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An Energy Budget for the Free-Living Nematode *Pelodera* (Rhabditidae)

R. Marchant* and W. L. Nicholas

Zoology Department, A.N.U., Canberra, A.C.T. 2601

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Summary. The energetics of a population of a free-living nematode *Pelodera* sp. that feeds on bacteria were studied in the laboratory. A budget was drawn up for *Pelodera* feeding on *Escherichia coli* labelled with ^{14}C. Measurements were also made of population growth, respiration and feeding rate. *In vitro*, *Pelodera* ingested on average 37.0×10^{-2} J h^{-1} mg^{-1} dry weight, of which 13.7×10^{-2} J h^{-1} mg^{-1} dry weight were respired, 15.0×10^{-2} J h^{-1} mg^{-1} dry weight were excreted and 8.3×10^{-2} J h^{-1} mg^{-1} dry weight were retained in growth. The measurements of feeding rate indicated that the values for the percentage energy flow depended partly on the concentration of bacteria present. These results are discussed and an energy budget is calculated for bacterial-feeding nematodes in bog soil, using published field data.

Introduction

Knowledge of the ecology and energetics of free-living nematodes is limited, in spite of their abundance in the soil and mud ecosystems. Several authors have tried to estimate their contribution to the energy flow in an ecosystem by combining data on their biomass in the field with laboratory data on their respiration (Nielsen, 1949, 1961; Bunt, 1954; Wieser and Kanwisher, 1961; Teal, 1962; Teal and Wieser, 1966). Cragg (1961) compared data from several of the above authors with that for other groups of soil invertebrates and concluded that nematodes probably contributed little to the energy flow. Nielsen (1961) calculated from respiration rates that nematodes ate 800 kg of bacteria out of an estimated total consumption by soil invertebrates of 9000 kg per hectare per year. Wieser and Kanwisher (1961) estimated that nematodes accounted for 33% of the oxygen consumed by the mud of a salt marsh. In contrast, Teal and Wieser (1966) reported that they accounted for only 3% in another. Previously, Teal (1962) had measured the density of free-living nematodes in this marsh and had calculated the rate that they assimilated energy. He used published data on their respiration and arbitrarily assumed that 75% of the energy assimilated was respired and 25% was used in growth. Gerlach (1971)

* Present address: Zoology Department, Monash University, Clayton, Victoria 3168, Australia.

in his review of the marine meiofauna believed nematodes contributed an important fraction to the total metabolism of marine sediments.

There are other parameters to consider, apart from respiration and biomass, however, if the flow of energy through nematode populations is to be understood. Yeates (1973) calculated the production and respiration of 29 species of soil nematodes from a beech forest. He used Nielsen's (1949) estimates of respiration and calculated a minimal value for yearly production by summing the increases in the population biomass between sampling occasions. With this data he determined annual assimilation but was unable to measure total energy flow and thus complete the budget because he had no data on the rate of ingestion of energy. In this paper we present laboratory data on complete budgets compiled for a fresh water nematode feeding on bacteria.

We selected a species which occurs in a local river with a view to future studies of its ecology in the field. The species belongs to the very common genus *Pelodera* (Rhabditidae) but the unsatisfactory state of rhabditid taxonomy makes the positive identification of species uncertain. Some pertinent data on feeding and growth of a related bacterial feeding soil nematode, *Caenorhabditis briggsae* (Rhabditidae) has been published by Nicholas *et al.* (in press), but nothing is known of its ecology and it has been kept in the laboratory for many years.

We began by drawing up carbon budgets from experiments in which *Pelodera* were fed on *Escherichia coli* labelled with ^{14}C. Then, the decline in bacterial numbers when a dense suspension was fed upon by a population of these nematodes was followed to relate changes in feeding rate to the concentration of food. The ecological efficiency, as defined by Slobodkin (1962), namely the ratio of production to consumption (P/C), was calculated from the experiments with ^{14}C. An independent estimate of this ratio was obtained by growing large populations of *Pelodera* from a few individuals in culture of known amounts of bacteria. To convert the weight of nematodes produced to calories and thus joules, the caloric value of *Pelodera* had to be measured. Finally the respiratory rate of the *Pelodera* was measured to check the values obtained using ^{14}C.

