Studies on the nematode fauna of moorland soils

B. Banage William

STUDIES ON THE NEMATODE FAUNA OF MOORLAND SOILS

by

WILLIAM B. BANAGE, B.Sc. (Lond.)

(St. Cuthbert's Society)

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There is certainly no royal road to the knowledge of the nematodes. The traffic in this direction has not justified the installation of through trains and sleeping cars; so he who takes this route must be prepared to put up with inconveniences, and to make the best of certain disgusting passages.

N.A.Cobb (1915). "Nematodes and their relationships," in: Yb. U.S. Dept. Agric., 1914.

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SUMMARY.

SUMMARY.

Ecological studies on the soil nematodes were carried out on the Moor House National Nature Reserve, where a rigorous montane climate gives rise to moist and acid soils and a variety of vegetation types. From the area, five sampling sites were studied. These represented areas of peat erosion, growing bog, Juncus squarrosus moor edge, alluvial Nardus stricta grassland and limestone Festuca-Agrostis grassland. Intensive study was limited to the moor edge site, where the largest nematode populations were found.

On the selected sites the qualitative and quantitative aspects of the fauna were studied by random sampling and by other methods which are fully described. Of a wide range of genera found, 38 were identified and a study of their gut contents facilitated their classification into feeding ecological groups. Of these, plant feeders were the most abundant on all the sites, followed by the microbial feeders. Miscellaneous feeders were few and predators very rare and localized. No nematodes were found to feed on

humus. Only 26 species, of which 9 were new, were identified.

A study of the distribution of the nematodes indicated that they were aggregated and also concentrated in the superficial soil layers, with no detectable seasonal vertical migration. A seasonal population variation was, however, found for the Juncus moor, but data from elsewhere failed to show it.

Among several soil factors affecting nematodes, soil aeration was considered the most important, especially in relation to the degree of waterlogging in the soil. Soil structure did not exercise much direct influence on the nematodes.

The biomass and role of nematodes in moorland soil respiration were estimated on the Juncus site and found to be very small.

I. INTRODUCTION

I. INTRODUCTION

As long ago as 1915 Cobb, re-echoing an earlier prediction by Bastian (1865), drew attention to the ubiquity and abundance of nematodes in nature. Indeed, on the merit of these considerations alone, the Nematoda are undoubtedly the most successful metazoan phylum. This may be due to the simplicity of their body pattern which is easily adaptable to any environment where water and food are abundant. The majority of them are vermiform and cylindrical in shape, tapering steeply to the head end and more gradually to the tail. Their 3-layered body, non-segmented and pseudocoelomate, is without any external limbs and is covered by a very resistant cuticle. There are so many variations on this apparently simple pattern that no satisfactory generalization can be made about a 'typical' nematode. Their structure and morphology as well as other facts about their biology have been summarized by Chitwood & Chitwood (1950) and Hyman (1951) to which reference should be made for details.

The species parasitic in man and other animals (the round worms) are fairly large and have been the subject of study since the times of the early Greeks. The free-living forms, or eelworms, are very small. The largest

among them are about 3 mm. and the majority are between 0.5 and 2 mm. in length. At their widest, their bodies are only about 1/50 of this in diameter.

Hidden in the soil and being so small, they were overlooked until the perfection of the compound microscope in the 17th century made their study possible (Peters, 1955a). According to Christie (1959, p.2), Bastian's monograph published in 1865 was the first really comprehensive work on the free-living nematodes. The latter described 100 new species but the known total was even then still under 190. Such is the abundance of this group, however, that according to a recent estimate (Peters, 1955a) probably half of all the 10,000 or so species of nematodes then known were free-living.

The discovery of plant parasitic forms and of the fact that the dividing line between the free-living and the parasite could hardly be drawn with satisfaction, resulted in research being concentrated on taxonomy and aspects of economic importance. Thus there is more information about the plant nematodes generally than about other free-living types. With some exceptions, such studies were carried out by plant pathologists with the result that a rather illogical and somewhat confused terminology has arisen to describe the habits and activities of the nematodes. Because it over-emphasizes the

plant rather than the nematode, such a terminology needs to be re-defined when adopted by an ecologist.

Most of the stylet-bearing nematodes probably depend, either partly or entirely, on plants for their food (Steiner, 1956 ; Jones, 1959). The majority of these puncture and suck the plant from the outside. They are capable of moving about in the soil. At the other extreme are those which at some stage in their life history are completely tied to a single plant and may possess a certain degree of host specificity. All these are regarded as parasites (Christie, 1959, p.7), although all nematologists are not agreed about this (see Jones, 1959), and depending on the extent to which they move about in the soil, are classed into 3 categories: migratory or vagrant, semi-sedentary and sedentary (Jones, 1959; Pitcher, 1959; Steiner, 1949b).

Overlapping with this classification is that which divides plant nematodes into endoparasites and ectoparasites. Not only are the full logical implications of these terms ignored, but also the same species is often regarded as being both endo- and ecto-parasitic (e.g. Pratylenchus pratensis). Some of the phytonematodes are also called obligate parasites, although the antithesis, facultative parasites, would hardly be apt for the majority of the other so-called parasites.

These classifications, useful as they may be for shorthand reference, are to a certain degree misleading. In no other major animal group is it so difficult to separate parasite from non-parasite, let alone distinguish the different types of parasitism, as it is in the nematodes. This is true both for those which affect animals as well as those which affect plants. In the writer's opinion, all those which suck plants should be regarded as plant feeders and be referred to as plant or phyto-nematodes.

The difficulty over the use of the word 'parasite' involves its opposite: 'free-living'. For the purposes of this work, free-living nematodes are those stages in the life history of any species which, after hatching, may be found fully capable of carrying on an independent and active existence when environmental conditions are favourable, regardless of how they obtain their food.

It has been emphasized by several writers that, while the marine nematodes are a more or less a distinct group, there is complete overlap between the soil and fresh water ones. These two ecological groups are sometimes called terrestrial nematodes. Free-living nematodes from soil, however, properly constitute part of the soil fauna, using free-living in the sense just defined. This is necessarily a wider concept of 'soil organisms' than that of Burges

(1958, ch.6) who defines them as 'those which live naturally in the soil without being associated with any higher plant and animal host' (p.10). This may be arbitrary or convenient but in the light of what has been said about the plant feeding nematodes it begs the question. The writer's concept, however, is broadly similar to that of Kühnelt (1955).

To evaluate the role of free-living nematodes in the economy of the soil it is necessary to obtain as much information as possible on the many aspects of their ecology and biology. Although some people have been alive to this in the past, among them Cobb and Steiner in the U.S.A. and Franz in Austria, the first and most outstanding work to incorporate ecological concepts into nematology was that of Overgaard Nielsen in Denmark. His studies not only encompassed the estimation of population levels in various soils, but also measurements of biomass and respiratory rates for several species. The shortcomings of this worker's studies, e.g. the taxonomy, reflect the magnitude of problems to be overcome in nematological investigations.

Progress has been made in this country in taxonomic and parasitological studies on soil and plant nematodes, witness the monographs by Goodey (1933, 1951) and the recent compilation by Southey (1959). Nevertheless, no ecological work of the kind that Overgaard Nielsen has

done has been attempted. Indeed, the only population estimates for soil nematodes published seem to be those of Robertson (1925) from Scottish soils. There is, therefore, little from Britain to compare the present writer's results with, although such comparisons may be made with continental and American work.

This study is a contribution to a comprehensive investigation of moorland ecology and was executed almost entirely as a field survey. Field work, the results of which are reported here, was carried out between March, 1958 and March, 1960.

II. THE STUDY AREA AND SAMPLING SITES

II. THE STUDY AREA AND SAMPLING SITES

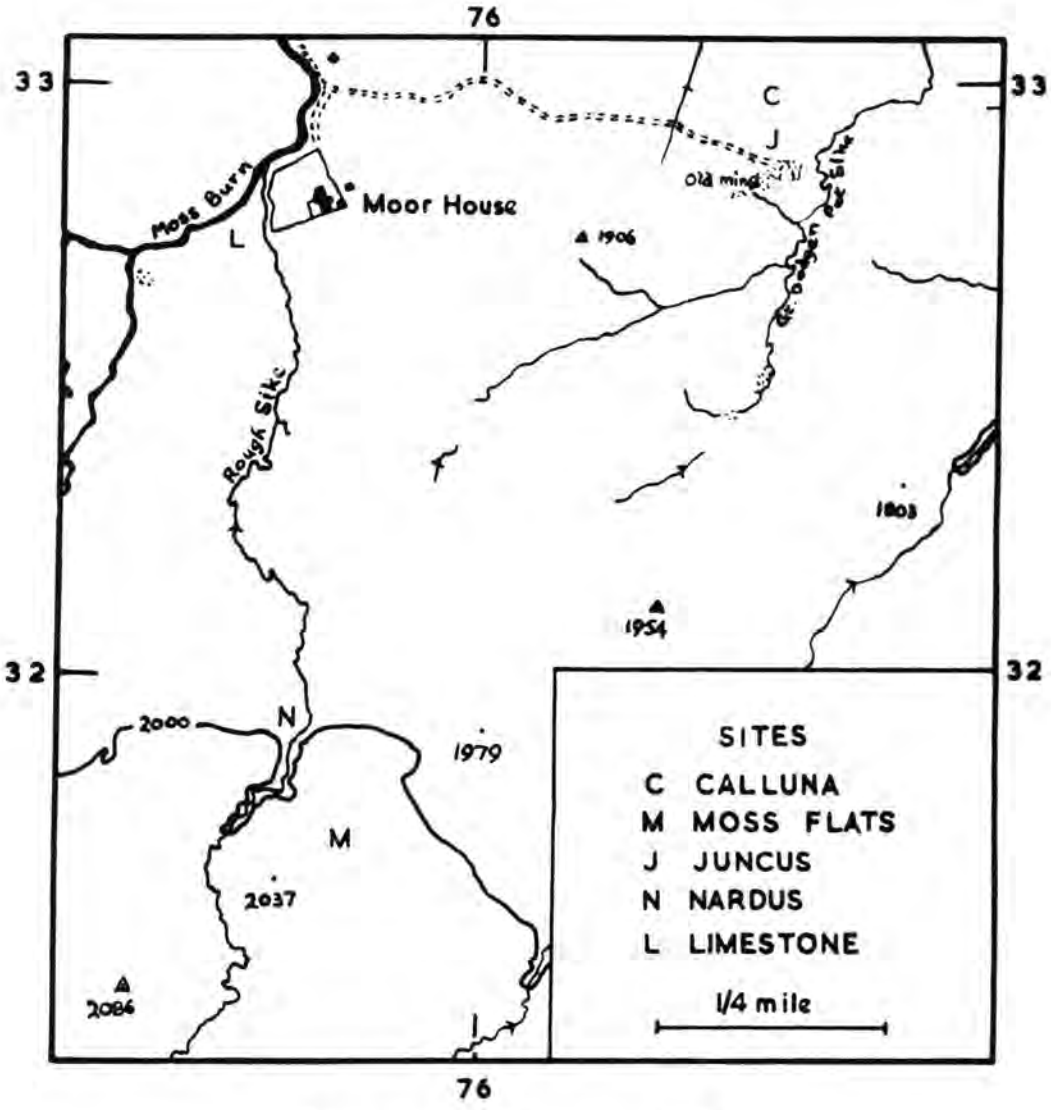
1. Location, physiography and vegetation.

The study area was in the Nature Conservancy's National Nature Reserve (N.R.80), Moor House (Nat. Grid Ref. 35/758329), Westmorland and descriptions of this have been given by Conway (1955), Coulson (1959) and Svendsen (1957). The reserve lies in the Northern Pennines some 12 miles (19.2 km.) east of Penrith and some 11 miles (17.6 km.) south of Alston. Its boundaries, covering about 10,000 acres (4,000 hectares) includes the three peaks of Little Dun Fell, Great Dun Fell and Knock Fell lying south-east of Cross Fell. From the fell tops, over 2,600 feet (7,800 m.), the greater part of the reserve slopes in an easterly direction to the River Tees, over 1,600 feet (4,800 m.), which bounds it on its northern and eastern sides.

The geology of the area (see Johnson, 1958) consists of stratified sandstones, shales and limestones showing the succession typical of the Carboniferous Yoredale Series to which they belong. The somewhat strongly dissected geology is buried under a widespread cover of superficial deposits consisting of glacial moraines, boulder clays and post-glacial solifluction clays derived

from the underlying formations. The drift is in turn covered by blanket peat which thus forms the dominant soil type, there being little exposure of mineral soil. On the occasional limestone outcrops, however, and also on the terraces of the many small streams, soils with differing admixtures of mineral matter (flushes) occur. Those on the limestone outcrops are often skeletal and probably of drift origin, while those covering alluvial terraces contain various amounts of re-distributed peat. The blanket peat, too, is in various stages of growth, erosion and regeneration and, in the summer months, the vegetation is intensively grazed by sheep which add their droppings to the soil.

There is, therefore, a very wide range of habitats distinguished by as many plant associations. Blanket bog with Calluna vulgaris, Erica spp., Eriophorum spp. and Sphagnum spp. predominate on the peat soils. On the moor edge where the peat is disturbed or re-distributed and on the solifluction drift, sandstone and limestone outcrops, other plants (e.g. Nardus stricta, Juncus spp., Deschampsia flexuosa, Festuca spp. and Agrostis tenuis) take their place. These often form mosaics of communities depending on the extent to which the soil is waterlogged.



THE STUDY AREA

FIG. 1.

2. The sampling sites.

From the area described, five sampling sites were selected for study (Fig. 1.). They represent the major divisions of the habitat mosaic found on the blanket peat (Table 1.).

Table 1. Classification of some Moor House soils following the scheme of Pearsall (1950, Fig. 16, p.77).

Soil	pH	Moisture	Group
Bare Peat	4.3 - 4.6	I.H. <7, damp	blanket peat
Calluna Moor	4.5 - 4.9	I.H. <10, wet	blanket bog
Juncus Moor	4.5 - 4.6	I.H. <7, damp	peat mor
Nardus Grassland	4.8 - 5.0	I.H. <1.8, normal	flush
Limestone Grassland	4.9 - 5.8	I.H. <1.6, normal	mull, lime-poor

Notes:

1. I.H. = Index of humidity (cf. Pearsall's Relative Humidity) for the explanation of which see Part III.2 (b).
2. The pH is that of the upper 12 cm. of the peat measured with a glass electrode (see Table 11, notes).

PLATE 1.

The Bare Peat site, showing the re-distributed peat on the beech layer.

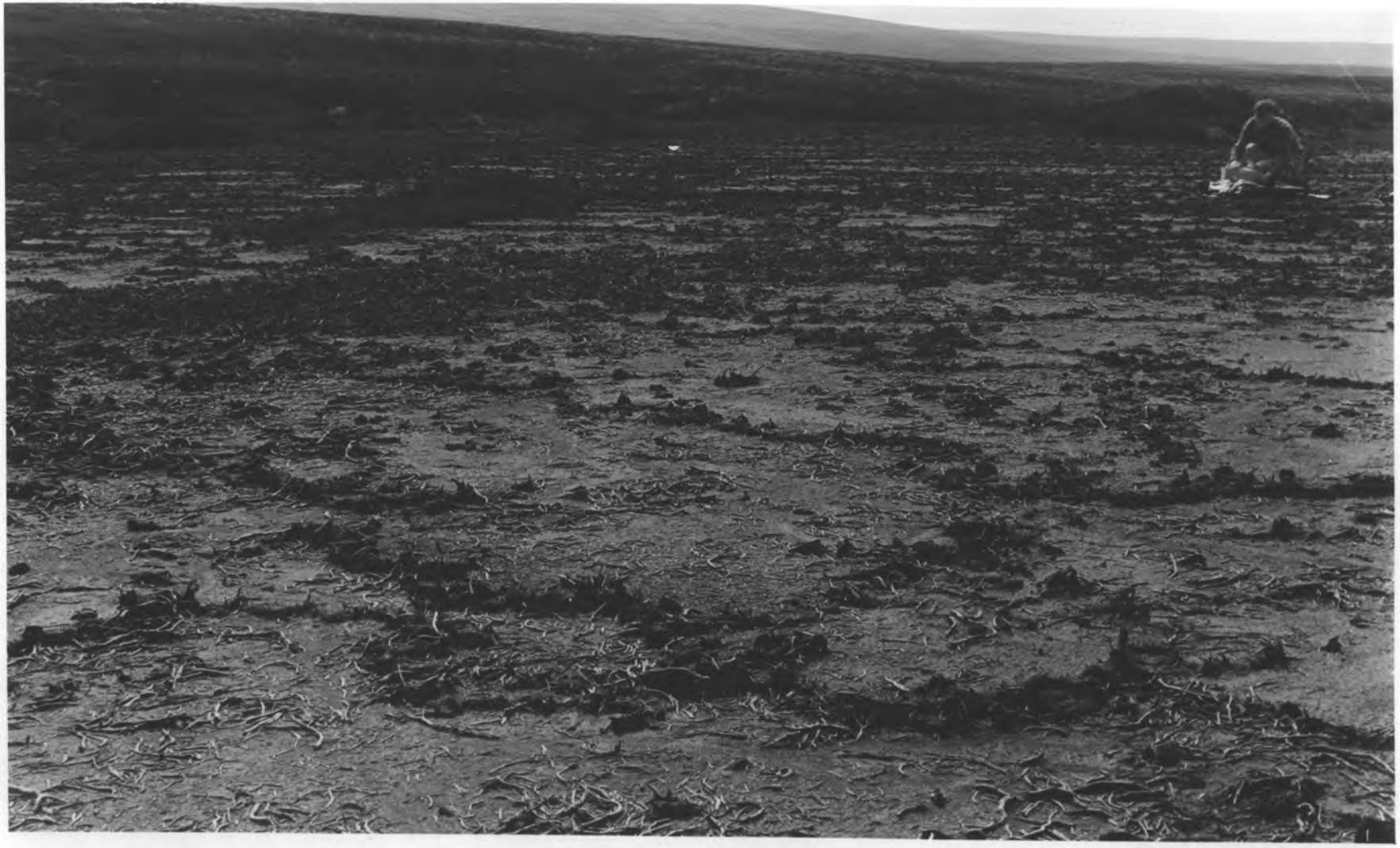
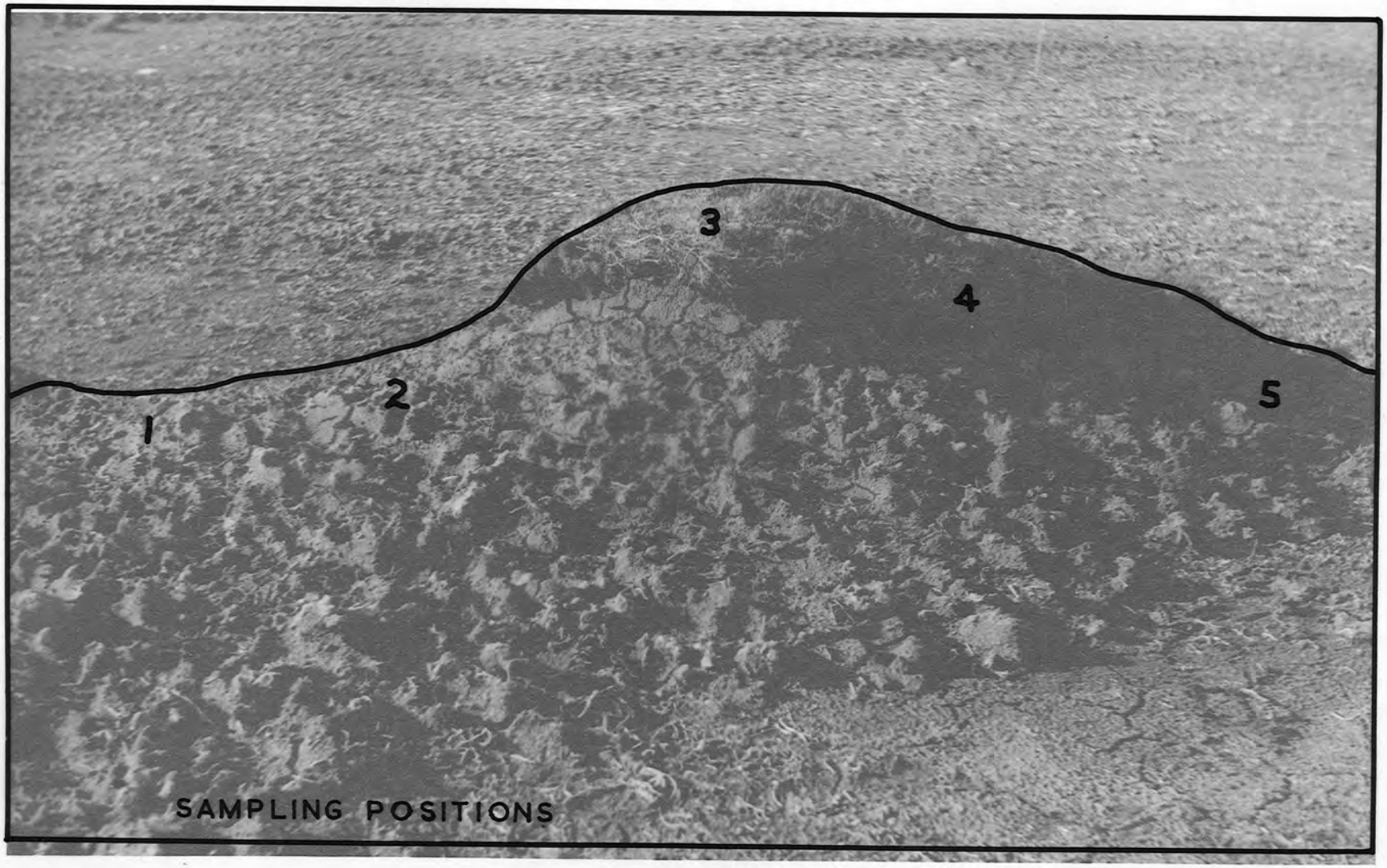


PLATE 2.

A windward view of a Residual *Calluna* Hummock on Moss Flats.

Note the eroded peat surface.


1
2
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5
SAMPLING POSITIONS

PLATE 3.

A leeward view of a Residual *Calluna* Hummock on Moss Flats.

(a) Moss Flats.

This is an area of eroded peat near the head of Rough Sike. Sampling was done on the bare peat as well as on one of the hummocks of Calluna to which the original peat layer has been reduced (the Residual Calluna Hummock). Each hummock has an elongated 'tail' of bare peat to the windward side (Plate 2.) rising to the 'crest', which represents the original peat surface, and a much shorter part covered with vegetation to the leeward (Plate 3). The vegetation on the hummocks consists of Calluna vulgaris, Erica spp., Empetrum nigrum and Cladonia spp. Below this is a layer of litter and fibrous roots of the plants to a depth of about 10 cm. where the more compact peat is found. The upper regions of the hummocks are relatively well drained.

The peat underlying the hummocks has been denuded and re-distributed over the wind-swept surface on which the birch layer is exposed (Plate 1). This surface formed the Bare Peat site. Table 2 gives the profile of the peat and its water content during the dry summer of 1959 is indicated in Table 8.

(b) The Calluna site.

This site is on the heather covered hill to the north and west of the Great Dodgen Pot Sike and just above the Juncus site described below. It is a typical blanket bog

Table 2. Soil profile of the Bare Peat.

A_oH	0 - 2 cm.	Black, well oxidized, crumbly peat, somewhat humified and largely redistributed by water and wind. Peat erosion has reached the Betula twig layer.
A_oH	2 - 18 cm.	As above but the peat is plastic and more humified; boundary merging into:
A_oH	18 - cm.	Brown, unoxidized and stratified peat formed in situ and containing many twigs, humified.
Base rock		Beds of limestone, shale and limestone between Tyne Bottom and Scar Limestones.

site (Plate 4) with a continuous cover of Calluna vulgaris as the dominant plant, interspersed with tussocks of Eriophorum vaginatum and hummocks of Sphagnum spp. Other plants include: Cladonia spp. as well as several other lichens, Eriophorum angustifolium, Polytrichum commune and Vaccinium vitis-ideae.

Table 3. Soil profile of the Calluna site.

A_0L	0 - 4 cm.	Thick litter composed of dead Calluna leaves, lichens, mosses, liverworts, etc. and with many procumbent stems of Calluna vulgaris.
A_0F	4 - 5 cm.	Fermentation layer, merging into:
A_0H	5 - 15 cm.	Dark, humified peat, slightly crumbly, with fibrous plant roots.
A_0H	15 - 60 cm.	Yellow-brown unoxidized peat with Calluna roots in upper parts; Eriophorum and Calluna remains distinguishable; lower layers more decomposed and compacted and merging into plastic peat with few recognizable plant remains; boundary clear.
A_2G	60 - cm.	Gleyed soil overlying boulder clay.
Base rock		Tyne Bottom Limestone.

Table 4. Soil profile of the Juncus site.

A_oL	0 - 3 cm.	Litter mainly composed of leaves, leaf bases and root-stocks of Juncus squarrosus and Deschampsia flexuosa, little humified and merging into the next layer.
A_oF	3 - 4 cm.	Fermentation layer, much as above but very slightly humified, merging into:
A_oH	4 - 19 cm.	Black, oxidized and crumbly 'grass type' peat formed in situ, with abundant fine, fleshy roots; well humified and merging into next layer.
A_oH	19 - 42 cm.	Peat as above but brown and unoxidized, less crumbly, stratified with a Betula twig layer at base; boundary clear.
A_2G	42 - 67 cm.	Gleyed, grey-buff, water-logged and plastic soil of drift origin, with iron mottling (red).
Base rock		Tyne Bottom Limestone.

The profile of the peat (Table 3) shows that it is deep and anaerobic in the deeper layers. When exposed it quickly oxidizes and turns from a yellow-brown to a dark colour. The peat, even in the driest period, contained a lot of water (Table 8).

(c) The Juncus site.

Plate 4 shows the location of this site just below the Calluna site on the hill slope. The Tyne Bottom Limestone which forms the base rock of the profile (Table 4) outcrops a few feet further down the slope where there is a road to a disused mine. Although the drainage is poor and there is considerable run-off, there seems to be some enrichment of the peat of this site, either from this base rock or, alternatively, from past disturbance.

The vegetation consists of Juncus squarrosus as the dominant plant and Deschampsia flexuosa and Festuca ovina as abundant and Galium saxatile, Polytricum commune, Potentilla erecta and Eriophorum angustifolium as the other common species. At the bottom of the slope there is a Sphagnum pool with S.recurvum and Juncus effusus round the margin. It is a sign of the artificiality of the site but, nevertheless, in agreement with its 'moor edge' position (Svendsen, 1957) that a few Calluna clumps occur on the lower side of the Juncus squarrosus.

PLATE 4.

A transect view of the Juncus (middle foreground) and the Calluna (background) sites.
Note the Juncus effusus in the foreground.

The water content of the soil (Table 9) as measured by the index of humidity seems to vary very little between the wettest and the driest periods of the year.

(d) The Nardus site.

This lies on the left bank of Rough Sike, downstream from Moss Flats. The soil (Tables 5 and 10) is a well drained peaty alluvium, though liable to short periods of flooding when the stream is in spate.

There is a thick vegetation mat with Nardus stricta as the dominant grass. Occurring with different degrees of abundance are Deschampsia flexuosa, Juncus squarrosus, Potentilla erecta, Agrostis canina, Anthoxanthum odoratum, Galium saxatile, Pleurozium schreberi, J.effusus, Luzula compestris, Rumex acetosa, Polytrichum commune and Viola riviniana.

Plate 5 is an upstream view of the site during the dry period and the sub-angular boulders from the drift below the alluvium are clearly visible.

(e) The Limestone Grassland site.

Located on an outcrop of the Tyne Bottom Limestone, this site is near the Field Station and between Moss Burn and Rough Sike. The soil is a rendzina-type brown earth derived from a rich limestone residual. Its rather skeletal nature is clearly shown by the limestone boulders

which protrude to the surface (Plate 6). The soil profile is somewhat ill-developed except where fewer boulders are found (Table 6). Good drainage on a north-west facing slope, a high pH by moorland standards (Table 11) and the consequent abundance of earthworms are further characteristics of this site. The vegetation is given in Table 7. It is a typical Festuca-Agrostis grassland (Pearsall, 1950) with a vegetation mat, about 3 cm., which is kept close cropped by sheep. This factor tends to obscure the rich floristic nature of the mat.

(f) Other collecting habitats.

In addition to the major sampling sites described above, casual collecting was done in the following habitats:

(i) Sphagnum Pool: with a pure stand of S.recurvum near the edge of an area of actively growing bog (Valley Bog) which has been described by D.H. Murphy (1955).

(ii) Alluvial Grassland: an area of alluvium very similar to the Nardus site except that it lies over a limestone outcrop in the valley of the Moss Burn near the Field Station.

(iii) Residual Calluna Hummock: on Moss Flats (see under Moss Flats, above).

(iv) Sheep Dung: some sheep droppings on the Juncus site were examined.

Table 5. Soil profile of the Nardus Grassland site.

A_oL	0 - 5 cm.	Litter mainly composed of very loosely packed living and dead horizontal basal portions of Nardus, merging into:
$A_oF + H$	5 - 6 cm.	Fermentation layer turning into humus, divided by a sharp and wavy boundary from the underlying layer.
A_1	6 - 40 cm.	Dark-brown, moist, sandy loam; soil often fluffy and crumbly, with mixed humus of alluvial peat origin; abundant fine, fibrous roots, particularly in upper layers; merging into:
B_2	40 - 53 cm.	As above though somewhat leached; deeper layers with common, prominent fine to medium iron mottling and passing into a layer of sub-angular stones and boulders of sandstone origin.
Base rock		Sandstone above Single Post Limestone.

Table 6. Soil profile of the Limestone Grassland site.

A_oL	0 - 3 cm.	Vegetation mat with some dead plant remains but very little distinct litter.
$A_oF + H$	3 - 6 cm.	Dark, humic layer forming a distinct zone 2 - 4 cm. wide, with many roots.
A_1	6 - 7 cm.	Dark band with wavy boundaries, distinctly separated from:
A_2	7 - 10 cm.	Fine sandy-silt layer, distinctly more leached than above and with occasional red iron mottles.
B_1	10 - 11 cm.	Humus band; boundary clear.
B_2	11 - cm.	Brown sub-soil with many earthworm burrows which are more humus stained and dark in colour. Many pebbles and stone fragments of shale and limestone clearly indicating drift origin. The sub-soil is at least 65 cm. deep.
Base rock		Tyne Bottom Limestone.

Table 7. The vegetation of the Limestone Grassland site.

Dominant	Festuca ovina
	Agrostis tenuis
Abundant	Thymus drucei
	Potentilla repens
	Polytrichum commune
Others	Selaginella selaginoides
	Luzula campestris
	Rumex acetosella
	Euphrasia confusa
	Galium hercynicum
	Anthoxanthum odoratum
	Rhacomitrium lanuginosum
	Mnium undulatum
	M. punctatum
	Achillea millefolium
	Carex caryophyllea
	Veronica officinalis
	Cardamine pratensis
	Cirsium arvense
	Prunella vulgaris
	Viola riviniana
	V. lutea
	Cerastium vulgatum
	Alchemilla vestita

These were the commonest plants out of about 40 species seen in an examination of the area. The protruding limestone boulders harbour a rich bryophyte flora, not included in the above list.

PLATE 5.

A general view of the Nardus Grassland site looking upstream from the Rough Sike.
The bed of the greatly reduced stream during the summer of 1959 is clearly visible.

