Nematode Numbers, Biomass and Respiratory Metabolism in a Beech Woodland – Wytham Woods, Oxford

J. Phillipson, R. Abel*, J. Steel, and S.R.J. Woodell

Animal Ecology Research Group and Botany School, Oxford University, Zoology Department, South Parks Road, Oxford OX1 3 PS, United Kingdom

Summary. The mean annual population density of nematodes in the litter and upper 6 cm of soil was found to be 368,000 m^{-2}. Mean individual live weight biomass approximated 0.2 µg and mean biomass was calculated to be 74.6 mg live weight m^{-2}. No evidence of seasonal vertical migration between the litter, 0–3 cm and 3–6 cm strata was found and on average these strata contained 21.9, 46.2 and 31.9% respectively of the total number of nematodes recovered. The equivalent biomass values were 26.14, 56.57, and 17.29%. Total numbers revealed a general picture of low densities in spring and high ones in early winter, whereas biomass m^{-2} was low in late summer — autumn and high in winter. The annual oxygen consumption of the extracted nematodes was calculated to approximate 0.21 l m^{-2} (≈ 4.0 kJ m^{-2}) but when corrected for the effect of individual biomass (weight specific oxygen uptake) was equivalent to an energy expenditure ≈ 6.0 kJ m^{-2} which in its turn, because of the efficiencies of extraction, probably accounts for only 87% of the total energy expenditure by the nematode fauna. The nematodes were estimated to be responsible for a minimum of 0.11% to a maximum of 0.13% of the total "soil" respiration. A production/biomass ratio of 5.16 was estimated as was a net population production efficiency of 36.63%.

Introduction

Nematodes occur in their thousands in almost every type of soil and yet our knowledge of the density and biomass of free living forms is strictly limited. Yeates (1972) provided one of the most recent summaries of the available information. He tabulated data from studies of ten habitats where densities were in the range 326,560 to 29,800,000 nematodes m^{-2} and biomasses were in the range 353 to 17 800 mg live weight m^{-2}. Clearly, nematode numbers and biomass per unit area vary markedly between habitats.

---

* *Present address*: Central Water Planning Unit, Reading, U.K.

The present work reports on nematode numbers, biomass and respiratory metabolism and forms part of a research programme designed to investigate the ecosystem dynamics of a beech (*Fagus sylvatica* L.) woodland known as Brogden's Belt (Nat. grid ref. SU 464077) in Wytham Woods, Oxford.

The Site

A description of the site and its characteristics (canopy cover, ground flora cover, standing crop of litter, soil depth, soil density and soil drying out properties) during the study period is given in Phillipson et al. (1976). An account of litter fall, litter decomposition and the evolution of carbon dioxide is given in Phillipson et al. (1975).

In brief, the study site was established as a series of 10×10 m grid squares and covered an area of 5130 km^2. The rendzina type soil is shallow (6–42 cm in depth), overlies broken Jurassic limestone ("Coral rag") of the Upper Corallian strata (Arkell, 1945; Elton, 1966) and, with a single exception (pH 6.3), has a range of pH's from 7.3 to 8.0.

Methods

Sampling

The study site was divided into 22 sampling strata. Each stratum comprised two adjacent 10×10 m grid squares and at approximately one month intervals from October 1971 to December 1972 one sample unit was selected at random from each of the 22 strata.

The split cylindrical soil corers used to take the sample units were 1.05 cm^2 in area and were thus similar in size to those used by Nielsen (1949), no undue soil compression was noted. Sample units were divided into litter ($L + F$ horizons), 0–3 cm and 3–6 cm soil depths. They were temporarily held at 10° C but were always extracted on the day of collection.

Extraction

Both litter and soil were extracted using the "tray method" of Whitehead and Hemming (1965). Extractions were completed within 12 h and approximately 150 ml of suspension was collected from each sample. The suspension was allowed to settle for 18 h before decanting and centrifugation at 4000 revolutions per s for 5 s. Tests involving repeated centrifugation allowed a spin efficiency of 88.77% to be calculated for the "single" period of centrifugation.

Counting

Extracted samples were preserved in 5% formalin. At a later date the preserved samples were placed in a petri dish over a sectored underlay (Solomon, 1945) such that the nematodes in 1/30 of the total area of the petri dish were counted. The counts were multiplied by the appropriate conversion factor to give numbers per square metre.

Biomass Determination

Approximately five nematodes per extraction were photographed with a scale under a microscope. The negatives were subsequently projected onto a screen at a magnification of approximately

×200 and the length and maximum width of each specimen was determined. A total of 4494 nematodes was measured in this manner. From these measurements biomass was calculated according to the method of Andrassy (1956) which employs the formula $\dfrac{W^2 \times L}{16 \times 10^5}$ and is in μg when W (maximum body width) and L (body length) are in μm. It should by noted that in employing the Andrássy formula, total worm length was recorded and thus tail lengths were not altered to allow for conoid tailed species.

    Mean individual biomasses were calculated for each month which, when multiplied by the appropriate monthly mean density, provided estimates of the mean monthly biomass.

Ancillary Measurements

From April 1969 to June 1971 field temperatures had been determined at seven randomly sited stations on the study area. At six of these a sucrose inversion technique (Berthet, 1960; Lee, 1969) was employed to calculate fortnightly integrated temperatures and at the seventh a Grant continuous recorder was installed. At each station temperature records from six vertical heights (+100 cm, +20 cm, air-litter interface, litter-soil interface, −5 cm and −20 cm) were used to construct monthly mean temperature profiles. Subsequent analysis did not reveal any significant difference between the seven stations and thereafter (July 1971 to April 1973) results were obtained only from the Grant continuous recorder. The results from this single station during the study period (October 1971–December 1972) can be assumed to be representative of the whole site.