Materials and Methods

The Experimental Animals

Pelodera sp. was collected from muddy sand on the banks of the Molongolo River, Australian Capital Territory, about 400 m downstream from the outfall of Canberra's sewage works. Initially *Pelodera* were cultured in nutrient agar with a mixed bacterial flora. Several specimens were then axenised with penicillin and streptomycin (Rothstein and Nicholas, 1967) and used to start axenic cultures. Thereafter, *Pelodera* were maintained in an axenic culture medium described by Nicholas *et al.* (in press), so as to supply large numbers of axenic nematodes for experiments.

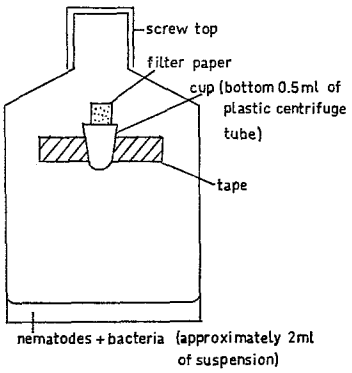

Fig. 1. Culture flask used in ^{14}C experiments showing arrangement for trapping $^{14}CO_2$ evolved. See Fig. 2 for further details

E. coli was the only bacterium used as food in experiments. A wild strain, BS (sensitive to streptomycin), was obtained from the John Curtin School of Medical Research in the Australian National University, and was kept on slopes of Brain Heart Infusion agar at 4°C.

The Carbon-14 Experiments

Sub-cultures of *E. coli* were prepared in 100 ml of Brain Heart Infusion broth (Oxoid Ltd., London). After 48–72 h the bacteria were separated from their medium and washed three times in distilled water by centrifuging. The bacteria were labelled in 2 ml of water containing 20 μCi of $NaH^{14}CO_3$ (57 mCi mM^{-1}, Radiochemical Centre, Amersham, U.K.) for 18–24 h. The next day the bacteria were washed again in the same way to remove unassimilated ^{14}C. Finally, streptomycin sulphate was added, 1000 units ml^{-1}, to the suspension of bacteria to inhibit bacterial reproduction which is stimulated by the release of nutrients from *Pelodera* during feeding.

Six cultures of *Pelodera* were used for each experiment. The nematodes were centrifuged to separate them for their culture medium and then washed as above three times. Rhabditidae can tolerate high concentrations of streptomycin. One withstands concentrations of 10^6 units ml^{-1} (Gochnauer and McCoy, 1954). The solutions of *E. coli* and *Pelodera* were pipetted into a culture flask producing a suspension of about 2 ml, and left for 48 h. Fig. 1 shows the experimental apparatus used. As controls experimental flasks containing the same amount of labelled *E. coli* but no nematodes were run concurrently. The flasks were kept at a constant temperature of 20 ± 1°C during the experiment. At the end of 48 h the contents of both flasks were treated as shown in Fig. 2 to determine the distribution of the isotope. Three types of flask were used in these experiments: a 250 ml tissue culture flask (Falcon Plastics, B–D Laboratories Inc., USA) with a screw top; a 200 ml Erlenmyer flask with a screw top and a 100 ml Erlenmyer flask with a serum cap. It was found that 48 h was sufficient for most of the bacteria to be eaten by the *Pelodera*, but not long enough for *Pelodera* to multiply significantly.

The dry weights specified in Fig. 2 were taken from samples which had been dried in an oven at 60 ± 1°C for at least 24 h, then transferred to a desiccator for

