

Soil Nematodes in Terrestrial Ecosystems¹

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Abstract: There has been much work on plant-feeding nematodes, and less on other soil nematodes, their distribution, abundance, intrinsic properties, and interactions with biotic and abiotic factors. Seasonal variation in nematode fauna as a whole is correlated with factors such as moisture, temperature, and plant growth; at each site nematode distribution generally reflects root distribution. There is a positive correlation between average nematode abundance and primary production as controlled by moisture, temperature, nutrients, etc. Soil nematodes, whether bacterial feeders, fungivores, plant feeders, omnivores, or predators, all influence the populations of the organisms they feed on. Although soil nematodes probably contribute less than 1% to soil respiration they may play an important role in nutrient cycling in the soil through their influence on bacterial growth and plant nutrient availability. *Key Words:* ecology, energetics, microcosms, nutrient cycling, primary production.

Nematodes, as one component of the soil ecosystem, interact with biotic and abiotic factors, producing economic crop losses but also having many other effects, largely unknown. The role of the nematode community in ecosystems is essential knowledge for managing plant nematode populations (42), clarifying the role of nematodes in dispersing algae, fungi, bacteria, phages, and viruses (103, 104), decreasing energy inputs to farming, disposing of organic wastes (57), and dealing with nematode tolerance to nematicides (80). Keys to understanding that role will be knowledge of the distribution and diversity of nematodes in ecosystems, as well as their population dynamics and their influence on food sources.

This paper, concerned mainly with nematodes in natural or lightly managed terrestrial ecosystems, relies heavily on data collected from such habitats during the International Biological Programme (1964–1974). The role of nematodes in ecosystems is understood more easily, and sampling effort reduced, in stable habitats where

nematode populations are more likely to be in equilibrium, albeit dynamic, with their environment, than in cultivated fields where conditions are subject to more drastic changes. In interpretation, however, knowledge of plant nematode biology and interactions derived from agriculture are used.

Nematodes feed on a wide range of foods, and this paper uses the following trophic groups: bacterial feeders, fungivores, plant feeders, omnivores, predators. In interpreting interactions, feeding and parasitism should be distinguished (109) as well as parasitism and pathogenicity (95). Soil samples may also yield soil stages of nematodes that parasitise invertebrates and vertebrates.

Any study of nematode populations, which repeated sampling has shown to contain up to 105 species (41) and 29,800,000 individuals per m² (94), must take into consideration the distribution in time and space not only of the nematodes but also of factors which may interact with them. The way in which each variable is measured may be crucial. There are many methods of extracting nematodes, each with its own efficiency (7), and ecologists have an added problem of assessing whether the nematodes recovered were active at the time of sampling so their metabolic contribution may be assessed (29, 64, 79). The typical aggregated distribution of all plant and soil

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nematode populations necessitates replicated sampling. Some nematologists work with individual cores (41, 110) and some bulk cores for extraction of subsamples (102); results are normally expressed per m² to a specified sampling depth, with some estimate of variability. Biomass and dry weight are often calculated so the respiratory activity and calorific content of the nematodes may be assessed and related to ecosystem dynamics.

POPULATION SIZE, STRUCTURE, AND DIVERSITY

Nematodes in differing ecosystems:

Nematode abundance and biomass from 115 places and habitats, including published and unpublished International Biological Programme data, show:

1) Population estimates range from 8,100/m², for rain forest in Puerto Rico, to 30,000,000/m² for meadow steppe in the USSR (69).

2) Wooded and non-wooded ecosystems have similar population ranges. In non-wooded habitats, mean nematode population densities tend to fall in the series mesic > wet > dry, and, when separated by the degree of organic matter on the soil surface, mineral soils have higher densities than organic mors and peats (69).

3) The relationship between abundance and dry weight suggests that mean individual biomass is greater for grassland nematodes than for woodland nematodes (69).

4) Nematode abundance and average individual weights appear lower for temperate coniferous forests than for deciduous forests (69).

Table 1 summarises data for 28 sites at which I have judged sampling to be adequate to calculate an annual mean population; use of annual means greatly reduces mean populations in grasslands (7,200,000 to 1,900,000/m²) and deciduous forests (6,100,000 to 1,700,000/m²) compared with those given by Petersen (69). Although based on a single site, deserts clearly have lower nematode density than other ecosystems. Petersen (69) had the impression of greater nematode abundance in deciduous than in evergreen forests; annual means show no significant differences. Deciduous

forests and temperate grasslands have similar densities. Nematodes from deciduous forests and temperate grasslands are also similar in total dry biomass and mean individual biomass, although considerably greater than nematodes from evergreen forests. Acid conditions prevailing in coniferous forest soils are inimical to lumbricid earthworms, millipedes, and woodlice, but soil fungi flourish much better than in looser base-rich soils of deciduous stands. In evergreen coniferous forests, fungal-feeding Tylenchida are likely to become more numerous; their small size is partly responsible for the smaller biomass in such forests.

Table 1 gives hourly respiratory rates at 2 C. In tundra the temperature is limiting for much of the year, whereas in deserts anhydrobiosis would be important. On an annual basis the more equitable microclimate in evergreen forests probably offsets the lower hourly respiratory rate: annual values are probably similar for temperate grasslands, evergreen forests, and deciduous forests.

