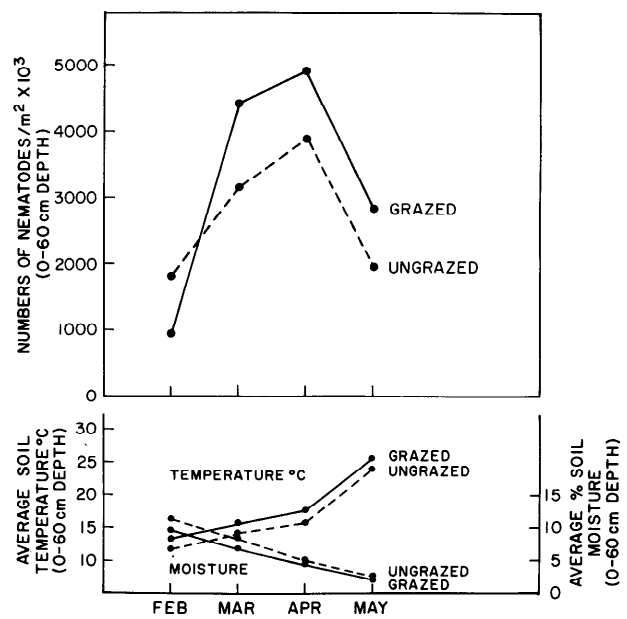

Fig. 2. *Total nematode numbers and soil moisture and temperature in grazed and ungrazed grassland at the San Joaquin Experimental Range, California, 1976.*

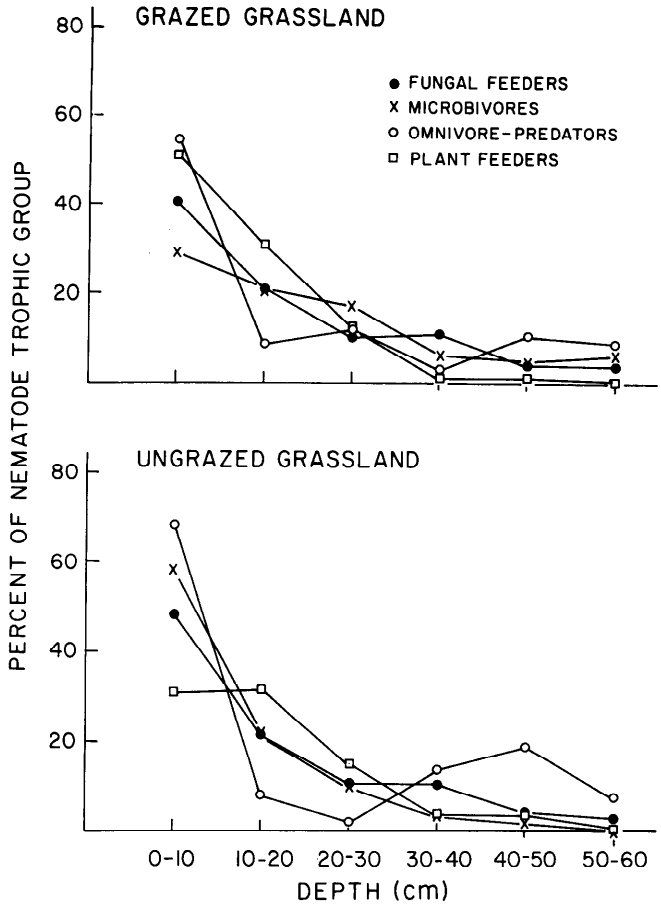

Fig. 3. *Vertical distribution of nematode trophic groups on grazed and ungrazed grassland at the San Joaquin Experimental Range, California, 1976.*

warmer and moisture levels declined to 4% to 5% in March and April, there was an increase in numbers of nematodes. Maximum nematode metabolism, production, and energy turnover probably occurred during this period when the range of soil moisture and temperature was more optimal for nematode activity. Nematode activity and density may have been minimal in May because some nematodes are known to enter an inactive state of cryptobiosis, which is brought about by unfavorable environmental conditions such as low soil moistures. Freckman (1978), working in desert soils, found the nematode community to be cryptobiotic when soil moisture was below 2.7%, and it is possible similar conditions occurred during this study. Cryptobiosis enables nematodes to survive until favorable conditions of moisture and temperature return.

A comparison of this more comprehensive study with the 1974 survey shows a reversal in numbers of nematodes on grazed and ungrazed sites. In March, 1974, there was a greater number ($7.35 \times 10^6/m^2$, 0–60 cm depth) and biomass (0.918 g/m^2, 0–60 cm depth) of nematodes in the ungrazed grassland. Results of the March 1976 sampling indicated a greater nematode density ($4.19 \times 10^6/m^2$, 0–60 cm depth) and biomass (0.175 g/m^2, 0–60 cm depth) on the grazed grassland. The trophic structure of the March, 1974, ungrazed and grazed area was respectively 80 and 60% saprovores, whereas in March, 1976, fungivores and microbivores represented the nematode community in the ungrazed area by 33 and 36% and in the grazed area by 49 and 26%, respectively (Table 4). Nematodes in all trophic groups were most abundant at the 0–10 cm depth, and numbers declined with increasing depth on both grazed and

Table 4. Monthly numbers and biomass of nematode trophic groups corrected for extraction efficiency in grazed and ungrazed grassland at San Joaquin Experimental Range, 1976.