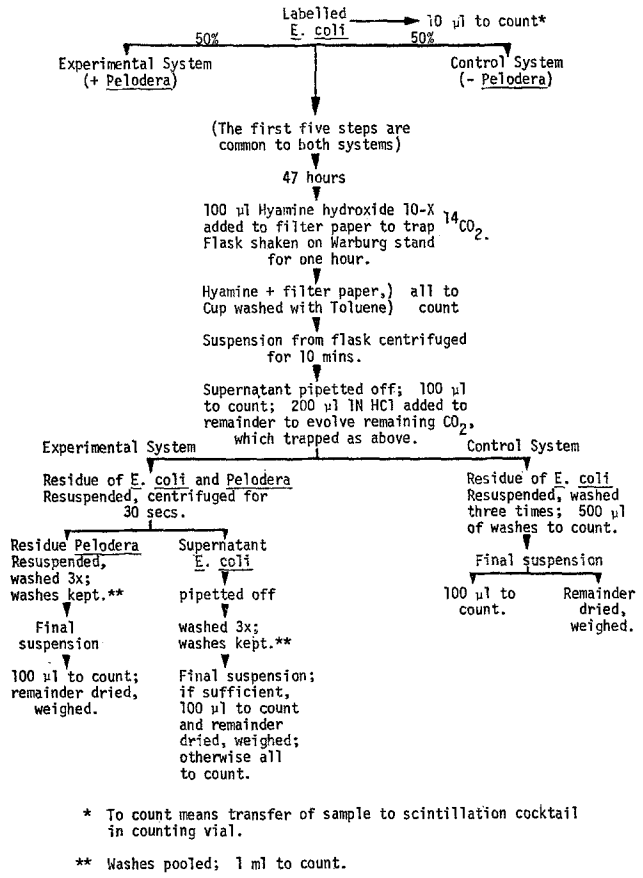

Fig. 2. Procedure used to determine redistribution of ^{14}C after 48 h in experimental and control systems

another 24 h, and finally weighed to ± 0.05 mg. The radioactivity of the various components indicated in Fig. 2 was measured with a liquid scintillation counter (Beckmann Liquid Scintillation System), following the techniques and advice of Kobayashi and Maudsley (1969). Each sample was pipetted into a vial containing 15 ml of a scintillation cocktail. The cocktail consisted of:

3 g PPO (2,5-diphenyloxazole) (Ajax Chemicals),
500 ml Toluene (Matheson, Coleman and Bell),
100 ml Triton X100 (Robert, Bryce and Co. Ltd.).

Efficiency and quenching were estimated by counting an internal benzoic acid-^{14}C standard. All vials were kept in the dark for at least 24 h before counting to prevent chemoluminescence and to provide enough time for the cocktail to penetrate the sample fully. All vials were counted for at least 20 min. Background counts

were subtracted and the resulting D.P.M.s increased according to the size of the sample taken from the total amount present.

The efficiency of trapping of $^{14}CO_2$ in the three types of flask was tested by adding different amounts of $NaH^{14}CO_3$ to five flasks of each type. $^{14}CO_2$ was evolved by adding 100 µl of lNHCl. The amounts of $NaH^{14}CO_3$ added covered the range or $^{14}CO_2$ released in the actual isotope experiments. Each flask was fitted with cups and paper as shown in Fig. 1. They were left for 48 h and then the $^{14}CO_2$ evolved was absorbed by the procedure given in Fig. 2 and the radioactivity measured. The pH at the end of the 48 h was always less than 2.5. The flasks had the following average efficiencies:

100 ml Erlenmyer flask with serum cap, 80%,
250 ml tissue culture flask with screw top, 70%,
200 ml Erlenmyer flask with screw top, 60%.

The self-absorbance of *Pelodera* was estimated by comparing the D.P.M. from a suspension of the untreated nematode (labelled by feeding on *E. coli*) with aliquots from nematodes pre-digested in a 100 µl of hyamine hydroxide 10 – X (Packard Instrument Corp., USA) for 1–2 h at 50°C in a closed vial. An average self-absorbance of 1.5 ($n = 3$) was calculated. Self-absorption of the bacteria was considered negligible.

Before performing any of the above procedures, our micropipettes were calibrated either by weighing distilled water or using radioactive standards. In particular, the volumes delivered when pipetting nematodes and bacteria were determined.

The Feeding Rate Experiment

The method described by Nicholas *et al.* (in press) in which the number of bacteria remaining in a suspension of bacteria and *Pelodera* was estimated after successive intervals by haemocytometer counts was used to make one experiment. At the end of the experiment the nematodes were dried and weighed as above. The results were recorded as concentration of bacteria versus time and then converted to dry weight of bacteria versus time by taking 10^{10} cells to weigh 4.0 mg (Nicholas *et al.*, in press). Linear regression lines were fitted to enable estimation of the ingestion rates.