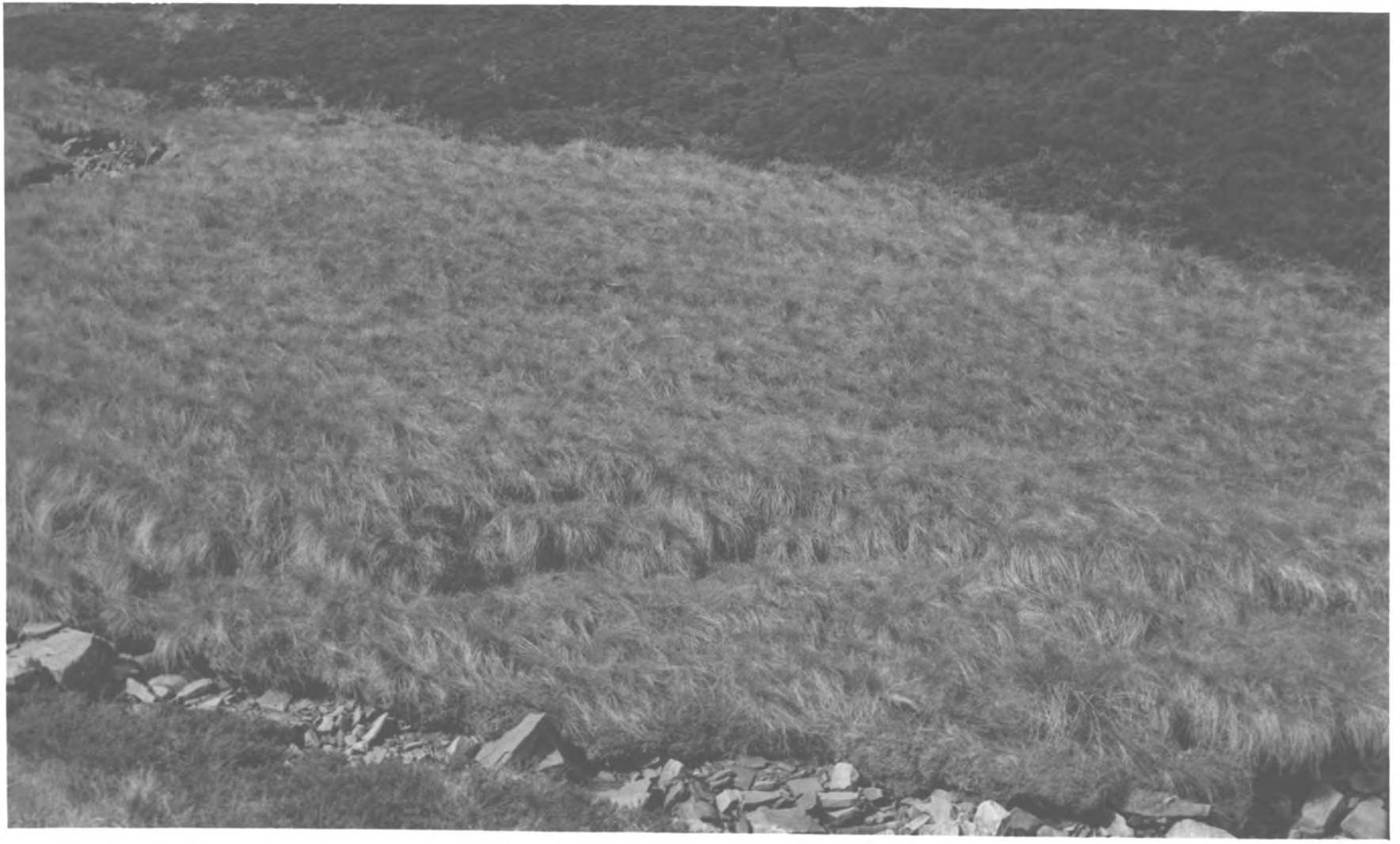
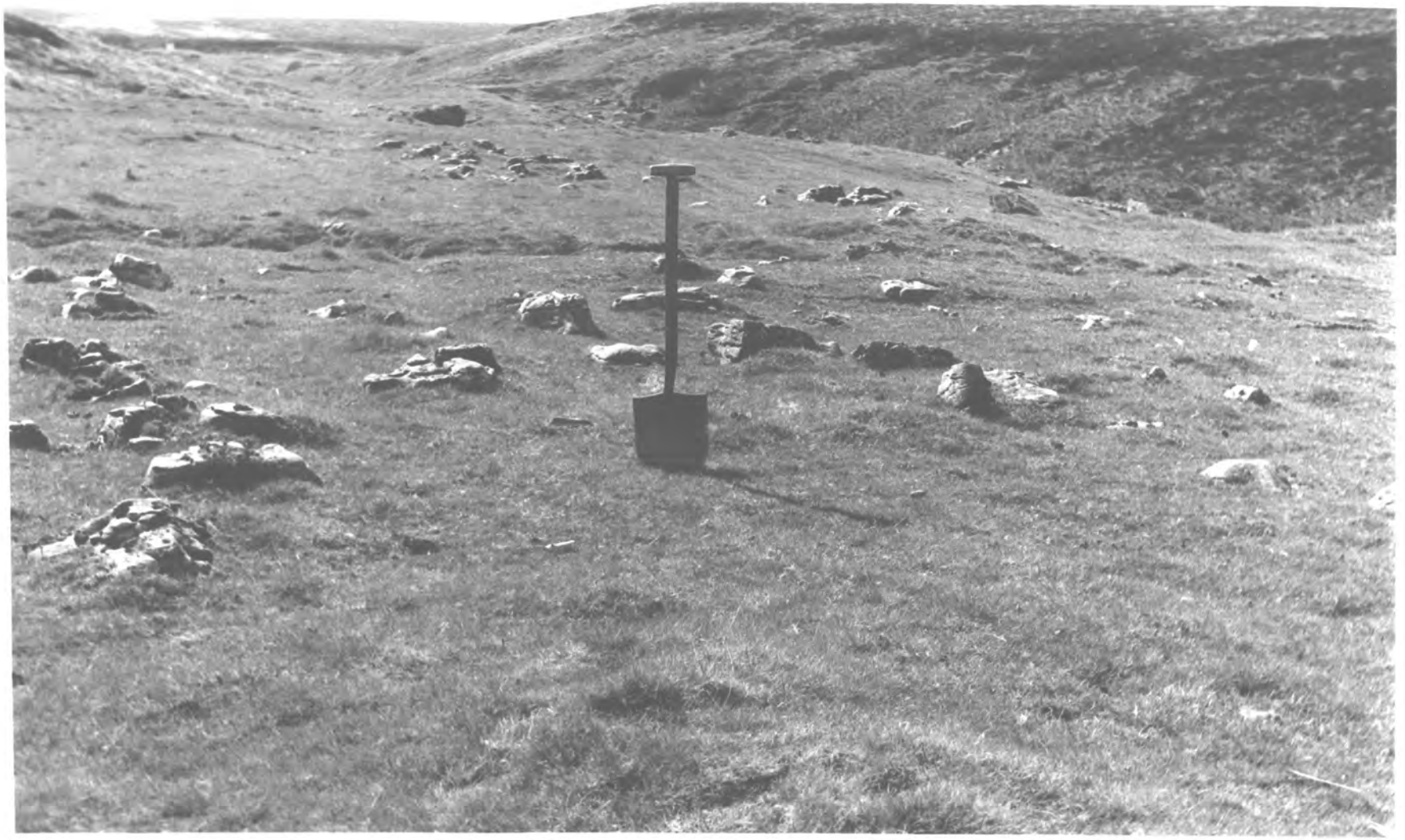


PLATE 6.

The Limestone Grassland site, looking westwards.
The valley of the Moss Burn separates the site from the heather covered hill in the background.



III. GENERAL HABITAT FACTORS.

III. GENERAL HABITAT FACTORS.

1. The structure of peat.

(a) Technique.

Microtome sections were cut at 20μ and 10μ for the study of the structure of peat, using Minderman's (1956b) technique. Small discs of frozen peat 1 cm. in diameter and 1 cm. deep were taken from a frozen peat core. The field core had been taken from a disturbed area dominated by Eriophorum vaginatum but with considerable quantities of Juncus squarrosus among other plants.

The procedure of embedding given by Minderman was closely adhered to. The peat discs were enclosed in plastic rings (cut 'polythene' glass tops) and wrapped in fine copper gauze. They were then gradually lowered for 2 hours at a time in 5, 10, 15 and 20% gelatine solutions in water, the solutions being maintained at 30°C. during this time. The beaker containing the gelatine was then allowed to cool and the blocks of impregnated peat cut out and fixed in 10% formalin before sectioning. Very little noticeable swelling took place because of the 'polythene' rings in which the peat was contained.

Since there was no sand in the material, it was not treated with hydrofluoric acid as advised by Minderman.

Sectioning was done using a microtome knife on an ordinary rocking microtome, the sections being stored in 4% formalin prior to mounting.

Some sections were mounted on glass slides with 15% gelatine, pressed hard with filter paper and left in a Petri dish of 4% formalin overnight to ensure good adhesion. They were then stained with a modification of Conant's quadruple stain (Johansen, 1940). This consisted in 1% aqueous solutions of:

Safranin	for 48 hours
Methyl violet	for 15 minutes
Fast Green F.C.F.	for overnight
Orange G	for 30 minutes.

The schedule is that recommended by Minderman. Mounting in Canada balsam was not successful because the sections did not stand dehydration very well. One stained section was, however, mounted in lactophenol and others were mounted unstained in 0.005% cotton blue lactophenol (Plates 7-9).

(b) Results and discussion.

The prepared sections were examined under a magnification of 80x. A higher magnification of 320x, although used, was less satisfactory due to the warping of the sections while being mounted.

PLATE 7.

A section of Moor House peat, stained with Conant's quadruple stain. 10μ thick. The gelatine-filled spaces are light-coloured.

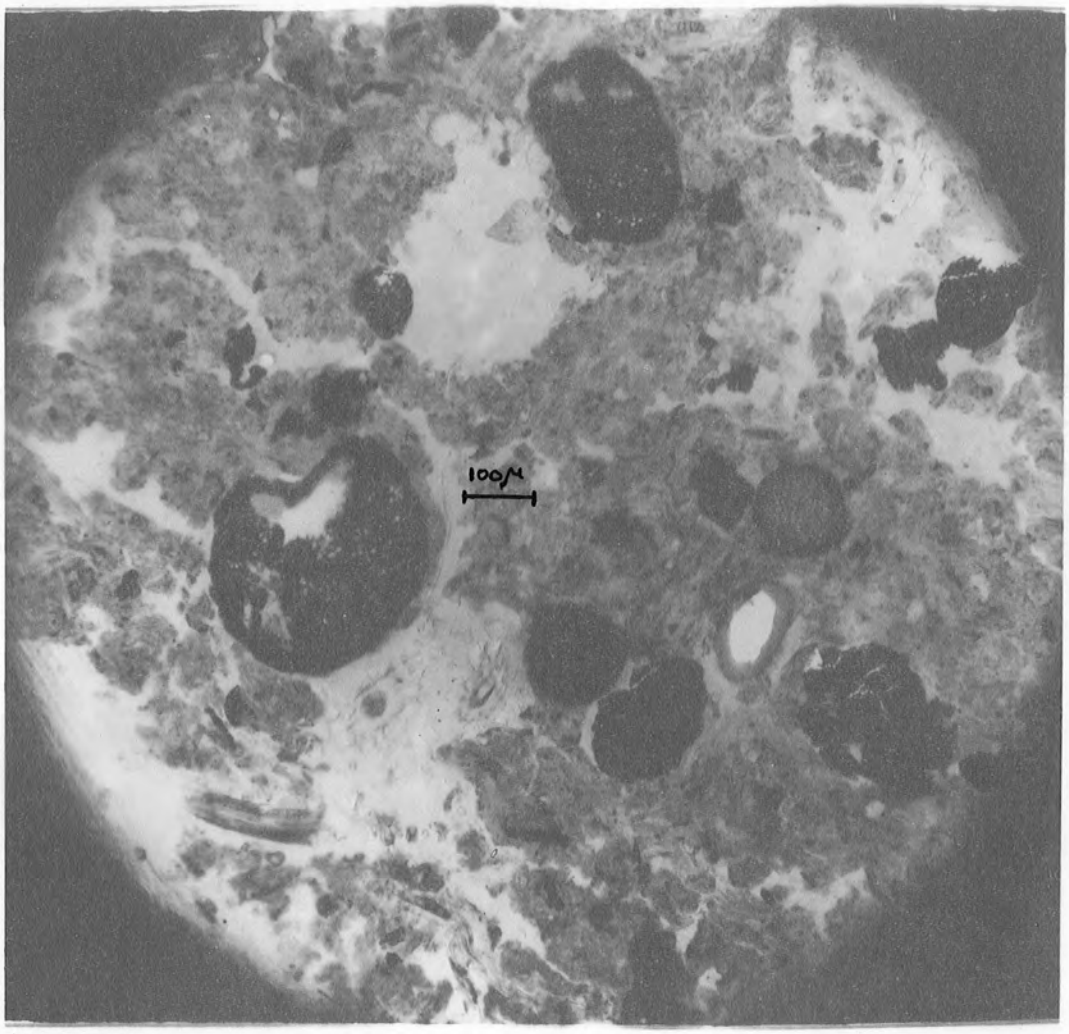

100μ

PLATE 8.

Another stained section of peat. 10μ thick.
Note the peat (darkly stained), spaces (light-coloured) and plant remains.
For the scale see Plate 7.

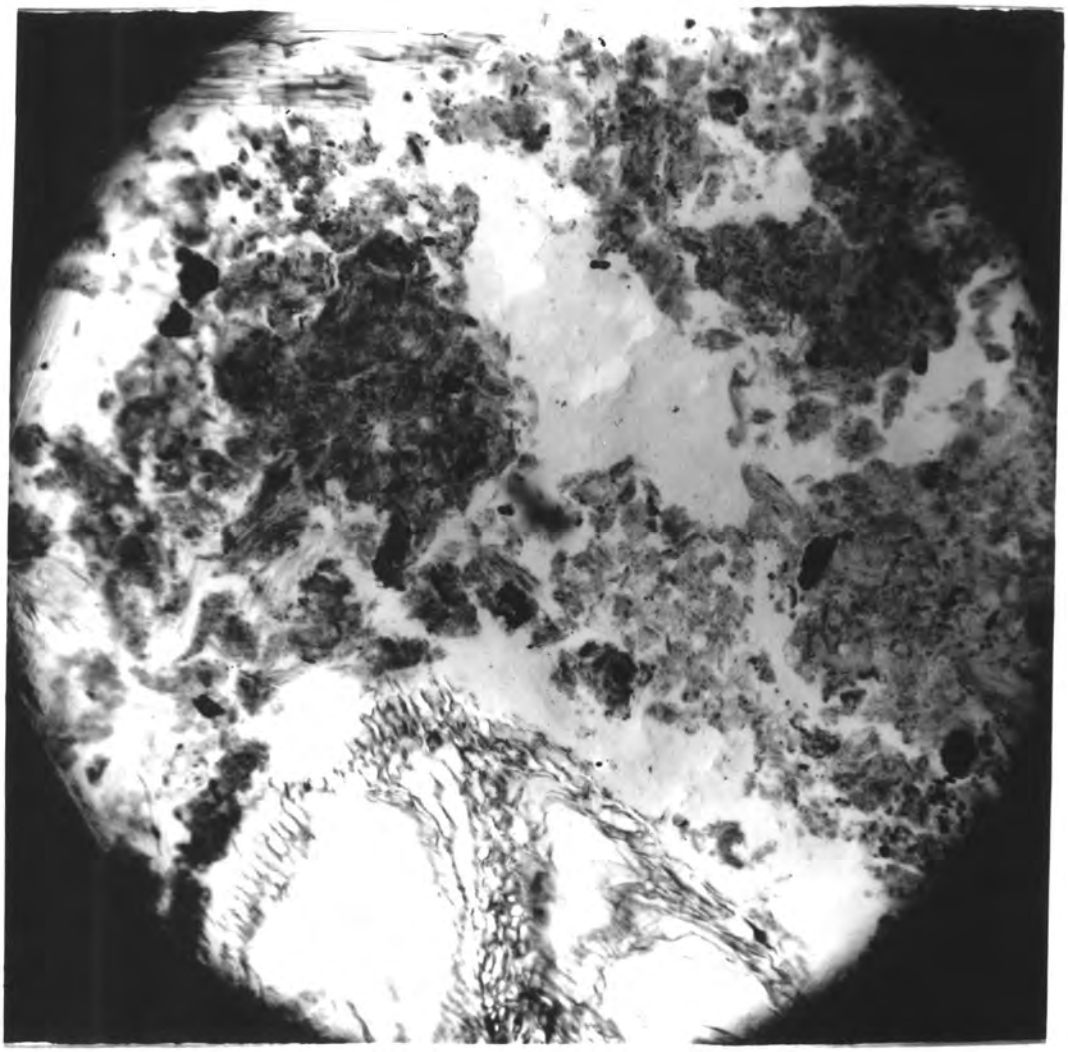
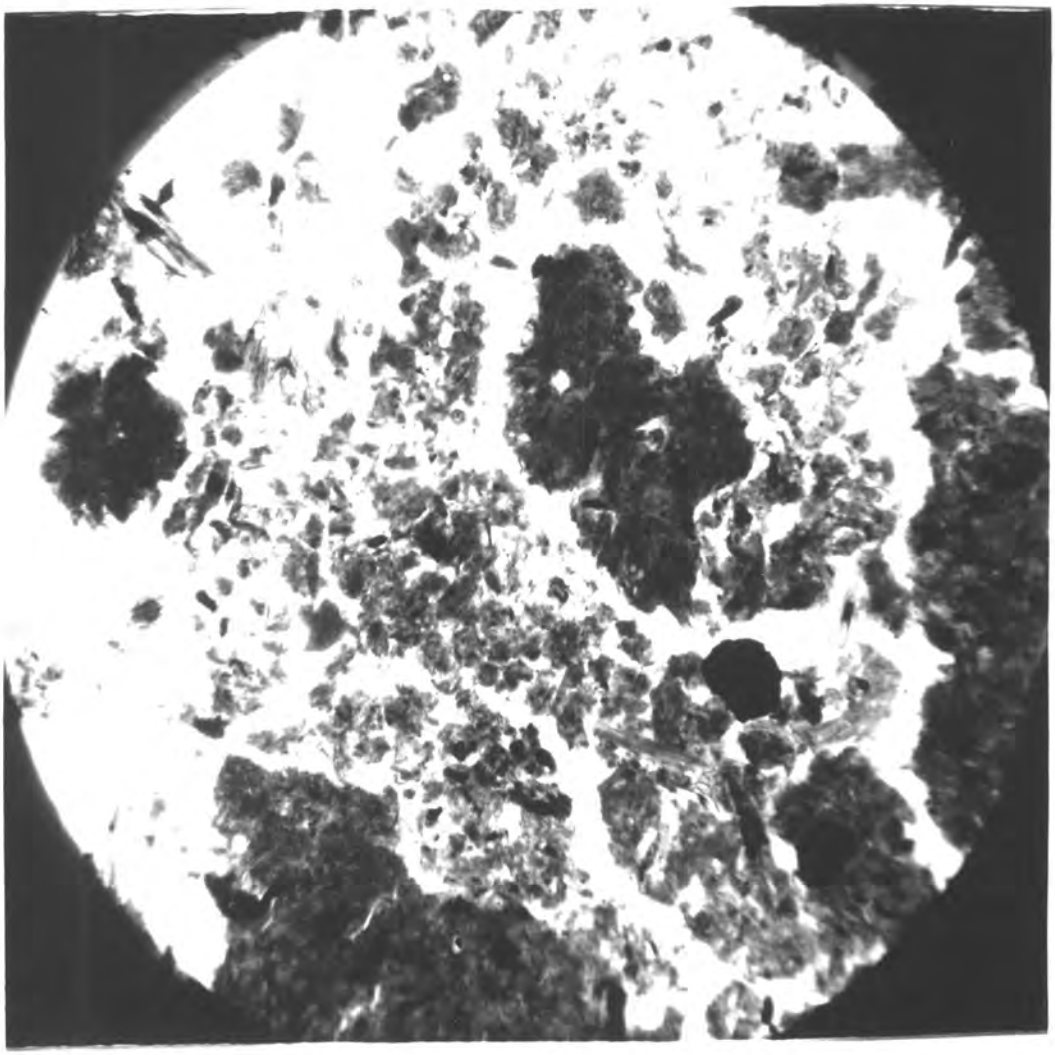


PLATE 9.

Peat section, unstained. 10μ thick.

Compare this section with Plates 7 and 8.

For the scale see Plate 7.



Examination revealed a lot of structures of plant origin but no parts of animals were identifiable. Furthermore, it was clear that the decomposing plant remains did not invariably provide definitely clear boundaries to the intervening spaces. These spaces have been called 'cavities' (Haarløv, 1955) or 'micro-caverns' (Weis-Fogh, 1948) by authors who have attached great significance to them in relation to the vertical distribution of the soil fauna.

Haarløv (1955) using the soil sectioning technique he developed in collaboration with Weis-Fogh (Haarløv & Weis-Fogh, 1953) has described: (1) the cavity percentage, (2) the total length of the boundaries of cavities and (3) the diameter of the largest circle lying free in the cavity of the sections. It is conceivable that using sections as thick as his (0.75 mm.), it would have been possible to obtain definite measurements, but even then his method of sectioning would invalidate some of the measurements in a sandy soil, since the sand would have been dislodged into the agar-filled spaces during sectioning. In thin sections like the writer's such measurements would be impossible and the same impression is gathered from the photographic plates of Minderman's sections which were cut at 7.5 and 10μ. In this context it is relevant to mention that Haarløv ignored spaces of less than 0.1 mm. diameter in his measurements.

Peat swells on absorbing water. A core taken from the Juncus site (a humified peat, see Table 4) contracted from 57.8 cc. to 12.6 cc. when left exposed under laboratory conditions for 6 months. Greater contraction in volume was noticed in peat cores dried for water content determination. The greater the amount of water in the soil, the more contraction there was, which means that the mineral soils, with little peat and therefore containing less water relative to their weight, contracted less than the peat on drying. Clearly, the spaces in the peat are to be regarded, ecologically, as different from the structural pores between mineral soil particles. They cannot offer the same physical restriction to the distribution of soil animals, especially microscopically vermiform ones like the nematodes, as has been postulated for micro-arthropods. The writer finds no reason to call them 'micro-caverns' because of the connotation that such a term carries with it.

Table 8. Water content of the soils from the Moss Flats and the *Calluna* sites.

The figures are indices of humidity.

Date	Upper 6 cm.	Lower 6 cm.
(a) Bare Peat.		
4.viii.59	3.9	5.1
17.viii.59	4.0	7.6
29.ix.59	3.8	6.9
(b) Residual *Calluna* Hummock.		
29.ix.59	1.8	3.4
(c) *Calluna* site.		
29.iv.59	8.8	8.3
3.vii.59	7.7	8.5
13.viii.59*	6.9	8.1
17.ix.59	5.6	7.3
29.ix.59	8.1	8.7

* Figures for this date are means of 2 cores in each case.

Table 9. Water content of soil from the Juncus site.
The figures are indices of humidity.

Date	Upper 6 cm.	Lower 6 cm.
24.xi.58*	6.1 I.H.	6.0 I.H.
7.iv.59	7.0	5.1
27.v.59	5.4	5.0
19.vi.59	5.0	5.9
3.vii.59	5.8	5.4
13.viii.59	4.9	5.4
17.viii.59	5.2	6.3
25.viii.59	5.2	3.8
17.ix.59*	3.8	5.0
29.ix.59	4.3	5.3

* Figures means of 2 cores.

Table 10. Water content of the soils from the grassland sites.

The figures are indices of humidity.

Date	Upper 6 cm.	Lower 6 cm.
(a) *Nardus* Grassland.		
17.iii.59	1.8	1.1
3.vii.59	1.1	1.1
17.viii.59	1.4	1.1
21.ix.59	0.6	1.4
29.ix.59	0.6	0.7
(b) Limestone Grassland.		
5.v.59	1.0	0.7
3.vii.59	0.9	0.5
28.vii.59*	0.8	0.7
17.viii.59	1.6	0.6
29.ix.59	0.5	0.4
16.x.59	0.6	0.5

* Figures for this date are means of 2 cores in each case.

2. Moisture content.

(a) Drainage.

The state of drainage of the sites will be found described under each individual site description. The following is a comparative summary.

All the peat sites were liable to waterlogging. At such times the peat, especially on the Calluna site, became plastic, slimy and difficult to sample with the corer. Waterlogging has given rise to the gleyed peaty drift which underlay the peat on these sites. The Nardus site was liable to flooding when the Rough Sike was in spate, but such periods did not last very long. It was, consequently, a well-drained site. A high proportion of sand and silt and a basement of angular sandstone boulders (Plate 5) were contributary factors to better drainage. The sloping aspect of the Limestone Grassland site and the base rock gave rise to good drainage.

(b) The index of humidity of the soil.

Tables 8-10 give the water content of the Moor House soils in 1959. The figures are the ratios of the weight of water to that of the dry weight of single cores except in a few cases where more than one was taken. They were the same size as the ordinary field sampling cores and were

dried at 100°C. for 48 hours before being weighed for dry weight determination.

It was not easy to make a comparative study of the water content of the different soils sampled. The concepts which have been developed in the study of soil moisture (Baver, 1956) do not seem to be applicable to highly organic soils like peat. Pearsall (1950) considered it 'convenient to use the water/humus ratio' since 'it was shown..... by W.B. Crump that the relative humidity of a peaty soil depends on its humus content' (p. 76). The present writer prefers the term 'index of humidity' for the ratios in Tables 8-10 rather than 'relative humidity' which is an inapt term since it is used with a different meaning in meteorology.

Because of the striking discrepancy in the organic matter content (see Table 11), the I.H. for the peat and mineral soils are not strictly comparable. This was not, however, a very serious drawback for this study. That the I.H. gave a fair picture of the water status of the soils was shown when it was used, in conjunction with pH, to fit the soils into the rough classification scheme for upland soils that Pearsall (1950, p.77) suggested (Table 1).

Table 11. Properties of some Moor House soils (see Notes below for explanations).

Depth	pH	% Organic Carbon	% Nitrogen	C/N ratio
(a) Bare Peat (Moss Flats).				
1.	4.34	38.12	1.33	28.66
2.	4.54	36.53	1.295	28.21
3.	4.62	38.35	1.260	30.44
4.	4.52	35.92	1.295	27.74
5.	4.52	38.30	1.120	34.20
(b) *Calluna* site.				
1.	4.54	33.85	1.575	21.49
2.	4.40	30.95	2.082	14.86
3.	4.62	35.09	2.024	17.18
4.	4.60	32.14	Unreliable due to frothing	
5.	4.98	33.21	2.38	13.95
(c) *Juncus* site.				
1.	4.50	No soil	No soil	-
2.	4.54	20.0	Not enough soil	-
3.	4.44	29.5	2.31	12.77
4.	4.66	30.0	2.05	14.66
5.	4.66	27.0	2.17	12.44

[continued

(d) Nardus site

1.	5.04	No soil	No soil	-
2.	4.96	16.30	0.98	16.63
3.	4.74	9.60	0.70	13.71
4.	4.80	7.50	0.45	16.48
5.	4.80	8.85	0.49	18.06

(e) Limestone Grassland site.

1.	4.95	7.43	0.978	7.60
2.	5.45	5.56	0.707	7.86
3.	5.64	3.74	0.495	7.56
4.	5.71	3.52	0.436	8.07
5.	5.80	3.19	0.500	6.38

Notes on Table 11.

The samples were taken on the following dates:

1. Bare Peat and Calluna site samples 7.iii.60
2. Juncus and Nardus site samples 5.x.59
3. Limestone Grassland site sample 1.ii.60

The depths to which the numbers 1-5 correspond are as follows:

1. 0-2 cm. (roughly the pure litter, when vegetation present)
2. 2-4 (roughly the fermatation layer)
3. 4-6 (sub-fermetation, humic layer)
4. 6-9
5. 6-12 cm.

All the analyses were carried out in the University School of Agriculture, King's College, Newcastle upon Tyne, by Mr. F. Hunter who has supplied the following information about the techniques.

The organic carbon was determined by the Walkley and Black chromic acid oxidation method with the Markham apparatus, except in the case of the Bare Peat and Calluna site samples for which the Tinsley modification of the Walkley and Black method was used. Apparently, the Walkley and Black method itself tends to give a somewhat low figure for carbon for some soils.

The nitrogen was determined by the standard Kjeldahl method and the pH was measured on a 1:5 soil-water suspension with a glass electrode.

3. The carbon/nitrogen ratio.

The C/N ratio is probably the best method of estimating soil organic matter although the results are not always easy to interpret (Russell, 1958, p.270) and the factors which affect the ratio are varied. It has, however, been found to be rather constant at about 10 for most arable soils examined, in spite of the agricultural treatment which the soils have received. This is because the decomposition of organic matter, with the release of carbon as carbon dioxide and nitrogen as ammonia, tends to proceed differentially until an equilibrium is reached (Russell, 1957, p.25; 1958).

Russell also says that the C/N ratio is typically higher under acid than neutral conditions. It is higher, too, under cold or any other conditions which limit decomposition. Furthermore, moorland plants are generally poor in nitrogen and rich in carbon (Pearsall, 1950). The C/N ratio in moorland soils might, therefore, be expected to be high. The results of the analyses for percentage organic carbon and percentage nitrogen of the soils from the main sampling sites are given in Table 11. Each figure is derived from one bulk sample of 5 field cores.

To the data given by Russell (1958, Table 58, p. 270) showing the range of the C/N ratio in 50 British arable soils, the writer has added a descriptive scale from which

it will be seen that all except one of the Moor House soils have C/N ratios above the normal for arable soils (Table 12). The only exception, the Limestone Grassland site, has rather low figures which could be partly due to the method of estimating the organic carbon (see notes to Table 11). It is noticeable, however, that even in the case of the Juncus and probably the Calluna and Nardus site soils, C/N ratios are not remarkably higher than those expected from arable soils.

Table 12. Scale of the C/N ratio in some British soils (after Russell, 1958) applied to Moor House soils.

	% of soils examined whose C/N ratio falls in the range				
C/N ratio range	<5.5	5.5 - 8.4	8.5 - 11.4	11.4 - 14.4	>14.5
%	-	6	76	18	-
Description	V.low	Low	Normal	High	V.high

Moor House soils:

Bare Peat	V. high
Calluna	High - v.high
Juncus	High - v.high
Nardus	High - v.high
Limestone Grassland	Low - normal

On the assumption that the C/N ratio is an indicator of the rate of turn-over of nutrients in the soil and hence is a guide to the level of active microbiological population (Pearsall, 1950, p.74), the Moor House soils might be arranged in a descending order as follows:

Limestone Grassland	→	Juncus Moor	→	Nardus Grassland	→	Calluna Moor	→	Bare Peat

This compares with the scheme in Table 1.

4. Climate.

(a) General.

Climatological information for Moor House covering the period between 1932 and 1942 has been published by Manley (1936, 1943; see also 1952) and regular meteorological observations have been made since the nature reserve was established in 1952 (see Green, 1958). Tables 13 and 14 summarize the salient features of the precipitation and temperature regimes at the Field Station (1930 feet O.D.), the information being taken from the Moor House Management Plan, 1959.

Snow may lie on the ground to as late as mid-May. From then to mid-October, 'summer' conditions (i.e. with mean daily temperatures >42°F) prevail but there is no month in which frost is not liable to occur. The rather

Table 13. Precipitation data for Moor House.

Annual rainfall	70 in. (178 mm.)
Wettest month	December
Driest month	May
Mean length of snow cover period	80 days

Table 14. Temperature data for Moor House.

Coldest months	January	33.0°F (0.6°C)
	February	32.6°F (0.3°C)
Warmest months	July	52.8°F (16.1°C)
	August	52.3°F (16.8°C)
Mean daily temperature		42°F (5.6°C)
Mean diurnal range		0 - 40°F (0-22°C)
Length of frost period (i.e. no. of days on which frost may occur)		>150 days

wide margins of the mean diurnal temperature range reflect weather conditions with damp, misty days on the one hand and dry, cloudless ones on the other. Table 15 taken from Pearsall (1950), shows that the mean January and July temperatures are comparable with those of some Scottish Highland localities after correction for altitude. Moor House is therefore typical of the montane zone of Britain which has been said to have features similar to those of the sub-actic climate at sea-level (Manley, 1936; Pearsall, 1950, ch.3).