    Rainfall data were kindly provided by the Geography Department, Oxford University.

Results

Numbers

It is generally accepted that nematodes are most abundant in the 0–3 cm stratum of the soil; that this was so in the present case can be seen from Figure 1. The figure shows nematode densities per square metre per month in the litter, 0–3 and 3–6 cm strata and also the percentage of the total nematodes recovered from each stratum. Litter accounted for 21.9% of the nematodes and the 0–3 and 3–6 cm contained 46.2 and 31.9%, respectively.

    Statistical comparisons (t tests) for seasonal variations in abundance in each of the strata revealed very few significant ($P < 0.05$) changes between consecutive months. In the litter there were no significant decreases and the only significant increase occurred between 25 August and 18 September 1972. At 0–3 cm depth a significant decrease occurred between 1 November and 30 November 1971 and significant increases were demonstrated between 30 November and 27 December 1971 and 31 October and 5 December 1972. Below 3 cm there was a significant decrease from 1 November to 30 November 1971 and a significant increase from 31 October to 5 December 1972. Despite the failure to demonstrate marked seasonal variation on a month to month basis it was shown that there were statistically significant lower nematode densities in all strata during Spring (March–May) while the highest densities occurred during early Winter (December).

    Figure 2 shows the total nematode densities per square metre per month and as would be expected reflects the same type of variation as revealed by
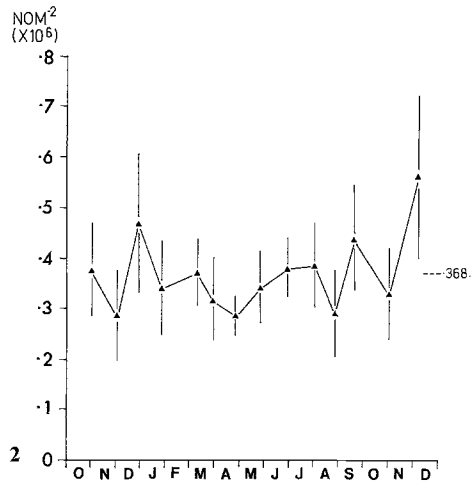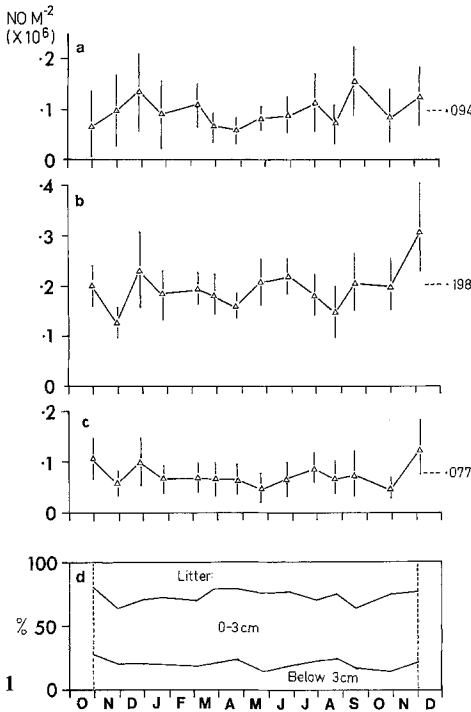
Fig. 1 a–d. Nematode numbers m^{-2} with 95% confidence limits. **a** Litter. **b** 0–3 cm. **c** Below 3 cm. **d** Percentage distribution in the three strata

Fig. 2. Total nematode numbers m^{-2} with 95% confidence limits

analysis of the data for the separate strata. A significant decrease in density occurred between 1 and 30 November 1971 and significant increases between 25 August and 18 September and 31 October and 5 December. Note that the population density of 5 December 1972 was not significantly different from that estimated for 27 December 1971, this possibly indicates stability in absolute numbers from year to year.

Figure 3 shows the monthly mean field temperatures at the air-litter interface, litter-soil interface and −5 cm below the soil surface. Comparison of Figures 1 and 3 make clear that the population density changes cannot be related in any direct manner to either temperature or rainfall.

Biomass

Figure 4 shows mean individual biomass per month in each of the three soil strata. In only 3 months were significant differences for the same sampling date demonstrated between the strata. Between litter and 3–6 cm on 27 December 1971, on 27 June 1972 between 0–3 cm and 3–6 cm, and on 5 December 1972 between litter and 0–3 cm and 0–3 cm and 3–6 cm.
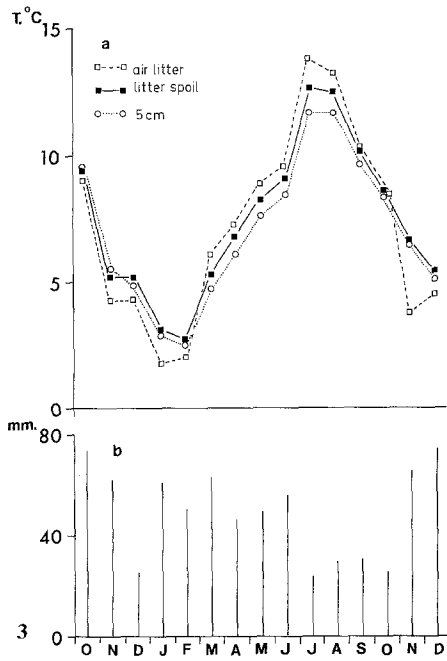
Fig. 3a and b. Microclimate data. **a** Monthly mean temperatures for the air-litter, litter-soil interfaces and −5 cm depth. **b** Monthly rainfall
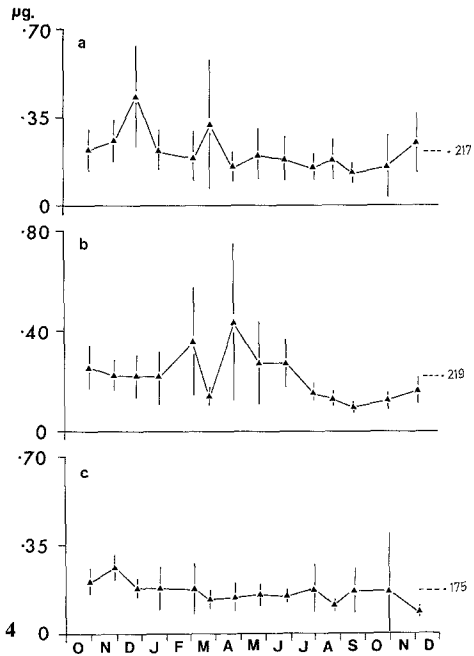
Fig. 4a–c. Individual mean live weight biomass with 95% confidence limits. **a** Litter. **b** 0–3 cm. **c** Below 3 cm

