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Cryptobiosis and Its Effect on Metabolism and Production Estimates of Desert Nematodes

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FINAL REPORT

CRYPTOBIOSIS AND ITS EFFECT ON
METABOLISM AND PRODUCTION ESTIMATES OF DESERT NEMATODES

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ABSTRACT

A technique was developed for extraction of nematodes in the anhydrobiotic state from dry desert soils. Morphologically, the anhydrobiotic nematodes were coiled and shrunken in size. Anhydrobiosis, as represented by the coiled form of nematodes from desert soils, was not confined to any particular life stage or trophic group. Studies on the soil moisture levels necessary to rehydrate anhydrobiotic nematodes and return them to metabolic activity indicate that metabolic activity resumes at a soil moisture level of about 2.7%. A more precise model for determining total numbers and biomass of the nematode community present in desert soils was developed. The annual mean number of nematodes was $.12 \times 10^6/m^2$ and the biomass was $.039$ g/m^2. The effect of a lowered, nondetectable metabolism was considered in all calculations of oxygen consumption. Cumulative annual metabolism, production, assimilation and consumption figures are presented for nematode trophic groups at Rock Valley, Nevada in 1974.

INTRODUCTION

The density, biomass, community structure and seasonal and spatial distribution of nematodes in relation to four plant species (*Lycium andersonii*, *Larrea tridentata*, *Krameria parvifolia* and *Ambrosia dumosa*) as well as abiotic factors in the Mohave Desert have been previously reported (Freckman and Mankau 1976). However, estimates of annual productivity and metabolic activity for nematodes in the Rock Valley, Nevada Mohave Desert ecosystem during 1974 (Freckman et al. 1975b; Freckman and Mankau, in press) were inflated since the influence of anhydrobiosis on nematode metabolic activity during the hot, dry summer months was not considered.

Nematodes in North American desert soils are often exposed to long periods of extremely dry conditions and apparently survive by some anhydrobiotic adaptation (Freckman et al. 1975a; Freckman and Mankau, in press). The ability of nematodes to survive without water, or in a state of anhydrobiosis, has been known since the early 1700's, when nematodes dissected from dry plant material revived when placed in water (Crowe 1971). Many studies of anhydrobiosis have described the revival and activity of nematodes in water after many years in dried soil.

Anhydrobiotic nematodes are characterized by: 1) a morphological change to reduce surface area exposure, i.e., from a vermiform, active nematode, to a motionless, tight, three-dimensional coil; and 2) a physiological change of a lowered nondetectable metabolism (Evans and Perry 1976). Because the latter characteristic would affect metabolic estimates for the desert nematode community, it was necessary to determine the length of the nematode anhydrobiotic state in desert soils.

The limiting factor in this study, and in developing biological and physiological knowledge of anhydrobiotic nematodes in soils, has been the extraction technique. All nematode soil extraction techniques use water, which initiates rehydration of anhydrobiotic nematodes and results in a change in their form, from a tight coil to an active or a straight eel-like worm.

OBJECTIVES

The purpose of this study was to:

1. Determine a technique for extraction of desert nematodes in their anhydrobiotic morphological state.

2. Determine the duration of the nematode anhydrobiotic state in Mohave Desert soils.

3. Complete estimates of nematode metabolic activity and productivity at Rock Valley, Nevada.

METHODS

EXTRACTION TECHNIQUE FOR ANHYDROBIOTIC NEMATODES

The following procedure was tested for varying concentrations (0.51, 0.75, 1.0, 1.25 and 1.50 M) of KCl, ethylene glycol and sucrose (Freckman et al., in press). Soil samples taken from Rock Valley during the extremely dry period of June-August 1976 were used as test soil. The method consisted of mixing 100 cm³ of desert soil samples with 300 ml of test solution + Separan® (Dow Chemical Co., Midland, Mich.). The mixture was allowed to settle 90 sec and was then poured through 100- and 325-mesh sieves. Nematodes were collected on the 325-mesh sieve and backwashed with the test solution. This nematode suspension was layered above 10 ml of 2.0 M sucrose in a conical centrifuge tube. The morphological form of nematodes extracted in these solutions was examined (40X) at 30, 60, 90 and 120 min following contact of the soil sample with the solution. The percentages of total nematodes which were either coiled, noncoiled but inactive, or active following extraction were determined for each range of concentrations with each solution at the previously noted time intervals.