Table 15. Mean and converted January and July temperatures for Moor House compared with those from Highland Scotland (after Pearsall, 1950, Table 3, p.34).

Station	Altitude ft. O.D.	Mean Temp. °F at named altitude		Calculated Temp. °F at 2,000 ft.	
		Jan.	July	Jan.	July
Ben Nevis	4406	23.4	41.7	31.8	50.1
Moor House	1840	33	53	32.5	52.5
Braemar	1111	34.9	55.1	31.9	52.1

(b) Precipitation and evaporation during the period of study.

The total rainfall at Moor House during 1958 was about average (68.4 ins.). That for 1959 was 63.1 ins. Table 16

shows the precipitation/evaporation ratio for the two years from which it will be seen that, taking monthly periods, at no time in 1958 did it fall below 1. In 1959, on the other hand, it was less than unity in May, August and September, and exceeded unity by a very small amount in February and June.

The P/E ratio is obtained by dividing the rainfall (P = precipitation) by the observed potential evapotranspiration (E). The latter is measured by the method described by Green (1959) who also states that, in general, the values obtained are in agreement with those computed by other methods.

Table 16. Monthly P/E ratio for 1958 and 1959.

Month	1958	1959
Jan.	15.40	4.58
Feb.	10.78	1.60
Mar.	2.52	3.31
April	13.80	7.60
May	3.04	0.45
June	2.44	1.11
July	2.65	2.07
Aug.	2.69	0.47
Sept.	4.18	0.90
Oct.	6.36	5.20
Nov.	2.61	17.40
Dec.	16.88	30.75
Year	4.68	2.89

IV. TAXONOMY AND SYSTEMATICS.

IV. TAXONOMY AND SYSTEMATICS.

1. Introduction.

Writing about the nematodes, Overgaard Nielsen (1949, p.5) says that, "for practical purposes nematode taxonomy is fairly simple (apart from technical difficulties) and the species are satisfactorily defined (with a few exceptions)." Despite this assertion, the taxonomy of the nematodes is far from being easy. Several authorities, among them Cobb, Chitwood & Chitwood, Steiner, and Peters have stressed this point in several of their writings. It is also strikingly demonstrated by the fact that wrong identifications, not only at the specific but also at the generic level, abound in the literature. This has led to an already large synonymy in some species and also to the state of affairs where many author's species lists are highly suspect. Thus many of the lists which have been produced by ecologists are only valuable in as far as they indicate the groups of nematodes which have been encountered. Beyond this, critical microscopic study is essential to establish species and, unless checked by a competent taxonomist, or accompanied by adequate figures on which checks can be made, the results are of limited value, or indeed highly misleading.

2. The taxonomy and systematics of the free-living nematodes.

The basis of modern systematic work on the free-living nematodes was laid by Chitwood (1933). His scheme of classification was further developed by Chitwood & Chitwood (1937) (see Chitwood & Chitwood, 1950). Jones (1959) mentions other schemes which have been proposed by other authors, but among phytonematologists, to whom all the work on soil nematodes is due, the Chitwood & Chitwood system has been universally adopted. It was basically used by Goodey (1951) who in his monograph on the "Soil and freshwater nematodes" accepted the raising by Thorne (1949) of the Tylenchida to the rank of an order.

If the rank of phylum advocated for the nematodes by the Chitwoods is accepted, the outline classification of the free-living nematodes is as follows:

Phylum: Nematoda

Class : Phasmidia

Order : Rhabditida

Order : Tylenchida

Class : Aphasmidia

Order : Chromadorida

Order : Enoplida.

Goodey (1951) collated a lot of systematic information which before had been widely scattered in the literature. Since then, however, there have been rapid advances in the study of the taxonomy of the free-living and phytonematodes. Many new species have been described and taxonomic revisions made in various groups, often involving the change of status of the original ranks. The writer does not feel competent enough to attempt a review of this abundant and more up-to-date literature, but brief remarks are offered in the next Section on what is relevant to this work.

3. The identification of the nematodes from Moor House soils.

(a) Techniques.

In the handling of nematodes for identification the techniques and methods of Goodey (1957) have been used. For routine work temporary mounts were made either in water or fixative and ringed with candle-wax, individual nematodes being manipulated with a mounted eye-lash hair or nylon bristle, the latter being in some cases even better.

Permanent preparations were made for critical examination of the nematodes. Specimens were transferred to a drop of water on a glass slide, cautiously relaxed over a small flame and then fixed in TAFG, a modification of the fixative TAF, recommended by Dr. J.B. Goodey. The formula for this is as follows:

Formalin	8.0 ml.
Triethanolamine	1.5 ml.
Glacial acetic acid	2.5 ml.
Distilled water	88.0 ml.

The nematodes were transferred to small quantities of this in small glass tubes or solid watch glasses, suitably covered and left for at least 24 hours. The rapid lactophenol technique of Franklin & Goodey (1949), or the rapid method to glycerine of Baker (1953), both of which are given by Goodey (1957), were then used in the staining and processing the nematodes. The worms were finally mounted in lactophenol or glycerine according to the method used in processing. The cover-slips were supported by pieces of glass-wool and ringed with 'Glyceel' on a turn-table.

The final mounts were examined under the high powers of the microscope (310X and over) and sometimes under oil immersion (over 1000X). For measurements and counting of small structures (e.g. head annules, etc.) camera lucida drawings were made.

The body indices were obtained from camera lucida drawings by the use of lead fuse wire recommended for the purpose and are expressed in the familiar modification of the de Man formula:

L = length of the nematode in mm.

$$a = \frac{\text{body length}}{\text{greatest diameter}}$$

$$b = \frac{\text{body length}}{\text{distance from head to end of oesophagus}}$$

$$c = \frac{\text{body length}}{\text{tail length}}$$

$$V = \frac{\text{distance of vulva from head end x 100}}{\text{body length}} .$$

For b, in all cases the measurements were taken behind the cardia or oesophago-intestinal valve, except when this protrudes into the lumen of the intestine. Where the oesophageal glands are separate the oesophagus has been presumed to end where the lumen of the dorsal gland joins the alimentary canal. The tail length is measured from the anus to the tail tip.

(b) The literature used.

Goodey (1951), while giving generic diagnoses and descriptions of typical species, does not include keys for the identification of the others. Cobb (1918c) gives a key to genera, again describing only typical species. A revision of this key has recently been made by Chitwood & Allen, but this came out too late to be used. Other keys have been made for continental nematode faunas by Schneider (1939) and Jägerskiöld (1909), but the most useful aid to

generic identification was the key, attributed to Chitwood, published by Pennak (1953). In all cases, however, reference was made to Goodey's descriptions and figures and so he is the ultimate authority except where, as indicated below, other sources have been drawn upon.

(i) Class Phasmidia.

For the Rhabditidae and Diplogasteridae no determinations beyond genera were attempted and then only Goodey's book was used. The Cephalobidae were identified using Thorne's key (Thorne, 1937).

The order Tylenchida is of special importance being the only Phasmidian group containing phytonematodes. Consequently, its taxonomy is in a state of flux due to constant revision and re-examination.

The order was erected by Thorne (1949) and accepted as such by Goodey (1951). The genus Tylenchus was revised by Andrássy in 1954 who, besides examining the validity of past authors' species also grouped them into four subgenera. Tylenchorhynchus has been revised by Allen (1955) and Sher & Allen (1953) have revised Pratylenchus. Golden (1956) reviewed the genus Helichotylenchus and gave the histories of the species which he finally established as Helicotylenchus multicinctus, H.erythrinae and Rotylenchus robustus. He came to the conclusion that his

H. erythrinae was the same species as that first described by Cobb in 1893 under the name of Tylenchus multicinctus, but different from that re-named and illustrated by Goodey (1932) as Anguillulina multicincta.

Confusion is very rampant too in the genus Rotylenchus. The authority for R. robustus which is given here is a drawing on the files of Dr. J.B. Goodey labelled as such and attributed to de Man, 1876. The figure and measurements are, according to this source, those of a neotype by Goodey & Seinhorst. Dr. J.B. Goodey's advice has been taken with regard to the identification, nomenclature and authority as given here. It is relevant, however, to mention briefly the source of the confusion referred to.

Thorne (1949), Golden (1956) and Loof & Oostenbrink (1958) all agreed that there had been misidentifications as far as this species was concerned. De Man described what he thought to be the same species in both cases in 1876 and 1880 but published the illustrations for the latter case in 1884. Filipjev (1934) made de Man's 1880 species the type of his new genus Rotylenchus but gave no specific descriptions. Later in 1936 he gave a diagnosis although he used figures from Goodey (1932) thus accepting the latter author's species as being the same as de Man's.

According to Thorne the discrepancies between de Man's figures and descriptions on the two occasions indicate that he had more than one species or that he confused his proper R. robustus with the closely similar Hoplolaimus uniformis, which Thorne himself described for the first time. Golden broadly agrees with Thorne. Loof & Oostenbrink re-examined the history of the species, studied de Man's original collection and made collection from his sites. From the evidence they present they conclude that a composite species has been created by both de Man and Goodey. Agreeing with Thorne, they also think that besides related species de Man may have had a Hoplolaimus as well as Helichotylenchus multicinctus.

The present position of the species is not clear. Loof & Oostenbrink attach the name Rotylenchus robustus to de Man's 1876 species (described as Tylenchus robustus) which they synonymize with the 1880 species and with Hoplolaimus uniformis Thorne, 1949, the latter being suppressed. The species which Goodey re-created as Anguillulina robusta (de Man, 1876) Goodey, 1932 is synonymized with Rotylenchus robustus (de Man, 1880) Filipjev, 1934. They think that it is the same as that named by Thorne (1949) and also by Golden (1956). A new name is given to this species viz: Rotylenchus goodeyi. Andrássy

(1958a) changed this name to Gottholdsteineria goodeyi when he revised the subfamily Hoplolaiminae. The result of all this controversy is clearly illustrated by the fact that Pitcher (1959, footnote on p.81) states that "Hoplolaimus uniformis becomes Rotylenchus robustus (de Man, 1876) Filipjev, 1934, and ... Rotylenchus robustus becomes Gottholdsteineria goodeyi (Loof & Oostenbrink, 1958) Andrássy, 1959."

Some nematologists do not agree with the views of Loof & Oostenbrink (Goodey, J.B., personal communication), at least until the taxonomy of the species has been thoroughly re-examined. The writer's species corresponded morphologically with that figured by Goodey (1932) and to make absolutely certain of its identity, this authority is quoted for it.

The subfamily Criconematinae was the subject of a paper by Taylor in 1936. Since then Raski (1952, 1958) has made studies on the genus Criconemoides and Chitwood (1957) has contributed to the taxonomy of the genus Criconema. Both authors give keys for identification to the species. These were used but also reference was made to the papers in which new species for both these genera have been described up to 1959.

Aphelenchoides has not been revised as a genus, but the writer was able to consult the collection of drawings of the known species which are in the possession of Dr. J.B. Goodey. Dr. M.T. Franklin who has re-examined the type species A. parietinus (Franklin, 1955) kindly checked the writer's material.

(ii) Class Aphasmidia.

The taxonomy of this group has, in general, been less extensively studied. The literature is, with a few exceptions, widely scattered and identification of species entails searching through all this and making comparisons between the specimen under study and the known species, one by one.

In the order Chromadorida, the genus Plectus was particularly abundant at Moor House but except for those species listed, the authorities for which are also given, no specific determinations were attempted. The Tripylidae (Enoplida) have never been revised either, and the process of comparison referred to above had to be used.

The Mononchidae have attracted considerable attention in the past because of their predatory behaviour. They have, consequently, been the subject of a number of both biological and taxonomic studies. Goodey (1951) followed Cobb (1917b) in regarding the family as consisting

of one genus Mononchus, sub-divided into subgenera of which he recognized six namely: Mononchus, Iotonchus, Sporonchulus, Anatonchus, Prionchulus and Mylonchulus. Pennak (1953) regarded these as full genera and also added Mononchulus to them. However, de Coninck (1939) had already treated Anatonchus and Prionchulus as full genera when he made the nomenclatorial combinations for the two species A.tridentatus and P.muscorum, also found by the present writer. There is no evidence that he did the same for the other subgenera. The most recent revision of the Mononchidae is that of Andrássy (1958b, 1959a). He sub-divided three of the subgenera of Goodey (1951) into two each. Thus, together with two new ones which he described and the other three already recognized, he obtained a total of eleven, all of which he regards as full genera. He, apparently, was not aware of either de Coninck's or Pennak's work. The groups subdivided and the new ones formed from them are:

Mononchus subdivided into Mononchus and Cobbonchus,
Iotonchus subdivided into Iotonchus and Miconchus,
Sporonchulus subdivided into Sporonchulus and Granonchulus.

The new groups he added are: Judonchulus and Brachonchus.

His key and classification, like those of his predecessors, are largely based on the pharyngeal morphology.

The effect of this taxonomic revision on the present work is referred to later.

The superfamily Dorylaimoidea was monographed by Thorne (1939) and the genera Dorylaimus, Aporcelaimus and Dorylaimoides were studied by Thorne & Swanger (1936). In both cases keys were given for identification to the species but they were not always found easy to use because often they combined characters for both males and females and the two sexes are not always found together in small samples. Furthermore, the genus Dorylaimus is a very large and common one. Andrássy (1959b, 1960) has recently broken it down into a number of genera. A type-script of his revision was made available to the writer by Dr. J.B. Goodey and from the attempt to work with it, the writer formed the impression that it was more based on the insufficient data in the literature than on actual examination of specimens.

Finally, the writer's specimens of Dorylaimus spp. were submitted to Dr. J.B. Goodey and he placed one species as near Eudorylaimus uniformis (Thorne, 1929) Andrássy, 1959 and the others as probably belonging to four species of the same genus. It is relevant to quote

his comments about the literature on the Dorylaims:

> "Having looked at the literature on the Dorylaims I conclude that except in very few cases it is doubtful whether there is sufficient data available for most of the species to be sure of their identification. Little indication is given of range of characteristics in a species for instance and although Thorne's monographs are impressive, when you look at them closely the data available is very meagre." (Goodey, J.B., in litt.)

One more difficulty was brought to the writer's notice by the statement of Williams (1959) about the nature and taxonomic use of the so-called 'spear guiding ring' in separating Dorylaimus (where it is present) from Aporcelaimus (where it is absent). Williams, rightly says, citing Altherr, that when Thorne & Swanger used the character, they did not fully describe it. Since a 'muscular ring' which he calls a 'spear guiding sheath', as opposed to a 'cutinized' or 'spear guiding ring' proper, is present in Aporcelaimus, the use of this character without fully describing it is liable to lead to errors. The present writer's determinations for Aporcelaimus were made on live specimens and so were not checked by a competent

Table 17. Identified nematode genera by sampling sites.

	Bare Peat (Moss Flats)	Residual Hummock (Moss Flats)	Calluna Moor	Juncus Moor (Moor Edge)	Nardus Grassland	Limestone Grassland	Alluvial Grassland	Sheep Dung	Sphagnum Pool (Valley Bog)
1. Tylenchus	+	+	+	+	+	+	+	+	
2. Tylenchorhynchus	+	+							
3. Helicotylenchus									
4. Rotylenchus									
5. Pratylenchus									
6. Paratylenchus									
7. Criconemoides									
8. Criconema									
9. Aphelenchoides	+	+	+	+	+	+	+	+	
10. Dorylaimus		+	+	+	+	+	+	+	
11. Aporcelaimus		+	+	+	+	+	+	+	
12. Tylencholaimus		+	+	?					
13. Enchodelus		+							
14. Actinolaimus		+							
15. Nygolaimus		+				?			
16. Tylencholaimellus		+				+			

Continued.

	17. Alaimus	18. Amphidelus	19. Rhabditis	20. Bunonema	21. Panagrolaimus	22. Macrolaimus	23. Eucephalobus	24. Teratocephalus	25. Plectus	26. Wilsonema	27. Rhabdolaimus	28. Anonchus	29. Aphanolaimus	30. Monhystera	31. Prismatolaimus	32. Diplogaster	33. Tripyla	34. Anatonchus	35. Iotonchus	36. Miconchus
Bare Peat (Moss Flats)									+				?							
Residual Hummock (Moss Flats)						+			+	+	+			+	+					
Calluna Moor									+	+		+	+	+	+					
Juncus Moor (Moor Edge)			+		+	+	+	+	+		+	+	+	+	+					
Nardus Grassland				+			+	+	+					+	+		+	+	+	
Limestone Grassland			+				+	+	+		+			+	+			+	+	
Alluvial Grassland									+	+										
Sheep Dung			+				+									+				
Sphagnum Pool (Valley Bog)														+	+					

Continued

37. Mononchus (s.l.)
38. Prionchulus

	Bare Peat (Moss Flats)
+	Residual Hummock (Moss Flats)
+	*Calluna* Moor
	Juncus Moor (Moor Edge)
+	*Nardus* Grassland
+ +	Limestone Grassland
	Alluvial Grassland
	Sheep Dung
+	*Sphagnum* Pool (Valley Bog)

Note:

\+ indicates 'present'

? indicates 'identification doubtful'

taxonomist, but there was no doubt that they had the combination of characters which Goodey (1951) gives for this genus.

4. Systematic notes on the nematode genera and species from Moor House.

(a) Introduction.

A list of nematode genera which were identified from Moor House, by sampling sites, is given in Table 17. Extensive collections were made on the first and third to sixth sites listed and only casual sampling on the others. Therefore, a comparison can only be made for the five sites. As nematode genera and species are known to fluctuate widely in their abundance, there is less than an even chance that random sample units selected for examination will contain a representative number of the genera or species in any particular habitat. Thorne (1939, p.11) stresses this fact and Cobb (1918b) had noticed it in connection with his study of filter-bed nematodes in American cities.

In Sub-section (b) the genera and species, when the latter were determined, are given with notes about their morphology and occurrence. The study on the species, as already indicated, was made on select, processed specimens.

It was not always possible to recognize and separate all identified species when encountered again under normal routine work, done under the low power of the microscope with live, temporary mounts. When a species was identified from more than one site, either through microscopic determination or because it was the only species in the genus and hence easily recognizable, this has been indicated in the accompanying site notes. This information is again summarized in Sub-section (c) which gives only the species for ease of reference.

(b) Observations on the genera and species.

The arrangement of the groups followed here is largely that of Goodey (1951) which has been discussed in Section 2 and the measurement indices used have been explained in Section 3 above.

(i) Order Rhabditida Chitwood, 1933.

Family Rhabditidae Chitwood & Chitwood, 1937.

Rhabditis spp. were present in sheep dung but occasionally specimens were found in cores taken from the Juncus and Limestone Grassland sites.

Bunonema sp., 4 undetermined specimens were found in one core taken from the Nardus site.

Correction to p. 54.

Between l. 16: '1♀ L=1.07mm, a=36.3, b=5.3, c=18.1, V=56.2' and l. 17: 'No ♂♂ seen', insert the following:

Macrolaimus spp. A specimen identified as belonging to this genus was found on the Juncus site. Several specimens including juvenile forms of another species were found in cores taken from a residual Calluna hummock at the Moss Flats site. This species, although with the oesophageal characters of a Macrolaimus as illustrated by Goodey (1951), had no cephalic papillae. One specimen had the following measurements:

1♀ L=0.5 mm,, a=20, b=3.3, c=17.2, V=60%.

Family Diplogasteridae Steiner, 1919.

Diplogaster sp., a single undetermined species was found in sheep dung on the Juncus site.

Family Cephalobidae Chitwood & Chitwood, 1934.

Cephalobidae were probably present on all the sites but it was not easy to separate the genera with certainty during routine examination of samples.

Panagrolaimus rigidus (Schneider, 1896) Thorne, 1937, was identified from the Juncus site. Only ♀♀ were seen. The specimen studied was slightly thinner than Thorne's. According to Goodey (1951), this genus is in need of revision, so although P.rigidus is apparently a common, even cosmopolitan, species it probably represents a conglommeration of closely related forms, The specimen studied had the following measurements:

I♀ L=1.07mm., a=36.3, b=5.3, c=18.1, V=56.2%.

No ♂♂ seen.

Eucephalobus sp. one ♀ from the Juncus site had these measurements:

I♀ L=0.77 mm., a=34.3, b=3.6, c=14.7, V=63.5%.

It occurred also in sheep dung on the Nardus and Limestone Grassland sites and was at times probably confused with Panagrolaimus rigidus. Eucephalobus is a difficult genus to separate into species. The present specimen is close to E.teres and E.laevis in measurements and lip characters

but these species are themselves not sufficiently differentiated from each other (Thorne, 1937).

Teratocephalus spp. were very common on all the sites, probably three species being present at the Juncus site alone. One of these was identified as Teratocephalus terrestris de Man, 1876, and had the following measurements:

1♀ L=0.54, a=32.9, b=4.4? c = 5.4, V=51.9%.

This is a worldwide species. (Goodey, 1951; Schneider, 1939).

(ii) Order Tylenchida Thorne, 1949.

Family Tylenchidae Filipjev, 1934.

Tylenchus was the most abundant genus especially on sites where peat formed a greater basis of the substratum than mineral - derived soil.

Tylenchus (Aglenchus) agricola de Man, 1884, was found on all the sites. It is a species widely distributed in moist soil and decaying matter of vegetable origin. It has in the past been confused with T.filiformis. (Andrássy, 1954). The specimen on which this record is based was identified by Dr. J.B. Goodey.

T.(Aglencus) costatus de Man, 1921.

1♀ L=0.44mm., a=27.2, b=4.7, c=4.9, V=63.3% spear 11.6μ.

These measurements fit those given by Andrássy (1954),

according to whom this is not a very abundant species but is known from Europe and the United States of America.

Tylenchus (Tylenchus) davainii Bastian, 1865.

1♀ L=0.97mm., a=59.8, b=7.3, c=6.8, V=61.8%.

A widely distributed species. (Andrássy, 1954; Goodey, 1951; Thorne, 1949).

Tylenchus (Filenchus) sp.n.

1♀ L=0.93mm., a=40.4, b=6.4, c=13.5, V=78%.

1♂ L=0.98mm., a=45.5, b=6.2, c=10.9.

Both specimens were found on the Juncus site.

Tylenchus (Filenchus) sp.n.

1♀ L=0.95mm., a=32.6, b=6.4, c=4.9, V=67%.

1♂ L=0.85mm., a=39.7, b=5.8, c=7.1.

This, too, was recorded from the Juncus site and, like the preceding species, did not fit any of the descriptions of the known species in this genus.

Tylenchorhynchus sp.n.

1♀ L=1.02mm., a=31.5, b=7.3, c=26.2, V=53.3%.

Spear 22.6μ, dorsal gland orifice 1.46μ behind spear base.

1♂ L=1.03mm., a=31.8, b=7.6, c=18.54, spear 21.85μ, spicule 33.6μ, gubernaculum 18.03μ.

Three very similar males were examined. All females examined had an incurved tail, not mentioned in the literature. This could be a population peculiarity or a

specific character. The specimens fitted none of the described species in detail but were closest to T.maximus, except that the latter is not known to have any males. Also, it has a longer tail (c=16-20), is thinner (a=37-47) and its head has 6 or 7 annules, whereas the species in question has 5. T.maximum is, however, a common species in the Netherlands and the U.S.A. and is also known from Canada.

The species was found in the grassland sites as well as in the residual hummocks on Moss Flats. The female specimen examined was found to be parasitized by an internal fungus. (Allen, 1955).

Helicotylenchus erythrinae (Zimmerman, 1904) Golden, 1956.

1♀ L=0.79mm., a=30.8, b=8.5, c=41.2, V=63.2%.

These measurements compare very well with those given by Goodey (1932) for Anguillulina multicincta Cobb, 1893 which, Golden says, is the same species. Goodey also gives measurements for males which, however, were not seen by the writer.

♀♀ L=0.595-0.86mm., a=20.3-31.8, b=5-7.6, c=33-54 V=57-67%.

♂♂ L=0.47-0.5mm., a=25-26.6, b=6.3, c=20-33, spear 25-28μ.

If this and the writer's species are both the same as the original erythrinae, it must be a cosmopolitan species. However, Golden (1956) has shown that since its description as Tylenchus erythrinae by Zimmerman in 1904 from the roots Erythrina lithosperma in Java, it has been variously synonymized and transferred from genus to genus by several authors. In particular, it has been confused with the species now established as Helicotylenchus multicinctus (Cobb, 1893) Golden, 1956.

H.erythrinae was common on the Nardus Grassland and Limestone Grassland sites. It was never found on the Juncus site. (Golden, 1956; Goodey, 1932).

Helicotylenchus sp.n.

1♀ L=0.84mm., a=25.5, b=5.7, c=31.9, V=55.3, spear 31.88μ.

The species is close to H.multicinctus (Cobb, 1893) Filipjev, 1936, but has a more equatorial vulva, a slightly longer stylet and a longer tail. The measurements given for H.multicinctus by Goodey 1940 are:

♀ L=0.63-0.680mm., a=23.8-28.5, b=4.5-6.0, c=48-63, V=64.6-71.8%, stylet 20-24μ

♂ L=0.435-0.556mm., a=27.2, b=3.76-4.8, c=28-35.6 spicules 20-22μ.

Although the three specimens studied came from the Limestone Grassland, it probably occurred also on the Nardus

Grassland site. No males were recorded. (Golden, 1956; Goodey, 1940).

Rotylenchus robustus (de Man, 1876), Goodey, 1932.

2♀♀ L=1.22mm., a=28.6, b=8.8, c=47.2, V=54.8%, spear 36.8μ.

The specimens identified came from the Nardus Grassland site but the species was also found on the Limestone Grassland site.

The history of this species has been adequately dealt with by Golden. (Golden, 1956; Goodey, 1932).

Pratylenchus pratensis (de Man, 1880) Filipjev, 1926.

1♀ L=0.5mm., a=25.8, b=5.9 (to end of bulb, 4.8), c=22.5, V=83.8%.

Large numbers of this species were occasionally found in some cores, taken from the Limestone Grassland site, which were reminiscent of the "nests" described by Steiner (1949b), otherwise it was not a common species, although it was sometimes encountered on the Nardus site.

It is a widespread species and a reputed plant parasite (the "root lesion nematode"). (Goodey, 1951; Sher & Allen, 1953).

Family Criconematidae Thorne, 1943.

Paratylenchus sp. was found on the Nardus and Limestone Grassland sites.

Criconemoides sp.n.

♂♀♀ L=0.46-0.56mm., a=9.4-16.6, b=4.2-5.5, c=11.6-24. V=80.0-94.5%, spear 51.1-57.2μ, body annules 71-79, not including head and tail end annules; in some cases annules anastomosed.

No ♂♂ seen.

A head end view of this species indicated the presence of small ventro-median lobes. Its characters did not, however, fit any of the diagnoses of the known species. It was common on the Nardus site. (Raski, 1958; Taylor, 1936).

Criconemoides sp.

A species otherwise closely similar to the one mentioned above except that it was longer and three males were found in the same core, taken from a residual hummock of Calluna on Moss Flat, which are presumed to belong to it. The female had about 85 body annules.

Criconema murrayi (Southern, 1914) Taylor, 1936.

♀L=0.44mm., a=9.6, b=3.8, c=5.4, V=80.8, spear 68μ, annule number 62, vulva on 12/13 annule from the terminus, anus on 11/12 annule from the terminus. (a is computed by excluding the spines and the width so measured is 0.0452 mm.).

This is very close to the type as described by Taylor (1936). The species was found on the Nardus site and the Calluna hummocks on Moss Flats. A single specimen has

also been obtained from the Limestone Grassland site.

Although originally found in moss from Ireland, it, or morphologically identical forms, may be widespread. (Chitwood, 1957; Southern, 1914; Taylor, 1936).

Family Aphelenchidae Steiner, 1949.

Aphelenchoides.

This genus was found on all the peat habitats but was not common if present at all, on the grassland sites.

Aphelenchoides saprophilus Franklin, 1957, was collected from the Calluna as well as the Juncus sites. Two females, no males were recovered, had the following mean measurements, the figures being means:

L=0.67mm., a=29.7, b=8.7, c=12.6, V=67.2%.

Franklin described this species as "frequently found in rotting plant tissue in contact with soil." She also says that it is very similar and easy to confuse with A.parietinus under which so many determinations have been lumped in this genus. It may, therefore, be that this is a common and very widespread, but hitherto unrecognised, species. (Franklin, 1957).

(iii) Order Chromadorida Chitwood, 1933.

Family Plectidae Chitwood & Chitwood, 1937.

Plectus spp. were present on every site but less common on the grassland than on the more peaty sites.

Plectus parietinus Bastian, 1865, was determined by Dr. J.B. Goodey from specimens collected from the Juncus site where it was very common, as it was also on the Calluna and Moss Flats sites.

Plectus tenuis Bastian, 1865, occurred abundantly on the Juncus site and in cores taken from Calluna litter.

This determination is according to Schneider (1939).

Wilsonema.

From the Calluna hummocks on Moss Flats a specimen was obtained and identified as probably:

Wilsonema auriculatum (Bütschli, 1873) Cobb, 1913.

1♀ L=0.3mm., a=18, b=3.6, c=7, V=?

(Goodey, 1951; Schneider, 1939).

Rhabdolaimus. spp. occasionally appeared, especially in the Limestone Grassland extracts, but one specimen was recovered from a Calluna hummock at Moss Flats.

Anonchus sp. was only once recorded, at the Juncus site.

Family Camacolaimidae Chitwood & Chitwood, 1937.

Aphanolaimus attentus de Man, 1880.

1♀ L=0.73mm., a=28.1, b=?, c=6.3, V=50.2%.

1♂ L=0.83mm., a=41.5, b=7.1 ? , c=6.4.

This species was exactly the same as/described by Goodey that (1951), except that the males seen all had three pre-anal papillae, as he illustrates them, although he describes

four in his diagnosis.

It occurs on most sites, but was never recovered from any of the extracts of the Limestone Grassland site cores. Casual examination of Sphagnum samples from Valley Bog yielded several specimens and in all cases when it was encountered, the males were as common as, if not commoner than, the females. (Goodey, 1951).

Family Monhysteridae Chitwood & Chitwood, 1937.

Monhystera spp. Cores from the Juncus, Nardus and Moss Flats sites had occasional specimens belonging to this genus, being a typically aquatic group. however, it was not surprising to find them most abundant in the Sphagnum samples from Valley Bog.

Monhystera villosa Bütschli, 1873, was identified from Moss Flats peat.

1♀ L=0.54mm., a=35, b=?, c=7, V=74.3%.

Prismatolaimus was a common genus, being represented by: Prismatolaimus dolichurus de Man, 1880, a characteristically long tailed species constantly present in samples from the Juncus site, but also turning up elsewhere. A somewhat smaller and shorter:

Prismatolaimus sp. was also seen on the Limestone Grassland site.

(iv) Order Enoplida Chitwood, 1933.

Family Tripylidae Chitwood & Chitwood, 1937.

Tripyla affinis de Man, 1880. The following measurements were made on specimens extracted from Limestone Grassland samples.

1♀ L=1.44mm., a=29.4, b=5.0, c=6.5, V=55.1%,

egg 103.2 × 51.6μ.

1♂ L=1.45mm., a=28.2, b=5.5, c=5.7.

The morphological characters agreed so well with Goodey's diagnosis and illustrations that it is, undoubtedly, the same species. (Goodey, 1951).

Tripyla sp.n., had features very close to those of T.setifera, including long cephalic papillae of which there were six, about $\frac{1}{3}$-$\frac{1}{4}$ of the head width in length. Smaller, thinner setae were also present about $\frac{1}{2}$ of the head width behind the head end. The cuticle was thick and apparently double or layered, with strong striation. A marked and more frequently repeated striation occurred on the sub-cuticle, itself a character of probable taxonomic significance as no mention of it was found in the diagnoses of this group.

The following measurements are means obtained from two specimens of each sex:

♀ L=1.30mm., a=29.0, b=4.7, c=6.0, V=52.9%.