Analysis for variation in mean individual biomass in any one stratum failed to demonstrate significant changes in consecutive months in the litter but revealed significant decreases between 27 June and 1 August and 25 August and 18 September 1972 in the 0–3 cm stratum. Below 3 cm the only significant change in consecutive months was a decrease from 30 November to 27 December 1971.

From a seasonal viewpoint no change in mean individual biomass was apparent in the 3–6 cm layer. In the litter and 0–3 cm strata lower mean individual biomasses occurred in late Summer and Autumn (July–October 1972).

Figure 5 shows the nematode biomass per square metre per month in each stratum. The values were obtained as products of the appropriate mean numbers per square metre and mean individual biomass. On a seasonal basis the stratal biomass data reflect the trend shown by individual biomass rather than that shown by the population density figures, namely low values in Summer and Autumn rather than Spring. Also shown in Figure 5 are the percentages of the total biomass contained in each stratum. Litter accounted for 26.14% of the nematodes and the 0–3 cm and 3–6 cm strata contained 56.57 and 17.29% respectively.

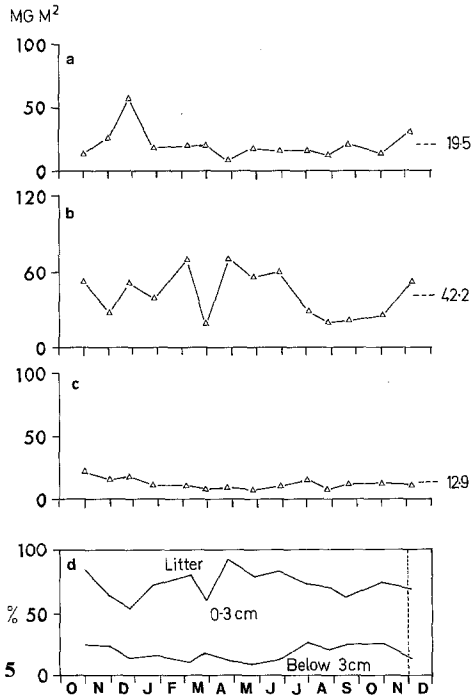Figure 6 shows the total nematode biomass per square metre per month,

Fig. 5a–d. Nematode live weight biomass m⁻². a Litter. b 0–3 cm. c Below 3 cm. d Percentage distribution in the three strata
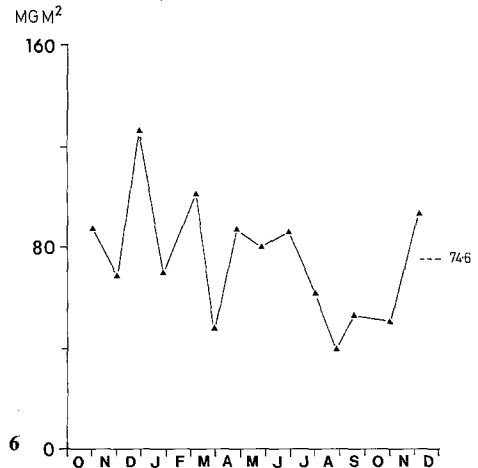
Fig. 6. Total nematode live weight biomass m⁻²

these values being obtained as the sums of the appropriate stratal values. The lowest biomasses occurred in the late Summer and Autumn (July–October 1972) and the highest in Winter (December 1971 and 1972).

Using the energy value of 2.152 cal mg⁻¹ (≈ 9.004 J mg⁻¹) for fresh nematode material given by Yeates (1972) the energy equivalent of the mean biomass of 74. 6 mg live wt m⁻² was calculated to be 160.539 cal m⁻² (671.698 J m⁻²).