DURATION OF THE NEMATODE ANHYDROBIOTIC STATE IN DESERT SOIL

The microenvironmental parameters affecting anhydrobiotic nematodes are difficult to observe, define and control. Simons (1973) considers the amount of soil moisture to be the most important influence in survival in dry soil, whereas in saturated or unsaturated soils it has an indirect influence. He further suggests that diurnal changes of the relative humidities of the soil air enable nematodes to survive. This probably applies only to nematodes located in the upper 5 cm of soil and it is this zone in desert soils where most of the biological activity takes place.

During 1974, soil temperatures and moistures were recorded between 9 and 10 a.m. for each of the 36 weekly samples (Freckman et al. 1975b). Soil temperatures were measured prior to removal of the soil sample by inserting thermistor probes to depths of 5, 15 and 25 cm at each of the

three sample positions (Table 1). Soil moisture was determined gravimetrically by drying at 105 C for 24 hr. Soil moisture varied considerably in these weekly samples (Freckman and Mankau 1976), with a high reading of 16% by weight and the majority of the readings falling between 1.5 and 6%.

To determine the amount of soil moisture necessary to rehydrate anhydrobiotic nematodes to activity, ± 20 g of Rock Valley soil obtained during August 1976 was placed in petri dishes and varying amounts of water (0-3 ml) were added to each dish to simulate the actual moisture range measured at Rock Valley in 1974. There were five replicates for each amount of water. The dishes and soil were weighed prior to and following addition of water. To ensure there was no evaporative loss of water, lids were placed on the petri dishes and each set of five dishes was placed in a plastic bag and sealed. All dishes were placed in an environmental chamber maintained at 28 C and 70% relative humidity. After 24 hr, the petri dishes were removed and the soil stirred into 1.25 M sucrose. Nematodes were extracted according to the new anhydrobiotic extraction technique to determine the form of the nematode at various soil moistures.

The amount of soil moisture at which active nematodes enter into anhydrobiosis was determined in a similar manner. Desert soil was premoistened and ± 20 g soil was placed into weighed petri dishes. The dishes were placed in the environmental chamber and the soil was allowed to dry slowly. At periodic intervals of 24 hr, 36 hr and up to 14 days, eight petri dishes were removed from the chamber; three dishes were weighed and oven-dried at 105 C for 48 hr and percent soil moisture determined. Soil from the other five dishes was removed and placed in 1.25 M sucrose for extraction and determination of the nematode morphological shape.

ESTIMATES OF ANNUAL METABOLIC RATES AND PRODUCTIVITY

Nematode density decreases linearly with depth and distance from the shrub base (Freckman et al. 1975b). To determine whether the density under the canopy of any shrub is constant, or is affected by absolute shrub size, correlations were calculated for average monthly shrub size and average monthly nematode density. At position 1 (0-10 cm depth at shrub base), position 2 (11-20 cm depth at the base), position 3 (21-30 cm depth at shrub base), r = .0176, .0744, .0376, respectively. There was no measurable effect of shrub size on density of nematodes at these positions. A slight increase in nematode density from position 1 (at the base of the shrub) to position 4 (at one shrub radius) was noticed only in 13% of the samples. Of this 13%, 24% was attributed to fungal feeders which occurred in the 11-20 cm depth at positions 2 and 5, and the remainder to the other three trophic groups.