♂ L=1.36mm., a=24.1, b=5.1, c=6.0.

A point of biological interest is that both the males and the one female studied revealed fusiform-shaped bodies in their reproductive systems, presumed to be spermatozoa. It does not seem to be reported that nematode spermatozoa are ever this shape, but if they are, it would be strong evidence that the males are functional.

The locality for the species was the Limestone Grassland site, but might have been also present on the Nardus site, from which unfortunately, the only studied specimen was a juvenile. (Bütschli, 1873; Cobb, 1893).

Family Mononchidae Chitwood & Chitwood, 1937.

The Mononchidae were never very abundant in any of the material examined. However, they were recovered fairly regularly from the grassland sites, indicating that they were widespread there, even if not abundant. At first they were all lumped together under Mononchus, following the system of Goodey (1951) or when possible, they were split into sub-genera. Taxonomic revision by Andrássy (1958b) had led to the situation where any identifications originally made on live specimens cannot be verified except in those cases where these were retained and permanently mounted. This procedure was not always practicable under

routine sampling conditions, with the consequence that the writer's original identifications have had to be abandoned. The following specific determinations were made by Mr. W.C. Clarke of the New Zealand Department of Scientific and Industrial Research, then at Rothamsted. The words sensu lato are attached to what has been retained of the writer's unconfirmed identifications which may, therefore, have been affected by Andrássy's taxonomic revision already mentioned.

Anatonchus tridentatus (de Man, 1876) de Coninck, 1939. Only two ♀♀ were obtained from the same core taken from the Limestone Grassland. Goodey (1942), who made a special study of this species in the soils from St. Albans, England, says of it, "it occurs here in greater numbers than any other species of Mononchus so far encountered."

Iotonchus sp., sensu lato, came from the Nardus site.

Miconchus sp., the determination was carried out on a juvenile extracted from the Nardus site.

Mononchus sp., sensu lato. Records of live identifications exist for the Calluna and Limestone Grassland sites, but in the case of the former only one specimen was ever found.

Prionchulus muscorum (Dujardin, 1845) de Coninck, 1939. Localities: Nardus and Limestone Grasslands. This species has been reported from all over the world by many authors.

Family Dorylaimidae de Man, 1876.

Dorylaimus is a very large genus. Goodey (1951) listed about 200 species and varieties inhabiting soil, fresh water or moss and the present state of their taxonomy is referred to in Sub-section 3(b) above where, too, the recent work by Andrássy is mentioned. Since the keys of Thorne & Swanger (1936) and Thorne (1939) were used for generic identification of the Dorylaimoidea, it has been decided to retain the name Dorylaimus for the purposes of this work.

Dorylaimus spp. were found on all the sites sampled though none were extracted from the bare peat on Moss Flats.

Aporcelaimus was a genus encountered only on the Limestone Grassland site.

Tylencholaimus: a small species was common on the Limestone Grassland site and a doubtful record for the genus also exists for the Juncus site.

Enchodelus macrodorus (de Man, 1880) Thorne, 1939. This was recorded on the Nardus and Limestone Grassland sites. Two ♀♀, one from each site, were measured and studied. The one from the Nardus site had the following measurements:

L=1.90mm., a=18.4, b=3.8, c=61.3, V=42.9%, spear 40μ.

The other from the Limestone Grassland had these measurements:

L=1.85mm., a=24.1, b=4.7, c=78.2, V=43.8%, spear 45μ.

No ♂♂ were seen and according to the literature these are rather rare.

A comparison of the measurements given by Thorne and Goodey for this species shows that the ♀♀ are very variable. Combining the two authors' observations the range of measurements is as follows:

L=1.6 - 1.93mm., a=24 - 37, b = 4.5 - 5.3, c =53 - 77, V=42 - 46.7%.

The species, if it is the same, must therefore be very variable and Thorne says that the variability is even greater if other workers results are taken into account. "European records give lengths: ♀ : 1.0 - 2.2mm; ♂; 1.12 - 2.16mm, with proportional measurements varying greatly, indicating that perhaps more than one species is involved." If it is actually the same species that has been collected, it seems to be cosmopolitan, having been collected from many European countries, from North America, Greenland, the Faroes, Nova Zembla and S.W. Africa. (Goodey, 1951; Thorne, 1939).

Actinolaimus sp. was found on the Limestone Grassland site, although it did not occur in large numbers. Unfortunately both the specimens mounted for critical examina-

tion turned out to be juveniles.

Nygolaimus sp. was doutfully recorded, from a single specimen, on the Limestone Grassland site.

Family Leptonchidae Thorne, 1935.

Tylencholaimellus sp.n. was identified from a single ♀ specimen recovered from a Limestone Grassland site extract. It did not fit any of the known species as given by Goodey and Thorne. The specimen did not survive the rigours of permanent mounting. That and the smallness of it account for the incomplete measurements.

1♀ L=0.49mm., a = 25.5, b =? c=? V=45.7%.

This seems to be the first record of this genus from this country. (Goodey, 1951; Thorne, 1939).

Family Alaimidae de Man, 1880.

Alaimus, Amphidelus and Adorus, the three genera in this family according to Goodey (1951), are separated mainly on their amphid shape and the characters of the male spicula. All the specimens seen, except one, had almost indistinct or pore-like amphids and were therefore placed in the genus Alaimus. The only one specimen which had elongate, slit-like amphids was found on the Juncus site and was placed in the genus Amphidelus.

Alaimus spp. were found on the Juncus and the Grassland sites. The descriptions of the species in the literature are meagre and the illustrations are inadequate, mainly because of the smallness of the species and the difficulty of making out clearly the anatomical details in prepared specimens. A common species on the Limestone Grassland site keyed out as A.parvus but due to the deficiency of detail observed and the vagueness in the characters used to separate the species this could not be confirmed. It had these measurements:

1♀ L=0.86mm., a=53.4, b=3.7, c=6.9, V=46.3%.

Thorne gives the following measurements for A.parvus:

♀ L=0.7mm., a=40, b=4.1, c=7.1, V=41%.

He says, however, that Steiner reported a specimen of A.primitivus with: L=0.606mm., a=33.7, b=3.7, c=8.2, V=43.9% which might have been a A.pavus. It will be clear that until the size range of the species is know, it would be unwise to include all the three specimens in the same species.

Amphidelus was recorded from one specimen found on the Juncus site. The species was not determined.

It is interesting that no males of the Alaimidae were ever seen amongst all the specimens that were examined.

(c) A list of nematode species from Moor House.

In the following list are given such species as were conclusively determined from various Moor House soils. After each species the sites from which it was identified are also given. A single record does not necessarily mean that the species does not occur anywhere else, but often means that the site indicated was the source of the specimens which were carefully studied. The following abbreviations are used for the site names:

A = Alluvial Grassland

B = Bare Peat (Moss Flats)

C = Calluna Moor

D = Sheep Dung

H = Residual Calluna Hummocks (Moss Flats)

J = Juncus Moor (Moor Edge)

L = Limestone Grassland

N = Nardus Grassland

V = Sphagnum Pool (Valley Bog).

No.	Species	Site
1.	Panagrolaimus rigidus (Schn.) Thorne	J.
2.	Teratocephalus terrestris de Man	?C, H, J, L, N.
3.	Tylenchus (Aglenchus) agricola de Man	A, ?B,C,H,J,L,N.
4.	T. (Aglenchus) costatus de Man	L.
5.	T. (Tylenchus) davainii Bastian	J.
6.	Helicotylenchus erythrinae (Zimmerman) Golden	L, N.
7.	Rotylenchus robustus (de Man) Goodey	L, N.
8.	Pratylenchus pratensis (de Man) Filipjev	L, N.
9.	Criconema murrayi (Southern) Taylor	H, L, N.
10.	Aphelenchoides saprophilus Franklin	C, J.
11.	Plectus parietinus Bastian	C, H, J, ?L, ?N.
12.	P. tenuis Bastian	C, J.
13.	Wilsonema auriculatum (Bütschli) Cobb	H.
14.	Aphanolaimus attentus de Man	?B, C, J, N, V.
15.	Monhystera villosa Bütschli	B.
16.	Prismatolaimus dolichurus de Man	C, J, H, L, N.
17.	Anatonchus tridentatus (de Man) de Coninck	L.
18.	Prionchulus muscorum (Dujardin) de Coninck	L, N.
19.	Enchodelus macrodorus (de Man) Thorne	L, N.

To these should be added a number of species which were identified as new since they did not fit any of the descriptions of known species.

No.	Species	Site
20.	Tylenchus (Filenchus) sp.n.	J.
21.	Tylenchus (Filenchus) sp.n.	J.
22.	Tylenchorhynchus sp.n.	A, B, H, L.
23.	Helicotylenchus sp.n.	L.
24.	Criconemoides sp.n.	N.
25.	Tripyla sp.n.	L, ?N.
26.	Tylencholaimellus sp.n.	L.

These species could not be described because not enough material was obtained. The specimens examined, however, are preserved on permanently mounted slides.

V. FEEDING BIOLOGY.

V. FEEDING BIOLOGY.

1. Introduction.

The earliest information on the food biology of eelworms was obtained by examining the gut contents and by directly observing feeding worms. Because of the ease with which these can be done, they still form the basis of much of our information. The literature contains many comments on this topic, derived from such sources, but being so scattered it is not easy to review them. Nonetheless, Menzel (1920) produced a review of the earlier literature and lately Overgaard Nielsen (1949a) has made this information available in English. Goodey (1951) collated what information was then known about the feeding habits of the different genera that he dealt with in his monograph and Hyman (1951) made reference to workers who had made observations on the feeding habits as well as those who had cultured free-living nematodes under experimental conditions.

In addition to making observations and experiments, various people have also attempted to deduce the probable food of the nematodes from the anatomical structure, an approach that is widely used in other animal groups e.g. insects and birds. The form of the buccal capsule, the structure or absence of the buccal armature and the struc-

ture of the oesophagus are all highly characteristic specializations of certain nematode groups for their methods of feeding and nature of their food. Overgaard Nielsen (1949a) divided soil nematodes on this basis into those feeding on: (1) liquid food, (2) particulate food and (3) large micro-organisms. It is interesting that Wieser (1953) later produced a very similar classification for marine nematodes. Like all classifications, however, these have their uncertain categories and border-line cases.

For ecological purposes, a classification based on the type rather than the state of the food is to be preferred. The latter can still be made using the same combination of methods of observation, experiment and inference from anatomical structure. A typical classification of this type is that given by Chitwood & Chitwood (1950, p.1) who divided the nematodes into scavengers, herbivores, carnivores and parasites. Overgaard Nielsen (1949a, p.80) quotes other examples from other authors. He, however, examined various types of evidence and concluded that free-living soil nematodes could best be divided into four feeding groups (p.91 and 1949b), viz.

(1) Root feeders

(2) Bacterial feeders

(3) Algal feeders

(4) Predators.

This terminology implies more precise knowledge and more rigid food requirements than the information available justifies and the present writer has considered it better to adopt the following modification:

(1) Plant feeders

(2) Microbial feeders

(3) Miscellaneous feeders

(4) Predators.

Further reasons for this usage will become evident in subsequent sections of this Part.

2. Aims and techniques of study.

From the information obtained in this study, it was hoped to evaluate the ecological role of nematodes in the moorland soils. The representatives of the different genera and species were examined when they became available in the course of sampling. Some of the nematode types were not very abundant and so only a few could be examined. The amount of information obtained from this study, although very valuable, is not therefore as extensive as might have been desired.

The specimens were often examined live, in temporary water mounts prepared according to the technique described in Part IV.3, below. Sometimes very active specimens were anaesthetized by mounting them in chloroform-water, the

strength of which depended on the activity of the worms. To observe the gut contents clearly it was preferable to have the live nematodes performing rather sluggish movements, but when such movements were not required or, sometimes, in order to obtain better results under oil immersion, the specimens were mounted directly in lactophenol and the cover slips ringed with candle wax or 'Glyceel'.

In addition to the specimens mounted alive, those prepared for taxonomic study were examined for their gut contents. Gut content examination was also done while carrying out routine feeding group classification. The latter classification was done to find out the percentage of the different feeding groups in order to assess their relative abundance and also to get information for biomass estimation.

For this routine operation, nematodes of one sample unit from the sample were examined. About 10 to 15 worms at a time were transferred by means of a mounted bristle to a drop of water on a glass slide having an area about 2.6 x 2.1 cm. marked into a 1 mm. square grid. A square cover slip was then lowered on to the preparation and the worms examined under the microscope. Actively moving specimens, e.g. Plectidae and Cephalobidae, were anaesthetized with chloroform-water and if the scanning was

likely to take a long time the preparation was ringed with candle wax to prevent drying up. The specimens were examined and identified to the lowest taxon possible or just put into their feeding group if identification was not possible. Some nematodes were lost during the transfer to the slide and some stuck to the edges of the cover slip, but in general at least 90% of them were examined.

3. Plant feeders.

The writer includes in this group the stylet-bearing nematodes which pierce and suck cryptogamic or parts of higher plants (nos. 1-9, Table 17) apart from the Dorylaimoidea (q.v. Section 5). These nematodes are widely regarded as plant parasites in the widest sense of that word (Christie, 1959, p.7) by phytonematologists and this parasitic aspect of the group has been very much emphasized. This is a reflection of the plant pathological approach, already referred to, which dominates the study of soil nematodes. Besides the standard manuals of plant nematology, this aspect of nematology has recently been reviewed by Chitwood & Oteifa (1952), Christie (1959), Fielding (1959) and Southey (1959).

In the present study no solid objects were ever found in the gut of any of the plant feeders. Some of the species have been cultured on agar plates of fungi by various workers.

In this way, for instance, Franklin (1957) cultured Aphelenchoides saprophilus although she found that after some time its length decreased slightly. Probably other plants besides fungi are necessary for their proper development in nature.

4. Microbial feeders.

Included in this group are all the genera numbered 17 - 33 in Table 17. They include, besides others, those which Overgaard Nielsen (1949a, Table 23, p.92) classified as feeding on particulate food. The writer did not examine Bunonema, Wilsonema, Rhabdolaimus, Anonchus and Amphidelus because they were not easily obtainable. All the others were studied and without exception bacteria were seen, sometimes in very large numbers, in their gut (Table 18).

Rhabditis spp. were kept on agar plates and were seen to ingest both the bacteria and the algae growing on the plates. They were found to ingest fungal spores when cultured with soil microfungi.

In almost all cases where bacteria were found in gut contents, they were of coccoid form (cocci and diplococci). They were often of different sizes and, especially in those specimens particularly amenable to microscopic examination (e.g. species of Plectus, Panagrolaimus, Eucephalobus and Tripyla), were usually clearly seen to be surrounded by

Table 18 The gut contents of some microbial feeders examined.

Genus	Gut contents
Rhabditis	bacteria, unicellular green algae, fungal spores
Bunonema	not examined
Diplogaster	bacteria
Panagrolaimus	bacteria
Macrolaimus	bacteria
Eucephalobus	bacteria
Teratocephalus	bacteria
Plectus	bacteria, fungal hyphae
Wilsonema	not examined
Rhabdolaimus	not examined
Anonchus	not examined
Aphanolaimus	bacteria, fungal spores
Monhystera	bacteria
Prismatolaimus	bacteria (small cocci, often in groups), fungal spores, clear or dark viscous matter common
Tripyla	bacteria (cocci) in viscous and sometimes detrital matter
Alaimus	when clear enough only bacteria seen
Amphidelus	not examined

a viscous fluid material. The same fluid bound other objects ingested, e.g. fungal spores. In Plectus spp. and Panagrolaimus rigidus it was noticed that the viscosity of the gut contents was different in the different parts of the intestine. Often there was a very tenacious plug in the fore-intentine, enveloping and stretching some distance behind the oesophago-intestinal valve. The mid-intestine contained more fluid material which was seen to flow backwards and forwards, past the constrictions imposed by the reproductive organs, as the nematodes wriggled or performed the well-known 'thrashing movements' (Hyman, 1951). Further back in the hind-intestine, the gut contents were again less fluid and, near the anus, often darker in colour.

Especially within the fore-intestine viscous plug, but also elsewhere in the gut, the ingested bacteria were usually found in distinct groups. Although it was possible that they had divided prior to being digested, the grouping probably arose from the nematodes having swallowed members of a colony. Alternatively, it might have represented successive portions of the viscous plug which had passed down the gut as they broke off.

It is probable that the viscous fluid in the gut serves a digestive function. The functional morphology of the intestine of the nematodes is related to the high

hydrostatic pressure of their body fluid (Harris & Crofton, 1957). This pressure would seem to be sufficient to empty the gut when the anal sphincter is opened and it may well be that the viscous fluid prevents all the gut being emptied at the same time, thus facilitating proper digestion of the food organisms before being voided. Nevertheless, Steiner (1949a) claims that bacteria pass, apparently unharmed, through the tracts of nematodes.

5. Miscellaneous feeders.

This includes all the families of the superfamily Dorylaimoidea (Goodey, 1951), except the Alaimidae which do not possess a stylet and are microbial feeders (see Table 18).

Overgaard Nielsen classified the genera Dorylaimus and Tylencholaimus as probably taking liquid food, and, without examining them, thought the same about Actinolaimus and Nygolaimus (1949a, p.92). This conclusion was based on the buccal and oesophageal morphology of the genera. His review of the literature, citing various authors (de Man, Steiner, Menzel, Micoletzky and Stöckli), was entirely about Dorylaimus spp. (p.76). Species of this genus according to these authors, feed on a variety of things, both plant and animal. This led Overgaard Nielsen

to conclude (p.81) that

> "nothing definitely can be said of the nutrition of the Dorylaiminae. Several occasional observations are at hand but they do not allow one to construct a general concept."

His own observations (p.84) indicate that 2 species of Dorylaimus could be maintained on moss or cultures of alga and bacteria for up to about 5 weeks. Tylencholaimus mirabilis lived in a water culture of algae for 6 weeks. Dorylaimus tritici could not be cultured for more than 10 days on alga, bacteria or moss, although it lived for 20 days on dead enchytraeid. This latter seems difficult to explain. The failure of the other nematodes to live in the bacterial cultures, however, was probably due to their drowning. Whatever the food merit of the algal growth was, it would certainly have aerated the medium.

The experiments of Overgaard Nielsen, as he admitted (p.84), did not therefore establish anything, especially as he did not, following his standards of reliability (p.81), record any direct observations of the nematodes feeding on the algae. His conclusions (1948b, p.52; 1949a, pp.84, 98 - 99, 118) when examined in the light of his evidence and that of the literature he quoted (1948b, p.50; 1949a, p.76) are inconsistent. The only general conclusion the present writer would have arrived at from his evidence is that this

group of nematodes feeds on a wide range of organisms, rather than definitely on algae.

Linford & Oliveira (1937) found that 10 species of Dorylaimus and the closely related genera Discolaimus and Actinolaimus fed on other nematodes. From the literature and observations they considered that Dorylaimus spp. feed on nematode and mite eggs and enchytraeids as well. Linford (1937) later added rotifers and infusoria to this list. Cobb (cited by Thorne & Swanger, 1936, p.10) considered some Dorylaimus spp. carnivorous.

The evidence of Overgaard Nielsen that some members of the Doryaimoidea are plant feeders is supported by other writers (see e.g. Thorne & Swanger, 1936; Thorne, 1939; Goodey, 1951) and, indeed, the apparent convergent evolution of this group's buccal armature, especially among the Longidorinae and Tylencholaiminae, with that of the Tylenchoidea would lead one to expect that (Steiner, 1936). Thorne & Swanger attribute the colouring often seen in the gut of the Dorylaimoidea to higher plants. More recently, Hollis and his co-workers were able to culture Dorylaimus ettersbergensis and found that given a number of micro-organisms it would live and reproduce best on a blue-green alga (Chroococcus sp.) although it would also feed on the others which included two green algae, a sporozoan and a fungus. These were thought to provide supplementary

Table 19 Recorded and observed food of the Dorylaimoidea.

Genus	Recorded in literature	Observed in present study
Dorylaimus	various, including microbial, plant and animal matter	Chlorophyllous plant, algal cells, brown humus, bacteria, fungal spores, red coloured matter and unidentifiable viscous fluid, red thread-like strands, protozoan cysts, setae-like objects.
Aporcelaimus	predatory on small oligochaetes (Thorne & Swanger)	no recognizable remains.
Tylencholaimus	chlorophyll (O. Nielsen)	chlorophyll and colourless matter.
Enchodelus	plant materials, chlorophyll in gut (Thorne)	colourless fluid with oil-like globules, no solid matter.
Actinolaimus	predatory	dark-bluish and brownigh matter.
Nygolaimus	predatory largely on oligochaetes (Thorne)	not examined.
Tylencholaimellus	no information	not examined.

nutrition. (Hollis, 1957).

The recorded food of some genera of the superfamily Dorylaimoidea together with the writer's observations on the gut contents are given in Table 19. The commonest gut contents consisted of a colourless, greenish or brownish tinted viscous fluid. When green it, no doubt, was of plant origin and when brownish or dark coloured, it might have had some humus in it. There was no evidence, however, that humus or debris were ingested in large amounts (see also Overgaard Nielsen, 1949a). A wide variety of other objects were seen in the gut of species of Dorylaimus but never in that of other genera.

The Dorylaimoidea may therefore be considered as consisting of three feeding types:

(1) those feeding on a wide range of organisms (animal, plant and microbial) e.g. Dorylaimus;

(2) those feeding on plants or parts of plants and which have the stylet modified or strengthened e.g. Tylencholaimus, Enchodelus and Tylencholaimellus (?);

(3) those predatory on other animals e.g. Aporcelaimus, Actinolaimus and Nygolaimus.

A clear-cut distinction between these groups does not seem to exist and consequently they are best treated as one group under the heading 'miscellaneous feeders'.

6. Predators.

According to Christie (1959) predatory nematodes are of three distinct types. One has a plain oesophagus which is capable of swallowing relatively large 'objects'. In this are included Tripyla and Monhystera. Another type has a cup-like pharynx, usually armed with grasping or puncturing teeth or both. These, of which Diplogaster and Mononchus are examples, suck the contents or entire bodies of their prey. The third type, for example the predatory species Aphelenchoides and some of the Dorylaimoidea, is armed with a stylet which is used like that of the plant feeders.

Goodey (1951) gives the food of Tripyla affinis as "small nematodes, many of which can be seen in the intestine of some of the writer's mounted specimens" (p.262). He also gives nematodes and rotifers as having been observed in the gut of 2 related species. None of the present writer's specimens of this genus showed any evidence of having fed on any nematodes or other animals. T. affinis was found to have dark, probably detrital, matter and bacteria in the gut. An undetermined species from the Limestone Grassland had relatively large and also smaller coccoid bacteria as the only identifiable gut contents. Overgaard Nielsen (1949a, p.78) cited Micoletzky's observation on T.papillata "feeding exclusively on diatoms."

Clearly, Tripyla spp. are not obligate predators and do not seem to be so at Moor House, for which reason the genus is included with the microbial feeders. For the same reason the genus Diplogaster, represented in sheep dung, was included in the same feeding group.

Monhystera spp. are obviously not predatory, both from their small size (about 0.5mm.) and the structure of their pharynx (see Goodey, 1951, p.209). Christie (1959, p.20) and Goodey (1933, p.278) both quoted Cobb as having speculated on the genus being predatory. The writer has not been able to find the original source of the quotation but there is no doubt that Cobb considered species of the genus microbivorous, since he wrote the following about them.

> "Of the numerous species of Monhystera I have had occasion to examine with respect to their food habits, all appear to be largely if not wholly vegetarian... If the filterbed Monhysteras are not an exception to the rule, they would seem to depend on fungi and bacteria as a source of food, except in open beds, where of course they would find an abundance of green microphytes" (Cobb, 1918b).

He found the marine species to be almost exclusively diatom feeders. Overgaard Nielsen (1949a) could not decide about the chief food of Monhystera but the present writer con-

siders the evidence sufficient to include the genus with the microbial feeders.

The predatory species of Aphelenchoides seem to differ morphologically from the plant feeding ones sufficiently ~~enough~~ to be put in a genus of their own; Seinura, (Christie, 1959, p.149; Chitwood & Oteifa, 1952). None of these, however, were encountered in Moor House soils. The position with regard to the Dorylaimoidea has already been discussed.

There remains the family Mononchidae of which at least 5 genera were found (Table 17, nos. 34 - 38). The predatory nature of this group is well established (Cassidy, 1931; Cobb, 1917b; Goodey, 1942; Menzel, 1920; Steiner & Heinly, 1922; Thorne, 1924, 1927). Following Cobb's suggestion (1920) attempts were made by Steiner & Heinly to use the Mononchids in biological control of plant parasitic nematodes. Although they found that M.papillatus voraciously preyed on nematodes during certain stages of its life cycle, they confirmed earlier workers' observations that there was no selective preference for the nematode species, or indeed for the other organisms, preyed on. Thorne (1927) studying field populations of 4 species of Mononchidae in Utah, U.S.A., found M.papillatus the most voracious nematode feeder, the other species preferring other micro-organisms. The food list of the Mononchidae is quite extensive (Table 20).

Table 20 Organisms fed on by Mononchidae (from the literature and observations in present study).

Nematodes (with the nomenclature brought up to date)

Tylenchus (Aglenchus) agricola

Pratylenchus macrophallus

(Tylenchulus semipenetrans)

(Heterodera schachtii)

(Meloidogyne sp.)

Rhabditis spp.

Panagrolaimus rigidus

(Turbatrix aceti)

Cephalobus spp.

Plectus spp. including P.parietinus and auriculatus

Aphanolaimus attentus

Monhystera spp.

Ironus sp.

Tripyla intermedia

Mononchus sp. and other Mononchidae

Dorylaimus spp.

Bacteria

Protozoa (Leptomonad flagellates reported by Goodey (1942) must be parasites)

Rotifera

Tardigrada

Oligochaeta probably entirely Enchytraeidae although 'small earthworms' is a commonly used expression

Collembola

Examination of the gut contents of juvenile and female Mononchus sp. (sensu lato) revealed bacteria (coccoid and rod forms), angular pieces of plant origin, plant (fungal ?) spores, corpulatory spicules of nematodes and spicule-like objects. Remains of small Plectidae and Aphanolaimus attentus were found in the gut of other Mononchidae. One Mononchus sp. juvenile had in its gut, besides bacteria and material of plant origin, two Chromadorid nematodes (with circular amphids and uniform oesophagi, probably Monhystera spp.)

A long tailed specimen of Dorylaimus kept with two female specimens of Anatonchus tridentatus was found with its anterior end chewed off, its oesophageal region punctured and part of its body contents sucked out. On examination, one of the specimens of A.tridentatus had at least 4 spears of Dorylaimus, all apparently the same species, in the gut. The other specimen had 2 spears of a different type and probably different species of Dorylaimus. It also had, besides another nematode in the fore-intestine, remains of an enchytraeid which was identified as probably a Mesenchytraeoides by Dr. J.E. Peachey, of Rothamsted Experimental Station.

Dark, probably detrital, matter together with bacteria, was usually seen inside juveniles of Prionchulus muscorum. Dark, unidentified matter, a rotifer mastax and

nematode spicules were other objects found inside this species. A female specimen was seen in the act of feeding on a Plectus and kept under observation for about 4 minutes, after which time the prey was released. The latter had been seized and punctured a short distance from the head end, where the predator was exerting very strong suction and both animals were struggling violently. The prey continued wriggling for 20 minutes after being released. Its hind end was twitching for another 10 minutes and it took 8 more minutes before becoming completely motionless. Meanwhile there was considerable loss of body contents through the punctured region. The predator paid no further attention to the disabled prey and although its wagging head made contact with several other nematodes, there was no attempt at feeding on them. Examination of the water containing this specimen showed 3 dead Plectus specimens, one with its tail and the others with their heads bitten off, presumably by this predator.

There are several records of how Mononchidae feed (see esp. Steiner & Heinly, 1922) but some of the descriptions in the literature of how these organisms capture their prey seem to be lyrical exaggerations. The writer's observation does not seem to confirm that these predators immobilize their prey by poison as has been postulated by

several authors. The length of time the prey took to die, in spite of very extensive damage, and the violence of the struggle do not support this view.

7. The relative abundance of the feeding groups.

The nematode feeding groups can be regarded as ecological groups (Overgaard Nielsen, 1949a) and their relative abundance estimated with regard to the sites and hence the soil properties.

As will be seen later in connection with the vertical distribution of the feeding groups (Part VIII.3), the plant feeders are the predominant group on the Moss Flats sites (Bare Peat and Residual Calluna Hummock). The microbial feeders are next in importance, but the miscellaneous feeders (Dorylaimoidea) and the predators are insignificant. The paucity of the figures, or the way in which they were obtained, on these areas do not permit a calculation of percentages which would be meaningful.

Table 21 shows the relative abundance of the feeding groups, on a mean percentage basis, for the rest of the Moor House sites. The genera of which these are composed will be found in Table 17 above. The striking fact is the predominance of the plant feeders on all the sites, followed, in order, by the microbial and miscellaneous feeders. This

Table 21 % relative abundance of the feeding groups.

	Plant feeders	Microbial feeders	Miscell. feeders	Predators	Unclas- sified	No.Units examined
Calluna	83	12	1	0	4	3
Juncus	65	29	4	0	3	8
Nardus	60	25	8	0.2	7	2
Limestone Gld.	48	25	22	1	5	4

is irrespective of the vegetation type or soil properties. The percentages of the microbial feeders may be slightly higher because a lot of those unclassified were probably microbial feeding types.

VI. SAMPLING AND EXTRACTION TECHNIQUES.

VI. SAMPLING AND EXTRACTION TECHNIQUES

1. Introduction.

The extraction of nematodes from soil presents great problems and there are several methods now available for this purpose. They can be divided into two broad categories: those employing the movement of the nematodes when externally stimulated (the so-called 'automatic' techniques) and those in which physical processes are used to obtain the worms without any reference to the worms' physiological reactions (the so-called 'physical' processes). Some methods, however, combine both these principles. The choice as to which of the available techniques one uses will depend on many factors, including: size of sample and sample units, time and handling facilities available, type of soil and degree of accuracy required. For obvious reasons, as Jones (1955a) has pointed out, in a numerical investigation the degree of accuracy needs to be as high as possible. Considerations of the other factors will, nevertheless, influence the degree of accuracy in as far as they will largely govern the principle used in extraction. Thus the aim of the sampling programme needs to be kept in mind. Although he does not deal with the nematodes as such, the problems of soil sampling are outlined by Macfadyen (1957, Ch. 6). In considering organisms of

the size of a nematode which have a short life span and thus are liable to fluctuate widely in numbers, the biological factors of reproduction, hatching, etc., have to be taken into account. With these considerations in mind several extraction methods for nematodes were examined.

Direct microscopy which is the equivalent of hand sorting as used for larger organisms, was used by Robertson (1925) and Stöckli (1943). Minderman (1956a) combined a staining method with direct microscopy and Capstick and his co-workers used this method (see Twinn, in press) with success in the detection of fungal predators of nematodes in leaf litter.

Cobb (1918a) devised an elaborate technique for extracting soil nematodes and their eggs. Its essential features were the combined use of floatation, decanting and sieving processes, the different sized nematodes being retained on wiregauze screens of different mesh sizes. Baermann (1917) described a technique of an 'automatic' type, using the funnel as its unit. There have been many variations on this theme (see Goodey, 1957). Christie & Perry (1951) combined the principles of Cobb's and Baermann's methods by passing the decanted suspension, with most of the debris discarded, through the funnel type of extraction. Overgaard's (1948) modification

which the writer used will be described below.

Centrifugal floatation with a sugar solution (Caveness & Jensen, 1955) and also with magnesium sulphate solution (Minderman, 1956a) have been used; the latter author has given modifications for different types of soil.

To obviate the difficulty of the nematodes drowning in the Baermann-type arrangement, Seinhorst introduced the 'mistifier' in which the sample is continuously sprayed with a mist of water. He also devised the Erlenmeyer flask and the elutriator methods which bear his name (see Goodey, 1957). The elutriator method used the same principle as that of Oostenbrink (1954, see Jones, 1955a and Williams & Winslow, 1955).