Respiratory Metabolism

Nielsen (1949) made a detailed study of nematode respiration rates and felt it justifiable for ecological purposes to establish three species groupings with regard to oxygen consumption, namely 1500 ± 200, 1200 ± 200 and 800 ± 300 ml O_2 kg⁻¹ h⁻¹ at 16° C. In the present study species groupings were not attempted and so a mean weight specific value of 1000 ml O_2 kg⁻¹ h⁻¹ at 16° C recommended by Nielsen (1967) was accepted as a possible conversion factor. However, as Yeates (1972) has indicated individual biomass estimates calculated according to the Nielsen (1949) method are 83% of those calculated by the Andrássy (1956) method employed in this study. To conform with the Andrássy

Table 1. The data used to calculate oxygen consumption m^{-2} mth^{-1}

Month (30.5 days)	Litter			
	Field temp	Wt. spec. resp. (ml O$_2$ g^{-1} h^{-1})	Biomass (g live wt m^{-2})	Monthly resp. (ml O$_2$ m^{-2} mth^{-1})
Oct–Nov 1971	9.30	0.39	0.014	3.997
Nov–Dec	4.80	0.22	0.025	4.026
Dec–Jan	4.80	0.22	0.058	9.340
Jan–Feb 1972	2.45	0.16	0.019	2.225
Feb–Mar	2.45	0.16	0.021	2.460
Mar–Apr	5.75	0.25	0.020	3.660
Apr–May	7.10	0.30	0.008	1.769
May–June	8.65	0.37	0.017	4.606
June–July	9.35	0.41	0.016	4.802
July–Aug	13.30	0.65	0.017	8.089
Aug–Sept	12.95	0.63	0.012	5.534
Sept–Oct	10.20	0.45	0.020	6.588
Oct–Nov	8.75	0.38	0.013	3.616
Nov–Dec	5.25	0.24	0.030	5.270
	$\bar{x}=7.51$	$\bar{x}=0.35$	$\Sigma=a$ 0.247 b 0.251	$\Sigma=a$ 57.096 b 57.959

Month (30.5 days)	0–3 cm depth			
	Field temp	Wt. spec. resp. (ml O$_2$ g^{-1} h^{-1})	Biomass (g live wt m^{-2})	Monthly resp. (ml O$_2$ m^{-2} mth^{-1})
Oct–Nov 1971	9.50	0.42	0.052	15.987
Nov–Dec	5.40	0.24	0.028	4.919
Dec–Jan	5.10	0.23	0.051	8.586
Jan–Feb 1972	3.10	0.18	0.039	5.139
Feb–Mar	2.70	0.17	0.069	8.586
Mar–Apr	5.10	0.23	0.019	3.199
Apr–May	6.55	0.28	0.070	14.347
May–June	8.00	0.34	0.056	13.937
June–July	8.80	0.38	0.060	16.690
July–Aug	12.25	0.57	0.029	12.100
Aug–Sept	12.20	0.57	0.020	8.345
Sept–Oct	10.00	0.44	0.021	6.764
Oct–Nov	8.65	0.37	0.025	6.764
Nov–Dec	6.15	0.26	0.052	9.897
	$\bar{x}=7.393$	$\bar{x}=0.33$	$\Sigma=a$ 0.541 b 0.511	$\Sigma=a$ 118.599 b 114.354

Month (30.5 days)	3–6 cm depth				Total
	Field temp	Wt. spec. resp. (ml O$_2$ g^{-1} g^{-1})	Biomass (g live wt m^{-2})	Monthly resp. (ml O$_2$ m^{-2} mth^{-1})	Monthly resp. (ml O$_2$ m^{-2} mth^{-1})
Oct–Nov 1971	9.50	0.42	0.022	6.764	26.748
Nov–Dec	5.50	0.24	0.016	2.811	11.756
Dec–Jan	5.00	0.23	0.018	3.030	20.956
Jan–Feb 1972	3.10	0.18	0.012	1.581	8.945
Feb–Mar	2.60	0.17	0.012	1.493	12.539
Mar–Apr	4.80	0.22	0.009	1.449	8.308
Apr–May	6.20	0.27	0.010	1.976	18.092
May–June	7.70	0.33	0.008	1.932	20.475
June–July	8.50	0.37	0.011	2.979	24.471
July–Aug	11.80	0.54	0.016	6.324	26.513
Aug–Sept	11.80	0.54	0.008	3.162	17.041
Sept–Oct	9.80	0.43	0.013	4.092	17.444
Oct–Nov	8.50	0.37	0.013	3.521	13.901
Nov–Dec	5.60	0.25	0.012	2.196	17.363
	$\bar{x}=7.171$	$\bar{x}=0.326$	$\Sigma=a$ 0.155 b 0.142	$\Sigma=a$ 37.593 b 33.735	$\Sigma=a$ 213.288 b 206.048

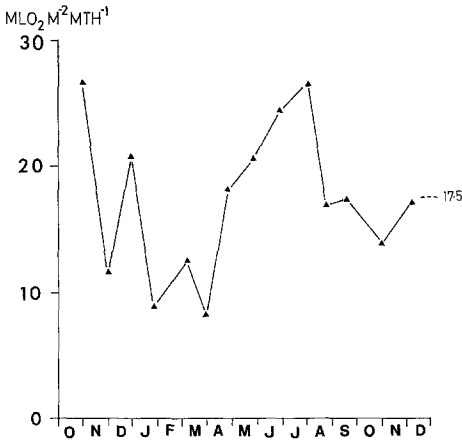$a=$ 1st 12 months (Oct 1971–Sept 1972); $b=$ 2nd 12 months (Dec 1971–Nov 1972)

MLO$_2$M^{2}MTH^1

Fig. 7. Oxygen consumption attributed to the extracted nematodes

method of calculating biomass the 1000 ml O$_2$ kg^{-1} h^{-1} at 16° C was adjusted to 830 ml O$_2$ kg^{-1} h^{-1} at 16° C.