The ratio between maximum and minimum nematode population densities over the year varies from 2× for an English beech woodland (71), 3× for a New Zealand sand dune (106), 4× for a French grassland (11), 5× for English moorland (6) and Danish beech forest (110), 6× for Finnish spruce (38) and Swedish pine forests (82), to 10× for a grazed New Zealand pasture (117). In part this reflects climatic differences, but nematodes are a component of ecosystems in which there are daily, seasonal, and annual fluctuations around the 'maximum persistent biomass', which itself is less than the 'maximum potential biomass', depending on the severity of the habitat.

Nematodes in climatic and vegetational sequences: Studying nematode populations in a sequence in which the climate, soil, or vegetation is constant is useful in illustrating the effect of these factors on population composition and species ecology.

Nematodes at six sites, with soils from similar parent material, supporting tussock grassland under precipitation of 350–5000 mm, were investigated using autumn samples (113). Total abundance declined with altitude, whereas diversity did not. *Para-*

TABLE 1. Average nematode population characteristics by ecosystem type for sites at which mean annual figures can be calculated. Based mainly on data in Petersen (69). Respiration has been calculated according to Klekowski et al. (50).

Ecosystem	Sites	Nematode abundance (thousands/m ²)	Dry weight (mg/m ²)	Mean individual dry wt (μg)	Mean individual fresh wt (μg)	Wt-specific O ₂ consumption at 20 C (μl × 10 ⁻³ /individual/hr)	Hourly respiration rate of population (μl O ₂ /m ² at 20 C)
Tundra	1	3,900	180	0.05	0.23	0.50	1950
Temperate grassland	6	1,919 ± 696 (204-3695)	217 ± 99	0.11	0.57	0.95	1820
Desert	1	423	25	0.06	0.30	0.60	250
Evergreen forests	11	2,811 ± 620 (911-6954)	128 ± 25	0.05	0.23	0.50	1410
Deciduous forests	9	1,731 ± 563 (178-4430)	200 ± 115	0.12	0.58	1.0	1730
Tropical forest	1	56	—	—	—	—	—

tylenchus was dominant at the two driest sites but at the next site was mixed with *Macroposthonia*, which occurred at all the wetter sites; *Radopholus* occurred at the wettest site and *Pratylenchus* at the preceding site. There was a high correlation (0.89***) between total nematodes and Truog P, a measure of readily available soil phosphorus, and a lesser correlation (0.69†) with percent soil organic carbon; both of these relate to plant growth in an area where phosphorus availability limits plant growth, and it is to this that the nematode populations are causally correlated.

In a series of 11 grazed *Lolium perenne*/*Trifolium repens* pastures the vertical distribution of total nematodes in 0–30 cm soil had an overall correlation of 0.95*** with Truog P and of 0.89*** with percent soil organic carbon (118). Fig. 1 shows the relationship between annual mean total

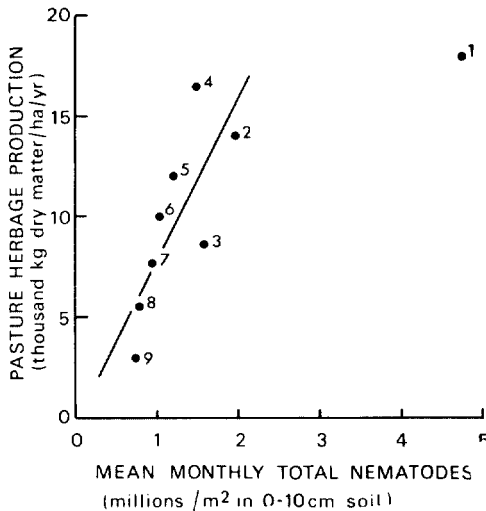


FIG. 1. Relationship between mean monthly total nematode populations and pasture herbage production at nine New Zealand pasture sites. Soil types on which the sites were situated are: 1, Levin; 2, Otiake with irrigation; 3, Rotoiti; 4, Tokomaru with irrigation; 5, Tokomaru dryland; 6, Kokotau; 7, Judgeford; 8, Pomare; 9, Otiake dryland. The regression equation for sites 2–9 is $y = 44.5 + 7.89x$; the regression coefficient is significant at 0.001%. See text for further information (118).

nematode population estimates and annual herbage dry-matter production for nine grazed New Zealand pastures over a wide range of soil types and conditions. There is a significant linear regression of herbage production on nematode population density at eight sites; the ninth aberrant site is one

at which neither soil moisture nor soil temperature is limiting during the year. On an annual basis, plant herbage yield was related more closely to nematode numbers than to soil phosphorus or percent soil organic carbon (118). Assessment of root production would be useful in such situations; the relations between root production and soil biota have been discussed by Coleman (15).

Wasilewska (97) reported on nematodes in six afforested dunes in Poland; four formed an establishment succession over 6–20 years, and the other two were 135-yr-old forests of differing composition. Nematode abundance, biomass, and metabolism had a strong positive correlation with soil humus content and the degree of vascular plant cover, particularly in the early (and presumably more productive) stages of the succession. The contribution of fungivores to numbers and biomass increased with time. The overall mean individual weight decreased through the succession, although most markedly in plant-feeding nematodes, corresponding to a shift from 60% plant-feeding nematodes at 6 yr to 15% at 17–20 years. Fungivores and plant feeders had maximum numbers in the spring, bacterial feeders maintained relatively large numbers and biomass throughout the year, and omnivores, fungivores, and plant feeders were reduced in winter. Omnivores and bacterial feeders made the greatest contribution to oxygen consumption.