A modification of the Baermann technique incorporating the use of 'physical' processes is that of Minderman (1956a), used and further modified by Capstick & Twinn (see Twinn, in press). In this method the efficiency of the extraction is improved by intermittently shaking the sample.

As far as the writer is aware there has been no thorough comparison of the many techniques mentioned. Each was devised for a particular problem and, therefore, unless an individual has actually tried them on the same type of soil, not much importance should be put on comparisons of population estimates obtained by other workers. Overgaard Nielsen (1949a, p.10), for instance, compared the estimates

obtained by Franz and Stöckli with his own, but the latter two authors used direct micrsocopy or decanting and, of necessity, must have taken different sized smaples besides working on different kinds of soil.

2. The applicability of the different extraction techniques.

In the present study it was intended to take several sample units (10 or 15) at a time, all of which were to be extracted and sorted under as uniform conditions as could be managed, and as rapidly as possible. A technique which could facilitate this was therefore needed. It had to be suitable for peaty soils whose properties made direct microscopy impracticable. Besides the larger, fluffy peat 'particles', the water used in their extraction assumed a dark, rather viscous character making it impossible to see the nematodes. It proved difficult, in fact, to isolate nematodes free enough from peat debris to be able to sort them easily. Techniques which work best with leaf litter or mineral soils and which involve shaking (e.g. Minderman's) or washing (e.g. Seinhorst's mistifier) of the sample were not practicable on this account. Nevertheless, several techniques were tried out on the Moor House soils to find out if they could be of use in the isolation of the nematodes.

Centrifugal floatation using a solution of magnesium sulphate was unsuccessful because not only were very small sample units necessary, but also the nematodes were killed in the process, thus making sorting in the peaty matter which passed through the sieves impossible.

A trial was made of the sieving technique (originally of Cobb) as described by Goodey (1957). This is apparently satisfactory for sandy soils but it is very laborious, uses large volumes of water, and where a single-handed worker is concerned, the multiplicity and changes of vessels involved lead to mistakes. The technique consists in dispersing the soil sample in a volume of water and, using the differential settling properties of the soil particles and the nematodes, separating the worms from the debris by decanting. The separation is facilitated by the use of wire mesh screens of different gauges. The different sizes of nematodes are caught on the appropriate sized mesh, washed into clean water and counted. For obvious reasons this was not a practicable technique.

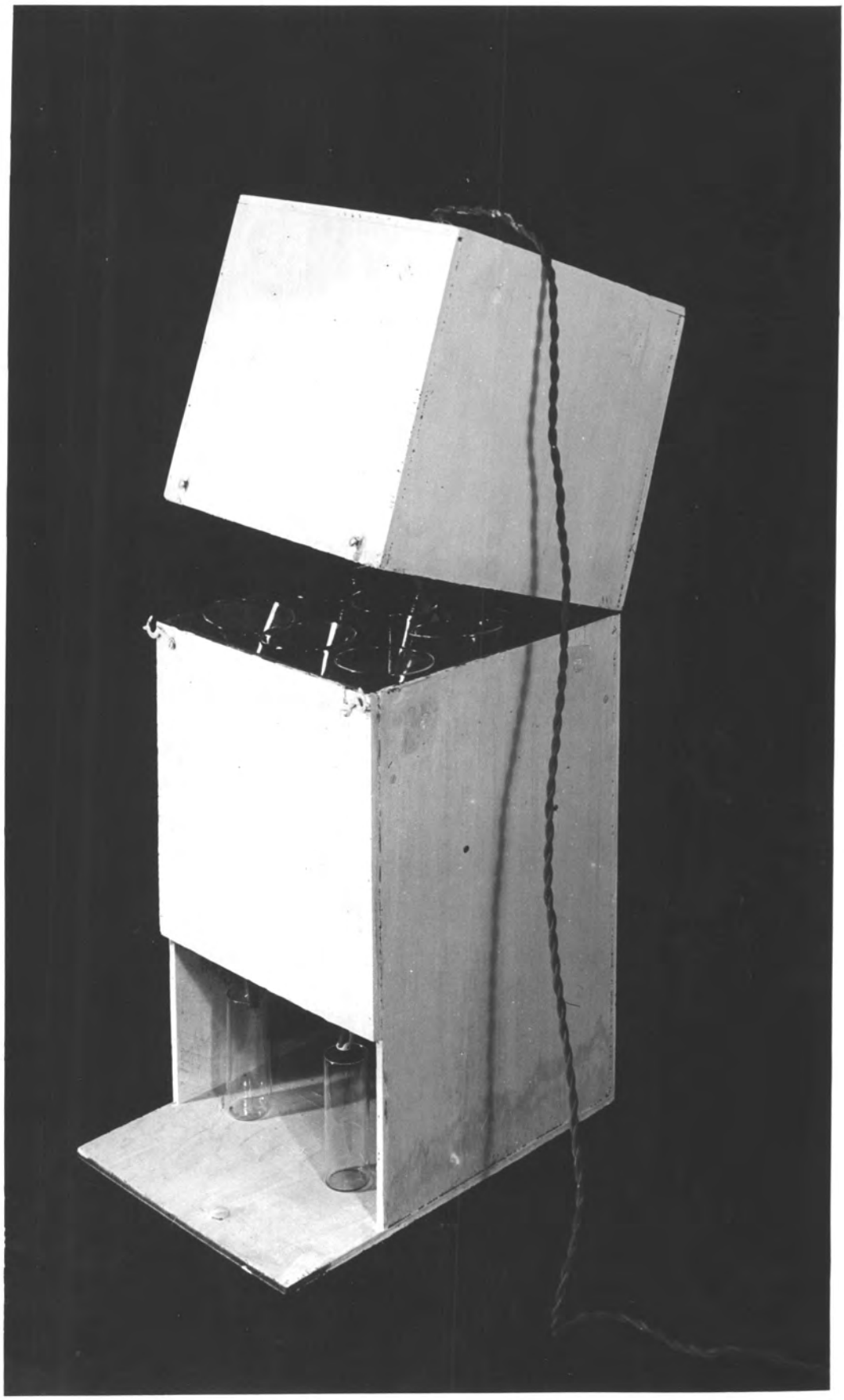
Seinhorst's Erlenmeyer flask technique was a failure, too. This uses two conical or Erlenmeyer flasks. One of these, full of the nematode suspension, is inverted over the other which contains clean water. They are connected by a wide tube formed by the stem of a 'polythene' funnel which is attached to the upper flask by a wide rubber

band. The soil particles fall under gravity into the lower flask and the water moves upwards to replace them. The nematodes, being lighter, are caught in the upward water current and retained in the upper flask. When this technique was tried by the writer, peat tended to fall down at intervals as large blobs or globules rather than as a trickle of particles, which would be the case with a mineral soil. These blobs not only carried the nematodes down with them when they fell, but also blocked the water connection between the flasks. Thus not enough turbulence was maintained in the upper flask neck to cause differential sedimentation of the nematodes from peat. The failure of this experiment indicated that elutrition methods could not be applied to peat.

A technique modelled on the Baermann funnel method seemed to be the best choice for the problem after these trial experiments. If carefully set up during extraction not too much peat would be shaken down the funnels to make later sorting too difficult. Furthermore, it would not require too much constant attention, thus time would be available for other aspects of the work. Lastly, larger sample units could be used than in some of the techniques described above. The Overgaard Nielsen modification (Overgaard, 1948a) was found to satisfy these conditions and was adopted. It is described below.

PLATE 10.

The extraction apparatus.



3. The sampling and extraction techniques used.

(a) The extraction apparatus.

Overgaard (1948a) described and illustrated his modification of the Baermann funnel technique. The apparatus is essentially a rectangular plywood box of 23.5 cm. by 22 cm. base and 55 cm. height, including the lid. A loose plywood board with holes to take 9 glass funnels is sunk into and supported 6 cm from the rim and 26.5 cm. from the top of the box lid. The lid is 20.5 cm. deep and has fixed in the middle of it an electric bulb as a heat source. All the measurements are, as in Overgaard's original version, taken externally.

The glass funnels have a diameter of 7 cm. Fig. 2 is an illustration of one such a funnel. To the stem of the funnel (A) is attached a piece of rubber tubing (B), about 15 cm. long with a tight joint (C). This is closed by a screw clip (D) and the whole funnel filled with cold water to within a short distance of the brim (E). The material to be extracted (F) is spread out on a piece of nylon cloth (G) and immersed in the water. The nematodes, under the ~~force~~ influence of the heat from the electric bulb (H) and also under the influence of gravity, fall to the bottom after passing through the nylon cloth. The collection of worms and the soil matter which inevitably falls down with them (J) is run off at the end of the extraction.

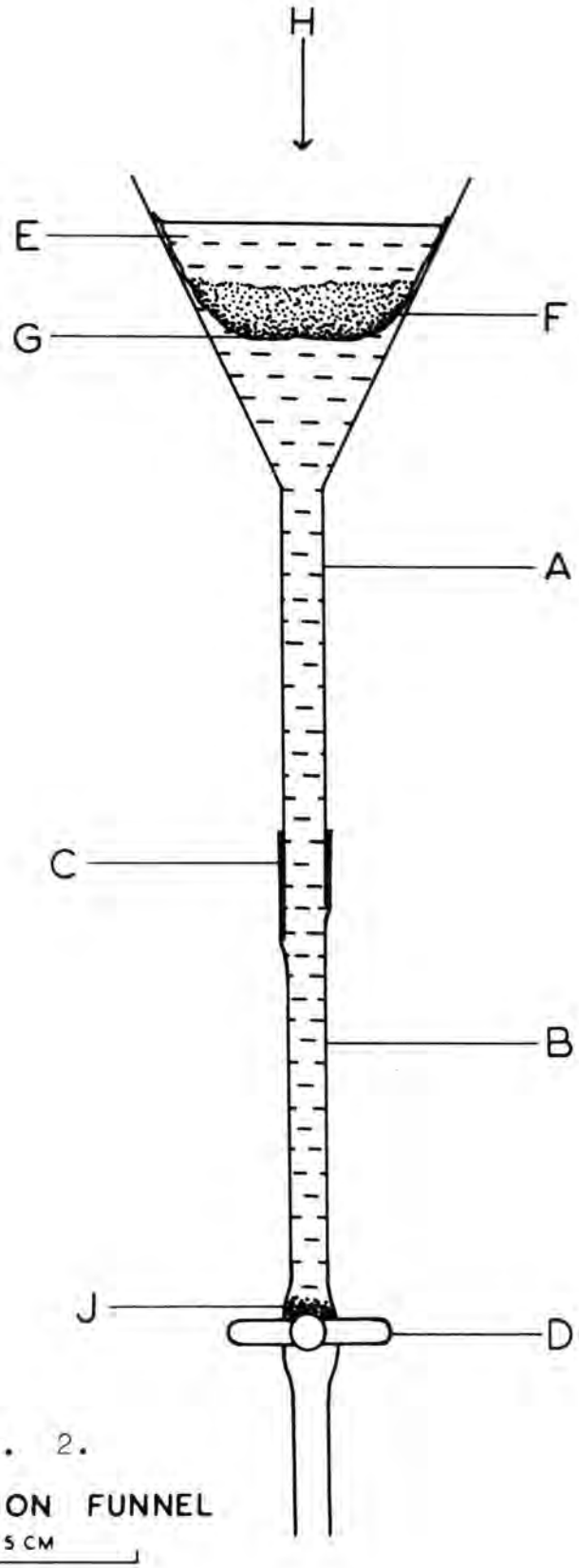


Fig. 2.

EXTRACTION FUNNEL

5 CM

For routine extractions two boxes with a maximum capacity of 18 funnels were set up, although normally only 15 were actually in use at a time. Material from more than this number could not be sorted in the time limit imposed by the factors discussed in Section 4 below. Each extraction box was regarded as one 'Extraction Unit', the material put into each funnel or the material run off from each funnel, including the number of nematodes in it, being the 'Sample Unit'. The term 'extract' is used to cover what was obtained as a result of extraction, including the nematode suspension before or after sorting.

Trial results from the two extraction units were compared by the 'Student's' t-test and no significant difference was found between them (t=1.020; with 13 d.f., P=2.160 at 5% level).

Overgaard's recommended the use of a "16W (10 CP) carbon incandescent lamp" but to obtain high enough temperatures a 25W pearl bulb was used and it was found necessary to close the ventilation holes in the sides of the boxes. Furthermore, to stop as much of the peat as possible from falling down the funnels, nylon cloth of 3 holes per mm. mesh was substituted for the coarse wire gauze which he used. As no nematodes larger than the holes were ever seen by microscopic examination, no errors due to differential or selective extraction can be attributed to this

substitution.

(b) The treatment of the sample.

Field and laboratory sampling equipment mentioned here is shown in Plate 11.

Cores were randomly taken in the field with a brass earth corer of the usual type, 3.5 cm. diameter (approx. 1/1000 m^2) and made to take a 6 cm. deep aluminium tin into which the inverted core was transferred. The tins containing the cores were covered with screw tops and stored at 5°C. prior to extraction. Most authorities are agreed that, within the limits of a few days there should be no change in the numbers of nematodes at such low temperatures. Overgaard found that storage at 0°C. did not affect the efficiency of his extraction up to 3 weeks. The writer did not make any specific tests on the effect of storage on extraction efficiency since all samples were extracted within a week of being taken.

Deep cores, when required, were obtained by taking a long core and cutting it into the required portions.

Before extraction, the large cores were sub-sampled in the laboratory. They were lightly frozen at 0°C. for 15 hours, taken out of their aluminium tins and each in turn transferred, the right way up, to a hollow wooden block. After a few minutes to allow slight thawing of the core a smaller core of 4.7 cc. was taken from the middle of each one. The micro-corer used was of the type that Haarløv & Weis-Fogh (1953) used for their work on soil

PLATE 11.

Field and laboratory sampling equipment.

A. Field sampling corer.

B. Sample tin with field core.

C. Wooden block with field core.

D. Small corer.

E. Glass rod for removing sample unit core from the small corer.

F. Sample unit core on nylon cloth circle.


A
B
C
D
E
F

sectioning.

The wooden block was made and used as follows. A hole wide enough to take a frozen core was drilled through a block of wood, base 6.5 cm. by 9.5 cm. and height 6 cm., a 1 cm. plywood bottom was put on and the block was sawn into half. The two halves were hinged together on one side and so could be opened out to remove the soil after sub-sampling. During sub-sampling, they were held together by a hook-and-eye mechanism on the front of the block.

Overgaard (Overgaard, 1948a, 1948b, and Overgaard Nielsen, 1949a) gives no details of how his samples were taken. He only says that "the samples were taken with a small steel cylinder with a cutting edge (area 1 sq. cm., effective height 5 cm.) (fig. 1), the total sample thus consisting of 5 cubic cm. of earth plus the moss growing on it" (1948b). It can only be assumed that he used the same method on all the range of soils which he worked with (1949a). The present writer's attempts to take direct samples from the field with such small corers were all unsuccessful. It was impossible to get any cores from moss or peat especially when the latter was very water-logged. Even on mineral soils it was impossible to avoid compaction due to the smallness of the core area. Cores were therefore frozen and sub-sampled in the laboratory to preclude squashing and also to obtain sample units of known length which

could be cut into protions of desired size. In the latter stages of the work the sample units were sub-divided in order to increase the efficiency of extraction.

(c) The extraction process.

The sample units, taken as described above, were placed on circles of nylon cloth of about 7 cm. diameter and mesh size of 3 holes /mm. and allowed to thaw but not to dry. The material was teazed out with dissecting needles and gently lowered into the funnels containing water at 7 - 9°C. This gives a starting temperature for the extraction of about 12 - 13°C., recommended by Overgaard.

The temperature rose to about 30°C. in the first hour of the extraction and then more gradually to a final reading of between 35 and 40°C. Slight differences occurred in individual funnels and between the two extraction units. Table 22 shows two mean temperature trends in the first 6 hours and the final temperatures for the two units. There were also slight variations due to soil type and water content of the soil. In view of the other sources of variation, it is not an easy task to evaluate the effect of this one. However, it has already been pointed out that there was no significant difference between the performance of the two units used.

Table 22 The course of mean extraction temperatures in the first 6 hours and the final temperature for two extractions of peat soils.

The temperatures are the means of 8 extraction funnels in all cases except for Unit B in (a) where the means are for 7 funnels.

(a) Time in Hrs. after start.	Extraction Unit A	Extraction Unit B
0	14.0°C	14.0°C
1	28.5	29.9
2	34.5	34.7
3	36.0	36.5
4	36.8	36.7
5	36.1	37.5
6	36.5	37.0
20	36.4	36.4

Date of sampling 3.vi.58, date of extraction 5 - 6.vi.58.

(b) Time in Hrs. after start.	Extraction Unit A	Extraction Unit B
0	13.0°C	13.0°C
1	30.3	30.3
2	34.6	35.1
3	35.0	36.0
4	35.6	36.9
5	36.7	36.6
6	36.0	36.9
20	37.0	35.6

Date of sampling 3.vi.58, date of extraction 11 - 12.vi.58.

Trial extractions were made at room temperature, but for all subsequent work the extraction units were maintained under regulated temperature conditions (21 - 23°C). All extractions lasted 20 hours after which the heating was switched off, but sometimes there was a short time lag between the switching off of the heating and the dismantling for sorting.

(d) The sorting process.

After an arbitrarily set time of 20 hours, the screw clips on the funnels were opened and the water containing the nematodes run off into glass tubes. These were then corked and cooled to about 5°C., a temperature at which the nematodes recovered from the heat paralysis. They could then be seen wriggling and moving in the peaty water extract and this facilitated counting. It was for this reason that sorting was done while the worms were still alive and, consequently, counting was never allowed to take more than 3 days. For other reasons, too, the 3 day limit was imposed on the duration of the sorting process. There was, firstly, the possible hatching of nematode eggs in the extract thus changing the final count of the worms, and secondly, the growth of micro-fungi in the extract which often became noticeably bad after two or three days. These factors will be dicussed further in Section 4 below.

The counting was done under a binocular microscope (magnification 30X) using transmitted light. After much of the water had been decanted off, the scanty, residual suspension in each tube which contained the nematodes was shaken up and transferred to a counting dish. The latter consisted of an ordinary small Petri dish with vertical and horizontal lines etched on the bottom. The fields so formed were scanned and the number of nematodes registered by an electric counter operated with the foot. Peat particles, micro-fungal growth and debris obscuring the worms were turned aside with a mounted nylon bristle. The same instrument was used to remove very actively moving or floating specimens.

The time taken to sort through one sample unit depended on the amount of contamination as well as on the number of worms present. In general it varied from 30 minutes to 1½ hours, a sample of 10 or 15 units taking 3 days.

Trials were made to find out if it was possible to estimate the number of worms in a suspension by counting aliquots drawn from it. A graduated 1 ml. counting slide, as used by Heal for testate amoebae (see Heal, unpub. thesis, 1959), did not give satisfactory results. Whereas total counting gave 259 nematodes, from a well stirred 50 ml. suspension of the same sample unit the number was estimated at 400 by counting 5 1-ml. aliquots under the

monocular microscope. This process took as long as the total counting. According to two separate estimates on a 25 ml. suspension of the same extract the number of nematodes was put at 500 and 437.5 respectively. Clearly, these estimates were too high. Total counting was therefore the only method whose results could be regarded as reliable. Probably a larger number of aliquots might have yielded a more accurate estimate since, if completely random dispersion in the suspension is assumed, the accuracy of the estimate depends on the number of individual counts made. This is the basis of bio-assay work in phytonematology and its validity derives from the properties of the Poisson series (see Jones, 1955a). It was doubtful, however, with the amount of contamination in the suspension whether a random dispersion of the nematodes was, in fact, obtained. Furthermore, increase in the number of aliquots would necessitate a more than proportionate increase in the labour involved and would thus be defeating the whole purpose of avoiding total counting.

4. A discussion of the sampling and extraction techniques used.

Some of the advantages and shortcomings of the techniques employed in the present study have already been given in the preceding sections, but further consideration will be given to these techniques.

(a) The sampling.

Due to its physical and chemical structure, the soil is a very heterogeneous medium and the smaller the sample unit taken from it the greater is this heterogeneity, both within and between the individual sample units. This means that many sample units must be taken, if they are small in size, in order to obtain a good estimate of the mean number of soil micro-organisms. The number of free-living nematodes in the soil is such that small size cores are necessary, but as was mentioned in Sub-section 3(b) above, direct field sampling was not possible. The freezing process was, therefore, introduced to ~~enable~~ allow sub-sampling in the laboratory.

Only by freezing was it possible to get cores from crumbly soil as, for example, that of the deeper layers of the Limestone Grassland site. The obvious solution to the problem of a crumbly soil is to estimate the number of nematodes per unit weight of soil, as is usually done, especially with the cyst-forming forms, in phytonematology.

Robertson (1925) used a combination of weight and area in expressing his population estimates. He found, by weighing, the 'capacity per unit weight' of his samples (i.e. their volume per unit weight). Each sample was 4 in. square and 6 in. deep. He thoroughly mixed the soil and then took 10 sub-samples each with a weight corresponding to that of 1 cu. in. and thus he estimated the population

per cu. in. and also per acre. While this might be valid for a well mixed sandy or mineral soil, when the soil has a vertical zonation, with an accumulation of organic matter in the upper layers, much doubt would be cast on the meaning of the 'mean per unit volume'.

Because it was not possible to take unfrozen cores of comparable size to those obtained by freezing, it was impossible to evaluate the effect of freezing on the extraction efficiency. A comparison was made between very lightly frozen cores and those treated for the normal length of time. Two samples of five cores each were randomly taken on the same day from the Juncus site. One was then frozen for 5 hours and the other for 15 hours before sub-sampling. The sample units were in each case divided into two 3 cm. portions, randomized and extracted under as similar conditions as the techniques described could allow. The total number of worms extracted from each sample unit and the mean for the sample are given in Table 23. No significant difference in the means was established by the t-test ($t=1.581$, with 8 d.f., $P>0.1$), although it should be pointed out that the samples were rather small.

(b) The extraction.

The reasons underlying the choice of the extraction technique have already been given. Whilst it was very convenient, its efficiency proved difficult to assess,

Table 23. A comparison of the means from two samples subjected to two different freezing treatments.

Site : Juncus.

Sampling date : 5.viii.58

Extraction date : Sample 1, 7.viii.58

Sample 2, 11.viii.58

Sample unit	No. nematodes from Sample 1 (frozen 15 hrs.)	No. nematodes from Sample 2 (frozen 5 hrs.)
1	359	287
2	296	310
3	149	205
4	147	327
5	148	490
Total	1099	1619
Mean	219.8 ± S.E. 42.80	323.9 ± S.E. 44.78

mainly due to the soil type which had to be handled. Overgaard (1948a) estimated that he obtained an extraction efficiency of at least 90%, running his extraction for 12 hours. Other workers to whom the writer has talked are not inclined to put it as high as that.

Two experiments were made by the present writer to try and assess the extraction efficiency on samples from the Juncus site. It should be stressed that the inadequacy of these experiments is fully realized. The first experiment was by sieving of the peat from one sample unit after the normal extraction procedure. The peat was mixed with a little water and washed through a series of wire gauze and nylon cloth sieves of decreasing mesh sizes. Finally, the suspension was passed through a paper tissue screen. At each stage the residue was examined under the binocular microscope and the final water extract was also inspected for any worms remaining. The total number of nematodes which was found, together with the number extracted by the 'automatic' process are given in Table 24, from which it will be seen that, for this sample unit, the efficiency was 88.8%. Although many of the nematodes recovered were inactive and probably dead, some were alive and active. Their failure to get out originally might therefore have been due to being trapped in the peat.

Table 24. An estimation of the extraction efficiency of one extraction funnel.

Site : Juncus.
Sampling date : 22.x.58
Extraction date : 23.x.58

No. of nematodes extracted in funnel	238
No. from extracted material obtained by sieving	30
Total	268
Extraction efficiency for sample unit	88.8%

The second experiment was rather less definitive in its execution for reasons which will become evident. After a sample of 15 units from the Juncus site had been extracted for 20 hours, more water was added to the funnels and the extraction continued for a further period of 12 hours. The number of nematodes obtained from both extraction runs are shown in Table 25. in which also the second extraction results are given as a percentage of ~~both the initial and~~ the final total extraction .

It is clear that a varying proportion of worms remained unextracted after 20 hours, but also that this was not related to the number initially extracted. The percentage of the nematodes obtained on re-extraction, in comparison with the total, is small (about 9%). Thus the initial mean figure of 140.20 worms, when compared with the total figure of 157.87, represents an extraction efficiency of about 90%. There is no reason to suppose that the further 12 hours re-extraction gets all the worms out, however, and the writer has considerable doubt whether, without using impracticably small sample units, complete extraction can be achieved with this technique in a short time. Partly for this reason, but also as a means of obtaining information on the vertical distribution of the nematodes, sample units were sub-divided before extraction in the later stages of the work. The sample size then

Table 25. The number of nematodes extracted after 20 hours compared with the number a further 12 hours re-extraction.

Sample unit	No. nematodes extracted (a)	No. nematodes by re-extraction (b)	Total (a) + (b)	(b) as % of Total
1	92	10	102	9.81
2	185	37	222	16.66
3	68	10	78	12.82
4	115	7	122	5.74
5	255	28	283	9.90
6	132	11	143	7.69
7	183	1	184	0.54
8	89	7	96	7.29
9	127	11	138	7.97
10	177	37	214	17.29
11	142	13	155	8.39
12	85	6	91	6.60
13	101	10	111	9.01
14	110	20	130	15.38
15	242	12	254	4.73
Total	2103	220	2323	139.82
Mean	140.20	14.67	154.87	9.32
S.E.	14.66			

had to be cut down to 10 units to obviate the increased number of extracts to be counted.

In the above described experiment the re-extraction took 12 hours, the total time of the extraction run then being about 30 hours. Minderman (1956a) found that after 48 hours the number of worms his 'shaking' technique extracted began to increase again after levelling off. He postulated that this was due to the number of newly hatched juveniles and actually found that in one experiment, of all the nematodes extracted between 2 and 4 days only one was adult. Any sample of soil containing a large number of nematodes will also contain an indeterminable number of their eggs. Although there seems to be no precise information about the effect of various factors like temperature, soil water content, etc. on the rate of development of the free-living nematodes, it would be reasonable to suppose that subjecting a soil sample to temperatures of the order of 30°-40°C., under moist conditions, would be liable to accelerate the hatching of any eggs the sample contained. Once the hatching had taken place the juveniles would appear in the extract and they would be indistinguishable from those juveniles which had been in the sample at the time it was taken. Overgaard Nielsen (1957) has, in fact, commented on this disadvantage of the extraction technique. A short extraction

duration, therefore, seemed ~~more~~ preferable to a long one. The attempt to assess the proportions of active and anabiotic nematodes in the soil by 'incubating' the soil suspension for a long period of time, as Renkonen (1949) did, would seem to overlook very fundamental considerations of nematode biology.

(c) The sorting.

As has been pointed out already, total counting of the extracts was found to be more accurate than aliquot sampling. This time consuming procedure put a limit both to the number of samples which could be taken and the frequency with which this could be done.

On a few occasions extracts were examined twice as a check and some of the results of such re-counts are given in Table 26 below.

Table 26. Some examples of sorting efficiency.

	1st count.	2nd count.	Difference.	Time lag between the counts in days.
1.	255	251	- 4	0
2.	185	183	- 2	0
3.	294	295	+ 1	0
4.	159	161	+ 2	0
5.	43	44	+ 1	0
6.	360	370	+ 10	3
7.	387	372	- 15	3
8.	269	269	0	0

It will be clear that when the precautions with regard to the floating and actively moving specimens mentioned in Sub-section 3(d) of this Part were taken, there was very little error in the counting, provided this took place very soon after extraction. In two cases in the Table 26 above re-counts were made 3 days after the time of extraction and it will be seen that the counting error was larger.

The sources of error which had to be considered when the extracts were kept for a long time have also been mentioned. The indeterminable problem of the hatching of eggs in the extracts and the difficulties it poses for the accurate estimation of the numbers of the worms in the sample has been dealt with. During sorting, and especially when specimens were isolated singly for identification into their feeding group, juvenile forms in different stages of development were noticed, but it was neither practicable nor always possible to treat them differently from the other specimens.

After a few days, the water extracts containing the nematodes, especially those of very peaty samples, underwent changes of a possibly chemical nature. A scum often formed on them and nematodes were more easily liable to float than when first extracted. Furthermore, many soil nematodes will die from drowning if kept submerged in water. It was noticed that Dorylaims and Mononchs grad-

ually became more sluggish and eventually died, as so did the Tylenchs. Extracts kept for up to a week had only some of the microbivorous types when re-examined. Often, too, and especially in extracts from soil under more or less dry conditions, there was a profuse growth of micro-fungi. The mycelia of these formed 'blobs' in which peaty plant remains and nematodes became entangled. Under such conditions counting was very difficult, it being necessary to teaze out each mycelial 'blob' to ensure that no nematodes were trapped in it. Some of the smaller species, especially Teratocephalus spp., were nearly always stuck to these micro-fungal growths, probably because they were not capable of enough vigorous action to break free as, for example, did the Dorylaimus spp. It was not found out whether any of these micro-fungi were nematode predators but evidence was obtained that some nematodes were parasitized by fungi.

VII. HORIZONTAL DISTRIBUTION.

VII. HORIZONTAL DISTRIBUTION.

1. Introduction.

O'Connor (1957), Overgaard Nielsen (see 1955) and Peachey (1959, unpub. thesis) have studied the details of distribution of Enchytraeidae (Oligochaeta). Studies on Collembola have been made by Hughes (1958, in press) and Wallace (1957) while Macfadyen has given some information on the horizontal distribution of three Oribatei (Acarina) and one Collembola species on a Molinia fen in Berkshire. In all cases there was evidence of patchy distribution or aggregation. This is a widespread and well-known distribution phenomenon (seeAndrewartha & Birch, 1953, ch. 13) which is to be expected in soil animals in the light of what has been said about the heterogeneity of this environment.

In the study of phytonematodes interest, as far as the details of distribution are concerned, has been in the cyst-forming types (Jones, 1955a, 1955c; Fenwick, 1959). Levels of cyst abundance are determined from bulk samples and the final population estimates are expressed in very general terms. The advantage of working with cysts is that a fairly even distribution in the bulk sample can be achieved by thorough mixing. The estimate of the field population can then be made fairly readily as the distri-

bution of cysts in aliquots drawn from the bulk sample conforms to the Poisson distribution. In the field, however, the cysts are aggregated and depending on the aim of study, two methods can be used to obviate this complication. In sampling programmes in which the determination of cyst population is the primary aim, many randomly taken sample units are necessary per bulk sample. For studies in which evenness of cyst distribution is required, Jones (1955b) has devised the 'microplot' method details of which are irrelevant for the present discussion.

Although numerous population estimates of non-cyst forming nematodes have been made, little close attention has been given to the details of how they are distributed in the soil. Some information which has been obtained in the present study is presented in the subsequent sections of this Part.

The ideal method to study the distribution of soil animals would necessitate firstly, a complete enumeration of all the animals to a known depth of soil. Secondly, this information would then be transferred to a map from which the relative density distribution could be easily determined. The method of complete enumeration, originally used by Salt & Hollick, has also been used, with or without mapping, by the workers on enchytraeids quoted above.

It is possible, however, only for those animals which are relatively slow moving and, further, can only be successfully employed when the animals are few and large enough to make complete enumeration easy. With the small size, large numbers and difficulties of extraction, handling and sorting encountered in the nematodes complete enumeration is not possible. A sampling method has therefore to be used.