The uniform respiration rate of 0.830 ml O$_2$ g^{-1} h^{-1} at 16° C was corrected for the mean temperatures prevailing in the different soil strata by a two stage process. First, the available temperature data for the air-litter interface, the litter-soil interface and -5 cm depth were used to calculate the prevailing temperatures in the litter ((air-litter $T°$ + litter-soil $T°$)/2), 0–3 cm ((litter-soil $T°$ + -5 cm $T°$)/2) and 3–6 cm (-5 cm $T°$) strata. Second, the "correction coefficients" calculated by Winberg (1971) from Krogh's (1914) "normal curve" (see also Bornebusch, 1930) and detailed in Duncan and Klekowski (1975) were used to determine the weight specific oxygen consumption at each of the estimated prevailing temperatures. The appropriate formula is $R_{x°} = R_{16°} \cdot q_{16°}/q_{x°}$ where $R_{x°}$ and $R_{16°}$ are oxygen consumption per unit wt per unit time at the prevailing temperature and 16° C respectively and $q_{x°}$ and $q_{16°}$ are the "correction coefficients" for these two temperatures.

Table 1 shows the data used in calculating respiration per square metre per month (30.5 days). Note that over the spread of mean temperatures experienced during the study period (2.45–13.30° C) the weight specific oxygen consumption ranged from 0.16–0.65 ml g^{-1} h^{-1}.

Figure 7 shows the total monthly oxygen consumption of the nematodes per square metre. Comparison of this figure with Figures 3 and 6 indicates the combined influence of temperature and biomass on monthly uptake while the effect of rainfall or its absence appears negligible in this study. Energy expenditure by the nematode population was generally below average in all seasons bar late-Spring and Summer (April to August).

Annual oxygen consumption was calculated to be 206.048 to 213.288 ml O$_2$ m^{-2} depending on whether the last or the first twelve months of the fourteen months of study were taken to represent a year. The energy equivalent of oxygen is 4.775 cal per ml O$_2$ (Heilbrunn, 1947), which equals 19.979 J ml^{-1} O$_2$, and thus the annual respiratory energy expenditure by the nematodes can be calculated to be 4116.633–4261.281 J m^{-2} ($\approx$983.879–1018.450 cal m^{-2}).

Discussion

Numbers

Comparisons of the three graphs presented in Figure 1 do not provide any evidence of seasonal movement between the three strata. The study of vertical distribution of the nematodes showed that 21.9% of the total number was recovered from the litter, and 46.2 and 31.9% from the 0–3 and 3–6 cm strata, respectively. The only available data which are strictly comparable with the present findings are those obtained by Yeates (1972) for a beech forest in Denmark (Hestehave). Results from twelve monthly sampling occasions in Hestehave indicate that the litter contained 13.6% of the nematodes recovered while the 0–3 and 3–6 cm strata held 57.7 and 28.7%, respectively. Yeates (1972) also made a special study of nematode vertical distribution at Hestehave but sampled on only four occasions throughout one year. He showed that of the nematodes occurring in the litter and top 6 cm soil 8.7% were found in the litter, 59.7% in the 0–3 cm stratum and 31.6% in the 3–6 cm stratum. The high percentage of nematodes found in the Brogden's litter is surprising when one recognises that Yeates (1972) homogenised the Hestehave litter before extraction, thereby increasing the litter extraction efficiency by a factor of 4.8. Apart from the existence of a real difference in vertical distribution, two possible explanations of the discrepancy between the two sites can be proffered (i) the standing crop of litter in Brogden's was approximately ten times that present in Hestehave, (ii) the litter stratum taken from Brogden's included more H layer than did that taken from Hestehave. The first explanation is unlikely but the second is quite possible because of the difficulty of detecting with certainty the exact boundary between the F and H layers. This is of importance when it is realised that the upper 1 cm of soil can contain between 25 and 50% of the total nematode fauna (Nielsen, 1949, Fig. 5).

Indirect evidence to support the second contention can be found in the comparisons, shown in Table 2, of the percentage of nematodes found in different soil strata in a variety of studies. When the litter and 0–3 cm stratal data are pooled for each of the two beech woodlands it is clear that together they contain approximately 70% of the nematodes occurring above 6 cm soil depth, a value which is in general accord with data from other studies where litter was not treated separately. It is thus probable that the boundary between the litter and 0–3 cm strata in the two beech studies was not distinguished in exactly the same manner.

Table 2 shows also that the percentage of nematodes occurring above 6 cm soil depth lay between 81 and 97% ($\bar{x}=87\%$) of the total number.

Efforts to demonstrate seasonal variation in the Brogden's Belt nematode population revealed a general picture of low densities in Spring and high ones in early Winter. An almost identical pattern was found by Berge et al. (1973) in an ancient grassland habitat in northern France. Other studies have demonstrated different seasonal patterns, for example Banage (1966) working at a moorland *Juncus* site found that the lowest densities occurred in Summer and the highest in Autumn. The seasonal pattern at Hestehave (Yeates, 1972) is

Table 2. The percentage of total nematodes found in different soil strata

Habitat	Nematodes as % of total in the top 6 cm		Nematodes in top 6 cm as % of total nematodes	Authority
	% above 3 cm	% at 3–6 cm		
Oak forest	67	33	81	Arpin (1975b)
Moorland heather	78	22	97	Banage (1966)
Moorland grassland	69	31	73	ibid.
Bog	67	33	96	Nielsen (1949)
Plain	89	11	97	ibid.
Beech forest	71	29	?	Yeates (1972)
	68	32	75	ibid.
Beech wood	68	32	?	This study

in complete contrast to that of Brogden's Belt for high densities were found in Spring and low ones in late Winter. The Hestehave pattern was accounted for in terms of temperature and soil moisture effects but no simple explanations were found to account for pattern in the present study or in those by Berge et al. (1973) and Banage (1966). Arpin (1975a, b) studied seasonal variation in individual species populations but was unable to demonstrate correlations of the type found at Hestehave. He suggested that a multiplicity of factors, both abiotic and biotic, interact to govern seasonal changes. Further studies are obviously needed before any definitive statements can be made about the factors controlling seasonal patterns.