Based on data for lateral distribution of nematodes from samples at 0, 1 and 3 radii from the shrub base, the nematode density appeared to decrease from the base to about 1.402 radii, beyond which densities remained constant. Therefore, since the effect of nematode density

Table 1. Sample position numbers with respect to soil depth and distance from the shrub base at Rock Valley

	Distance from shrub base determined by canopy radii		
Depth (cm)	0	1	3
0-10	1	4	7
11-20	2	5	8
21-30	3	6	9

was small at these intershrub spaces, a uniform density of nematodes will be assumed at the intershrub area. Because samples 1, 2 and 3 are at 0 radius, 4, 5 and 6 are at 1 radius and 7, 8 and 9 are at 3 radii from the shrub base, then each set of nine samples can be used to calculate the best fit for a linear regression from 0 to 1.402 radii. The equation used was: y = ax + b, where y = no. of nematodes/cm^2, x = the distance from the shrub base in centimeters, a = the slope of the line and B = the y-intercept calculated from the regression.

Therefore, the number of nematodes in the area of influence of a shrub can be calculated by:

$$\text{no. of nematodes} = \int_0^{10} \int_0^{2\pi} \int_0^{R} [x(ax + b)dx - d\theta]dz \quad (1)$$

where R in centimeters is 1.402 times the mean shrub radius, 2π is the angle in radians through which the function is rotated and 7 is the depth variable. Then, solving this gives $\frac{1}{3}\pi x^2 y$. Dimensional analysis then shows the expression is in $(cm^2)\cdot(n\cdot cm^{-2})$, or n, the number of nematodes.

Again, following a procedure similar to that of Edney et al. (1976) and using data which show that plant species (Freckman et al. 1975b) and shrub size (Edney et al. 1976) have no effect, the number of nematodes/ha can be determined. From data given by Ackerman et al. (1975b), Bamberg (1973) and Bamberg et al. (1974), the weighted mean radius, including solitary shrubs and clumps, of a shrub is .3114 m, the mean density of solitary shrubs is 2299 and the mean density of clumped groups is 4953. Assuming from data based on sets of nine samples, that the influence of a shrub on nematode density extends to 1.402 times its own radius and using Equation 1 to obtain nematode numbers in the area influenced by the average shrub, the total number of nematodes in influenced areas under the shrubs can be determined. The number of nematodes per hectare in the uninfluenced areas can be likewise obtained from densities at a distance of 3 radii from a shrub base (i.e., positions 7, 8 and 9). The sum of these two numbers gives the total numbers of nematodes/ha.

The method for determining productivity of each nematode trophic group has been partially described (Freckman et al. 1974) and is as follows: 100-150 nematodes in each of the respective trophic groups were measured to determine average length and width of the group; mean individual weight was determined according to Andrassy

Table 2. Actual sampling dates and weekly numbers used in analysis of nematode data at Rock Valley, Nevada, 1974

Months	Actual Sampling Dates	Weekly numbers
January	1/13 – 2/9	3–6
February	2/10 – 3/9	7–10
March	3/10 – 4/6	11–14
April	4/7 – 5/4	15–18
May	5/5 – 6/1	19–22
June	6/2 – 6/29	23–26
July	6/30 – 7/27	27–30
August	7/28 – 8/24	31–34
September	8/25 – 9/21	35–38
October	9/22 – 10/19	39–42
November	10/20 – 11/16	43–46
December	11/17 – 12/14	47–50