Hughes' approach (1958, in press) was to estimate the mean radius and the number of the animal aggregates by the use of paired samples. One sample in this method is taken randomly but another sample is taken 'tied' to it by a fixed distance between them (the tie-line). The use of the "ratio of the area of an aggregate to the length of its perimeter", calculated from this tie-line sampling, according the Hughes "defines the amount of break-up of areas of high-population density, and if certain assumptions can be made, provides an estimate of the mean radius of aggregates, and thus their number." The method has been applied to Overgaard Nielsen's and Peachey's enchytraeid maps and seems to confirm the centres of aggregation even if doubt is reserved about the validity of the concept of descrete aggregation foci from which a radius and a perimeter could be measured.

The third method of studying aggregation is by the analysis of results of random sampling. Macfadyen (1952) analysed sampling results from a combination of random and paired sampling in his study of the Acarina and Collembola of the Molinia fen. The present writer has analysed the data from random sampling at Moor House and the results are given below. The purpose of this attempt has been to detect the presence rather than to analyse the degree of aggregation with precision. Although these two ends are inextricably linked, a full analysis requires more precise data than could be assembled in the present study. Nevertheless, an analysis however incomplete is valuable and, related to environmental and biological factors of the organisms, may help to clarify the ecological processes operating on the organisms concerned.

Spatial distribution in soil nematodes, as in other soil micro-organisms, has to be considered under three aspects: (1) horizontal and (2) vertical distribution on a wide scale, and (3) both horizontal and vertical distribution on a small scale. This is because depth is a necessary component of any sampling procedure. For the third aspect of distribution the writer has borrowed the term 'micro-distribution'.

2. Methods of study and the results.

(a) The detection of aggregation by the coefficient of dispersion.

The coefficient of dispersion, originally due to Fisher (see Salt & Hollick, 1947), is used to find out whether animals are aggregated or not. It is, in fact, the ratio of the variance and the mean:

$$C.D. = S(x - \bar{x})^2 / \bar{x}(n - 1), \text{ or } s^2 / \bar{x}.$$

When this is <1 there is even distribution (over-dispersion), when it is 1 there is random distribution and when it is >1 there is aggregation (under-dispersion). Thus a random distribution is Poisson and has its variance equal to the mean. The divergence from unity is regarded as being significant if it exceeds:

$$1 \pm 2\sqrt{\frac{2n}{(n - 1)^2}}$$, where n = number of sample units. For 15 and 10 sample units this value is 1 ± 0.783 and 1 ± 0.994 respectively.

A similar test which involves X^2 and makes allowance for sampling has been given by Healy (1958, in press):

$$X^2 = (n - 1)s^2 / \bar{x}, \text{ d.f.} = (n - 1).$$

The coefficient of dispersion was worked out for the samples of all nematodes from the Juncus site and was never found to be less than 10 (Table 27). The lowest and highest values observed from other sites are given in Table 28. The hypothesis that these sampling figures are from a random distribution was not supported.

Table 27. Frequency distribution of the coefficient of dispersion on the Juncus site.

Coefficient of dispersion range	Frequency 1958 - 59	Frequency 1959 - 60
10 - 20	1	2
20 - 30	6	0
30 - 40	4	2
40 - 50	2	1
50 - 60	1	0
60 - 70	0	0
70 - 80	0	0
80 - 90	1	1
90 - 100	0	0
100 +	1	0
Total	16	6
No. cores / sample	15	10
Lowest C.D.	10.3	19.5
Highest C.D.	118.8	80.5

Table 28. The range of coefficients of dispersion on three sites other than the Juncus site.
The number of cores / sample is given under 'n'.

Site	Lowest C.D.	n	Date	Highest C.D.	n	Date
Calluna	17.6	15	10.vi.58	412.9	10	13.viii.59
Nardus	14.9	15	21.v.58	98.5	10	3.vii.59
Limestone	11.0	10	28.vii.59	67.3	10	5.v.59

(b) The frequency distribution of the sample unit values compared with the normal distribution.

The sample unit values were grouped into frequency distributions round their individual means with multiples of the S.D. as the class boundaries. Table 29 shows how this was done for the Juncus site. With the mean at 0, negative S.D. classes contain frequency values for sample units smaller than the mean and vice versa. The date for each sample is given in column 1.

Table 29. Distribution of the sample unit values in S.D. classes from the mean.

S.D. classes	-3	-2	-1	0	1	2	3	4
6.iii.58	-	3	4	6	1	1	0	
7.iv.58	-	1	11	2	0	0	1	
30.iv.58	-	2	4	8	0	1	0	
6.vi.58	-	3	6	3	2	1	0	
24.vi.58	-	2	7	2	4	0	0	
22.viii.58	-	1	9	3	2	0	0	
26.viii.58	-	2	8	4	0	1	0	
1.ix.58	-	3	6	3	2	1	0	
23.ix.58	-	0	9	5	1	0	0	
7.x.58	-	0	11	3	0	0	1	
22.x.58	-	3	5	5	2	0	0	
3.x.58	-	2	6	4	3	0	0	
17.xi.58	-	2	6	5	1	1	0	
9.xii.58	-	1	10	2	1	1	0	
17.xii.58	-	2	7	3	3	0	0	
21.i.59	-	3	5	4	2	1	0	
7.iv.59	0	1	4	3	2	0	-	
27.v.59	1	4	2	0	3	0	-	
19.vi.59	0	0	7	1	2	0	-	
25.viii.59	0	0	4	3	3	0	-	
17.ix.59	0	2	3	4	1	0	-	
7.iii.60	0	2	5	1	1	1	-	
Total	1	39	139	74	36	9	2	
% of Total	0.3	13.0	46.3	24.7	12.0	3.0	0.7	

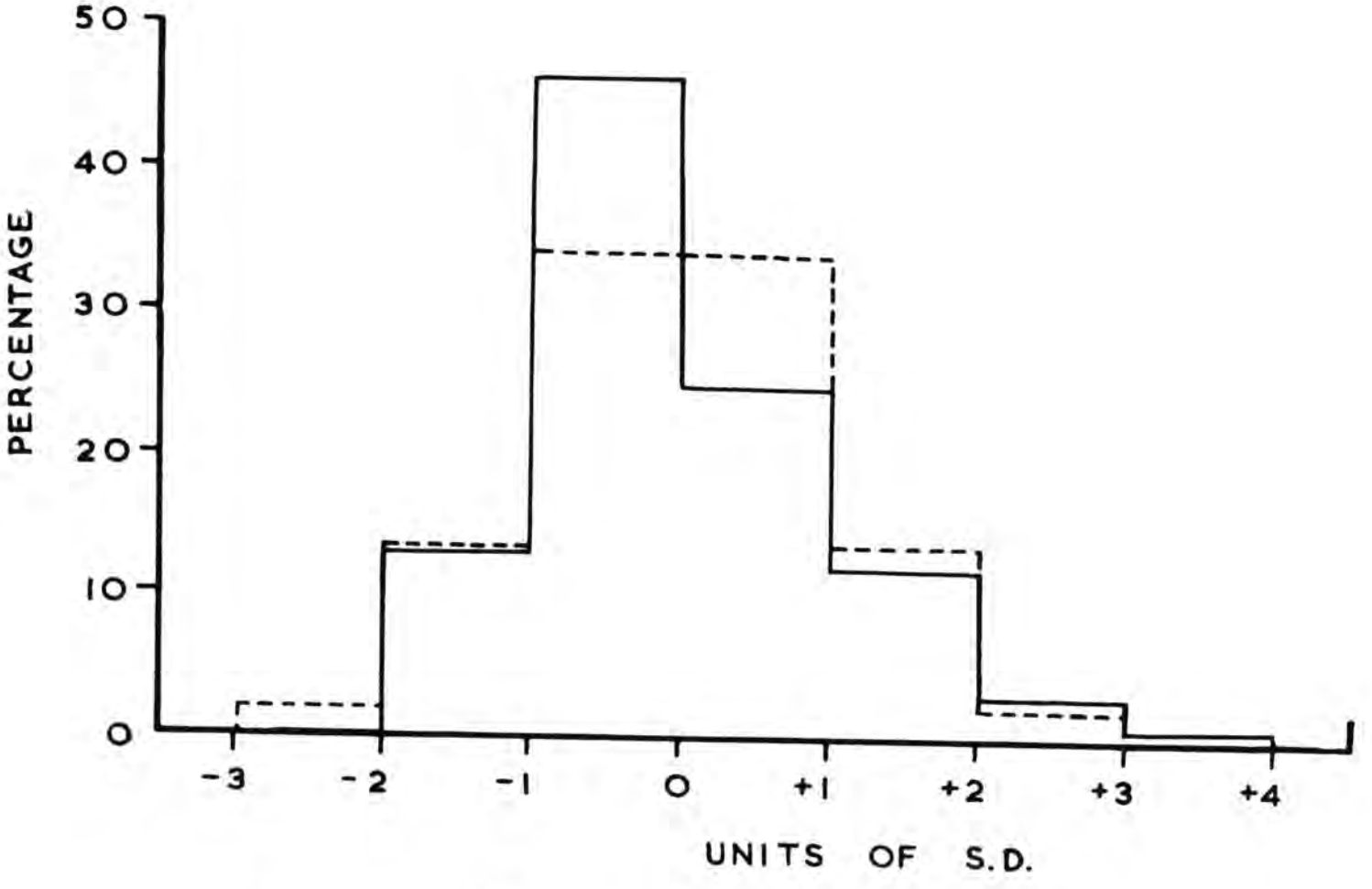


Fig. 3. The % distribution of Juncus site sample unit values.

Between the sample for 21.i.59 and that for 7.iv.59 the sample size and extraction treatment were changed. Therefore the samples for March 1958 - January 1959 and those for April 1959 - March 1960 were first treated separately in comparing them to the normal distribution (Table 30). The total frequency distribution derived from Table 29 was then treated as a whole since there seemed to be no essential difference between the data for the two periods.

Table 30. Deviation from normality of the sample unit frequency distributions.

Site	No. of units	X^2	d.f.	P
Calluna	50	42.685	3	0.01
Juncus 58 - 59	240	23.737	4	0.01
Juncus 59 - 60	60	11.743	3	0.01
Juncus Total	300	28.031	5	0.01
Nardus	55	7.532	3	0.10
Limestone	30	0.729	1	0.30

Fig. 3 shows the percentage frequency distribution for all Juncus site samples compared with the theoretical normal distribution and from this, as well as Table 29, two features of the frequency distribution are noticeable.

(i) An excess of values just below the mean (-1 S.D.) and lack of balancing values above the mean in the same class.

(ii) A tail of a small percentage of relatively large values (> +2 S.D.) and a much steeper fall off on the negative side (only 0.3% of the frequency distribution is between -2 S.D. and -3 S.D.).

Skewed distributions of this kind have been recorded by the workers on enchytraeids (O'Connor, 1957; Peachey, 1959, unpub. thesis).

Table 31. Percentage distribution of the sample unit values in S.D. classes from the mean.
The number of the sample units on which the results are based is given after each site.

Site	No.	-3	-2	-1	0	1	2	3	4	5
Calluna	50	.	10.0	48.0	20.0	10.0	2.0	6.0	4.0	
Juncus	300	0.3	13.0	46.3	24.7	12.0	3.0	0.7		
Nardus	55		7.3	45.5	34.6	10.9	1.8			
Limestone	30		6.7	50.0	30.0	6.7	3.3	3.3		
Theoretical normal		2.3	13.6	34.1	34.1	13.6	2.2	0.1	0.0	

Although less extensive data had been gathered from the other sites, frequency distributions were, nevertheless, made and compared with the normal distribution.

What limited results are available show a longer tail of small positive deviates for the Calluna site (Table 31) but a greater approximation to the symmetrical pattern for the two grassland sites (Tables 30 and 31). The grassland sites still, however, show the tendency to the tail of large positive deviates (> +2 S.D.). Probably not much importance should be put on these data in the light of their meagreness. It is interesting, nevertheless, to find that the frequency distribution for the Calluna site was similar to that for the comparable number of sample units from the Juncus site taken between April and September, 1959. This same frequency for the Juncus site, was, however, significantly different from that of the Nardus site (Table 32), a fact already demonstrated by Table 30.

Table 32. X^2 values for the comparisons of sample unit frequencies from the Calluna, Juncus 59 and Nardus sites.

Sites compared	Sample units	X^2	d.f.	P
Calluna & Juncus 59	50 50	1.104	3	> 0.70
Juncus 59 & Nardus	50 55	20.291	2	< 0.01

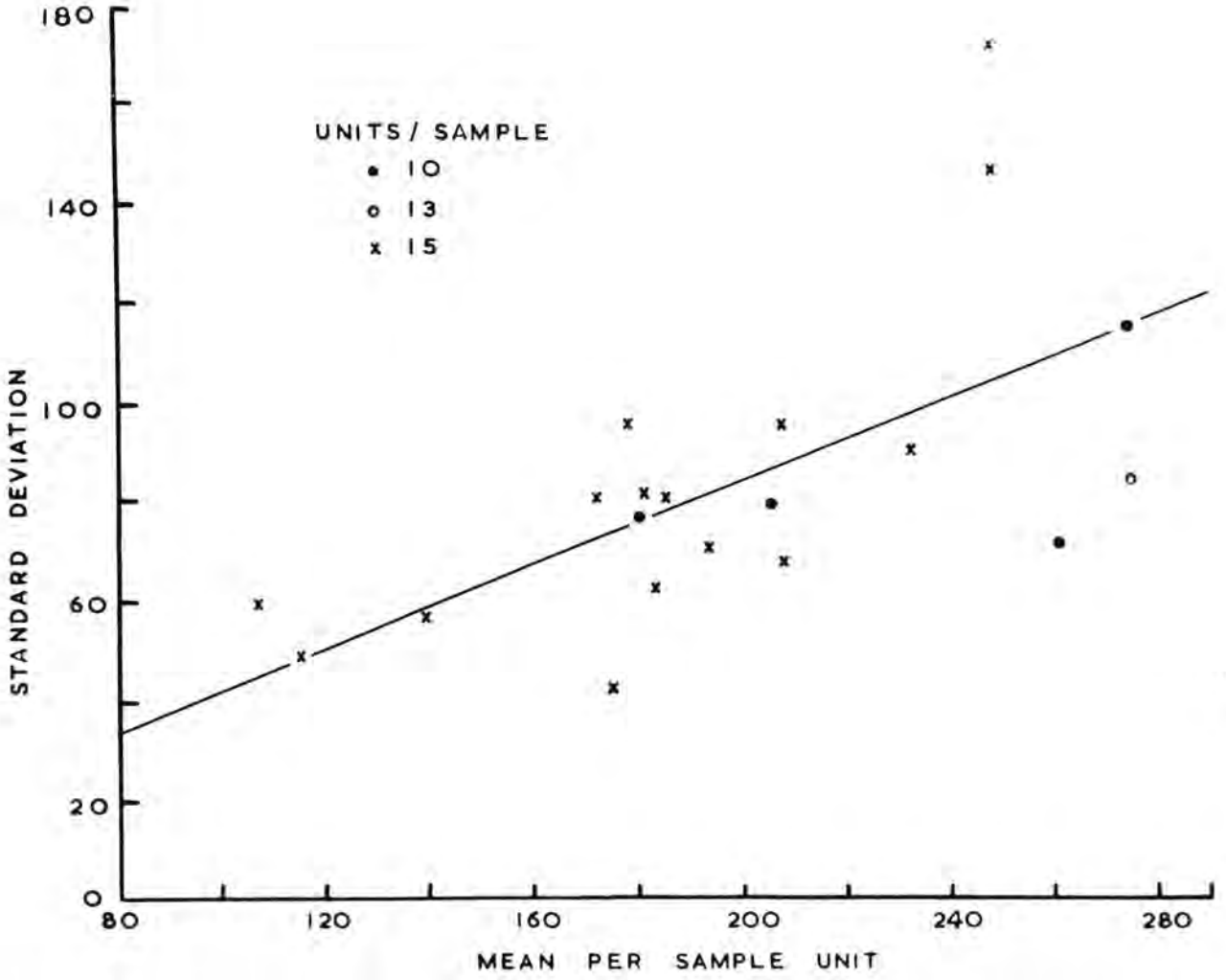


Fig. 4. Relation of S.D. to mean of Juncus site samples.

(c) The relation between the mean per sample and the S.D.

In Fig. 4 sampling results from the Juncus site are graphically represented by plotting the S.D. against its mean per sample unit. Although a general upward trend of the S.D. is detectable with the increasing mean, the scatter of the points and their limited number cannot permit a rigorous interpretation. What seems to be the best representation of a trend line has, however, been drawn in by eye. Two 10-unit sample results could not be fitted on this final graph. The mean and S.D. of one were 513 and 100 and those of the other 469 and 194 respectively. Since the pattern of deviation from the mean has been shown to be similar, it is not surprising to find that this graph is again reminiscent of what has been found in the enchytraeids.

3. Conclusion.

The deviation from normality of the sampling results makes it desirable to transform the data before normal distribution statistics are applied and the increase of the S.D., and hence the variance, with the mean indicates the logarithmic transformation as the most suitable (Quenouville, 1950, p.163). However, in view of the limited data available, only a limited scope of conclusions is possible and for this elaborate statistical

treatments would seem unnecessary. Errors attributable to other sources (e.g. sampling, extraction, etc.), although indeterminable, could be expected to be large. Consequently, the inefficiency of using normal distribution statistics would result in not detecting small differences rather than in indicating non-existent ones.

Aggregation as a biological rather than as a statistical phenomenon has to be studied by other means (e.g. mapping; see Overgaard Nielsen, 1955) which were not possible to apply to the present study.

VIII. VERTICAL DISTRIBUTION.

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1. General introduction.

Nematodes when associated with plant roots can penetrate very deep in the soil. Distribution down to 25 feet (about 7.6m.) has been recorded by Steiner & Heinly (1922). These authors remarked, however, that normally nematodes are found in the top 2-3 inches (5.0-7.6 cm) of the soil. Overgaard Nielsen (1949a, p.53) investigated their vertical distribution in various soils in Denmark and, in the sandy, coastal plain soils, he found them down to 80 cm. deep. He only gave percentages from which it is not possible to find out what numbers he actually encountered at these depths. He was of the opinion that, like other soil micro-organisms, the nematodes are largely superficial in their vertical distribution. In a cultivated field in Utah, U.S.A., Thorne (Thorne & Swanger, 1936, p.113) found the bulk of Dorylaimus obscurus in the upper 10 inches (25.4 cm.) of the soil, but between 1 and 10 worms were found in the deeper layers down to 2 feet (about 61 cm.)

The relation of the vertical distribution of some nematodes, among other soil microfauna, to the soil layers was studied by Volz (1951) in woodland soils in Bavaria. Taking soil layers to about 15 cm. deep, he

found that different species were abundant in the various (litter, fermentation, humus and soil) layers.

There is, therefore, a shortage of information on this topic of nematode ecology against which the findings from Moor House go to contribute. Results for vertical distribution were obtained by sub-dividing sample unit cores, before extraction, into 3 cm. portions.

2. Vertical distribution of all nematodes.

(a) Introduction

As Tables 34-40 show, it was not possible to sample all the sites under study either at the same time or even at corresponding times during the year. The Juncus site was sampled over a period of 12 months between August, 1958 and September, 1959. One winter sample of 5 units was obtained in January, 1959 before which date, in December, 1958, a pilot sample of 2 units had been taken. The results of these samples are shown separately in Table 37. Only limited data, none covering the winter period, exist for other sites. The number of sample units on which the study is based is given in Table 33.

Table 33. Sample units taken from different sites and their analysis for vertical distribution of all nematodes.

Site	No. of Sample units taken	No. analysed for 6 cm.		No. analysed for 3cm.	
			Upp. 6	Low. 6	All
Bare Peat	35	10	10	10	10
Residual Hummock	10	10	10	10	10
Calluna	50	10	10	10	10
Juncus	300	42	75	35	30
Nardus Grassland	55	19	40	15	14
Limestone "	30	15	30	15	15

'Upp. 6; 'Low. 6' and 'All' mean that either the upper 6 cm., the lower 6 cm. or all the sample unit core (of 12 cm. length) was divided into 3 cm. layers. The figures in different columns are independent and not additive.

(b) Vertical distribution of all nematodes in 3 cm. layers.

(i) The Moss Flats and Calluna sites.

The number of nematodes in the bare peat was found to be negligible (Table 34). On the residual Calluna hummock

(Moss Flats), sampled twice within the period of four weeks in 1958 (see Table 35), there was an increase in the numbers of nematodes found from the bare peat (position 1) to the part of the hummock bearing vegetation (positions 3-5). This is better seen in the upper 6 cm. figures for the 28.x.58 sample, especially when individual feeding groups are considered (Table 44). Anything clearer could not be expected to emerge from such few figures.

Judging by the erratic vertical distribution shown by the figures (Table 35), fairly marked aggregation of nematodes occurred within individual sample cores from the residual Calluna hummock. Examination of the nematodes extracted showed that aggregations of both plant and microbial feeders occurred and in both cases juvenile forms often composed a large proportion of the extracted worms.

On the Calluna site (Table 36) there was a marked concentration of the nematode fauna in the upper 6 cm. of the cores. Even the dry summer of 1959 had little effect on this steep vertical distribution gradient.

Table 34. Vertical distribution of all nematodes in 3 cm. layers on the Bare Peat.
Nos. 1-5 are sample unit cores.

13.v.59

cm.	1	2	3	4	5	Mean
0 - 3	0	0	0	0	0	0
3 - 6	0	0	0	0	0	0
6 - 9	0	5	0	0	0	1
9 - 12	0	1	0	0	3	0.8

4.viii.59

cm.	1	2	3	4	5	Mean
0 - 3	1	2	1	0	1	1
3 - 6	0	0	5	2	3	2
6 - 9	0	0	0	3	1	0.8
9 - 12	1	1	0	0	0	0.4

Table 35. Vertical distribution of all nematodes in a residual Calluna hummock on Moss Flats.

Position on hummock		1	2	3	4	5
Date	Depth in cm.					
23.ix.58						
	0 - 3	0	32	21	36	21
	3 - 6	1	7	0	30	7
	6 - 9	1	4*	6	112	2
	9 - 12	1		2	48	2
28.x.58						
	0 - 3	8*	1	51	257	420
	3 - 6		18	57	49	55
	6 - 9	23*	44	24	0	36
	9 - 12		11	10	0	2

* Extracted undivided.

The position nos. 1 - 5 correspond to i - v in Table 44.

Table 36. Vertical distribution of all nematodes in 3 cm. layers on the Calluna site.

29.iv.59

cm.	1	2	3	4	5	Mean	%
0 - 3	17	235	238	149	103	169.0	83.8
3 - 6	5	74	14	41	10	28.8	14.3
6 - 9	0	6	1	1	4	2.4	1.2
9 -12	0	3	0	0	0	1.4	0.8

13.viii.59

cm.	1	2	3	4	5	Mean	%
0 - 3	45	199	112	341	269	193.2	67.6
3 - 6	40	30	12	204	121	81.4	28.5
6 - 9	13	19	2	1	9	8.8	3.1
9 -12	2	2	0	2	7	2.6	0.9

(ii) The Juncus site.

Table 38 summarizes the sampling data for the Juncus site between November, 1958 and September, 1959 and Table 37 presents some data for the winter period, 1958 - 59. A consistently high percentage of nematodes were in the upper layers of the soil though, unlike the Calluna site, appreciable numbers still occurred down to 12 cm. below the surface, This is especially noticeable in the figures for the 17.ix.59. From the data obtained for micro-distribution (Table 52), it was found that in November, 1959, between 2 and 8 nematodes per 3 cm. portion of the core were to be found at a depth of 12 - 15 cm. Therefore, while on the relatively water-logged Calluna site sampling to 12 cm. probably hit the limit of the fauna, this could not be assumed to be so on the Juncus site. It certainly does not seem to have been so during the dry and warm summer of 1959.

The mean numbers of worms per 3 cm. layer given in Table 38, plotted on a histogram (Fig. 5), show a consistent pattern of vertical distribution throughout the sampling period. One occasion (19.vi.59), however, merits comment as it was the only one on which the mean and percentage for any layer exceeded the corresponding figures for the layer immediately above it. This happened at the

Table 37. Vertical distribution of all nematodes on the *Juncus* site by 6 cm. layers in Winter 1958 - 59.

Date	16.xii.58		21.i.59	
Depth in cm.	0 - 6	6 - 12	0 - 6	6 - 12
Sample Block No.				
1	142*	8*	92*	8
2			421*	43
3	266*	36*	111*	7
4			111*	18
5			235*	10

* Cores not sub-divided before extraction.

One core was taken from each sample block.

Table 38. Mean and percentage distribution of all nematodes in 3 cm. layers on the Juncus site. The mean number of nematodes/3 cm. layer is based on 5 units.

Date		0 - 3 cm.	3 - 6 cm.	6 - 9 cm.	9 - 12 cm.
24.xi.58	No.	183.2	48.0	11.8	6.2
	%	73.5	19.3	4.7	2.5
7.iv.59	No.	213.0	69.4	28.6	11.0
	%	66.1	21.6	8.9	3.4
27.v.59	No.	145.2	60.8	12.4	5.0
	%	65.0	27.2	5.6	2.3
19.vi.59	No.	104.4	40.2	10.6	17.6
	%	60.4	23.3	6.1	10.2
25.viii.59	No.	237.2	91.0	31.6	13.6
	%	63.5	24.4	8.5	3.6
17.ix.59	No.	324.2	214.6	63.4	39.2
	%	50.5	33.5	9.9	6.1

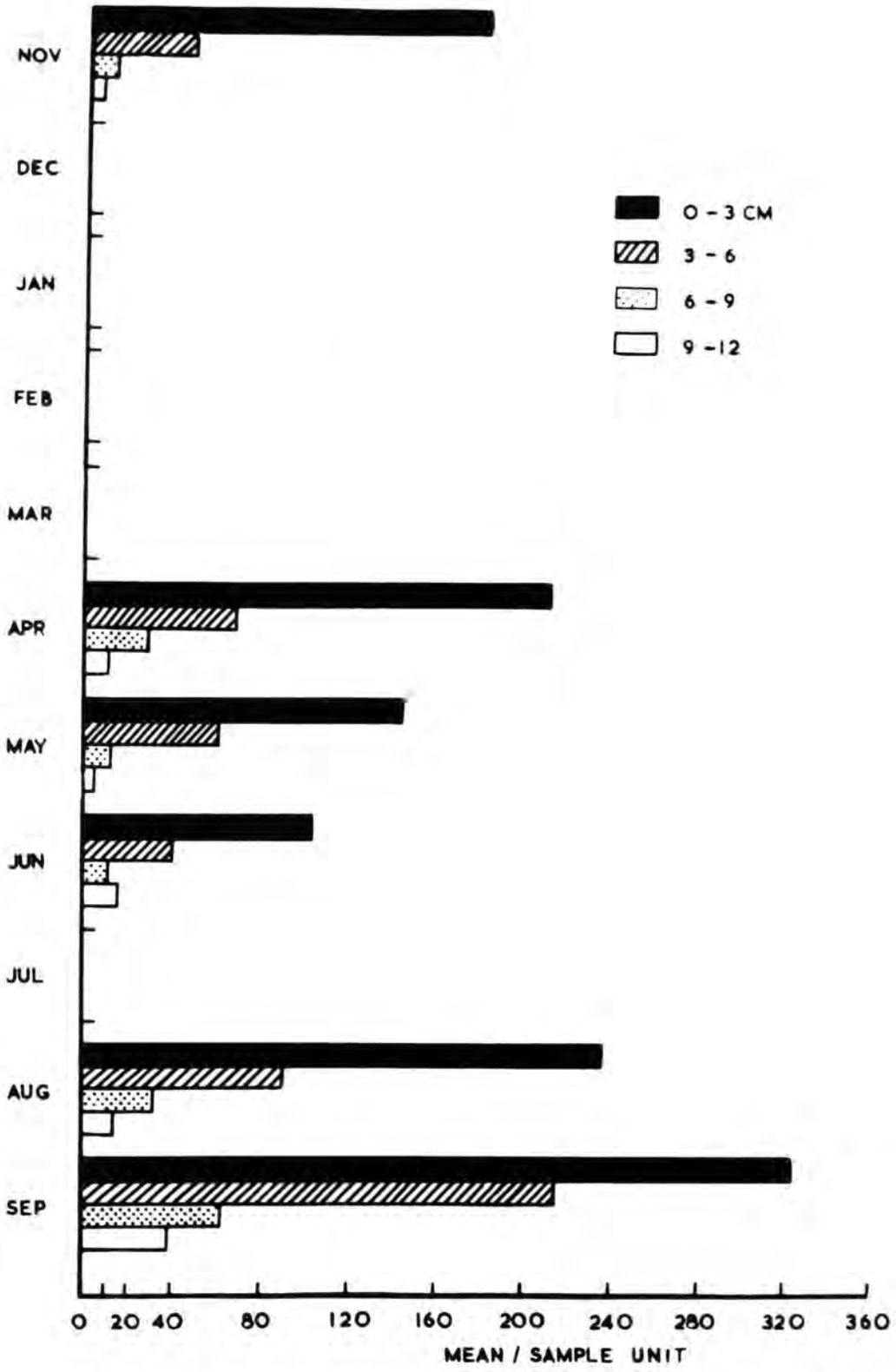

Fig. 5. Nematode vertical distribution on the Juncus site, 1958/59.

time when the sampling estimates of the population for 1959 - 60 was lowest, and at the start of the exceptionally dry summer of 1959.

(iii) The Nardus and Limestone Grassland sites.

Sampling results from these two sites are more comparable since they were taken over more or less the same period (Tables 39 and 40). On both sites there was an increase in the percentage of nematodes in the deeper layers of the soil, i.e. 6 - 9 and 9 - 12 cm., from the spring through the summer to the autumn.

On the Limestone Grassland site the mean number for the 6 - 9 cm. layer exceeded that for the 9 - 12 cm. layer in the July and October samples. In the May sample, too, the mean number for the 9 - 12 cm. only very slightly exceeded that for the immediately overlying layer. This 'inversion' in the vertical distribution trend seems to have been due to aggregations of certain nematode groups.

The coprogenous, crumbly soil, riddled with earthworm burrows, was very difficult to sample when it was dry. The division into 3 cm. layers of the lower 6 cm. portion of a core was at such times approximate. Some of the 'inversion' in the vertical distribution trend might have been due to this experimental error. However, several facts would seem not to support this. No 'inversion' was seen on the Nardus site, for all nematodes, in the summer

although the sandy silt there was almost as difficult to sample. Secondly, except for the May sample, the phenomenon of 'inversion' never occurred between the two lower 3 cm. layers (i.e. never between the 6 - 9 and the 9 - 12 cm. layers) which were the ones difficult to sample. The May sample was taken when the soil was quite moist (see Table 10) and no difficulty was experienced in separating the different portions of the cores. The relative increase in the number of nematodes, in fact, occurred at the level below the zone of maximum root development (see Table 6) and where earthworm burrows began to be very noticeable. Direct observation on the walls of some of these burrows revealed a rich growth of fungal mycelia, evidence of the existence of conditions suitable for nematodes. Probably in May these burrows were too damp and less well aerated but the dry weather ameliorated these conditions and local build-ups of nematodes occurred. The discussion of the vertical distribution of the individual groups in the next section will show that these build-ups or aggregations were common to plant and microbial feeders on the Limestone Grassland site but only occurred, as far as could be detected, in the plant feeders on the Nardus site (see especially Table 47).

Table 39. Mean and percentage distribution of all nematodes in 3 cm. layers on the Nardus site.

Date	17.iii.59		3.vii.59		28.ix. 59	
	No.	%	No.	%	No.	%
	311.5	75.6	268.6	61.0	255.2	57.6
	78.5	18.6	97.6	22.2	99.4	22.4
	15.5	3.8	44.4	10.1	57.4	13.0
	8.5	2.1	30.0	6.8	31.0	7.0

Table 40. Mean and percentage distribution of all nematodes in 3 cm. layers on the Limestone Grassland site.

Date	5.v.59		28.vii.59		16.x.59	
	No.	%	No.	%	No.	%
	111.2	56.5	122.8	48.3	142.4	47.3
	55.8	28.4	47.2	18.6	62.8	20.9
	14.8	7.5	54.6	21.5	64.0	21.5
	15.0	7.6	29.6	11.6	32.0	10.6

3. Vertical distribution of the feeding groups.

(a) Introduction.