Nielsen (63) sampled a 25-m beach transect and found a fourfold population increase to the seaward end, where there was a significant contribution by marine species. Sampling *Corynephorus* slopes showed a gradation in abundance and diversity from bare areas (175,000/m²; 10 spp) to under *Ononis* (1,200,000/m²; 18 spp). Nielsen correlated the degree of vegetative cover with nematode density.

Relation between nematodes and primary production of ecosystems: Primary production is the biomass which is incorporated into a plant community during a specified period; normally respiration losses are ignored and net production given, and often only the above ground portion is assessed. Nielsen (63) considered total nematode populations and suggested that nematode abundance is linked with lux-

eriant vegetation cover (i.e., greater primary production), while Stockli (87) suggested a link with readily decomposing organic substrate. Andrews et al. (3) reported that in a shortgrass prairie ecosystem "Grazing by cattle has a minor effect on primary production. In contrast, it is postulated that grazing by invertebrates, such as plant-parasitic nematodes, may have a major impact on primary production" (seasonally limited nematode activity has since been reported for the prairie (79) but does not basically alter relationships). Some of these relationships can be demonstrated experimentally [e.g., multiplication of *Panagrolaimus rigidus* reflects the amount of decaying organic material (53)], but the overall picture can be obtained only from comparative studies of ecosystems. This section considers total nematode populations in relation to environment. Preference is given to mean annual figures based on monthly or quarterly sampling, although some data used are less-well based.

Environmental management commonly leads to changes in plant productivity and in total and specific nematode populations. Relationships between nematode population size, rate of multiplication, and the growth of host plants have been reviewed (8, 45), but those relate primarily to plant-feeding nematodes in agricultural systems, including their interaction with climatic stress. However, comparisons of management regimes differing in intensity, or the replacement of one ecosystem by another, can give useful information on the components of the nematode fauna. That is particularly true when the nematology is on a strictly comparable basis.

In a *Phalaris tuberosa*/*Trifolium repens* pasture at Armidale, Australia, nematode abundance decreased in a strong correlation with decreased plant herbage and roots when stocking rates with sheep were higher (Table 2) (48). Although only total nematode abundance was assessed, the smaller root weights and litter production at the higher stocking rates would clearly reduce food available to plant- and bacterial-feeding nematodes. Results were similar for two adjacent mowing trials at Masterton, New Zealand, where the significant difference in cumulative pasture herbage yield (16,900 cf 9,800 kg D.M./ha) is reflected in

TABLE 2. Influence of stocking rate (sheep/ha) on nematode abundance in 0–25 cm soil, and standing pasture in Australian *Phalaris*/*Trifolium* pastures. After King et al. (48).

Sheep/ha	Mean nematodes /m ² (1,000s)	Green herbage	Dead herbage	Washed roots
		(kg dm/ha)		
10	270	3125	4225	6800
20	191	1959	1238	4263
30	101	620	104	2516

total nematode abundance [663,000 cf 344,000/m² in 0–10 cm soil depth (118)]. From a grazing trial at that site, Yeates (114) reported that an increase in stocking rate, liming, and phosphate fertilizer significantly increased total numbers of nematodes and of certain components (e.g., *Pratylenchus*, Mononchidae). This result is similar to that from Armidale, where pasture herbage production was greater (12,300, vs. 12,000 kg DM/ha/yr) in the year when there were significantly more nematodes from the highly stocked area (1,950,000/m² at 22.2 sheep/ha, vs. 1,610,000/m² at 14.8 sheep/ha).

Preliminary results from a study in which *Pinus radiata* seedlings were planted at a range of densities in pasture, and grazing continued, also indicate a clear relation between decreased pasture herbage production and decreased total nematode abundance in 0–10 cm soil in plots containing more trees/ha (118).

Cattle grazing for 28 years at the Cottonwood grassland site in South Dakota was correlated with a decrease in biomass of plant-feeding nematodes due to the absence of *Xiphinema americanum*, the largest species at the ungrazed site, a slight decrease in total nematode biomass, and a slight upward displacement of vertical distribution patterns with vegetation changes which apparently led to a general increase in *Tylenchorhynchus* spp. (78). Treating the grazed site with Vydate reduced nematode populations by 52–82% and increased herbage yield by 28–59%; with the dominance of plant-feeding nematodes (69% of numbers; 40–45% of biomass) it appears they may limit productivity. Smolik (78) used a relationship between nematode biomass, respiration, assimilation efficiency,

and activity to calculate the net food intake by nematodes, and found they consumed more than grazing cattle (Table 3). Subsequent work (79) suggests the nematodes were active only from June to September, not April to October as assumed in calculating Table 3; this is a reduction to 4/7, which would reduce nematode intake to about 22 and 32 g/m², which is still comparable to intake by cattle. A similar adjustment should also be applied to Smolik's results as used in assessing the importance of nematodes in ecosystems (3, 16), but that affects the conclusions only slightly.

The Cottonwood study showed the effects of 28 years of grazing. In a shrub-steppe ecosystem in Washington (81), 3 years of grazing and natural fire were not found to influence nematode abundance or biomass. The lack of change may be due to the initial absence of the large *Xiphinema americanum*, or the time elapsed since treatment may have been insufficient for population changes to become significant.