(1956); biomass was determined in g/m² or kg/ha; respiration was measured according to the formula: $R = 1.40W^{0.72}$ (Klekowski et al. 1972), where R = amount of oxygen consumed per individual per time and W = body weight; effect of soil temperature on nematode respirate rate was corrected to 20 C according to Winberg (1971); and a calorific equivalent of 4.8 cal/ml O_2 was used according to Yeates (1973). Cumulative respiratory metabolism per year was calculated as a sum of the monthly metabolic rates. Production was evaluated according to Engelmann's (1966) formula: $\log R = 0.62 + 0.86 \log P$, where R = the amount of calories used for respiration by poikilothermic invertebrates·m⁻²·yr⁻¹ (Wasilewska 1974). Consumption was estimated following the assumption of Kitazawa that nematode consumption is twice as high as their assimilation, i.e., both production and maintenance costs (Wasilewska 1974). Results are based on analysis of 1974 data. All four plant species were considered as single replicates, because the differences between them were less significant than other effects (Freckman et al. 1975a and b). To analyze data on a monthly basis, the Rock Valley data from January 15, 1974 to January 1, 1975 (48 weeks) were divided into 12 four-week periods (Table 2).
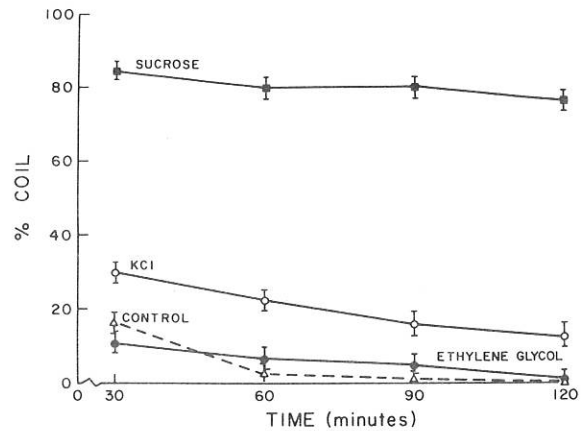

Figure 1. Anhydrobiotic nematodes (160X) 30 min after extraction with A) 1.25 M KCl; B) 1.25 M ethylene glycol; C) 1.25 M sucrose; D) 5% formaldehyde.
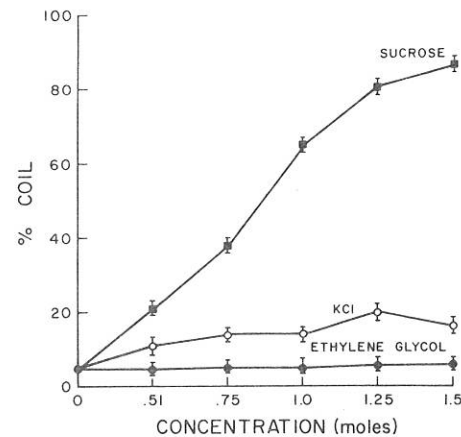

Figure 2. Average percent coiled nematodes extracted from desert soils in H_2O, .51 M, .75 M, 1.0 M, 1.25 M and 1.5 M KCl, ethylene glycol and sucrose, from 0-120 min after extraction. Brackets indicate limit of standard errors. The total average nematode yield per 100 cm³ of soil for each chemical at all molar concentrations: H_2O, 1174; KCl, 739; ethylene glycol, 1051; sucrose, 633.

RESULTS

EXTRACTION TECHNIQUES FOR ANHYDROBIOTIC NEMATODES

The most effective of all concentrations and solutions tested in maintaining the coiled anhydrobiotic form of the nematode was found to be 1.25 M sucrose (Table 3, Figs. 1 and 2). To determine if the use of sucrose at this concentration produced a coiled form (i.e., was the coiled form an artifact), the following experiments were performed: 1) Nematodes were revived after being extracted from desert soil samples. When placed in sucrose, these nematodes did not coil. 2) Desert soil was poured into the fixatives, formalin and gluteraldehyde. Dry, dead and living nematodes did not coil when placed in fixatives. The anhydrobiotic form of the nematodes in desert soils is a tight three-dimensional coil. Anhydrobiosis, as represented by the coiled form of nematodes extracted from desert soils with 1.25 M sucrose, was not confined to any particular life stage or trophic group. Adults and larvae of many genera were observed after coiled nematodes were rehydrated. Preliminary longevity experiments have shown that 85% of the coiled anhydrobiotic nematodes extracted in 1.25 M sucrose will revive in water after 30 days in the sucrose solution.

To determine if the noncoiled vermiform nematodes recovered in 1.25 M sucrose were metabolically alive, individual specimens were hand-picked and placed in water. The conclusion, after examination of many of these specimens, is that the noncoiled vermiform nematodes extracted in 1.25 M sucrose can be equated with metabolically active nematodes.