Another aspect of interest that requires closer investigation is the amplitude of fluctuations in nematode numbers in different habitats. In the present study density changed twofold over the period of investigation while Berge et al. (1973) demonstrated a threefold difference and Banage (1966) and Yeates (1972) found a fivefold change.

Biomass

Nielsen (1961) suggested that in nematodes (where there are several overlapping generations per year) there will be drift towards the demographers' "stable age distribution" (Lotka, 1939; Leslie and Ranson, 1940) and that some stabilisation of the mean body weight will take place. This was generally true in the present study (Fig. 4) although in the litter and 0–3 cm layers lower mean individual biomasses occurred in late Summer and Autumn. These lower mean body weights probably indicate a high recruitment of individuals to the population during the period July–October as this accords with an overall increase in numbers during and shortly after this time (Figs. 1 and 2). Because high recruitment probably occurred during the hottest and driest months it is not thought that drought affected the populations under study in the way that Nielsen (1961) suggested for the nematodes at his stations 1 and 4.

Total nematode biomass per unit area (Fig. 6) was low in late Summer

and Autumn and high in Winter thereby reflecting the trend shown by individual biomass values. Low Summer biomasses are in general agreement with a study of woodland nematodes by Huhta and Koskenniemi (1975) but contrast with the Hestehave site studied by Yeates (1972) where the influence of nematode density on total biomass was pronounced. However, in the Hestehave situation low mean individual biomass was not as closely correlated with periods of highest temperature as they were in the present study.

Respiratory Metabolism

Monthly respiratory metabolism values (Fig. 7) were clearly influenced by the prevailing soil temperatures. This is not surprising when one recalls that the application of seasonal temperature corrections to a standard rate of 0.83 ml g^{-1} h^{-1} at 16°C varies weight specific oxygen uptake between 0.16 ml g^{-1} h^{-1} at 2.45° C and 0.65 ml g^{-1} h^{-1} at 13.3° C. Nielsen (1961) and Yeates (1972) applied temperature corrections of this type to their data.

In the absence of contemporary microclimate data Nielsen (1961), on the basis of studies by Kristensen (1959), reasoned that during his study period 16° C would represent the mean temperature slightly below the soil surface for a period of 100 days centred around 10 June. He further reasoned that in the absence of drought effects the total annual respiration of the nematodes could be calculated by multiplying the respiration per 100 days by a factor of 2.12. Thus, at Station 18, the total annual respiratory metabolism of 14 g live weight of nematodes per square metre was 71 1 O_2 (≈ 0.579 ml g^{-1} h^{-1}). But an annual oxygen uptake of 71 1 O_2 m^{-2} is also equivalent to oxygen consumption at 16° C over 212 days, i.e. 0.997 ml g^{-1} h^{-1}. From either Krogh's (1914) curve or Winberg's (1971) "correction coefficients" it can be calculated that a reduction from 0.997 to 0.579 ml O_2 g^{-1} h^{-1} requires a temperature drop of approximately 5° C, hence the annual mean temperature at Nielsen's station 18 should have approximated 11° C (16−5° C). For strict comparison of the weight specific oxygen uptake in Nielsen's (1961) and the present study it is necessary to correct uptake in both studies to a standard temperature and at the same time allow for the different methods of estimating biomass. At 16° C the respective weight specific uptakes were taken to be 0.997 and 0.830 ml O_2 g^{-1} h^{-1}, correcting for the methods of biomass estimation these values become very similar at 0.828 and 0.830 ml O_2 g^{-1} h^{-1} thus justifying in part the use of the general conversion factor of 0.830 ml O_2 g^{-1} h^{-1} recommended by Yeates (1972) who followed Nielsen's (1967) generalisation of 1.0 ml O_2 g^{-1} h^{-1}. However, the mean individual biomass in Nielsen's (1949, 1961) study was 1.4 μg compared with 0.2 μg in the present one; this difference could, following Nielsen (1949, pp. 68–69), give rise at the same temperature to a weight specific oxygen consumption at mean individual biomasses of 0.2–0.25 μg some 1.33 times greater than at a mean individual biomass of 1.4 μg. It is probable therefore that a conversion factor of 1.1 ml O_2 g^{-1} h^{-1} at 16° C and not 0.830 ml O_2 g^{-1} h^{-1} at 16° C should have been applied to both the present and Yeates (1972) data (mean individual biomasses of 0.2 μg

Table 3. A summary of nematode numbers, biomass and respiratory metabolism in three different studies