Wasilewska (98, 99) studied a mountainous Polish pasture. Although the penning-up of sheep increased annual pasture production from 200 g/m² to 396 g/m² (18), there was a depression in annual nematode abundance and its estimated metabolism. In ungrazed pasture, total nematode abundance and metabolism decreased with increase in the intensity of fertilizing with sheep manure. Analysis by feeding groups, however, shows some increase in bacterial feeders, fungivores, and plant-feeding nematodes with increased manure, while omnivores and predators decreased greatly. That differs from results in Australia and New Zealand. While the difference may be due to a single event rather than sustained management, the

TABLE 3. Estimated annual intake of primary production by cattle and nematodes at the Cottonwood grassland site, South Dakota, U.S.A.; their biomass is also given; all measurements are dry weights. After Smolik (78).

	Intake (g/m ²)		Biomass (g/m ²)	
	Cattle	Nematodes	Cattle	Nematodes
Ungrazed	—	57	—	0.54
Grazed	22	39	1.69	0.38

production increase may reflect the input of readily available nutrients, the great increase in ammonifying bacteria (18), and the decomposition processes that may occur in manure on the surface of soil, where nematodes were not assessed (47). Unfortunately, the factors normally limiting pasture production are not specified, and the methods of assessing herbage production may lead to significantly different annual production estimates. There may also be a significant difference in nematode feeding habits, in that the (unassessed) natural manure microbivores increased in Poland whereas in New Zealand there was a marked increase in plant-feeding *Pratylenchus*.

In a Polish *Arrhenatheretum* pasture receiving two rates of NPK fertilizer in three successive years, there were no significant changes in abundance, biomass, or metabolic activity of nematodes (100). Urea as the nitrogen source may have bypassed some steps of the normal nutrient cycle, as is suggested by the failure to increase root biomass (72) despite a fourfold increase in hay yield (90).

In a Swedish Scots pine (*Pinus silvestris*) plantation with a herb layer including *Calluna*, *Vaccinium*, and lichens, the best relation between nematode abundance and plant weight was a negative association between *Tylenchus* spp. and the below-ground standing crop of *Calluna vulgaris*. There was a positive relation between numbers of root- and fungal-feeding nematodes and biomass of fine roots of *P. silvestris* and *Vaccinium vitis-idaea*. These results suggest that *Pinus* and *Vaccinium* or their mycorrhizae are food sources for *Tylenchus*. Slight correlations may be due to sampling technique, to non-limiting food resources, or to the problem of partitioning the nematode food supply between fungi and plant roots (83).

In five American deserts the rate of nematode population decrease below and between plants appears to be related to average annual rainfall and plant biomass (i.e., primary production) (30).

The results discussed above indicate a close relationship between herbage and root production in grasslands and between the vertical distribution of nematodes and roots in the soil. Annual production of below-ground matter and the below-ground/

above-ground ratios are significantly greater in herbaceous plants than trees, and the absence of significant differences between herbs and trees in total dry-matter production shows the importance of including root production in any assessment of productivity (13). Half to two-thirds of organic matter in the soil is from dead roots. Under grazed pastures, 70% of roots are concentrated in the upper 10 cm of soil (90), as are the nematodes (116). Under forests, a smaller proportion of plant biomass is found in the soil, and although the bulk of this comprises large roots at considerable depth, small feeder roots and mycorrhizae occur near the surface. In forests, nematodes are typically most abundant in the decomposition zone (F horizon), where there is great microbial activity (92); in mor soils, where decomposition takes place above the mineral soil, there are relatively few nematodes in the mineral soil itself. Pastures and forests also differ in the origin of their litter, and there may be a very rapid cycling of decaying root material during the growth of herbs (76). Other ecosystems differ similarly. Where vegetation is patchy, nematode population may differ greatly between vegetational types (55, 85). Such differences naturally make comparisons of nematode populations between ecosystems difficult even when the total metabolic activity of the soil is considered. However, again, total nematode abundance appears positively correlated with primary production if one avoids agro-ecosystems in which plant-feding nematodes may be dominant.

Population density and diversity: Nematode population diversity has been discussed (89, 107) but has not been related to population density in soils. Table 4 gives correlations between nematode abundance and species diversity for single sampling events. Values range widely, with no apparent trend. For 34 single-sampling events the correlation between abundance and diversity is not significant (+0.17). For 10 habitats (Table 5), repeated sampling gives a correlation of +0.81**, and when six other results from limited sampling are included the correlation is +0.80***.

There are many populations with 10–30 species and densities of 29–8,389 nematodes/100 g; significant correlations emerge only when more extreme populations (1–92

TABLE 4. Correlation between nematode abundance and number of species for single sampling events in a range of publications. († denotes $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Habitat	Sites	Correlation	Reference
Various	38	+0.60***	60
Moss	18	+0.86***	66
Soil under moss	12	+0.81**	66
Dune sand	6	+0.03	105
Tropical soils	12	+0.33	112
Tussocks	8	-0.16	113
Dune sand	10 depths	+0.29	106
<i>Festuca</i> clumps	6 depths	+0.85*	54

TABLE 5. Mean annual nematode abundance /m² and total number of nematode species identified in different habitats.

Habitat	Nematodes /m ²	Species	Reference
Mixed prairie	6,513,000	80	Smolik (69)
Oak-hornbeam forest (summer)	5,288,000	92	Saly (69)
Beech forest	1,432,000	75	109
Oak forest	1,000,000	22	4
Mixed fen	719,000	13	108
Alder-buckthorn carr	416,000	20	108
Dune sand	215,000	50	106
Sedge	204,000	17	108
Buckthorn carr	178,000	12	108
Reed bed	2,400	1	108

species) and the range is from more favourable habitats to less. Within sets of samples from similar climate (112) or similar vegetation (113), other factors influence density and diversity, and the predominance of such sets biases the calculation. Arpin (4) found that the mull soil of a hornbeam (*Carpinus betulus*) forest contained more species (30, vs. 22) but fewer total nematodes (255,000, vs. 1,000,000/m²) than the acid soil of a nearby oak (*Quercus sessiliflora*) forest. The sampling in the hornbeam forest did not cover a full year.