The Growth Experiment

A suspension of unlabelled *E. coli* in streptomycin (1000 units ml^{-1}) was prepared as before, except that sterile water was used for washing. Five sterile culture flasks were each inoculated with 4 ml of this suspension; 1 ml was dried and weighed as above. Then each flask was inoculated with less than fifty *Pelodera* at all stages of maturity. The flasks were stored at 20 ± 1°C and aerated every day. All manipulations were done taking precautions to maintain sterility. When almost all of the bacteria had been eaten as determined by the clarity of the suspension under the microscope, the mixture was pipetted from each flask and the *Pelodera* and remaining bacteria were separated by differential centrifugation and dried and weighed. Nematode growth was measured in ten of these cultures (five cultures in each series). In each of the flasks traces of fungal contamination became evident, but as soon as this was noticed a few grains of mycostatin was added to each. The fungus had disappeared completely by the time the nematodes and residual bacteria were separated for weighing.

The caloric value of *Pelodera* was measured in a microbombcalorimeter, as described by Phillipson (1964) following the methods recommended by Cummins

and Wuycheck (1971). The caloric value of *E. coli* was taken at 5.028 cal or 21.1 J mg^{-1} dry weight (Cummins and Wuycheck, 1971).

Respriation

Respiration was measured at a constant temperature of $20 \pm 1°C$ with a Warburg manometer using the direct technique of Umbreit, *et al.* (1957). *Pelodera* were fed on *E. coli* for at least 24 h before making the measurements. They were then washed free from bacteria and placed in Warburg flasks in 1.0 to 1.5 ml of water. Each determination lasted for 2–3 h after which the nematodes were dried and weighed. The nematodes did not stop swimming in the flasks and appeared as active at the beginning and end of the measurement as in their culture medium. Respiratory rates and respiratory quotients (*R.Q.*) were calculated with formulae and nomograms from Umbreit *et al.* (1957).

Results

The Carbon-14 Experiments

Table 1a shows the distribution of the ^{14}C in the experimental system and Table 1b the distribution in the control system for four experiments. Table 2 presents the weights of *Pelodera* and bacteria used in each. An estimate of the mean weight of bacteria present in each experimental system was used to calculate how much of the ^{14}C in the supernatant, washes and CO_2 came from the metabolism of the bacteria before they were eaten. The average of columns 2 and 3, in Table 2, was taken as the best estimate of this value in each experiment. Using these means, the counts in the appropriate control experiments were reduced proportionally and then subtracted from the experimental system. The error from doing this is not large because the bacterial metabolism is largely inhibited by streptomycin in the control (see Table 1b) and thus the experimental systems. Of more significance is the fact that some ^{14}C was unaccounted for at the end of each experiment. In our view it was lost as $^{14}CO_2$ thus implying that the correction factors applied to allow for such a loss in the various flasks were too low. Consequently the D.P.M. released as respiration were increased by the appropriate amounts and the budgets completed (see Table 3).

To convert the D.P.M. in Table 3 to joules the caloric value of *E. coli*, 5.028 cal (21.1 J)mg^{-1} dry weight, and the weight of the *E. coli* fed to the nematodes (column 2, Table 2) were used to calculate the number of joules per D.P.M. for each experiment. By dividing the figures thus obtained by the dry weight of *Pelodera* and by time, the results were converted to a rate in units of J h^{-1} mg^{-1} dry weight of *Pelodera* (Table 4). The joules in the supernatant and the washes were considered as total excretion by the nematodes during the experiment. The joules retained by the *Pelodera* were divided into those that were

Table 1a. The distribution of ^{14}C measured as disintegrations per minute (D.P.M.) in the experimental system

Expt. no. and flask used	^{14}C added as *E. coli*; 0 h	$^{14}CO_2$ 48 h[a]	*Pelodera* 48 h[b]	Supernatant 48 h	Uneaten *E. coli* 48 h	Washes 48 h	DPM total 48 h	DPM unaccounted for	% recovery
1 100 ml Erlenmyer flask	76663.1	24929.9	17320.9	19936.9	1281.0	6407.7	69876.4	6766.7	91.1
2 250 ml tissue culture flask	75016.1	23129.0	17181.0	15474.5	7146.0	4063.1	66993.6	8022.5	89.3
3 200 ml Erlenmyer flask	176019.4	48645.1	47180.3	49935.4	16044.4	13631.1	175436.3	583.1	99.7
4 250 ml tissue culture	251330.6	42207.7	80292.0	78197.1	5280.3	13775.4	219752.5	31578.1	47.4

[a] Figures corrected for loss of CO_2 from flasks using appropriate factors.
[b] Figures corrected for self absorbance.