Table 3. Percent coiled nematodes of total nematode yield extracted from desert soils in various molarities of KCl, ethylene glycol and sucrose and water controls at different time intervals following contact with extracting solution[a]

Time (min)	H₂0 Control	KCl (M)					Ethylene glycol (M)					Sucrose (M)				
		0.51	0.75	1.0	1.25	1.5	0.51	0.75	1.0	1.25	1.5	0.51	0.75	1.0	1.25	1.5
30	16	19	15	20	30	27	12	12	12	11	13	33	47	71	85	90
60	4	10	12	17	23	18	5	7	6	7	8	18	38	65	80	90
90	1	10	16	11	16	13	1	2	2	5	5	17	35	61	81	85
120	<1	6	11	9	13	9	1	1	0	1	2	18	35	65	78	82
Avg.	4	11	13	14	20	17	5	5	5	6	7	21	39	65	81	87
Yield[b]	1174	536	672	928	824	736	688	928	1112	1272	1256	536	520	704	800	608

[a]Data are averages of 3 replicates.

[b]Avg. total yield of nematodes per 100 cm³ soil.

LSD(P=0.05)=7

The extraction of nematodes using this technique has allowed us, for the first time, to examine nematodes from dry soils in a state of anhydrobiosis. It enables us to use the coil as a marker of the anhydrobiotic soil form to: 1) perform laboratory studies using extracted anhydrobiotic nematodes from soils that have been manipulated in various environmental conditions; 2) study the nature of entry into anhydrobiosis and the revival in soil; 3) determine the duration of the nematode anhydrobiotic state in desert soils.

DURATION OF THE NEMATODE ANHYDROBIOTIC STATE IN DESERT SOILS

Data from the soil moisture experiments indicate that the metabolic activity resumed at 2.7%. All nematodes were rehydrated and vermiform in dishes of soil with moisture levels of 11.7% in 42 hr (Table 4). Some species became active more rapidly than others. Reactivation of *Acrobeles* and *Stegelleta* occurred with 30 min, and was followed by reactivation of *Chiloplacus*, *Aphelenchoides*, *Aphelenchus*, *Paraphelenchus* and *Tylenchorhynchus*. *Eudorylaimus* and other members of Dorylaimina usually took several hours to resume activity.

Experiments to determine the percentage of soil moisture necessary for nematodes to enter anhydrobiosis were inconclusive. In order for nematodes to enter anhydrobiosis there must be a slow drying of the soil. The petri dish system in the environmental chamber proved to be inadequate, partially due to techniques for controlling soil moisture in small containers.

Although a portion of these experiments were inconclusive, results indicate that nematodes are metabolically active at soil moistures as low as 2.7%. This information is useful in estimating nematode metabolic rates and productivity. For purposes of this report, the total nematode community will be considered metabolically inactive and anhydrobiotic when average monthly soil moistures at each depth increment (0-10, 10-20, 20-30 cm) are below 2.7% (Table 5). The effect of temperature on respiration has been accounted for using Winberg's (1971) corrections.

Table 4. Percentage of anhydrobiotic nematodes[a] rehydrated at various soil moistures 24 hr after addition of moisture to desert soil in petri dishes

% Soil Moisture	% Rehydrated Nematodes	% Coiled Nematodes
Control (0-2%)	<11	89
2.7	12	88
3.2	30	70
4.1	38	62
4.7	50	50
5.0	69	31
6.5	72	28
7.3	76	24
9.1	81	19
11.2	88	12
12.8	89	11
15.0	88	12

[a]Means of 5 replicates.