Volz's (94) data for beech and oak-ash forest are not strictly comparable with those above, being obtained by direct examination of the soil, but indicate 11,903,000 nematodes/m² and 26 species in beech forest, compared with 29,815,000/m² and

47 species in the oak-ash forest. In arable soils, populations tend to be greater but diversity less (25, 88).

Trophic structure of nematode populations: Since Nielsen's (63) work, a series of papers have reported the relative abundance of various trophic groups of nematodes in a range of soils; because many omnivores and predators are large Dorylaimida, this increases their relative contribution to biomass. Vertical distributions of trophic groups have been reported (6, 86); some give seasonal changes (86, 98), and some also consider the influence of extraction method (31).

The dominance of bacterial feeders in Antarctic mosses, tundra, taiga forests, and deserts is noteworthy; in those habitats Angiosperms may be rare and, although bacterial feeders may start feeding as soon as climate permits, other trophic levels may need to await the development of a food chain. In the first four stations in a *Pinus* time sequence on sand studied by Wasilewska (97), bacterial feeders tended to increase with age, and that was offset by a decrease in omnivores. Nielsen's (63) results can be recalculated to show similar trends of bacterial feeders and omnivores with increasing vegetation cover and humus levels. Reversion of Broadbalk grassland to wilderness is reflected in a change from plant and fungal feeders to bacterial feeders (119), and replacement of forest by pasture in New Zealand increased plant-feeding nematodes (21).

In grasslands, Wasilewska (100) found that of total nematodes fungivores were 3-65% and plant feeders 7-66%. With increased stocking (unutilized pasture: pasture: sheepfold) bacterial and plant feeders tended to increase at the expense of omnivores. Bacterial feeders and omnivores made the greatest contribution in a grazed New Zealand pasture, but under more arid conditions plant feeders, particularly drought-resistant *Paratylenchus*, predominated (118).

Although the contribution of various feeding types may range from 100% bacterial feeders (86) to 93% plant feeders (88), it is clear that there may be definite trends along climatic or vegetational gradients, and it is in the light of those that detailed comparisons should be made (when

data are available) and account taken of differing distributions of feeding types with time and depth. Assigning nematodes to feeding groups is difficult because observations are lacking (88) and specific feeding habits are diverse.

Nematode community structure: Statistical analyses of the composition of nematode populations by cluster analysis (generally using a 'resemblance equation' or 'three-dimensional community ordination', and showing the relationships in dendrograms) are available for soybean fields, prairies, streams, and forest woodlots. Studies which emphasize the diversity or trophic aspect of community structure are discussed above.

In 14 soybean fields, community structures were similar in highly productive dark soils but in more diverse lighter soils differed between sites and from dark soils (26). Sampling different habitats in three prairies and using the maximum abundance of each species, indicated that variation was greater between prairie habitats than between prairies, and that similar species occur in similar habitats in all prairies (77). These results express mathematically the community types which were recognised by early nematologists as reflecting soil and vegetation types.

Sampling of 16 sites in two streams showed that species presence/absence data used in a resemblance equation do not relate nematode species to physical conditions at the sites, although community ordination (analysis of quantitative data by which communities are arranged in multi-dimensional order) did (27). In soybean fields, however, presence/absence data (based on a minimum density) gave good similarity indices, although the pattern was somewhat different from that obtained using population densities. When ordination was based on six predominant species, instead of 154, there was a closer relationship of these species to the physico-chemical factors measured. This suggests that these six species are the ones influenced most by the factors measured and the ones that are most important in cluster formation: results were similar for data from different years. Future studies might be able to assess the disturbance of benthic nematode communities from quantitative data for only a few dominant species (27).

Nematode communities in 18 Indiana forest woodlots were analysed by several methods. Of 175 nematode species, only 18 occurred at all sites, but almost 50% occurred at nine of the sites, and similarity indices gave groupings which reflected plant species associations and soil drainage (41). Quantitative ordination analysis gave a range from swamp forest communities (dominated by *Helicotylenchus platyurus*) to climax oak or beech-sugar maple communities (dominated by two *Tylenchus* spp. and *Tylenchorhynchus silvaticus*), but no clear relationship to edaphic factors was found, although correlations with soil and vegetation were better than when similarity indices were used (39). Analysis of abundance and live biomass of Tylenchida, Dorylaimida, and other nematodes showed that Dorylaimida were more diverse but less abundant than Tylenchida (40). Dorylaimida were depressed at two 'disturbed' sites. Ordination generally reflected the different communities at the sites, and when biomass was used the larger Dorylaimida dominated (40).

Analysis of nematodes extracted by centrifugal flotation from a 16.4-ha area in Michigan showed that Longidorinae and Criconeematinae had large 'prominence' and 'importance' values (52), and detailed analysis of 15 criconematid species showed their overall association with moderately drained sandy loams under woods, although difference between species did occur.

These statistical techniques are useful in pinpointing key factors influencing nematode communities and have confirmed the use of dominant species in assessing changes in streams.