		Nielsen (1961) Station 18	Yeates (1972) Recalculated		Present study
1.	Annual mean number per m^2 ($\times 10^3$)	10×10^3	1.09×10^3		0.37×10^3
2.	Mean individual biomass (μg)	1.4	0.26		0.20
3.	Annual mean biomass (g m^{-2})	14	0.28		0.08
4.	Annual mean temperature (°C)	$\approx$11.0[a]	6.9		7.4
5.	Uncorrected annual respiration at prevailing temperature (l O$_2$ m^{-2} a^{-1})	71.00	1.62[b]	0.80	0.21
6.	Weight specific respiration at prevailing temperature (ml O$_2$ g^{-1} h^{-1})	0.579	0.660[c]	0.326	0.299
7a.	Weight specific respiration corrected to 16° C from values given in 4 and 6 (ml O$_2$ g^{-1} h^{-1})	0.972	1.837	0.907	0.790
7b.	Weight specific respiration to 16° C from values given in 4 and 6 (ml O$_2$ g^{-1} h«^{1})	0.997[d]	1.826[e]	0.830[e]	0.830[e]
8.	Weight specific respiration at 16° C when corrected for differences between mean individual biomass (ml O$_2$ g^{-1} h^{-1})	0.997	2.429[e]	1.100	1.100
9.	Fully corrected weight specific respiration at prevailing temperature (ml O$_2$ g^{-1} h^{-1})	0.579	0.872[e]	0.395	0.422
10.	Fully corrected annual respiration at prevailing temperature (l O$_2$ m^{-2} a^{-1})	71.00	2.13[e]	0.98	0.30

[a] Estimated
[b] Annual respiration value from Yeates (1972)
[c] Calculated using Yeates (1972) value of 1.62 l O$_2$ m^{-2} a^{-1}
[d] Calculated from Nielsen's (1961) use of oxygen uptake for 212 days at 16° C to represent annual respiration
[e] Assumed

and 0.26 µg, respectively). This correction has been included in the general summary shown in Table 3.

Yeates (1972) reports weight specific oxygen consumption over the mean range of temperatures experienced (-0.6 to 15° C) to be 0.541–0.799 ml O$_2$ g^{-1} h^{-1}. Such values are difficult to reconcile with his reported use of Krogh's (1914) curve and a weight specific oxygen uptake of 0.830 ml O$_2$ g^{-1} h^{-1} at 16° C, the latter value when corrected by the curve reduced to 0.756 ml at 15° C and almost 0.10 ml at 0° C. Having noted this anomaly the temperature data of Yeates (1972), in his Table 4, were used in applying temperature corrections to the general conversion factor of 0.830 ml O$_2$ g^{-1} h^{-1} at 16° C. The

corrected values were used in conjunction with the biomass data (Yeates' Table 5) to recalculate monthly oxygen consumption and gave rise to an annual oxygen uptake estimate of 804.31 ml O_2 m^{-2} which is 49.54% of the value of 1623.4 ml O_2 m^{-2} given in Yeates (1972).

The 804.31 ml O_2 m^{-1} a^{-1} and a mean biomass of 0.282 g m^{-2} at Yeates (1972) study site is equivalent to a weight specific respiratory rate of 0.326 ml O_2 g^{-1} h^{-1} at 6.93° C. This value is much closer to the theoretically expected value of 0.300 ml O_2 g^{-1} h^{-1} at 7° C than the 0.660 ml O_2 g^{-1} h^{-1} at 6.93° C calculated from the published account. It has been assumed that some error arose in Yeates' (1972) calculations of respiratory metabolism and that his annual values for this parameter should be reduced to approximately one half of the published figures.

Table 3 summarises the data for Nielsen's (1961) station 18, those of Yeates (1972) as published and as corrected in this paper, and also those from the present study. The "fully corrected" annual respiration values were 71 l m^{-2} (Nielsen, 1961), 2.13 and 0.98 l m^{-2} (Yeates, 1972) and 0.3 l m^{-2} (this study), but it should be noted that these values apply only to those nematodes above 6 cm depth which, on average, comprise only 87% of the total.

The oxygen uptake per animal in Nielsen's study (0.007 ml indiv^{-1} h^{-1}) was six to nine times greater than the recalculated values for Yeates (1972) nematodes (0.0011 ml indiv^{-1} h^{-1}) and those of this study (0.0008 ml indiv^{-1} h^{-1}). These differences are easily accounted for by the knowledge that after correction to the Andrássy (1956) method of weight calculation Nielsen's (1961) individuals were seven to nine times heavier on average than those of the Hestehave and Brogden's study areas. Clearly, taking the product of Nielsen's rates of oxygen consumption per individual and population density (where the mean individual biomass is unknown) could lead to an error of magnitude in estimating nematode population respiration.

Conversion of the "uncorrected" annual oxygen consumption of the Brogden's nematodes (Table 3, item 5) to energy equivalents indicated that the annual respiratory energy expenditure was between 4116.633 and 4261.281 J m^{-2}. Using the "fully corrected" values for annual respiration (Table 3, item 10) the estimated energy expenditure of a biomass of 0.08 g m^{-2} ($\approx$671.698 J m^{-2}) approximates 5993.7 J m^{-2} a^{-1} ($\approx$1432.5 cal m^{-2} a^{-1}). It should again be recalled that this probably represents 87% of the total energy expenditure by the nematode fauna.

Production by nematodes is obviously difficult to measure but knowing the energy equivalents of the respiratory costs of the extracted Brogden's nematodes to be 5993.7 J m^{-2} a^{-1} it is possible to estimate production by the regression equation for short lived poikilotherms given in McNeill and Lawton (1970). The equation is $\log P = 0.08262 \log R - 0.0948$, where P is production and R is respiration, and gives rise to an estimate of extracted nematode production of 3464.8 J m^{-2} a^{-1} ($\approx$828.1 cal m^{-2} a^{-1}). Accepting this value the production/biomass (P/B) ratio equals 5.16 and the net population production efficiency ($P/A \times 100$) becomes 36.63%.