Table 5. Soil moistures at Rock Valley, Nevada, 1974. Moistures were measured by drying at 105 C for 24 hr and are expressed as water content percentage of wet weight

	Soil Moisture		
	0-10 cm	10-20 cm	20-30 cm
January	6.62	10.50	10.73
February	5.45	6.79	7.05
March	4.14	5.79	6.60
April	1.69	4.04	5.49
May	1.35	2.77	4.41
June	1.07	1.65	2.59
July	3.47	3.25	2.17
August	2.44	4.49	4.17
September	1.10	1.60	2.13
October	5.15	2.16	2.28
November	5.94	4.37	3.00
December	5.48	6.40	4.52

ESTIMATES OF ANNUAL MATABOLIC RATES AND PRODUCTIVITY

The annual mean number of nematodes per year, corrected for extraction efficiency, is .12 x $10^6/m^2$, which has a biomass of .03 g/m^2 (Table 6). Biomass was at a maximum in March and December and is reflected by an increased density for those months. The annual cumulative metabolism of the total nematode community was 1.157 $kcal \cdot m^{-2} \cdot yr^{-1}$, which takes into consideration the effect of anhydrobiotic nematodes. Results of metabolism estimates for each trophic group are shown in Tables 7-10. The nematode respiration of 1.157 $kcal \cdot m^{-2} \cdot yr^{-1}$ was apportioned as follows: microbivores, .53 kcal (46%); omnivore-predators, .38 kcal (33%); plant parasites, .15 kcal (13%); and fungivores .096 kcal (8%). The duration of the nematode anhydrobiotic state was considered to be from April, when the soil began to dry, through October.

Production of nematodes was .23 $kcal \cdot m^{-2} \cdot yr^{-1}$. The total energy flow (assimilation) was 1.387 $kcal \cdot m^{-2} \cdot yr^{-1}$. Thus, 17% of the energy assimilated is used for production. Based on Kitazawa's (1967) assumption that consumption of nematodes is twice as high as assimilation, it was calculated that all nematodes consumed 2.77 $kcal \cdot m^{-2} \cdot yr^{-1}$.

Using data of Ackerman et al. (1975a, b), the net primary productivity (NPP) is 19.8 g/m^2, and assuming an energy equivalent for plant litter material of 4.3 kcal/g, the three detritus-dependent nematode trophic groups respired about 1% of the annual energy input.

DISCUSSION

The major objectives of this study on the effect of anhydrobiosis on nematode metabolism and productivity in desert soils have been achieved and, when combined with another study (Mankau et al. 1973; Freckman et al. 1974; Freckman et al. 1975b; Freckman and Mankau 1976), present the most detailed information available on the ecology of nematodes in desert soils.

The development of a technique for the extraction of anhydrobiotic nematodes from dry desert soils is of potential use because it will enable studies of nematode survival in dry soils. Previously, nematodes used in studies of anhydrobiosis have been obtained from desiccated plant material or monoxenic cultures. Using this technique, the effect of soil moisture levels on anhydrobiotic nematodes from desert soils was examined. Although some of the soil moisture experiments designed to induce nematodes into anhydrobiosis were inconclusive, it was determined from other experiments that metabolic activity appears to resume when soil moisture levels reach 2.7%.

Table 6. Annual numbers, oxygen consumption and calorific equivalents for nematodes in desert soils at Rock Valley, Nevada in 1974

Nematode Trophic Groups	Annual mean identified (x $10^4 \cdot m^{-2} \cdot yr^{-1}$)	Metabolism (ml $O_2 \cdot m^{-2} \cdot yr^{-1}$)	Calorific equivalent (kcal $\cdot m^{-2} \cdot yr^{-1}$)
Fungivores	1.45	20	.096
Microbivores	5.43	111	.53
Omnivore-Predators	3.35	79	.38
Plant parasites	1.86	31	.15
Annual Mean	.12x10^6	241	1.16

Table 7. Average monthly numbers, oxygen consumption and calorific equivalents of nematodes for each of 12 months in 1974 at Rock Valley, Nevada