ACTIVITY OF NEMATODE POPULATIONS

Production ecology: Ecological units can be analysed as systems, and the balance measured between a population's intake and output of carbon or energy. Three basic equations describe this flow through a biological unit, whether at an individual, population, or trophic level:

$$\begin{aligned} \text{MR} &= \text{NU} + \text{C} \\ \text{C} &= \text{P} + \text{R} + \text{F} \\ \text{A} &= \text{P} + \text{R} \end{aligned}$$

where MR is energy in material removed

from the previous trophic level, NU is energy not used, C is food ingested, some of which is not assimilated but passes as faeces (F). The assimilated energy (A) is incorporated in new tissue and reproductive products (P), used for vital processes, and dissipated as heat; this part of the process, normally measured as gaseous exchange, is termed respiration (R). Since assimilation is the part of the matter, or energy, involved in metabolism it can be described as the energy flow, and few studies of nematodes have gone beyond estimating this. An introduction to ecological energetics is given in International Biological Programme Handbooks (35, 70), and methods of calculating the above parameters have been given for enchytraeids (65), Collembola (36), and annelids and arthropods (68). Although the Joule is the S.I. unit of energy, the calorie (1 cal = 4.184 J) is often used in energetics. Respiratory measurements can be converted: 1 ml O₂ = 4.775 cal = 19.979 J for animals feeding on a mixed substrate.

Some ecologists divide complex systems (defined, however, by habitat boundaries) into relatively simple units (e.g., species populations in the ecological sense), whereas others divide them into few relatively complex units (e.g., trophic levels). Much ecological information is potentially applicable from studies of plant-feeding nematodes, but, as regards trophic levels, "creation of correct ecological classification of nematodes is a somewhat difficult task with the amount of knowledge so far available" (97). When specimens are identified to genus or species before allocation to a trophic group, more data are available if the species information appears beside that for trophic groups; that is especially true of Dorylaimida, which have large individuals but have food habits so poorly known that many are regarded as omnivores.

Laboratory feeding studies: *Plectus parietinus* feeding on *Acinetobacter* sp. ingested 5000 cells per minute, a daily rate of 1.94×10^{-6} g dry weight (dw) or 650% of body weight; assimilation efficiency was 12%, while production was 82% of assimilated energy but 10% of consumed energy (20). Marchant and Nicholas (56) found the assimilation efficiency of *Rhabditis oxyerca* to vary with bacterial concentra-

tion; on average, 37% of ingested food was respired, 40% defecated, and 22% used in growth. In *Caenorhabditis briggsae* the efficiency of conversion of *E. coli* was about 13% (61). Feeding in *Pelodera chitwoodi* increased endogenous respiration sixfold, and, of energy ingested, juveniles used 27% in respiration and adults 21%; during their life span females ingested more than three times as many bacteria as did males (59). *P. chitwoodi* migrates to and feeds selectively on bacteria; resting and dead bacteria did not attract nematodes, and nematode feeding reduced the proportion of viable bacteria in the population (103).

The study of *Aphelenchus avenae* feeding on the fungus *Botrytis cinerea* (84) is complicated by an underestimation of ingestion. Net production efficiency (P/A) was 52% in the youngest juveniles, increasing to 80% in the fourth stage. P/A ratios of 6–20% were calculated for *A. avenae* feeding on *Alternaria tenuis* (101). However, the lack of a significant influence of initial nematode numbers on fungal growth suggests that either the populations were too small to influence fungal growth or the use of the reduction in fungal weight to estimate food intake ignores a significant effect of grazing.

Although these results are similar to results from the field (82, 99, 111, 115), they need to be related to environmental fluctuations and the microcosms discussed below.

Dry-matter content: Petersen (69) used 20% of fresh weight (fw), based on several published results, which generally involved direct weighing of nematodes collected from mass cultures, drying at 75–100 C, and reweighing. Values for *Aphelenchus avenae* range from 20% (84) to 32% (23), and may be explicable in terms of the state of hydration, since the moisture contents of *Aphelenchoides besseyi* can range from 5 to 80% without 100% mortality (37). However, nematodes extracted in water would be expected to be fully hydrated. Interference microscopy, using single nematodes, generally indicates a dry-matter content of 25% (67).

Yeates (110) gave a dry weight 58.5% of the fresh weight, derived from the relation $\text{biomass} = (W^2 \times L) / (16 \times 100,000)$, where biomass is in μg , W is maximum body width, and L is adjusted body length in

μm (2). This value was based on mixed species from field collections dried at 60 C and 10 mm Hg; volatiles, which are 11–48% of the dry weight of soil nematodes (10), are less likely to have been lost than from material dried at higher temperatures. In addition to a different fresh-weight assessment, the use of field rather than culture material may also be important; only in earthworms is attention normally given to the influence of gut content on dry weights (69).

In a hornbeam-oak forest, Saly (75) found average total nematode biomasses of 9.615 g/m² by Andrassy's method and 4.013 g/m² by drying at 20 C; this suggests a dry-matter content of 42%.

There is need for further work on this subject, including use of interference microscopy, but an average dry-matter content of 25% can generally be applied.

Calorific value: Known calorific equivalents of soil nematodes include 4.284 cal/mg ashfree substrate for *Plecticus* + *Poikilolaimus* (110), 5.453 cal/mg dw for *Aphelenchus avenae* (84), 6.300 cal/mg dw for *Rhabditis oxycerca* (56, 62), and 6.316 cal/mg dw for *Caenorhabditis elegans* (62). Those are compatible with values for soil microarthropods (96) and a wide range of animals (34). According to Yeates (110), his value is equivalent to 2.152 cal/mg fw.