Tables 43-48 show, by sites, the vertical distribution of the feeding groups into which the nematodes have been divided. For the purposes of this and subsequent discussion the term Dorylaimoidea will be used for the feeding group which, in Part V, was called 'miscellaneous feeders', since it was then shown that these all belonged to this superfamily. In the tables a dash means that no material was examined for that case while a zero indicates absence of that group in material examined. For the techniques used in the feeding group classification reference should be made to Part V.

The number of nematodes given for each date is derived from examination of one sample unit, except in the case of the Moss Flats sites. The figures for the Bare Peat on this site are the totals derived from 15 and 10 sample units for the two respective dates. Those for the Residual Calluna Hummock are individual sample unit counts there being five units for each date. The numbers of the units, given in Roman numerals, correspond with the sampling positions in Table 35.

(b) Microbial feeders, Dorylaimoidea and predators.

The microbial feeders and Dorylaimoidea are concen-

trated in the upper 6 cm. of the soil. Only on the Limestone Grassland did appreciable numbers of the Dorylaimoidea occur below 6 cm., but even there however, less than 20% were below 6 cm. and less than 5% below 9 cm. The actual percentages, calculated from the data available, are given in Table 41. On the peat soils, e.g. of the Juncus and Calluna sites, not only were the Dorylaimoidea absent from the lower layers but also their numbers in the upper 6 cm. were very small.

Table 41. Percentages of microbial feeders and Dorylaimoidea found in different 3 cm. layers of Limestone Grassland soil.

Depth in cm.	Microbial feeders	Dorylaimoidea
0 - 3	45.9	50.0
3 - 6	24.6	31.2
6 - 9	23.2	14.4
9 - 12	6.3	4.4

Similarly, only the Limestone Grassland site had appreciable numbers of microbial feeders below 6 cm. (Table 48). Although relatively more of the microbial feeders, as compared with the Dorylaimoidea, were found in the deeper layers of the soil (Table 41), nevertheless,

there was a general trend of vertical distribution showing decrease with increasing depth. This trend, obtained from data for four sample units, obscures the fact that individual cores in any sample often showed aggregations of certain microbial species e.g. Prismatolaimus dolichurus, Rhabditis sp. and Alaimus sp. Although similar build-ups might have occurred on other sites, there was no evidence of them from the sampling results. On the Juncus site, especially, the microbial feeders were found in the deeper layers, mainly represented by a few specimens of Cephalobidae, Plectidae, Alaimus and Teratocephalus. Such occurrences could be attributed to experimental error in the division of the cores before extraction. They could also be due to chance strays.

The predators were very rare and so no general conclusions could be made about their vertical distribution.

(c) Plant feeders.

Except on the two grassland sites and the Calluna hummock on Moss Flats, the plant species consist almost entirely of species of Tylenchus. The only other genus identified from the peat sites, Aphelenchoides, was represented by very few, usually 2 -3 specimens from the upper layers. Consideration of the vertical distribution of the plant feeders, therefore, largely involves a single genus. It is clear from Tables 43 - 48 that the group was

largely concetrated in the upper 6 cm. Nevertheless, unlike the microbial feeders and the Dorylaimoidea, appreciable numbers occurred in the deeper layers of the soil.

Twenty-five sample unit cores taken from the Bare Peat site yielded only 8 plant feeding nematodes in the upper 6 cm. and none in the lower 6 cm. (Table 43). This would seem to support the hypothesis that what plant feeders occurred on bare peat were all in the superficial layers. The figures for the Calluna hummock (Table 44) are too inconsistent and meagre to be interpretable. Probably more data would have yielded clearer information.

On the grassland sites, several other genera occurred besides Tylenchus (Table 17). Some of these e.g. Pratylenchus (represented by P. pratensis) and Paratylenchus, were found to occur in large numbers in some of the sample unit extracts thus indicating local aggregations. However, similar aggregations of Tylenchus spp. did occur in certain layers, as is shown by the examples in Table 42 below.

Table 42. The numbers of *Tylenchus* spp. in 3 cm. layers of 2 sample cores taken from the grassland sites.

Site	Date	0 - 3 cm.	3 - 6 cm.	6 - 9 cm.	9 - 12 cm.
Nardus Limestone Grassland	3.vii.59	56	17	6	20*
	28.vii.59	53	15	31*	9

* Aggregation causing vertical distribution inversion.

Aggregations of certain microbial species of nematodes, similar to those of the plant feeders here described, have already been mentioned in connection with the Limestone Grassland site.

Table 43. Vertical distribution of nematode feeding groups on Bare Peat (Moss Flats).

	Plant Feeders		Microbial Feeders		Dorylaimoidea		Predators	
Depth in cm.	0 - 6	6 - 12	0 - 6	6 - 12	0 - 6	6 - 12	0 - 6	6 - 12
6.v.58	5	-	2	-	0	-	0	-
13.v.59	3	0	0	7	0	0	0	0

Table 44. Vertical distribution of nematode feeding groups on a Residual *Calluna* Hummock (Moss Flats). i - v are position numbers (see text).

		Plant Feeders		Microbial Feeders		Dorylaimoidea		Predators	
Depth in cm.		0 - 6	6 - 12	0 - 6	6 - 12	0 - 6	6 - 12	0 - 6	6 - 12
23.ix.58	i	1	1	0	0	0	0	0	0
	ii	15	3	17	0	2	1	1	0
	iii	9	8	11	0	0	0	0	0
	iv	13	158	27	0	7	2	0	0
	v	22	4	4	0	0	0	0	0
28.x.58	i	4	20	4	1	0	0	0	0
	ii	17	50	2	0	0	0	0	0
	iii	32	30	56	3	8	1	0	0
	iv	201	0	75	0	0	0	0	0
	v	335	33	134	0	0	0	0	0

Table 45. Vertical distribution of nematode feeding groups on the Calluna site.

	Plant Feeders		Microbial Feeders		Dorylaimoidea		Predators	
Depth in cm.	0 - 6	6 - 12	0 - 6	6 - 12	0 - 6	6 - 12	0 - 6	6 - 12
27.v.59	159	0	48	0	3	0	0	0
13.viii.59	213	19	7	0	3	0	0	0
13.viii.59	301	10	38	3	2	0	0	0

Table 46. Vertical distribution of nematode feeding groups: Juncus site.

(a) Plant Feeders

Depth in cm.	5.viii.58	3.xi.58	24.xi.58	7.iv.59	25.vii.59	17.ix.59
0 - 6	101	171	54	138	229	237
6 - 12	24	-	5	55	38	87

(b) Microbial Feeders

Depth in cm.	5.viii.58	3.xi.58	24.xi.58	7.iv.59	25.vii.59	17.ix.59
0 - 6	10	96	99	112	101	30
6 - 12	0	-	0	11	2	2

(c) Dorylaimoidea

Depth in cm.	5.viii.58	3.xi.58	24.xi.58	7.iv.59	25.vii.59	17.ix.59
0 - 6	4	10	4	12	4	1
6 - 12	0	-	0	0	0	0

(d) Predators. None seen.

Table 47. Vertical distribution of nematode feeding groups on the Nardus site.

	Plant Feeders		Microbial Feeders		Dorylaimoidea		Predators	
Depth in cm.	0 - 6	6 - 12	0 - 6	6 - 12	0 - 6	6 - 12	0 - 6	6 - 12
12.viii.58	54	7	13	0	5	0	0	0
3.vii.59	93	39	102	1	16	2	1	0

Table 48. Vertical distribution of nematode feeding groups on the Limestone Grassland site.

	Plant Feeders		Microbial Feeders		Dorylaimoidea		Predators	
Depth in cm.	0 - 6	6 - 12	0 - 6	6 - 12	0 - 6	6 - 12	0 - 6	6 - 12
5.v.59	27	11	5	0	13	0	0	0
5.v.59	46	26	37	3	40	10	5	3
28.vii.59	85	49	57	41	24	6	1	0
16.x.59	142	47	82	18	48	20	0	0

4. Concluding remarks.

As would be expected, the more waterlogged peat habitats have a greater superficial concentration of the nematodes, mainly in the litter and fermentation layers of the soil. Amelioration of the conditions in the deeper soil layers during the drier periods was reflected in a higher percentage of worms found in those layers, but this was more noticeable on the mineral than on the peat soils. The data, however, do not give evidence of any vertical migration with season.

The vertical distribution of the different groups is characteristically different, with the Dorylaimoidea, which are less abundant on the more moist sites, being more superficial except on the Limestone Grassland site. Thus the soil properties and the relative abundance of the nematode groups help to explain the differences in vertical distribution patterns, especially on the two grassland sites. Furthermore, while the results from Moor House agree with the general observation that soil microorganisms are concentrated near the surface, they show that, unlike the findings of the other authors quoted above, this concentration is more marked in moorland peat soils.

IX. MICRO-DISTRIBUTION

IX. MICRO-DISTRIBUTION

1. Micro-distribution of nematodes on the Juncus site.

An attempt was made, by small scale sampling on the Juncus site, to find out if there was any general pattern of micro-distribution of the nematodes.

The number of nematodes from paired sample units taken from the same large core were compared and it was found that the means of two such paired samples did not differ significantly from each other. Eight paired sample units gave means of 209.38 (S.D. = 69.57, S.E. = 19.54) and 211.63 (S.D. = 69.12, S.E. = 19.42). These gave a $t = 0.0649$ which, with 14 d.f., has a $P>0.90$ (see Table 50). When compared for homogeneity, however, the X^2 for one pair (No. 2) was significant ($P<0.05$) and that for two other pairs (Nos. 1 & 4) was highly significant ($P<0.01$), (see Table 51).

A comparison, layer by layer, was made on two pairs of sample units, one pair being from a patch of Juncus squarrosus and another pair from an adjacent patch of Festuca ovina. The large cores were taken within 2.5 cm. of each other in the field and extended to a depth of 15 cm. From each field core 2 sample units were taken after the usual laboratory treatment. Each of the sample units was cut up into 5 layers of 3 cm. each as follows:

Table 49. Length of sample unit portions.

Layer	Depth in cm.
1	0 - 3
2	3 - 6
3	6 - 9
4	9 - 12
5	12 - 15

This numbering is used in Tables 53 - 56.

The various sample unit portions were randomized before extraction and the number of nematodes obtained from each layer is given in Table 52. In this, as in the subsequent Tables 53 - 56 derived from it, F refers to Festuca ovina and J to Juncus squarrosus. In each case sample unit 1 was taken at the centre and 2 from near the outside of the core.

Tables 53 & 54 show the X^2 of the equivalent layers in each pair of sample units. No clear pattern of micro-distribution can be derived from the inspection of these results, nor can any pattern be found when the inner sample units (Table 55) or the outer sample units (Table 56) from both cores are compared.

On the basis of these limited results, it does not seem as if the two plants, Juncus squarrosus and Festuca ovina, or the position in the frozen core from which the final sample units were taken, had any consistent effect on the final estimation of nematode numbers in the sample. The absence of pattern or trend in the X^2 comparisons is a demonstration of the heterogeneity in the distribution of the nematodes. The clear vertical distribution is not accompanied by a similarly clear horizontal pattern.

Only three out of the eight pairs of sample units in Table 51 differ significantly within themselves but it will be noticed that the differences within each of these is about the same magnitude as, or less than, the S.D. of the mean. This variation between paired cores is, in other words, much less than that often observed between the different items of a sample.

Table 50. A comparison of paired sample units from the *Juncus* site.

Sampling date : 6.iii.58.

Sample unit No.	Core 1	Core 2	Mean	Diff.
1	199	131	165	68
2	117	150	133.5	33
3	161	194	177.5	33
4	222	286	254	64
5	289	303	296	14
6	262	230	246	32
7	295	264	279.5	31
8	130	135	132.5	5
Total	1675	1693		
Mean	209.38	211.63		+18
S.E.	19.54	19.42		

Mean difference = +18

S.D. = 34.68

$t = 0.0649$, with 14 d.f., $P > 0.9$

Table 51. A comparison of paired sample units from the *Juncus* site by the X^2 test.

Date of sampling: 6.iii.58.

Sample unit No.	Core 1	Core 2	Total	Diff.	x^2	P
1	199	131	330	68	13.990	<0.01
2	117	150	267	33	4.079	<0.05
3	161	194	355	33	3.068	>0.05
4	222	286	508	64	8.063	<0.01
5	289	303	592	14	0.331	>0.05
6	262	230	492	32	2.081	>0.10
7	295	264	559	31	1.719	>0.10
8	130	135	265	5	0.094	>0.70
Total	1675	1694			33.425	<0.01
Mean	209.38	211.63				
S.D.	69.57	69.12				

Table 52. The number of nematodes from adjacent cores on patches of Juncus squarrosus and Festuca ovina : Juncus site.

Date of sampling: 5.x.59.

Depth in cm.	Juncus squarrosus			Festuca ovina		
	J_1	J_2	Mean	F_1	F_2	Mean
0 - 3	338	408	373	370	478	424
3 - 6	103	128	115.5	141	181	161
6 - 9	43	116	79.5	143	140	141.5
9 - 12	19	9	14	40	29	34.5
12 - 15	7	2	4.5	8	5	6.5

Table 53. A comparison of F_1 and F_2 by the X^2 test.

	1	2	3	4+5
F_1	370	141	143	48
F_2	478	181	140	34
Diff.	108	40	3	14
X^2	11.375	14.969	0.042	1.239
P	<0.01	<0.01	>0.80	>0.20

Table 54. A comparison of J_1 and J_2 by the X^2 test.

	1	2	3	4+5
J_1	338	103	43	26
J_2	408	128	116	11
Diff.	70	25	73	15
X^2	6.568	2.705	33.515	8.035
P	<0.02	0.10	<0.01	<0.01

Table 55. A comparison of F_1 and J_1 by the X^2 test.

	1	2	3	4	5
F_1	370	141	143	40	8
J_1	338	103	43	19	7
Diff.	32	38	100	21	1
X^2	1.446	5.918	53.760	7.474	0.066
P	>0.20	<0.02	<0.01	<0.01	>0.70

Table 56. A comparison of F_2 and J_2 by the X^2 test.

	1	2	3	4+5
F_2	478	181	140	34
J_2	408	128	116	11
Diff.	70	53	24	23
X^2	5.531	9.090	2.250	11.755
P	<0.01	<0.01	>0.10	<0.01

2. Micro-distribution of nematodes on the other sites.

No small scale sampling for micro-distribution was undertaken on the other sites, but the analysis of the results for vertical distribution yielded information on micro-distribution. The data have already been given in Part VIII. Evidence for the aggregation of nematodes was found, especially on the Limestone and Nardus Grassland sites and was discussed in connection with the phenomenon of 'inversion' in the vertical distribution trend. Also the examination of sample unit extracts during routine counting and feeding group analysis indicated that certain species of nematodes were probably more aggregated than others. The occurrence of 'nests' of Pratylenchus pratensis, for example, which are very reminiscent of the 'egg batches' of soil micro-arthopods (cf. Macfadyen, 1957, p. 81), have been mentioned already.

X. SEASONAL POPULATION VARIATION.

X. SEASONAL POPULATION VARIATION.

1. Introduction.

Information on the seasonal variation in the numbers of free-living nematodes is scanty. What exists is rather difficult to assess, largely because of the sampling methods used but, also, because of the way in which the results are expressed in the literature. Thus Overgaard Nielsen (1949a, p.23) claimed that no seasonal variation occurred on a site that he sampled in Denmark, although his results were not analysed statistically. Bunt (1954) working in Macquarie Island, claimed that he found a tendency for the numbers to increase from winter to summer. Many of his results, however, were based on one sample and his whole sampling programme consisted of only three sampling occasions. In the Alps, Seidenschwarz (1923) and Burkhalter (1928) found, over the period of 12 months, a summer increase and a winter decline of nematode numbers. In spite of lack of adequate replication, their results seem to be the only data covering the period of a year known to the writer.

Seidenschwarz gives monthly fluctuations for total nematodes and for 14 individual species, the figures being expressed in numbers per 30 cc. of soil. The general pattern of fluctuation was similar for all the species.

Burkhalter's study showed seasonal fluctuation to exist in four soil types: moss, 'alpine', woodland and pasture. The general pattern showed low numbers in May, a rapid increase to a peak in July and a gradual decline to December. With individual differences, this pattern of late spring minimum and summer - autumn maximum was general in the four soils.

Franz (1942) commented on the findings of Seidenschwarz and denied that a seasonal fluctuation could be detected in the nematode numbers in the soils of the Austrian Alps. He claimed that the only factors of importance were the soil type and the severity of the winter. It is probably this author whom Overgaard Nielsen (1949a, p.10) has in mind when he ways that Seidenschwarz's findings have not been confirmed by 'later authors'.

The writer is not aware of any study that has been done on the type of seasonal population fluctuation covering the free-living nematodes of British soils.

2. The Juncus site.

(a) Sampling programme.

Sampling was carried out in 1958 and 1959 and a single sample was taken in March, 1960. The results, except for the last mentioned are presented in Fig. 6. In the majority of cases in 1958, two samples of 15 units each were taken one in the early and the other in the late part of the month, with an interval of about 2 or 3 weeks

between them. The mean and S.E. were then found for the 30 units. The only 1958 results not obtained in this way are those for May, July, August and November. The figure for November is based on 28 units, 15 of which were taken early in the month. The figures for the other 3 months are based on 15 units only in each case, and so is that for January, 1959. After this date the sample size was changed to 10 units (see Part VI) and, also, because of other work, it was not possible to sample regularly on this site. The few occasions when sampling was done are, nevertheless, considered to cover the most important periods of the year as judged by the 1958 results.

For the sampling programme the site was divided into five blocks of three strata each as shown in the diagram below. Each stratum was 3 m. long by 1 m. wide.

3	4	9	10	15
2	5	8	11	14
1	6	7	12	13

Sampling strata.

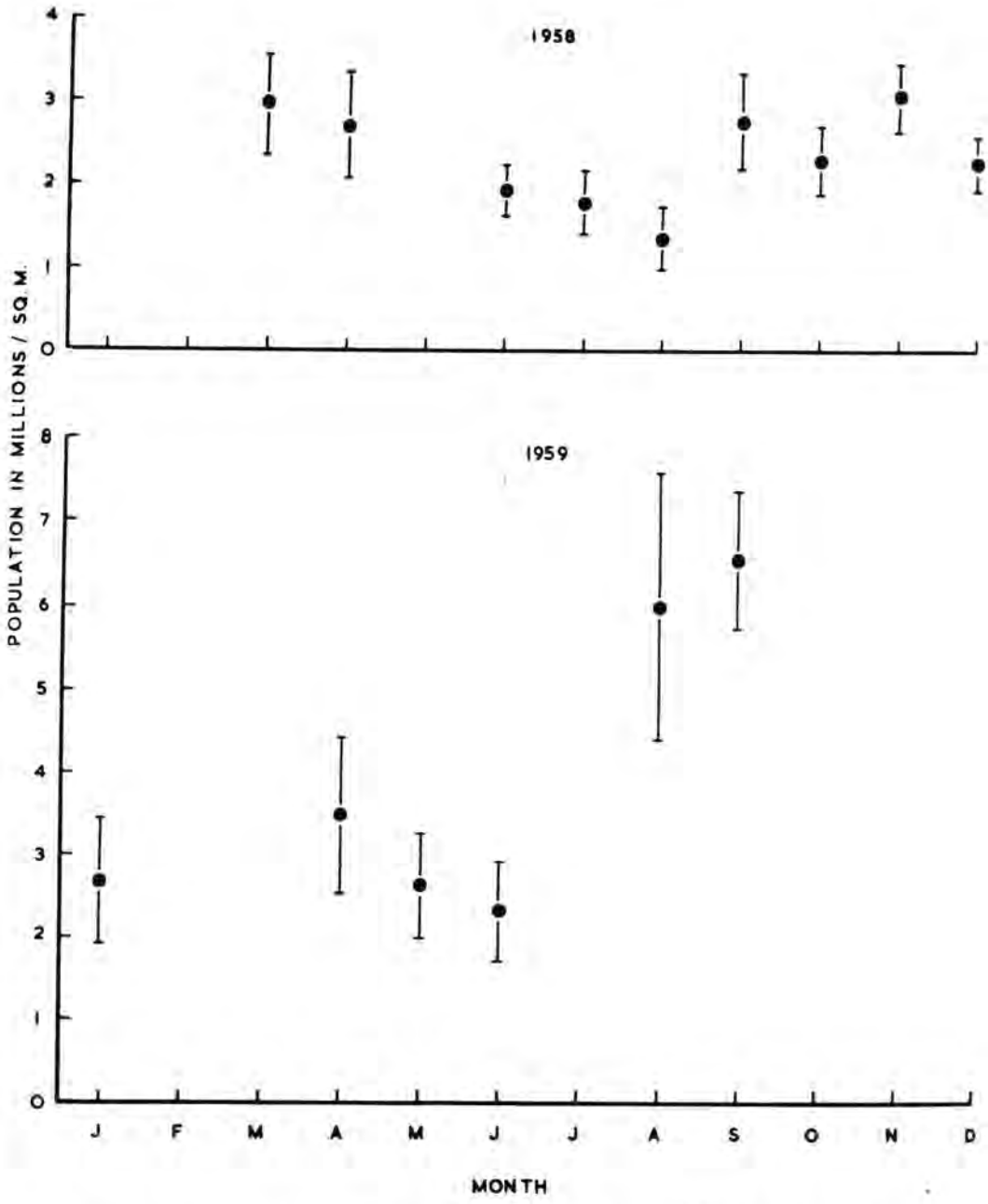

Fig. 6. Seasonal population variation on the Juncus site.

(b) Results.

Fig. 6 shows that the nematode population in 1958 decreased from spring to summer and suddenly increased in early autumn. It remained at about 2.5 million/m^2 during the winter of 1958-59. An analysis of variance (Table 57) of 1958 samples showed that sampling occasions were responsible for a greater source of variation than sample strata (i.e. position on the site). The seasonal differences were therefore real. It is interesting that the data available for 1959 indicates that as in 1958 there was a population decrease in the summer and a recovery in the autumn. The one 10-unit sample taken on the 7.iii.60 yielded an estimated population of 3.324 ± 0.291 million/m^2, a figure very much comparable with that for April, 1959 based on a similar sized sample, and that for March, 1958 based on a 15-unit sample. It would seem that a winter decrease of a somewhat less magnitude than the summer one is also a feature of the nematode population on the Juncus site.

Table 57. Analysis of variance of the 1958 sampling results from the Juncus site.

Source of variation	Sum of squares	d.f.	F
Sampling occasion (Date)	331,401	13	2.8591
Sample strata (Position)	88,593	14	1.4090
Residual	1,622,694	182	
Total	2,042,688	209	

Note: A plan of the sample strata is given in the text. One core was taken from each stratum on each sampling occasion.

3. Other sites.

Not enough information was obtained from the Bare Peat (Table 58) and the Calluna (Table 59) sites to enable conclusions on seasonal variation to be made.

Table 58. Nematode population estimates for the Bare Peat /m^2.

Date	Cores	$\bar{x}$/core	S.E.	Population	± 1 S.E.
6.v.58	15	0.47	0.18	5,820	4,580
13.v.58	10	0.30	0.18	3,820	2,290
4.viii.59	10	3.20	1.18	40,740	15,020

Table 59. Nematode population estimates for the Calluna site in millions/m^2.

Date	Cores	$\bar{x}$/core	S.E.	Population	± 1 S.E.
3.vi.58	15	36.40	11.37	0.463	0.145
10.vi.58	15	65.73	8.79	0.837	0.112
29.iv.59	10	120.20	20.30	1.530	0.258
13.viii.59	10	182.60	27.49	2.324	0.563

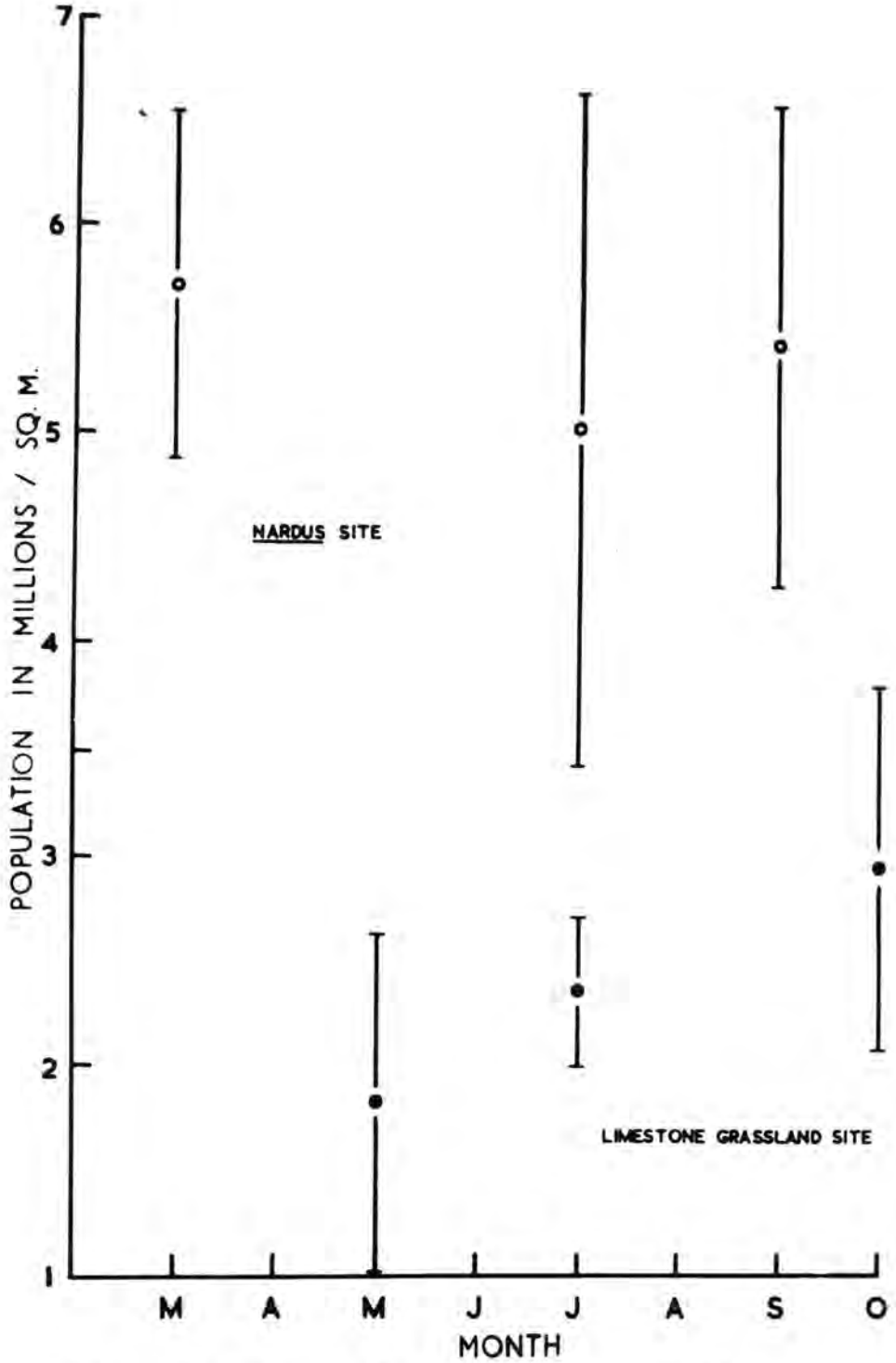

Fig. 7. Seasonal population variation on the Grassland sites, 1959.

From the Nardus and Limestone Grassland sites samples of 10 units each were taken in 1959 at the periods in the year when a change in the population level might have been expected. Fig. 7 shows the mean population levels and their ± 2S.E. ranges for both sites.

There was no significant difference between the samples of the Nardus site in 1959, although the mean for the 17.iii.59 indicated a real increase on that for the 12.viii.58 ($t = 3.22$, 18 d.f., $P < 0.01$) in Table 60. The latter, however, was of the same order of magnitude as that for the 21.v.58 despite the different sample size. It may be, therefore, that the general level of population, which is all that these data can indicate, was higher in 1959 than in 1958 but that in each year it did not vary very much.

Table 60. Nematode population estimates for the Nardus site in millions/m^2.

Date	Cores	$\bar{x}$/core	S.E.	Population	± 1 S.E.
21.v.58	15	67.87	8.23	0.864	0.105
12.viii.58	10	126.60	15.50	1.612	0.197
17.iii.59	10	448.20	35.17	5.706	0.448
3.vii.59	10	394.10	62.30	5.017	0.793
28.ix.59	10	425.20	126.28	5.413	0.563

The data for the Limestone Grassland site seem to show the same lack of seasonal variation. An analysis of variance of the 3 samples (Table 61) for the seasonal and sample variation gave an $F = 1.58$ with $P>0.5$. The apparently higher mean for the 16.x.59 was due to two large counts, both having juvenile 'swarms'.

Table 61. Nematode population estimates for the Limestone Grassland site in millions/m^2.

Date	Cores	$\bar{x}$/core	S.E.	Population	$\pm$ 1 S.E.
5.v.59	10	144.50	31.23	1.839	0.398
28.vii.59	10	184.90	14.26	2.354	0.182
16.x.59	10	231.30	36.05	2.944	0.459

XI. ESTIMATION OF NEMATODE BIOMASS AND ROLE IN SOIL RESPIRATION.

XI. ESTIMATION OF NEMATODE BIOMASS AND ROLE IN SOIL RESPIRATION.

1. Biomass.

(a) Problems and methods.

There are three chief problems which have to be faced in estimating the biomass of total free-living nematodes. One concerns the relative proportions of the different species which occur on the site being sampled. Ideally, one should find the population density of each and every species on the study area, find their individual biomass and so work out the total figure for all the species. This is very nearly an operational, if not a physical, impossibility. One can, therefore, either ignore all except the very common forms, or build on a set of assumptions and approximations which make allowance for the rare ones. The latter seems to be the better of the two courses to take, especially as many of the rare forms are relatively small species. Correction for these may not make much difference in the order of magnitude of the biomass, but, as Overgaard Nielsen has shown (1949a, p.68), the smaller species generally have a higher respiratory rate than the larger ones and they are, therefore, to be reckoned with from this point of view.

Whether only the common species are considered or allowance is made for the rare ones and those which it would not be possible to identify taxonomically, it is still not possible to examine all or even a very large proportion of the population. The percentage composition of the latter by species or any other groups will be, in the final analysis, an indeterminate approximation. It is, in any case, continuously changing under field conditions. In the present study this percentage composition has been found, not for any particular date, but from 6 sample units taken at different times. The figures are, therefore, means.

The second problem is that the different species sampled will be represented by specimens in various stages of development. The biomass, on the other hand, is estimated on the assumption that all the population is composed only of adult nematodes since the weights which form the basis of the calculations are those of adult specimens. This is not as serious as it might seem because the nematodes do not have a definite reproductive cycle such that at any one time most of them will be either adults or juveniles. In fact, with the short generation length that many have, the error is likely to be small compared to the real nematode biomass produced over any length of time.

The last problem is perhaps the most difficult. It is the practical one of how to obtain the weight of the worms themselves. Their small size and the smallness of the numbers encountered in the samples make direct weighing impracticable and an indirect method has to be resorted to for obtaining their weight. Three past workers have attempted this: Overgaard Nielsen (1949a, p. 14), Volz (1951, p. 58) and Andrássy (1956).

Overgaard Nielsen calculated the volume of a nematode from the formula for a cylinder : $\pi r^2 l$, taking the mean diameter as that at the base of the oesophagus. In spite of having found the specific gravity of nematodes as 1.02, he assumed, as a mathematical approximation ~~correction~~, that it was 1. He obtained his biomass figures by this method but used a much lengthier and more complicated one for the weights which he used in his determination of oxygen consumption. This other one was based on weighing paper models of nematodes and, according to him, gave results generally about 2% less than the simpler method.