	Mean No. (x $10^5 \cdot m^{-2} \cdot month^{-1}$)	Biomass (g/m^2)	Oxygen consumption[a] (ml O_2 consumed $\cdot m^{-2} \cdot month^{-1}$)	Calorific equivalent of oxygen consumption[a] (cal $\cdot m^{-2} \cdot month^{-1}$)
January	1.14	.027	6.3	30.1
February	1.43	.034	12.6	60.7
March	1.53	.037	28.0	134.5
April	1.24	.029	22.0[b]	105.3[b]
May	1.04	.025	31.6[b]	151.6[b]
June	1.08	.026	0[b]	0[b]
July	1.01	.024	54.3[b]	260.4[b]
August	.64	.015	26.0[b]	124.8[b]
September	1.29	.031	0[b]	0[b]
October	1.01	.024	18.0[b]	80.1[b]
November	1.53	.036	26.3	126.3
December	1.56	.037	16.1	77.5

[a]Correction factors used in all calculations to account for anhydrobiosis.

[b]Anhydrobiosis of nematodes occurred during this period.

Table 8. Mean numbers, oxygen consumption and calorific equivalents of fungal-feeding nematodes for each of 12 months in 1974 at Rock Valley, Nevada

	Mean no. x10^3·m^{-2}·month^{-1} (0–30 cm)	Oxygen consumption[a] (ml O_2 consumed·m^{-2}·month^{-1})	Calorific equivalent of oxygen consumption[a] (cal/m^2)
January	13.6	.5	2.5
February	17.2	1.1	5.0
March	18.4	2.3	11.1
April	14.8	1.8[b]	8.7[b]
May	12.5	2.6[b]	12.6[b]
June	13.0	0[b]	0[b]
July	12.1	4.5[b]	21.6[b]
August	.77	2.2[b]	10.3[b]
September	15.5	0[b]	0[b]
October	12.2	1.5[b]	7.1[b]
November	18.4	2.2	10.5
December	18.7	1.3	6.4

[a]Correction factors used in all calculations to account for anhydrobiosis.
[b]Anhydrobiosis of nematodes occurred during this period.

Table 9. Mean numbers, oxygen consumption and calorific equivalents of microbial feeding nematodes for each of 12 months in 1974 at Rock Valley, Nevada

	Mean no. x10^3·m^{-2}·month^{-1} (0–30 cm)	Oxygen consumption[a] (ml O_2 consumed·m^{-2}·month^{-1})	Calorific equivalent of oxygen consumption[a] (cal·m^{-2}·month^{-1})
January	51.0	2.9	13.8
February	64.4	5.8	27.9
March	68.8	12.9	61.8
April	55.5	10.1[b]	48.4[b]
May	46.9	14.5[b]	69.7[b]
June	48.5	0[b]	0[b]
July	45.4	25.0[b]	119.7[b]
August	29.0	12.0[b]	57.4[b]
September	58.0	0[b]	0[b]
October	45.6	8.2[b]	39.6[b]
November	68.9	12.1	58.1
December	70.1	7.4	35.6

[a]Correction factors used in all calculations to account for anhydrobiosis.
[b]Anhydrobiosis of nematodes occurred during this period.

Table 10. Mean numbers, oxygen consumption and calorific equivalents of omnivore-predaceous nematodes for each of 12 months in 1974 at Rock Valley, Nevada

	Mean no. x10^3·m^{-2}·month^{-1} (0–30 cm)	Oxygen consumption[a] (ml O_2 consumed·m^{-2}·month^{-1})	Calorific equivalent of oxygen consumption[a] (cal·m^{-2}·month^{-1})
January	31.4	2.0	9.9
February	39.8	4.2	19.9
March	42.4	9.2	44.1
April	34.3	7.2[b]	34.5[b]
May	28.9	10.4[b]	49.7[b]
June	29.9	0[b]	0[b]
July	28.0	17.8[b]	85.4[b]
August	17.9	8.5[b]	29.2[b]
September	35.7	0[b]	0[b]
October	28.1	5.9[b]	28.2[b]
November	42.5	8.6	41.4
December	43.2	5.3	25.4

[a]Correction factors used in all calculations to account for anhydrobiosis.
[b]Anhydrobiosis of nematodes occurred during this period.