However, Saly (75) found 9.44 cal/mg, apparently using the weight of nematodes dried for 24 h on cotton wool at 20 C.

The calorific value of soil microarthropods varies seasonally and with feeding habits (96), and other factors influence the calorific value of animals (34). Further studies are needed on inter- and intraspecific variation in calorific values of nematodes.

Reproductive cycles in the field: The reproductive cycles of *Heterodera* and *Meloidogyne* have been studied in annual crops, but only *H. mani* and *H. trifolii* have been studied in perennial crops. Assessing the reproductive cycles of most other genera is more difficult because of the difficulty in extracting eggs from soil, the absence of discrete egg masses, and lack of gross change in body form during maturation. Thorne (88) studied *Clarkus papillatus*, *Mylonchulus parabrachyurus*, and *M. sigmaturus* and concluded that their main period of reproduction was March-

May, with probably only a single generation a year. Volz (94) gave sex ratios ranging from 6♂:6♀ for *Heterocephalobus elongatus* to 1♂:148♀ for *Plecticus cirratus*. The occurrence of gravid females in 32 species under marram grass has been reported (106), while seasonal changes in the percentage contribution of juveniles, females, and males to populations under beech forest and grazed pastures have been given (111, 117). Various Longidoridae have been studied, and the monthly population composition of *Paralongidorus maximus* illustrated (12). Analysis of population structure during the year indicates periods of recruitment and mortality.

Given adequate field population and climatic data it should be possible to use results from laboratory cultures to interpret dynamics in the field; Jones's work, particularly on cyst-nematodes, shows approaches to integration and modelling (43, 46). Laboratory data on *Mononchus aquaticus* (44) clearly show the influence of temperature on the duration of each stage; the basal temperature appears to be 8 C, and up to 29 C there is a nearly linear relation between temperature and development. *Panagrolaimus rigidus* has a temperature curve similar to that of *M. aquaticus* (33), although the developmental rate is greater.

Reproduction and survival are inter-related; one stage may better survive adverse conditions (e.g., eggs in *Heterodera* cysts, second-stage juveniles of *Anguina tritici*, third-stage "dauer" juveniles of *Rhabditis*, fourth-stage and adults of *Aphelenchoides ritzemabosi*) (24), but survivorship is relative and detailed field studies are necessary before laboratory results can be used in interpreting population dynamics.

Nematode biomass production: Several methods have been used to make estimates of nematode production in the field. From monthly changes in the biomass of 29 species, Yeates (111) calculated an annual minimum production equivalent to 3.23 kcal/m² in a Danish beech forest, while Wasilewska used the equation $\log R = 0.62 + 0.86 \log P$ to calculate a production of 10–12 kcal/m² in meadows (100) and 14–25 kcal/m² in Polish mountain pastures (98). The expression $\log P = 0.8262 \log R - 0.0948$ (58) gave 1.08 kcal/m² in an English woodland (correction to published value;

J. Phillipson, pers. comm.) (71), while Sohlenius (82) used carbon-energy budgets to obtain nematode production of 456 mg C/m² (= 5.07 kcal/m²) in a Swedish pine forest. Production in seven California peatlands was estimated at 0.05–0.20 g wet wt/m²/yr (mean 0.106 g/m² ÷ 0.23 kcal/m²) (22).

Using the amended annual respiration of 1091 ml O₂/m² (= 5.21 kcal/m²) for the Danish beech forest (115) and $\log P = 0.8262 \log R - 0.0948$, production is 3.14 kcal/m², similar to the direct calculation. The same equation gives almost unchanged production estimates of 17.29–25.29 kcal/m² for Polish pastures in which juveniles were assumed to have twice the respiration rate of adults (98), and 4.57 kcal/m² for the Swedish pine forest.

If Yeates's (111) results are recalculated using monthly changes in total biomass rather than summing the 29 species, the figure obtained is 25% smaller. Species production estimates ranged from 714 µg fw/m²/yr (= 1.54 kcal) for *Teratocephalus terrestris* to 209,000 µg fw/m²/yr (= 449.8 kcal/m²) for *Aporcelaimus superbus*.

Until further estimates of biomass production are made, either directly or using fully adjusted respiration rates, no firm conclusions can be reached on the productivity of soil nematode populations, although the 17 available estimates give a correlation of 0.69** between mean annual nematode numbers and estimated biomass production. Several approximations have been made of total energy flow through nematode populations and their estimated efficiency (28, 71, 82, 98, 111).

Respiration: The respiratory metabolism of soil nematode populations is found by multiplying estimated live nematode biomass by an experimental respiration rate over the elapsed time, with adjustment for field temperature. Information provided by Nielsen (63) on respiration of soil nematodes has been widely applied (5, 71, 97, 110) using a basis figure of 1 ml O₂/g fw/hr at 16 C, which was adjusted to 0.830 ml O₂/g fw/hr at 16 C by Yeates (110) to allow for biomass calculations with Andrassy formula (2).

Klekowski et al. (50) reviewed data for 73 species at 20 C and calculated the rela-

tionships $R = 1.40 W^{0.72}$

$$MR = 1.40 W^{-0.28}$$

where R is the respiratory rate ($\mu\text{l} \times 10^{-3}/\text{ind.}/\text{hr}$), W is weight ($\mu\text{g fw}$), and MR is the metabolic rate R/W ($\mu\text{l} \times 10^{-3}/\mu\text{g fw}/\text{hr}$). They found a clear relation between body size and weight-specific respiration rate. When nematode activity is known (cf. cryptobiosis, anhydrobiosis, etc.), respiratory calculations should include both weight and temperature-specific oxygen consumption, with the 20 C weight-specific rate being determined from $R = 1.40 W^{0.72}$ and then corrected for temperature using $R_{x^{\circ}} = R_{20^{\circ}} \times q_{20^{\circ}}/q_{x^{\circ}}$ (q values are given by Duncan and Klekowski (19)). Sohlenius (82) followed such a procedure.