Volz calculated the weight of nematodes from models made in materials of known specific gravity. Andrássy criticized both these methods as being too simplified (e.g. assuming that the nematode is cylindrical) or too complicated to use. He also drew attention to the discrepancy between the results of the two workers for allegedly similar species. The method which he evolved

is really a combination of the mathematical and model ones of the earlier writers in the sense that it makes a correction for tapering in the nematode body while still utilizing a mathematical formula.

Andrássy determined the specific gravity of the nematodes to be between 1.082 and 1.086 with a mean of 1.084, a figure which is not far different from Overgaard Nielsen's 1.02 and Caveness & Jensen's (1955) of 1.05 - 1.06. He found the volume of the nematodes from the formula: $V = a^2b / 1.7$, where a = the greatest body diameter and b = the length of the nematode, all the measurements being in μ. 1.7 is a correction factor for using the body diameter and for the non-cylindrical shape of the organisms. Multiplication by the mean S.G. 1.084 gave the formula for the weight: $W = a^2b / 1.6\ \gamma$. He showed that the use of the so-called mean body diameter, i.e. the diameter at the oesophagus base, gave similar but somewhat higher results. On the other hand, the results obtained by his method differ by only about 0 - 3% from those obtained by the lengthy mathematical calculation, regarding the nematode as a series of cylinders and cones.

Andrássy's seemed the best of the methods and had the advantage of being applicable to a field ecological inquiry, although beyond producing a weight list of 50 species Andrássy does not seem to have used it himself.

(b) The biomass of nematodes on the Juncus site.

Biomass estimates (Table 63) based on the data for the best/lowest and highest population estimates on the Juncus in 1958 were made utilizing the method of Andrássy already described. It being impossible to examine a large enough number of sample units, in the course of routine sampling, to enable a reliable estimate of the proportion of the different feeding groups to be made, recourse was made to the use of 6 sample units taken at different times between May and September, 1958-59. 1478 nematodes from these sample units had been examined and classified into species, genera or feeding groups (see Part V.2) and from this classification the percentage of each group was calculated (Table 62). These latter were then used to find the proportions of the groups in the estimated population. Finally, the estimated proportions so obtained were multiplied by the weights (in γ) found by the Andrássy technique.

Allowances had to be made for the microbial feeders not determined and also for the other unidentified specimens of various kinds. Since the unidentified microbial feeders were 1/9 of the total identified specimens of this group, an appropriate correction was accordingly made. All other unidentified nematodes ~~composed~~ comprised 4% of the total and were forms lost because of the experimental hazards

Table 62. The percentages and computed weights on which the biomass estimates are based.

Group of genus	%	Wt. in γ	Remarks
Tylenchus	63	0.2079	mean of 10 assorted specimens
Aphelenchoides	1	0.0214	1 A.saprophilus.
Total plant feeders	64		
Cephalobidae	2	0.4178	mean of Panagrolaimus rigidus, Macrolaimus sp. and Eucephalobus sp.
Teratocephalus	8	0.1037	2 T.terrestris.
Plectidae	12	0.2310	6 assorted specimens.
Aphanolaimus	1	0.1257	1 specimen of A.attentus.
Prismatolaimus	3	0.1257	1 P.dolichurus.
Alaimus	1	0.0702	1 specimen.
Unidentified microb. feeders	3		
Total microbial feeders	30		
Dorylaimoidea	2	2.3733	mean of 5 assorted specimens.
Unidentified specimens	4		

Table 63. Juncus site biomass estimates, 1958.
See text for explanations.

Date	June	November
Population/m^2	1,949,000	3,059,000
Biomass in mg./m^2 wet weight		
Plant feeders	255.69	401.31
Microbial feeders	112.03	175.93
Dorylaimoidea	92.46	145.22
Allowance for the unidentified group	17.88	28.56
Total	478.06	751.02

mentioned in Part V.2. None of these, however, were Dorylaims which, being large, are easy to handle and recognize. The allowance for this group was calculated as 4/91, or approximately 0.05, of the identified plant and microbial feeders, the Dorylaimoidea being excluded. The biomass estimated in Table 63 may therefore be taken as that likely to be found on the Juncus when the population was lowest and highest in 1958. The data for 1958 were used rather than those for 1959 because the former were based on a larger number of sample units and, therefore, gave better mean monthly population estimates (see Part X.2).

It was not considered worth while carrying out biomass estimates for the other sites. The degree of approximation involved would have been much greater than that for the Juncus site because the number of sample units for which the nematodes had been sufficiently identified and analysed was too small (cf. Table 21, column 7).

2. The role of nematodes in the Juncus site soil respiration.

The importance of a group of soil organisms as regards its role in the energy turn-over in the soil may be found, relative to the other groups, by estimating its proportional oxygen consumption (Bunt, 1954). This is

as difficult a problem as that of estimating the biomass, already discussed, when as in this case, several species are involved. Therefore, as in the case of the biomass, it was attempted only on the Juncus site. Use was made of Overgaard Nielsen's measurements of the respiration of nematodes in Danish soils (1959a, p.68) and preliminary results of soil respiration for samples of Juncus site soil (Cragg, unpub.).

Overgaard Nielsen found that the differences between the respiratory rates for many of the species were slight. He therefore established groups of genera to which general oxygen consumption figures could be assigned. From these groups and also from his Table 20 (p.68) giving the respiratory rates of individual species, the writer worked out Table 64. This was then used, with the biomass figures already found (see Section 1), to obtain an estimate of a mean oxygen consumption for the nematodes on the Juncus site (Table 65). The population estimate for June, 1958 was used as the best minimum estimate available for any month.

Small soil cores from the Juncus site were found to have a mean weight of 4.40 g. (sampling date 17.ix.59). Since each was 1/12730 m^2 in circular area (see Part VI), the oxygen consumption by nematodes per individual unit (i.e. small sample core) was calculated from Table 65 to

Table 64. Nematode respiratory rates in cc. O_2 /kg./hr. (after Overgaard Nielsen, 1949a, see text).

Group or genus	O_2 consumption	Remarks
Tylenchus	1110	rate for T.filiformis.
Aphenchoides	1060	rate for A.parietinus.
Cephlobidae	800	average rate for Cephalobus spp.
Teratocephalus	1200	rate estimated only.
Plectidae	1200	average rate for Plectus.
Aphanolaimus	1200	average rate for Plectus.
Prismatolaimus	1400	average for P.dolichurus.
Alaimus	1200	average estimated only.
Dorylaimus	840	average for D.carteri.

Note: 'rate estimated only' means that no measurements were given for any species of that genus and so, considering its size, an estimate considered reasonable has been assumed. In other cases the respiratory rate of the species similar to those found at Moor House have been used.

be 0.00002967 cc./hr. or 0.000006742 cc./g wet weight of soil/hr. Soil samples taken from the same site on the 9.v.60 indicated that the soil respiration was about 0.04863 cc. O_2/g. wet weight of soil/hr. From this it would seem that nematodes were responsible for 0.014% of the total soil oxygen consumption.

Table 65. Nematode oxygen consumption estimates, Juncus site.

Population 1,949,000 (June, 1958 mean)

	Biomass: mg./m^2	Respiration: O_2 cc./m^2/hr.
Plant feeders	255.69	0.2838
Microbial feeders	112.03	0.0154
Dorylaimoidea	92.46	0.0777
Allowance for the unidentified group	17.88	0.0007
Total	478.06	0.3776

Note: This Table should be compared with Table 63 the explanation of whose derivation is given in the text on 'Biomass' (Section 1).

The soil respiration experiments referred to were carried out with a modified Swaby and Passey respirometer (see Birch & Friend, 1956) at 20°C. while Overgaard Nielsen's nematode respiration measurements are given for 16°C. His experiments with Mononchus papillatus (p.74) indicated that an increase in respiratory activity of about 20% took place for a temperature increase from about 16°C. to about 20°C. If an adjustment is made on this basis to the present writer's calculations, the oxygen consumption attributable to nematodes becomes 0.017% per gram of wet soil per hour. This is a very small proportion of the total soil respiration compared with 0.9% (range 0.5 - 1.2%) which Bunt (1954) estimated for Macquarie Island soils at 7°C. Its smallness will be even more strikingly realized when it is remembered that the population figures on which the calculation was based were means for a whole month. In actual fact the species composition of the population is bound to fluctuate and so the figure for respiration, as indeed that for the biomass, may at times be even smaller.

XII. GENERAL DISCUSSION.

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1. Nematodes in ecological studies.

In common with other soil micro-organisms, free-living nematodes are not easy to study ecologically. The technical difficulties and taxonomic demands (see Goodey, 1959) involved have been considered elsewhere. It is unjustifiable to dismiss these (cf. Hyman, 1959, p. 754 - 56) as a fastidious 'exaggeration of the worth of morphological differences' in the nematodes. The use of vague or inaccurate keys by ecologists who, understandably, resist being side-tracked into taxonomy is not commendable because it invalidates the zoogeographical importance of their findings.

Partly for this reason, extensive species lists produced by various continental authors (e.g. Franz, 1942; Gadea, 1956, 1957; Overgaard Nielsen, 1948b, 1949a; etc., also for other refs.) have not been given much attention. The second reason for ignoring species lists is that for the general aspects of nematode ecology dealt with in this work, which may be said to be 'synecological' (see Macfadyen, 1957), specific differences were not always found to be of vital significance and feeding-cum-ecological groups, as used by Overgaard Nielsen (1949a), have been found sufficient. This is not to deny that further advance in the study of the population ecology

of the free-living nematodes can only be possible when taxonomic knowledge will permit work with individual species. A start in this direction may be detected in the study of the boxwood spiral nematode by Golden (1956).

Enough has been said about the various problems associated with the sampling, extraction and handling of nematodes for biomass and respiration measurements. Further discussion is here reserved for other matters of wider implication which emerge in spite of, rather than because of, these problems. These matters comprise : the effect of the habitat factors and of the nematodes on each other and the role of these organisms in the energy turn-over in the soil.

2. Factors affecting free-living nematodes.

(a) Soil factors.

The soil in which the free-living nematodes and other micro-organisms live is a very complex substratum (Baver, 1956). It is basically made of mineral particles, the intervening spaces and pores being filled with differing proportions of soil water, air and organic matter in progressive stages of decomposition. The living conditions in such a medium depend on (1) the chemical and physical effects of these constituents, (2) the external influence of temperature and (3) the interrelation of the soil organisms. The relationships which emerge are so complex,

perhaps more so than in other media where life is found, that they can only be explained by invoking the well-known concept of the 'ecosystem' (Tansley, 1935).

It is, therefore, hardly surprising that no general agreement can be found in the literature about which factors most significantly affect soil nematodes. Soil mineral properties, moisture, pH, aeration, climatic factors, food and organic matter are among some that have been considered (Bunt, 1954; Dropkin, 1956; Franz, 1942; Overgaard Nielsen, 1949a; Steiner, 1952). Experimental work to assess the role of specific factors has demonstrated how these may operate to influence, for instance, hatching, migration and movement (see Wallace, 1959, 1960), but such work has further emphasized the enormity of the problem when it comes to explaining the field observations in terms of experimental results. It is especially difficult when, as in the present study, the nematode populations being dealt with are composed of different genera and species.

The soils at Moor House are characterized by low pH and excessive moisture (Table 1). In these properties, as well as in apparent productivity (Part III.3), they show a marked gradation. But this is not entirely paralleled by that of the nematode population sizes as estimated in this work (see Table 66). The grassland soils, a limestone mull with abundant earthworms on the one hand

and an alluvial flush on the other, did not yield the highest nematode population estimates. Thus in the Moor House habitats, nematodes do not seem to be necessarily more abundant under 'mull' than under 'mor' conditions (cf. Overgaard Nielsen, 1955, p. 207).

The percentage of the feeding ecological groups in the fauna also shows gradations. The plant feeders (all Tylenchoidea) increase, relative to the other groups, in the peaty habitats. The miscellaneous feeders (all Dorylaimoidea) increase from the peaty to the more mineral soils. Except on the Juncus site, the microbial feeders show a similar increase. A remarkable fact noticeable from Table 21 is the relative numerical insignificance in these moorland soils of the Dorylaimoidea and Mononchidae. According to Thorne the former group generally constitute 20 - 50% of the free-living nematodes (1939, p. 1) and the latter can make up as much as 13 - 22% (1927). At Moor House the only site on which the Dorylaimoidea were abundant was the Limestone Grassland. Examination of Overgaard Nielsen's Table 25 (1949a) shows that he found this group common in his raw humus areas. Mononchidae, however, were entirely absent from the Calluna and Vaccinium raw humus and bog soil habitats that he examined.

The differences in the vegetation of the areas sampled do not give any indication why, for instance, the

the grassland sites should possess a rich and more or less similar plant feeding nematode fauna while the Juncus moor, sharing certain elements of the vegetation with the Nardus grassland, should have only two genera (Tylenchus and Aphelenchoides). Similar inconsistencies in the distribution of the microbial feeders and predators are seen when, for example, the Calluna moor is compared with the residual Calluna hummock on Moss Flats. Neither in the case of both the microbial feeders and predators nor in that of the plant feeders can these distributional peculiarities be attributed to differences in food abundance. This is not intended to mean that when more is known about the food preferences of the microbial feeders, certain micro-organisms, perhaps less widely distributed, may not be found to play a greater part in the nematodes' food requirements than others. There is, in fact, some evidence that food selectivity may turn out to be important, not only for microbial but for plant feeders as well (see Hollis, 1957; Golden, 1956). But at Moor House no reason can be found to suppose that this factor was of great importance.

The pH of the soils did not vary very much from one site to another, with the possible exception of the Limestone Grassland site. However, in soils of this kind reducing and oxidising conditions may succeed each other with season as the water content of the soils changes

(Pearsall, 1950, p. 71). It is partly for this reason that the aeration of the soil is thought to be so important. Unfortunately, it was not possible to measure the 'redox' potentials in the peat but, especially during the wet periods, reducing anaerobic conditions extending to very near the surface, as in the waterlogged tropical swamps (Beadle, 1957), must often occur. The possibility of such a situation in some Moor House soils might explain the vertical distribution of the nematodes (Part VIII).

The general aeration of the soils on moorlands has been regarded as a critical factor in the abundance of the fauna in general (Pearsall, 1950, p. 214 - 15). In relation to the drainage of the different Moor House soils, it is probably the chief factor determining the faunal qualitative composition (Table 17). Thus the Dorylaimoidea which generally drown so easily (cf. Clapham, 1931), are more abundant on the better drained soils of the grassland sites. Also, they extend deeper where, as in the limestone mull, soil aeration is increased by earthworm burrows. Some mention may also be made of plant feeders. Most of the species, e.g. Rotylenchus robustus and Pratylenchus pratensis, which are generally recorded as 'found in meadow soils' are at Moor House to be found in the grassland site soils. Through influencing the qualitative composition of the fauna, soil aeration seems also to influence the general

population levels as estimated by the sampling techniques used here. This will be obvious from what has been said about some nematode species tending to form local aggregations.

The writer has rejected the view that the pore spaces of the peat might have a direct effect on the distribution, vertical or horizontal, of the nematodes because it will be clear from Plates 7 - 9 that the spaces available within the peat are vastly wider than the body diameter of even the largest of the nematodes encountered. Furthermore, Wallace (1960), working with Heterodera rostochiensis in fen peat, has found that the nematodes did not have a peak mobility at a single optimal water suction as they did in other soils. He postulated that this was because they could perform gliding movement aided by the 'smoothness' of the peat.

In Table 66 some of the nematode population densities obtained by various authors are given, together with those from Moor House soils. In view of what was said in Part VI about the sampling and extraction methods used by different workers, it is not intended that stringent comparisons be made between the data here presented.

Table 66. Some population densities of soil nematodes. Part of the Table is based on Peters, 1955b, Table 1.

Soil type	Millions/m^2	Source
From Moor House.		
Bare Peat	0.006 - 0.04	1958/9 samples
Calluna moor	0.5 - 2.3	1958/9 samples
Juncus moor	1.4 - 3.1	1958 samples
	2.3 - 6.5	1959 samples
Nardus Grassland	0.8 - 5.7	1959 samples
Limestone Grassland	1.8 - 2.9	1959 samples
From other areas.		
Arable (Scotland)	0.3 - 1.1	Robertson (1925) *
Arable (China)	0.5 - 1.5	Brown (1929)
Arable (U.S.A.)	0.25	Thorne (1927)
Arable (Austria)	10	Franz (1942)
Meadows (Austria)	8	Franz (1942)
Pasture (Denmark)	up to 20	O.Nielsen (1949a)
Pasture (China)	0.2	Brown (1929)
Sandy plain (Denmark)	0.8 - 1.3	O.Nielsen (1949a)
Raw Humus (Denmark)	2.4 2.7	O.Nielsen (1949a)
Woodland (Austria)	7	Franz (1942)

* Robertson used 'billion' for '1,000 million' in his original Table (see Russell, 1937, footnote p. 449).

(b) Climatic factors.

On the Juncus moor site there was, undoubtedly, a seasonal fluctuation in nematode numbers of the type that Seidenschwarz (1923) and Burkhalter (1928) observed in the Alps (Fig. 6). Although the results of sampling from the grassland sites were not extensive, they did not show any indication of a summer population decrease (Fig. 7). It is therefore conceivable that soil type and no doubt the qualitative composition of the fauna play a part in influencing the pattern of seasonal variation.

This seasonal variation pattern is, on the Juncus site, similar to that generally found for soil micro-arthropods (see Macfadyen, 1952; Evans, 1955). A summer decrease in numbers, with or without a subsidiary minimum in winter, has been found for enchytraeids (Peachey, 1959, unpub. thesis; Overgaard Nielsen, 1955) and protozoa (Cutler & Crump, 1935). According to Russell (1921, p. 279) some work has shown that, both in numbers and biochemical activity, bacteria may behave in the same way. Burges (1958, pp. 68-70) has discussed the variation of other microbial populations.

Climatic factors are assumed to be primarily responsible for these variations, although soil factors may play a contributory role. Both these affect, not

only the reproduction and development of the organisms, but also their survival and, in some cases, vertical migration and thus influence the findings of census sampling. The nematodes at Moor House were not found to perform seasonal vertical migrations like some of the enchytraeids (Peachey, 1959), nor was there any evidence that drought was responsible for the lower summer numbers on the Juncus area. Table 16 shows that there was no drying out of the peat in 1958 and that in 1959, although Fig. 6 shows that they had high nematode numbers, August and September had P/E values less than unity.

Seasonal food availability has also been suggested as probably responsible for the seasonal variation in the numbers of soil organisms (see Macfadyen, 1952, p. 105). Although this may be an ancillary factor, it cannot be the whole answer. It might be expected that the summer, with the generally increased temperatures and presumably better soil aeration would be a more favourable period for the soil organisms and they would increase rather than decrease in numbers. It may be that at present a comprehensive answer can not be given to this problem, because we are far from fully understanding how soil populations are regulated. In some cases, factors related to the population densities of the micro-organisms may be involved, possibly in conjunction with the soil factors. Thus, for example, the summer decrease could be related to the much higher

competition effects during the period of much larger densities in the spring. It is possible, too, that for the bacteria and other microflora, biochemical and antibiotic interactions (see Burges, 1958, p. 127 - 29) are operating. It is, therefore, difficult to make generalizations which would apply to all the groups.

Finally, it may be found, when investigations are carried out, that other micro-organisms on the Juncus site vary seasonally in the same way as the nematodes. Table 67 represents the subjective impression gained about the abundance of some micro-organisms in the nematode samples during the period March, 1958 to January, 1959. The extraction process used was not suitable for the estimation of these groups, but the relative increase in 'abundance' shown by the table is not unlike that shown in Fig. 6 for the nematodes.

3. Soil structure and the soil fauna with reference to the nematodes.

Much attention has been given to the soil fauna in relation to the structure of the soil. As a result of this pre-occupation, the soil animals have been divided into a microfauna and a macrofauna. The oft quoted criterion for this division is that the first group are independent of soil structure because they can burrow, while

Table 67. The abundance of some soil microfauna seen in sampling for nematodes: Juncus site, 1958 - 59.

Group	M	A	M	J	J	A	S	O	N	D	J
Ciliata	+	+	?	+		+	X	+	+		
Rotifera	+		?	+			+	+	+	+	X
Turbellaria (Prorhynchus)			?					+	+	+	X
Copepoda		+	?	+	+		+	+	+	X	X
Tardigrada	+	+	?		+		+	+	X	+	+
Chironomidae (Larvae)			?							+	X
Acari			?	+		+	+		X		

Key: + commonly found

? month not sampled

X very abundant

the second group cannot alter the physical structure of the soil and so must live in the pre-existing soil spaces (Overgaard Nielsen, 1949a, p.58; Russell, 1959, p.95; Stöckli, 1946; Weis-Fogh, 1948, p.239). According to this system, however, depending on the structure of the soil, an organism could belong to the microfauna in one locality and to the macrofauna in another. Apparently this could even hold for the nematodes.

Another group of authors has taken the absolute size of the organisms in question and the methods used in their extraction and study as a basis for their classifications (Fenton, 1947, p.76; Gilyarov, 1941; Murphy, 1953, 1955; van der Drift, 1951). The size ranges that these authors have erected are shown in Table 68 from which it will be clear that they are arbitrary and cut across the taxonomic groups.

Besides being arbitrary, the two schemes of soil fauna classification place undue emphasis on the mechanical influence, or the lack of it, that the soil fauna has on its environment, ignoring the fact that at the 'microhabitat' scale the distinction between the fauna's physical and chemical effects on the soil cannot be satisfactorily drawn. For many of the taxonomic groups there is no detailed knowledge about their effect, whether physical or chemical, on the soil. The writer's use of

Table 68. Classifications of the soil fauna according to size.

Group	Eumicrofauna	Microfauna	Mesofauna	Macrofauna	Megafauna
Gilyarov (1941)	microscopic and invisible to naked eye	non-microscopic, small forms; up to several mm. long.	non-microscopic, larger invertebrates; several mm. to several cm. long.	non-microscopic invertebrates inhabiting soil	-
Fenton (1947)	-	1 - 40μ long	just visible with hand lens to several cm. long	large vertebrates	-
Van der Drift (1951)	-	0.02 - 0.2 mm. long	0.2 - 2 mm. long	2 - 20 mm. long	2 - 20 cm. long
Murphy (1953)	-	<100μ long	200μ - 2 mm.	2 mm. - 2 cm.	-
Rapoport (1959)	-	0.02 - 0.2 mm. long	0.2 - 2.0 mm. long	2.0 - 20 mm. long	> 20 mm. long

the term 'micro-', with various combinations, has neither of the implications of pedological function or size ranges. It is just applied to organisms which it is impossible to handle and study without a microscope.

The distinction between the micro- and macro-fauna on the basis of burrowing activity can be shown to be rather false (see Kühnelt, 1955, p.6). Oligochaete enchytraeids as well as most of the soil micro-arthropod groups depend on decaying litter, soil fungi or plant roots as the major source of their food. These substances are acknowledged as important complements to the mineral fraction in making up the soil. By 'eating their way' through the soil in this way the micro-organisms are acting differently from the earthworms, for example, only in degree and not kind. Furthermore, it is now realized that the casting activity for which the earthworms have been celebrated since the time of Darwin's studies (1881), is, to a certain extent, carried on also by the microfauna (Kubiena, 1955). These micro-organisms build, through their faecal pellets, 'coprogenous' humus forms (see Kevan, 1955).

Although nematodes do not burrow or 'eat their way' through soil organic matter, the plant feeders among them cause modifications in the root systems of the plants on which they feed. Such modifications range from simple

devitalization of root tips, through necrosis and root rot to severe curtailment of the root system as a whole, a phenomenon which sometimes leads to the roots giving off an excessive number of branches (see Christie, 1959, p.12 - 17). This is all well known from the agricultural side, but recently Golden (1956), working with a free-living nematode Rotylenchus buxophilus (= Gottholdsteineria buxophila according to Andrássy, 1958), has been able to demonstrate how nematode infestation affects the size of the root system. He found a 5% significance difference between the weights of the roots of inoculated and control English boxwood plants (Buxus sempervirens var. suffruticosa) after 8 months' growth, the root system of the controls weighing 6.4 g. more. After 12 months this difference was almost doubled.

By affecting the development of plant roots in this way nematodes, undoubtedly, affect soil structure indirectly, even if, despite their numerical abundance, their direct mechanical effect may be presumed to be almost non-existent.

4. The role of nematodes in energy turn-over.

Besides the arbitrariness and the false emphasis they put on the mechanical effect of the soil fauna, there is a third objection to the schemes of soil organism classification discussed above. They do not help in the evaluation

of the organisms in the soil pyramid of numbers.

The concept of the 'pyramid of numbers' (Elton, 1927) integrates the food-chain relations of communities, using the word 'community' in the sense of Macfadyen (1957, p. 238). The latter author has also reviewed the allied concepts of the 'trophic levels', 'biomass' and 'activity of communities' (see ch. 9 - 10). As he makes it clear, the objective of these concepts is to help in understanding how energy is mobilized in communities. In a soil community, this problem resolves into that of understanding the role of the soil organisms in the carbon cycle, on the one hand, and in the mineral cycles, to which the nitrogen cycle really belongs, on the other. These cycles are dealt with by Burges (1958, ch.vii). As was stated in Part III. 3, the carbon and nitrogen cycles are linked, their 'tempo' in the soil being roughly expressed by the C/N ratio and to some extent by the biomass of the living organisms in that particular soil habitat.

The functional food-chain relations of soil organisms, with special reference to forest soils, have been reviewed by Birch & Clark (1953). In spite of criticisms which have been advanced against them (see Macfadyen, 1957, p. 119 - 20), their review can be regarded as pointing in the right direction. They arranged soil organisms into trophic levels starting with the litter as the primary

source of food. Fig. 8 is a food-chain diagram modified from theirs. Overgaard Nielsen (1949a, p. 103) has illustrated the feeding relations of nematodes and his information was drawn upon by Birch & Clark.

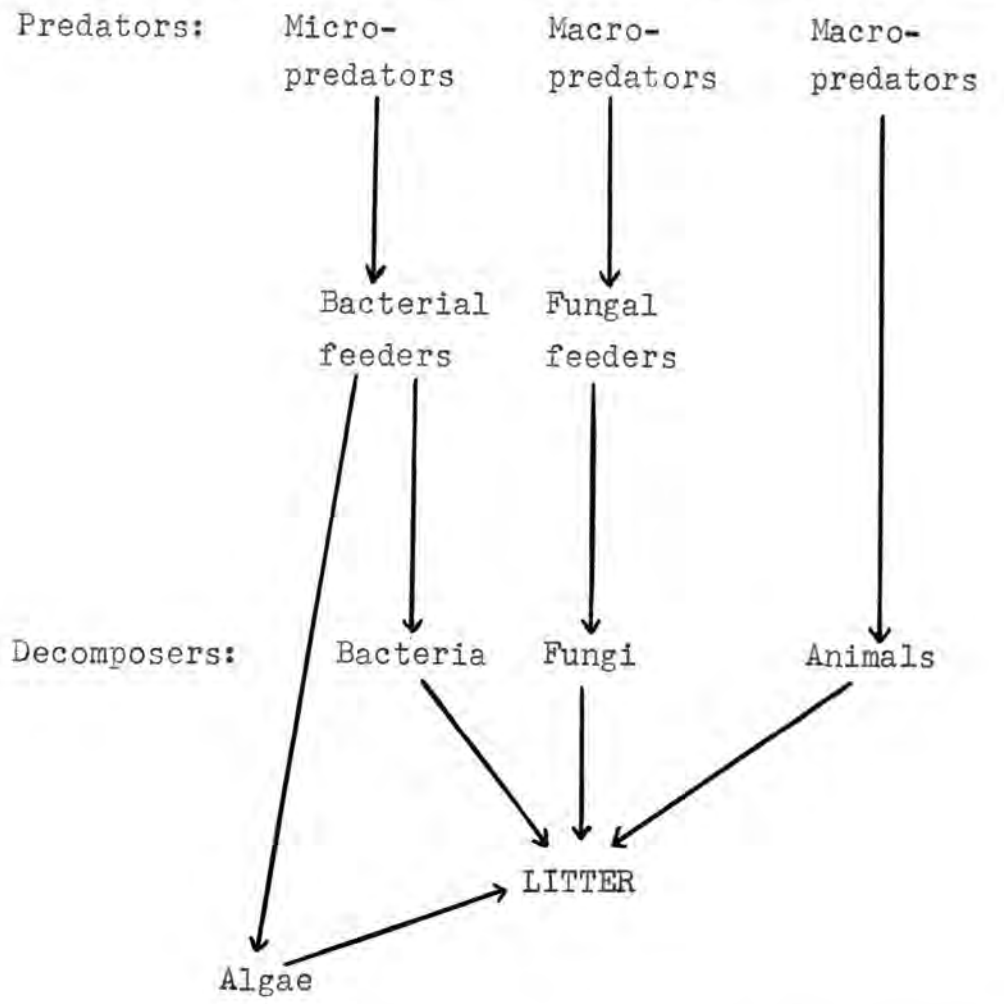

Fig. 8. Food-chain relations of soil organisms (modified after Birch & Clark, 1953).

⟶ indicates 'feed on'.

Both Overgaard Nielsen's and the present writer's results have shown that the nematodes come higher in the trophic level hierarchy than the decomposers. Also, there is strong evidence from the work on the axenic culture of the Rhabditid Caenorhabditis briggsae that a labile protein substance, so far termed Factor Rb, is important for their development and reproduction (Dougherty, E.C., et al, 1959; Nicholas, W.L., et al., 1959). Such a substance might not be expected to occur in humus.

The view, so widespread, that nematodes are 'saprophagous' must, therefore, be completely abandoned, as Overgaard Nielsen (1949a) has said. They do, however, play an important role in as far as some of the plant feeders (probably all the plant feeding genera in Table 17 except Tylenchus and Aphelenchoides) utilize the organic matter of living roots, thus by-passing the stages of the decomposers and the litter in Fig. 8. It is worth remembering that Birch & Clark (see p. 13), because of their emphasis on humus formation, minimized the importance of animals feeding directly on plant roots while a moment's reflection on, for example, wireworms will show how important they can be. As regards the nematodes, the work on the boxwood spiral nematode, referred to in Section 3, is an example.

In Part XI figures for the biomass and for the estimate of the respiratory role that the nematodes play on an area of Juncus moor were given. The calculations were based on the mean monthly population estimates, but it is, nevertheless, striking how small they are. They would have been even smaller on the waterlogged Calluna moor although on the grassland sites the abundance of larger nematode forms might have slightly counter-acted against the smaller population figures. Investigations which have been carried out on the Juncus moor habitats for Lumbricidae, Enchytraeidae and Tipulidae have shown that "total biomasses of the order of 200 g. per square metre can occur" (Cragg, 1959, unpub.), against which the nematode figures appear insignificant. Table 69 shows the writer's biomass figure together with two other estimates given by continental authors.

If the soil respiration measurements on which the calculation for the nematode respiratory role in Part XI, 2 is based turn out to be of the right order of magnitude, the part of nematodes in moorland peat soil respiration would seem to be very small. Indeed, it would appear that most of the contribution to the oxygen consumption in these soils is attributable to the microflora. Since few animal groups have so far been investigated, it would be premature to make further comparisons at present.

Table 69. Some estimates of nematode biomass in g./m^2 fresh weight.

Author	Biomass	Pop. in millions/m^2	Habitat and depth
Stöckli (1946)	5.0		Swiss grass field, 15 cm.
O. Nielsen	4.5	1.7	Danish spruce raw humus, 5 cm.
Banage	0.48 0.75	1.9 3.1	Juncus moor peat, 6 cm.

Note: the figure by Stöckli is taken from Overgaard Nielsen (1949a).

The present study indicates that a clear picture of the ecological importance of the free-living nematodes will necessitate a lot of future work, keeping in mind fundamental ecological principles. The results obtained here have a wider significance not only in outlining some of the problems to be overcome in future studies, but also in indicating how much caution should be taken in looking at work published in the past. In particular, caution should be exercised with regard to the sweeping generalizations that are often encountered.

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