Table 11. Mean numbers, oxygen consumption and calorific equivalents of plant-parasitic nematodes for each of 12 months in 1974 at Rock Valley, Nevada

	Mean no. x10^3·m^{-2}·month^{-1} (0–30 cm)	Oxygen consumption[a] (ml O_2 consumed·m^{-2}·month^{-1})	Calorific equivalent of oxygen consumption[a] (cal·m^{-2}·month^{-1})
January	17.5	.8	3.9
February	22.0	1.6	7.9
March	23.5	3.6	17.4
April	19.0	2.8[b]	13.6[b]
May	16.1	4.1[b]	19.6[b]
June	16.6	0[b]	0[b]
July	15.6	7.0[b]	33.7[b]
August	9.9	3.4[b]	16.2[b]
September	19.9	0[b]	0[b]
October	15.6	2.3[b]	11.2[b]
November	23.6	3.4	16.4
December	24.0	2.1	10.0

[a]Correction factors used in all calculations to account for anhydrobiosis.
[b]Anhydrobiosis of nematodes occurred during this period.

Table 12. Numbers, biomass and metabolism of nematodes (per m²) in several habitats

Habitats	Author	Numbers x10⁶	Biomass g	Metabolism (kcal/yr)
Salt Marsh, Massachusetts, USA	Teal 1962		2.76	64
Moorland, England	Banage 1963	1.9-3	0.5-0.8	19.8
Afforested dunes, Poland	Wasilewska 1971	0.5-7	0.2-0.7	5.7-23.5
Mixed forest, Poland	Wasilewska 1971	5	0.5	13.8
Dry pine forest, Poland	Wasilewska 1971	2	0.2	5.8
Mojave Desert, Nevada, USA	Freckman (unpubl. data)	.12	.03	1.16

This information, combined with the effect of soil temperature, was necessary before estimates of metabolism for nematodes in desert soils could be completed. Previous workers (Nielsen 1949) have simply assumed a reduced respiration under drought conditions. This assumption could not be made for desert soils, where soil moistures are characteristically low for long periods of time, and where nematodes survive in anhydrobiosis.

Briefly, some of the results from this previous Rock Valley study (Freckman et al. 1975b; Freckman and Mankau, in press) include: 1) the distribution of nematodes was not affected by shrub species; 2) the density of nematodes decreased with increasing depth and distance from the shrub base; 3) nematode populations reached a maximum density in March and November 1974; 4) population density increased in September following a sudden rain in August. These latter two results appear to be related to higher soil moisture levels in the winters, but further work would be appropriate to determine the actual abiotic effect on nematode density.

This is the only in-depth study of nematodes in desert soils and has as its strong points: 1) a technique which was 75% efficient in extraction of nematodes representing all trophic groups; 2) weekly samples -- each monthly average presented in Tables 6-11 is an average of 144 weekly samples/month; 3) soil temperature and moisture data for each sample taken; 4) consideration of anhydrobiosis on metabolism estimates.

Inaccuracies in this estimation of nematode productivity could result from: 1) not determining the life stages of the various species; and 2) individual weights were based on individuals in trophic groups and not for each individual species. It is known that juvenile respiration is 1-3 times greater than the adult (Klekowski et al. 1974) and, therefore, would affect total metabolism. However, in examining other data for nematodes in various habitats, it appears that some inaccuracy, ranging from too few samples to differences in estimation of metabolism, is usually a problem with studies of this type.

Comparison of data with those of other workers is shown in Table 12. Yeates (1973) reported that annual production of nematodes in a Danish Beech forest was 20.7% of assimilation. The estimates of the annual production of nematodes in desert soils was 17% of the total energy flow. This corresponds with Reichle's (1971) estimates of 17-18% for saprovores. It will be interesting to compare estimates of the role of the nematode trophic groups involved in the decomposer food chain from other habitats with nematodes in desert soils that respired about 1% of the NPP.

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