Table 1b. The distribution of radioisotope measured as disintegrations per minute (D.P.M.) in the control system

	D.P.M.						
Expt. no.	^{14}C added as *E. coli*; 0 h	$^{14}CO_2$ 48 h[a]	*E. coli* 48 h	Supernatant 48 h	Washes 48 h	DPM total	% recovery[b]
1	66696.6	3679.2	59997.4	1458.4	1886.8	67021.8	100.5
2	75016.0	5539.7	69589.1	423.1	286.7	75838.6	101.0
3	176019.4	4863.5	169115.6	1831.7	979.7	176790.5	100.4
4	251330.6	7784.9	249147.0	2863.4	3236.4	263031.7	104.7

[a] Figures corrected for loss of $^{14}CO_2$ from flasks using appropriate factors.
[b] The percentage recovery in the control system is slightly high indicating errors in the correction factors. Therefore the percentages recovered in the experimental system have probably been overestimated.

Table 2. Dry weights in the ^{14}C experiments calculated from the weight of samples

Expt. no.	Estimate of *E. coli* at 0 h[a], mg dry weight	Weight of uneaten *E. coli* at 48 h, mg dry weight	*Pelodera* recovered at 48 h, mg dry weight
1	10.5	0.2	15.1
2	17.2	1.7	25.1
3	18.4	2.6	15.0
4	15.9	0.4	14.7

[a] Weight derived from the weight of bacteria recovered from controls at 48 h.

Table 3. A ^{14}C budget (in D.P.M.) when *Pelodera* feeds on ^{14}C labelled *E. coli*[a]

Expt. no.	Respired as $^{14}CO_2$	Retained by *Pelodera*	Excreted by *Pelodera* into Supernatant	Lost from *Pelodera* in washes	Total
1	29556.9	17320.9	19080.8	5300.1	71258.7
2	28076.9	17181.0	15239.7	3904.0	64401.6
3	46455.3	47180.3	48891.3	13073.5	155600.4
4	69799.9	80292.0	76761.6	12118.4	238971.9

[a] The estimated contributions from the metabolism of uneaten *E. coli* have been subtracted.

Table 4. A carbon budget when *Pelodera* feeds on *E. coli*; D.P.M. given in Table 3 have been converted to joules

Expt. no.	Ingestion[a]	Production[a]	Respiration[a]	Excretion[a]
1	28.6 (100)	5.5 (19.1)	12.6 (44.4)	10.5 (36.5)
2	26.0 (100)	5.0 (19.3)	12.2 (47.4)	8.8 (33.3)
3	47.9 (100)	10.9 (23.1)	15.5 (32.7)	21.5 (44.2)
4	45.4 (100)	11.7 (25.8)	14.6 (32.0)	19.1 (42.3)
Average	37.0 (100)	8.3 (22.4)	13.7 (37.4)	15.0 (40.2)

[a] In joules $\times 10^{-2}$ h^{-1} mg^{-1} dry weight of nematodes; percentages in brackets.

incorporated into compounds of low molecular weight, *e.g.* metabolic intermediates and those incorporated into compounds of high molecular weight *e.g.* proteins, glycogen, nucleic acids, lipids. Nicholas and Viswanathan (in preparation) fed ^{14}C labelled *E. coli* to *C. briggsae* for 24 h, and then fractionated the nematodes. In three experiments

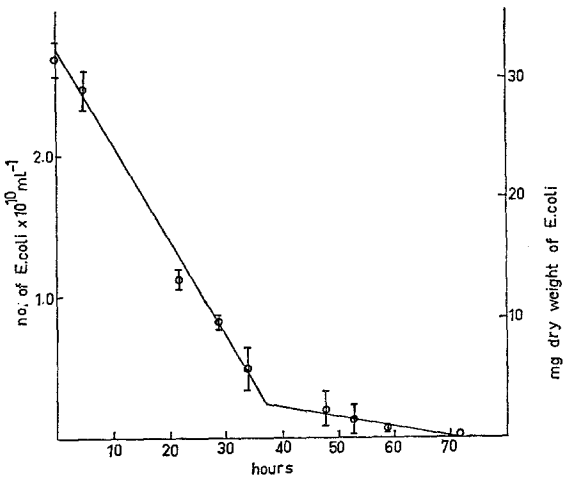

Fig. 3. The progressive decrease in *E. coli* when fed upon by *Pelodera*. Each point is the mean of 12 counts; the vertical lines indicate one S.E. about the mean. Regression line for the steeper slope is y (mg) $= -0.80\,t$ (h) $+32.49$; the other regression line is y (mg) $= -0.08\,t$ (h) $+5.92$