Phillipson et al. (1975) found the annual carbon dioxide evolution from the Brogden's Belt site to be 239.481 l CO_2 m^{-2} a^{-1}. Assuming an RQ of

0.9 for the "soil" respiration, oxygen consumption by the "soil" would be 263.429 l O_2 m^{-2} a^{-1} ($\approx$5263 kJ m^{-2} a^{-1}). The Brogden's nematodes in 1971–1972 were thus responsible for 0.11% (0.13% when corrected for the total nematode fauna by $\times$ 100/87). These estimates are lower than Bunt's (1954) estimate of 0.9% (range 0.5–1.2%) for Macquarie Island soils and lower than the 0.6–0.7% calculated by Banage (1963) for moorland nematodes. They are similar to the 0.008 to 0.21% at Signy Island (Spaull, 1973). On the current evidence nematode contribution to total soil repiration is relatively small.

References

Andrássy, I.: Die Rauminhalts- und Gewichtsbestimmung der Fadenwürmer (Nematoden). Acta zool. hung. **2**, 1–15 (1956)

Arkell, W.J.: The geology of Wytham Hills. Unpublished ms. of survey done in 1943. Geology Department, Oxford University (1945)

Arpin, P.: Sur quelques aspects des intéractions sol-nématodes dans des biocénoses forestières ou herbacées. Rev. Ecol. Biol. Sol. **12**, 57–67 (1975a)

Arpin, P.: Etude systématique et dynamique de deux Nématocénoses en climat tempéré. Rev. Ecol. Biol. Sol. **12**, 493–521 (1975b)

Banage, W.B.: The ecological importance of free-living soil nematodes with special reference to those of moorland soil. J. anim. Ecol. **32**, 133–140 (1963)

Banage, W.B.: Nematode distribution in some British upland moor soils with a note on nematode parasitizing fungi. J. anim. Ecol. **35**, 349–361 (1966)

Berge, J.B., Dalmasso, A., Kermarrec, A.: Etude des fluctuations des populations d'une nématofaune prairiale. Rev. Ecol. Biol. Sol. **10**, 271–285 (1973)

Berthet, P.: La mesure écologique de la température par détermination de la vitesse d'inversion du saccharose. Vegetatio **9**, 197–207 (1960)

Bornebusch, C.H.: The fauna of forest soil. Forst. Forsøgsv. Danm. **11**, 1–224 (1930)

Bunt, J.S.: The soil inhabiting nematodes of Macquarie Island. Aust. J. Zool. **2**, 264–274 (1954)

Duncan, A., Klekowski, R.Z.: Parameters of an energy budget. In: Methods for ecological bioenergetics (W. Grodzinski, R.Z. Klekowski, A. Duncan, eds.), pp. 97–147. Oxford: Blackwell 1975

Elton, C.S.: The pattern of animal communities, pp. 1–432. London: Methuen 1966

Heilbrunn, L.V.: An outline of general physiology, 2nd ed., pp. 1–384. Philadelphia-London: Saunders 1947

Huhta, V., Koskenniemi, A.: Numbers, biomass and community respiration of soil invertebrates in spruce forests at two latitudes in Finland. Ann. Zool. Fennici **12**, 164–182 (1975)

Kristensen, K.J.: Temperature and heat balance of soil. Oikos **10**, 103–120 (1959)

Krogh, A.: The quantitative relation between temperature and standard metabolism in animals. Int. Z. phys-chem. Biol. **1**, 491–508 (1914)

Lee, R.: Chemical temperature integration. J. appl. Meteorol. **8**, 423–430 (1969)

Leslie, P.H., Ranson, R.M.: The mortality, fertility and rate of natural increase of the cole (*Microtus agrestis*) as observed in the laboratory. J. anim. Ecol. **9**, 27–52 (1940)

Lotka, A.J.: Théorie analytique des associations biologiques. II. Analyse démocratique avec application particuliere à l'espèce humaine. Actualités Scientifique et Industrielle, No. 780, Paris (1939)

McNeill, S., Lawton, J.H.: Annual production and respiration in animal populations. Nature (Lond.) **225**, 472–474 (1970)

Nielsen, C.O.: Studies on the soil microfauna. II. The soil inhabiting nematodes. Nat. Jutl. **2**, 1–31 (1949)

Nielsen, C.O.: Respiratory metabolism of some populations of enchytraeid worms and freeliving nematodes. Oikos **12**, 17–35 (1961)

Nielsen, C.O.: Nematoda. In: Soil biology (A. Burges, F. Raw, eds.), pp. 197–211. London-New York: Academic Press 1967

Phillipson, J., Abel, R., Steel, J., Woodell, S.R.J.: Earthworms and the factors governing their distribution in an English beechwood. Pedobiologia **16**, 258–275 (1976)

Phillipson, J., Putman, R.J., Steel, J., Woodell, S.R.J.: Litter input, litter decomposition and the evolution of carbon dioxide in a beech woodland – Wytham Woods, Oxford. Oecologia (Berl.) **20**, 203–217 (1975)

Solomon, M.E.: Tyroglyphid mites in stored products. Methods for the study of population density. Ann. appl. Biol. **32**, 71–75 (1945)

Spaull, V.W.: Distribution of nematode feeding groups at Signy Island, South Orkney Islands, with an estimate of their biomass and oxygen consumption. Br. Antarct. Surv. Bull. No. **37**, 21–32 (1973)

Whitehead, A.G., Hemming, J.R.: A comparison of some quantitative methods of extracting small vermiform nematodes from soil. Ann. appl. Biol. **55**, 25–38 (1965)

Winberg, G.C., ed.: Methods for the estimation of production of aquatic animals (A. Duncan, transl.), pp. 33–64. London-New York: Academic Press 1971

Yeates, G.W.: Nematoda of a Danish beech forest. Oikos **23**, 178–189 (1972)