	Number × $10^6/m^2$		Biomass (mg/m^2)	
trophic groups	Grazed	Ungrazed	Grazed	Ungrazed
Fungivores				
February	0.37	0.75	14.6	28.3
March	2.04	1.03	81.7	41.1
April	0.67	1.10	27.1	43.7
May	1.16	0.53	46.3	21.1
Total	4.24	3.41		
Microbivores				
February	0.15	0.52	6.1	20.5
March	1.08	1.12	43.4	44.6
April	0.48	0.85	19.3	33.8
May	0.99	0.94	39.7	37.8
Total	2.70	3.43		
Omnivore-predators				
February	0.15	0.12	6.4	5.1
March	0.74	0.12	29.4	5.3
April	0.09	0.25	3.6	9.7
May	0.26	0.26	10.1	10.1
Total	1.24	0.75		
Plant parasites				
February	0.18	0.31	7.1	12.7
March	0.31	0.53	12.6	21.5
April	0.12	0.10	5.3	3.7
May	0.30	0.19	11.9	7.4
Total	0.91	1.13		
Unidentifiable				
February	0.09	0.12	4.0	5.3
March	0.02	0.33	8.2	13.4
April[1]	3.45	1.55	138.1	62.0
May	0.12	0.07	4.8	2.9

[1] Ninety-five percent of all April data represents nematodes from 0–10 cm depth which were damaged when the refrigerator malfunctioned.

ungrazed areas (Fig. 3). Omnivore-predators were the most numerous trophic groups at the 0–10 cm and 40–50 cm depths. The percentage of plant feeders was greater at the 0–10 cm depth (52%) on the grazed plot than on the ungrazed plot (32%) and at the 10–20 cm depth on both plots; plant feeders were the most abundant trophic group.

On the basis of this study and the 1974 study, it would appear that the interaction of soil moisture and temperature appears to be a more important factor controlling the nematode populations and trophic structure than grazing. For example, the 1974 data were taken in a year of abundant rainfall, and soil moisture was not a limiting factor. Total numbers of nematodes were much greater in the March sampling in 1974 than in 1976 on both grazed and ungrazed plots. The highest nematode density in 1974 occurred on the ungrazed areas, where higher organic debris and soil microfloral activity probably provided a greater abundance and quality of food sources for the fungivorous and microbivorous nematodes. However, in 1976, although low soil moisture (±2.5%) limited total nematode density later in April and May, soil in the 0–10 cm depth grazed area was always several degrees warmer (28.5°C) than the ungrazed soil (26.5°C) (Fig. 2). A temperature optimal for nematode activity and reproduction was reached much sooner in the grazed area in March when moisture was not limiting than in the ungrazed area. This may explain why the numbers and biomass were higher in the grazed area than in the ungrazed area in 1976.

Evidence from two previous studies on the importance of nematodes on grazed and ungrazed grasslands have been inconclusive. Smolik (1974) found a greater nematode biomass on ungrazed pastures and Smolik and Rogers (1976) found no differences in nematode density and biomass between grazed, ungrazed, and burned shrub-steppe areas. This San Joaquin study further indicates that grazed or ungrazed grasslands are not the sole determinants of nematode density and biomass. Other factors influencing the nematode community appear to be abiotic (i.e., soil moisture and temperature).

Grazing may influence nematode populations indirectly by causing a shift in plant vegetation. For example, in 1974, grasses were predominant with 70% grass on the grazed plot and 88% grass on the ungrazed plot. By March, 1976, the grazed area consisted of only 19.5% grass, whereas the ungrazed area was 100% grass (Table 2). Forbs were the predominant vegetation in the grazed area. Other differences in nematode density between the 1974 and 1976 plant growing seasons at the San Joaquin site could be in part due to extraction methods, extraction efficiencies, and taxonomic and trophic groupings.

Conclusions

Results of this study, although of an exploratory nature and obtained in a season of unusually low rainfall, indicate soil-dwelling nematodes are an important component in the annual grassland ecosystem and deserve further, more detailed study, particularly on different sites with different soils and vegetation. In comparison, soil microarthropod biomass ranged from 53–22 mg/m^2 for 0–10 cm depth samples taken in April and May, 1973[2]. This was lower than the nematode biomass of 117–40 mg/m^2 for a similar depth in April and May, 1976. Smolik's (1974) South Dakota studies showed more nematodes on grazed rangelands, while a Washington study (Smolik and Rogers 1976) revealed little difference between grazed and ungrazed areas. These 1976 California tests indicated more nematodes on a grazed area where the vegetation was mostly forbs than on an adjacent ungrazed area with almost exclusively grass vegetation. Nematode community structure varied with fungivores > microbivores > omnivore-predators > phytophages in the grazed grassland and microbivores = fungivores > phytophages > omnivore-predators for the ungrazed grassland.

Nematode numbers and biomass in 1976 were much lower than found in preliminary tests in 1974, when more than twice as much rainfall fell in the months of March and April. However, relative seasonal nematode densities were very similar to the usual seasonal pattern for aboveground live plant biomass of the annual plants at the San Joaquin site. Nematode numbers were low in winter when soil temperatures were low, even with relatively abundant soil moisture. Numbers rose and peaked in April with rising soil temperatures and intermediate soil moisture supplies. As temperatures rose more and soil moisture rapidly declined in May, nematode numbers dropped.

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