approximately 30% was recovered as soluble in 80% aqueous ethanol, giving an estimate of the fraction of ^{14}C and thus joules in low molecular weight metabolites. Because the compounds of high M.W. constitute the structure or biomass of the nematode, production during the experiment was calculated by multiplying the data from Table 3 for retention of the isotope by 0.7. The resulting figures imply that there was an increase in the weight of the nematodes during the experiment. This increase would not alter significantly the weights given in Table 2 which were taken as the most reliable measure of the weight of *Pelodera* present during the 48 h. The 30% of the ingested joules that went into compounds of low M.W. were joules ingested by the nematodes during the experiments, but which they had not metabolised. For simplicity, these unused joules were divided according to the ratios of the joules already present in each of the components of the budgets.

The Feeding Rate Experiment

The figures in Table 4 indicate that the isotope experiments fall into two groups: experiments 1 and 2 and experiments 3 and 4. Each pair has very similar energy flux. The results of the feeding rate experiment shown in Fig. 3 can explain the differences between the two pairs. The dry weight of *Pelodera* present during this experiment

Table 5. The ingestion rates from the ^{14}C experiments compared with those derived from the feeding rate experiment

Expt. no.	Ingestion rates from ^{14}C expts.[a]	Time taken to reach critical concentration (h)[b]	Ingestion rates from the feeding rate expt.[a]
1	28.6	9	34.4
2	26.0	9	34.4
3	47.9	17	53.8
4	45.4	15	48.7

[a] In joules $\times 10^{-2}$ h^{-1} mg^{-1} dry weight of nematodes.
[b] Equivalent to 2.4 mg in 2 ml of suspension (expts. 1 and 4) or 3.0 mg in 2.5 ml of suspension (expts. 2 and 3).

was 13.2 mg. Using this and a caloric value for *E. coli* of 21.1 J mg^{-1} dry weight, the regression coefficients from Fig. 3 can be converted to ingestion rates in units of J h^{-1} mg^{-1} dry weight of *Pelodera*. The steeper slope equals a rate of 127.7×10^{-2} J h^{-1} mg^{-1} dry weight; the other is equivalent to 13.0×10^{-2} J h^{-1} mg^{-1} dry weight.

The rates of ingestion in Table 4 are intermediate between these two. This indicates that the feeding period of 48 h falls on both slopes of Fig. 3. In other words, the rates of ingestion derived from the isotope experiments are not constant over the feeding period, but fall continuously as the density of food decreases. As an approximation the rates can be resolved into two rates. The factor that determines what fraction of the 48 h period proceeds at each rate is the time it takes the nematodes to reduce the bacteria from their initial concentration to the critical concentration, about 3×10^9 cells ml^{-1}, at which the rate changes. This time was estimated from the absolute ingestion rates in mg per hour which can be calculated for each experiment from the larger of the above two ingestion rates and the weight of nematode present (Table 3). Using this data weighted averages of the two rates in question were determined (Table 5). Although these are only approximately equal to the rates of ingestion measured with ^{14}C, they illustrate the dependance of the rate of ingestion on the density of the food and help to explain the grouping of the results in Table 4.

The changing proportions of ^{14}C recovered as respiration can probably be explained by the fact that below the critical concentration of *E. coli* the rate of ingestion approximately balances the respiratory rate (as measured with ^{14}C) resulting in a shift in the use of energy from growth and reproduction to maintenance. The increasing percentage of ^{14}C

Table 6. Results of the growth experiments

Weight (mg) of bacteria eaten	Weight (mg) of *Pelodera* produced
17.2	1.2
18.0	1.5
17.6	1.6
17.4	1.4
17.4	1.4
24.8	1.8
23.6	1.2
22.0	0.4
23.8	1.2
24.2	1.4

excreted as ingestion rate rises perhaps indicates that the percentage available for nematode growth is limited.