Many parameters are usually poorly known, and extensive correction of respiration, usually derived from non-feeding specimens in a water drop without soil particles around which to move, may give a false impression of precision. However, a basic temperature correction is normally made. A uniform respiration rate (e.g., 1.52 ml/g fw/hr at 16 C assuming a mean individual biomass of 0.2 $\mu\text{g fw}$) can be adopted, or weight-specific rates calculated, whether overall, for each sampling, or for a range of biomass classes. Other calculations use different rates for different feeding groups (from omnivores, $0.7 \times 10^{-3} \mu\text{l}/\mu\text{g fw}/\text{hr}$, to unknown food preferences, $1.5 \times 10^{-3} \mu\text{l}/\mu\text{g fw}/\text{hr}$ at 16 C, without temperature correction) (97) and, following experimental results for *Panagrolaimus rigidus* (51), assuming that juveniles have twice the respiratory rate of adults (98).

Nematode contribution to ecosystem metabolism: The International Biological Programme placed emphasis on relations within ecosystems. Respiration was used to assess the contribution of nematodes more accurately than abundance or biomass figures. Problems in estimating respiration have been discussed, and results for the percentage that nematodes contribute to soil respiration are unadjusted published figures. Bunt (14) extrapolated Danish results (63) and calculated 0.5–1.2% for sites on Macquarie Island; and the *Juncus* moor results of 0.6–0.7% (5) were adjusted to 0.2% by Spaul (86) to compensate for differing sampling depths. In Polish pastures, nematodes respire 0.29% of plant

root and shoot production (47). Results have attributed to nematodes 0.08–0.21% of the soil respiration at nine sites on Signy Island (86), 1.94% in an American deciduous forest (73), 0.13% in an English beech woodland (71), 0.52% in a Japanese coniferous forest (49), 1% of energy input to a desert soil ecosystem (28), and 0.33% of the annual carbon input in a Swedish pine forest (82) to nematodes. These results all indicate a relatively small role for nematodes in soil respiration, which is regarded as similar to carbon cycling in the ecosystem.

In agriculture, the great influence on plant growth of a relatively small plant-nematode biomass is well known, whether from direct effects or through increased susceptibility to climatic or nutritional stress. Twinn (92) using published data (32) to calculate that, ignoring turnover, the production of 15 mg biomass of *Rotylenchus buxophilus* led to a 12-g reduction in plant material. It has been calculated that the loss in pasture production due to the presence of 150,000 *Heterodera trifolii* cysts/m² is about 13 times the energy required to produce these cysts (118).

Nematodes have been studied in a wide range of experimental systems, ranging from hanging drops to agar plates, pots, and microplots. The dynamic interactions of nematodes with other organisms and nutrients have recently been studied using models of portions of natural ecosystems, or microcosms (1, 74). Just as grazing of bacteria by Protozoa (10) and of fungi by Collembola (93) increases nutrient cycling within the microcosm, so does grazing of bacteria by amoebae and nematodes. Using a bacterium (*Pseudomonas* sp.), an amoeba (*Acanthamoeba* sp.), and a nematode (*Mesodiplogaster* sp.) recovered from the rhizosphere of grass, Coleman et al. (17) studied the effect of these organisms on processes in microcosms in 50-ml flasks. Their results (Table 6) show that bacterial grazing by nematodes stimulates not only respiration but also the net mineralisation of phosphorus and nitrogen (i.e., the availability of plant nutrients). Although, as in agronomic pot trials, information obtained from microcosms is valuable, the results are difficult to extrapolate to natural ecosystems. More work with microcosms is ex-

TABLE 6. Influence of microbiota on dynamics of experimental microcosms; from results over 0-24 days (17).

Parameter	Microbiota present		
	Bacteria	Bacteria + amoebae	Bacteria + nematodes
CO ₂ evolution ($\mu\text{g CO}_2\text{-C/g dw}$) to day 24	1500	1750	1800
% increase in net phosphorus mineralisation to day 17	30	40	73
% nitrogen mineralised to day 17	31	76	81
Extractable ATP (ng ATP/g dw) at day 24	660	360	180
Live bacteria ($\times 10^9/\text{g dw}$) at day 24	1.9	1.1	0.8
Bacterial biomass (mg/g dw soil) at day 24	0.88	0.20	0.08

pected, and it should be supported by field studies.

CONCLUSIONS

Results for total nematode populations in lightly managed terrestrial ecosystems suggest that the populations are correlated with primary production but make only a small contribution to soil respiration. Faunas differ greatly in their food sources, as far as determined, and the diversity of feeding habits shows the degree of biological interaction in the soil. Full understanding of the role of nematodes in the soil requires study, in field and laboratory, of individual genera and species to obtain data so that their feeding, respiration, reproduction, and population dynamics can be modelled. Then the effects of their feeding on the food sources and on nutrient cycling can be put in perspective. That should help us understand the complementary roles of plant-feeding nematodes and those of the detritus food web in limiting or stimulating plant growth by making nutrients more readily available.

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