The Growth Experiments

The carbon-14 budgets, then, describe the situation when a stable population of nematodes feeds on a suspension of bacteria. A different situation occurs when a small population of *Pelodera* grows and reproduces in an abundant food supply. Table 6 presents the results of a long term culture of *Pelodera* on a diet of *E. coli*. The average weight of bacteria eaten and of *Pelodera* produced were multiplied by their caloric values and converted to a percentage to calculate the average ecological efficiency. The caloric value of *Pelodera* was 6.3 ± 0.7 (S.E; $n = 8$) cal or 26.5 J mg^{-1} dry weight.

The result was an efficiency of 8.0% which is lower than the average efficiency of 22.4% calculated from the ^{14}C experiments (Table 4). This may have been due to significant mortality during these long term cultures, although large numbers of dead nematodes were not observed. Other causes may have been the fungal contamination of the suspensions or the accumulation of waste products from the nematodes, both of which may have inhibited growth.

Respiration

The rate of O_2 consumption in the Warburg manometer was 4.2 ± 0.2 (S.E.; $n = 3$) $\mu l\ h^{-1}\ mg^{-1}$ dry weight. The *R.Q.* was 1.0 indicating carbohydrate was being used for which 21.2 joules are released per ml of O_2 consumed (Petruscwiczs and Macfadyen, 1970). This give a standard

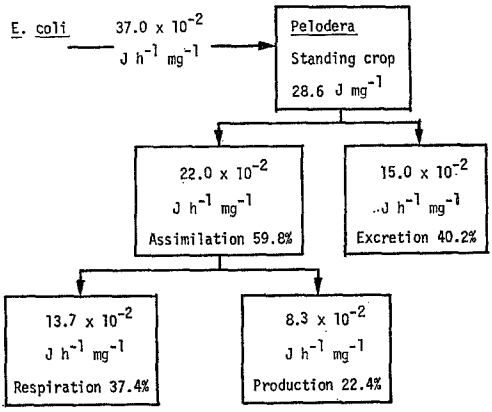

Fig. 4. Energy budget for the laboratory system

metabolic rate of 8.8×10^{-2} J h^{-1} mg^{-1} dry weight. This is significantly less ($0.01 > P > 0.001$) than that recorded from the ^{14}C experiments as one might expect because the nematodes were not feeding. Nevertheless, the values from the two types of determination are of the same order of magnitude thus providing independent support for the estimates of energy flow from the ^{14}C budgets. The respiratory rates measured by Nielsen (1949), Wieser and Kanwisher (1961) and Teal and Wieser (1966) range from 2.1 to 17.0×10^{-2} J h^{-1} mg^{-1} after correcting their values to dry weight (0.25 of wet weight).

Discussion

In our view, the most accurate data from the ^{14}C budgets are those on the percentage utilisation of the ingested energy. The accuracy of these percentages does not depend on conversion factors whereas the accuracy of the rates at which this energy is used does. We have shown by our feeding rate experiment that the values of these percentages depend partly on the concentration of food present. It is very likely that they also depend on the size and thus maturity of the nematodes, but we cannot determine the influence of this factor because we used populations of *Pelodera* which were at *all* stages of growth. The data from these budgets can be summarised by presenting the average rates of energy flow from Table 4 in a flow diagram (Fig. 4).

The average ecological efficiency is 13.0% if data from Fig. 4 and the growth experiments are combined. Slobodkin (1962), reviewing

available data, found that the value of this efficiency varied from 5 to 20%. Teal (1962) calculated an efficiency of 6.8% for the nematodes in a saltmarsh while Nicholas *et al.* (in press) calculated that 13% of the *E. coli* eaten is incorporated, by dry weight, into *C. briggsae*. The percentage of food assimilated in our budget is 59.8%. Engelmann (1966) stated that the percentage assimilated by poikilotherms was not more than 30%. The assimilation efficiency in our budget is high perhaps because the food contains less indigestible matter than that found in nature. Also differences between the physical and chemical conditions of our system and the natural system may have an effect. The turnover time for the biomass in our system is about 14 days. Wieser and Kanwisher (1961) calculated a time of 1 year, Teal (1962) of 1.6 months, and Nielsen (1949) of 1 month for field populations of a number of species of free-living nematodes. Again, the shorter time for *Pelodera* may be due to the above factors as well as the absence of competitors. It should be noted from Fig. 5, that production accounts for about 38% of total assimilation, whereas Teal (1962) assumed it accounted for only 25%. Yeates (1973) found that it accounted for even less, 21%, but he considered that he had underestimated production by a half in which case it would have accounted for 36%.

At this stage our efficiencies must be regarded as tentative until we have more data, especially on the influence of the maturity of the nematodes on them. The basic assumption of our method is, of course, that the ^{14}C labelled molecules are distributed evenly throughout the bacterial cell. Although this is probably not strictly true, any such error and any sampling error in our methods are probably insignificant compared to the errors which result from losses of the isotope when separating the components of the budget to measure their radioactivity. These losses are mainly due to pipettes that deliver a smaller volume than they should and incomplete trapping of the $^{14}CO_2$ evolved. Table 1 (a and b) shows that approximately 10% of the isotope initially added still remains unaccounted for even when correction factors for these two losses have been applied. Finally, an error, though less significant than these two, is made when basing our estimates of the amount of isotope retained as biomass by *Pelodera* on measurements made for a different, but related, bacterial feeding nematode.

It is possible to extrapolate our laboratory budgets to naturally occurring ecosystems. Before this can be done it must be realised that they are only short term determinations (48 h) of how incoming energy is used. They ignore mortality and predation both of which would have a significant effect on the long term energy flux in a naturally occurring

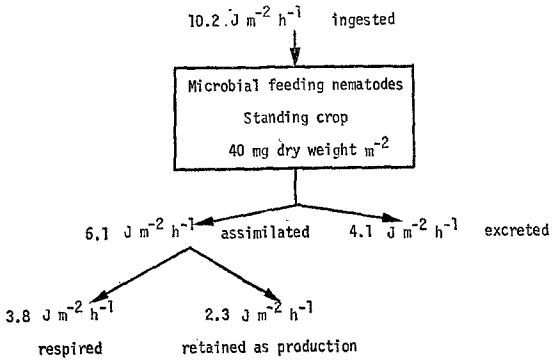

Fig. 5. Energy budget for nematodes in bog soil

population, especially on the amount that is transformed into nematode production. The only way round this problem if we wish to extrapolate our data is to take regular measurements of the nematode biomass in a natural ecosystem. This data would take into account mortality and predation and then, by applying data from laboratory budgets, field budgets could be calculated for each measurement of biomass. Summing such budgets would give a total budget for the period considered. Also if data was collected on age structure which indicated whether the population was just maintaining itself, *i.e.* composed mainly of non-reproducing adults, or actively growing and reproducing *i.e.* composed mainly of juveniles and reproducing adults, then the investigator would be better able to decide whether all the energy that was assimilated was respired as assumed by Nielsen (1949, 1961) or whether some was used for growth. Unfortunately this would not always be a clear decision because our laboratory data suggest that the ability of a population to grow actively depends partly on the concentration of available food.

Despite the fact that we do not have this information we think it is useful to compare our data with some published by Nielsen (1949) for a mixed population of bacterial feeding nematodes in bog soil. In our opinion the nematode fauna of this habitat is likely to be similar to that found in the mud of a river bank, the habitat where we collected *Pelodera*. Nielsen (1949) found that bog soil contained 3.4×10^5 or 160 mg wet weight of bacterial feeding nematodes per square meter which respired 182 $\mu l O_2$ m^{-2} h^{-1} at 16°C or 3.8 J m^{-2} h^{-1} (21.2 J released per ml O_2 consumed). Assuming that the dry weight of a nematode is a quarter of its wet weight and correcting to 20°C using Winberg's values (Winberg, 1971) of Krogh's normal curve, this rate of respiration equals 13.6×10^{-2} J h^{-1} mg^{-1} dry weight of nematodes which is very close to

the average value measured in our budgets. Furthermore, if we assume that the percentages for the efficiency of energy flow from our budget, Fig. 4, are those found in the field then a complete budget can be calculated from Nielsen's data (see Fig. 5). The rate of ingestion in Fig. 5 equals 36.5×10^{-2} J h^{-1} mg^{-1} dry weight at 20°C which again is very close to our own value. These facts perhaps indicate that the energetics of *Pelodera* are similar to those of other bacterial feeding nematodes. The problem still remains whether the rates of energy flow and the efficiencies measured in the laboratory are comparable with those existing in the field.

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Mr. R. Marchant
Department of Zoology
Monash University
Clayton, Victoria 3168, Australia