

# THE FAUNA OF GRASSLAND SOILS WITH SPECIAL REFERENCE TO ACARI AND COLLEMBOLA

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## INTRODUCTION

Soil animals may be classified into various categories depending on size (Fenton 1947; van der Drift 1951), degree of dependence on the soil (Jacot 1940), mode of locomotion (Kühnelt 1955) or life form (Gisin 1943; Klima 1956). The first is the most widely used and a simple division is into micro-fauna (0.001mm–0.1mm), meio—or meso—fauna (0.1mm–10mm) and macro-fauna (over 10mm). The micro-fauna includes protozoa, nematodes, tardigrades; the meso-fauna, mites, collembolans, enchytraeids; and the macro-fauna, earthworms, molluscs and many insects, myriapods and spiders. This classification is obviously arbitrary, and some groups (e.g. spiders) have representatives in more than one category.

Grassland soils contain many individuals and many species from each of these groups. Acari and Collembola are generally the most abundant arthropods, and in this paper their ecology will be considered with particular reference to their population density, communities and role in certain soil processes.

## POPULATIONS OF ACARI AND COLLEMBOLA IN GRASSLAND SOILS

The population densities and numbers of species in different grassland soils in Britain, continental Europe and northern United States

of America are shown in Table 1. Despite their variety the first seven habitats (moorland, fenland and old pasture soils in England, an old pasture in Denmark and an old meadow in northern U.S.A.) have remarkably similar population densities (178,000/m.<sup>2</sup>–298,000/m.<sup>2</sup>). Considering the populations in mosses of 280,000/m.<sup>2</sup> (Wood 1963) and in natural heathland of 162,000/m.<sup>2</sup> (Murphy 1963), it appears that population density of these small arthropods cannot be usefully used as a distinguishing characteristic of a particular habitat. This suggestion is not necessarily discredited by the very low population densities (35,000/m.<sup>2</sup>–59,000/m.<sup>2</sup>) recorded from the last six sites shown in Table 1, as the extraction methods used in these particular investigations (with the possible exception of Dhillon and Gibson's method) almost certainly incurred serious losses of certain groups, thus making an unknown contribution to the low recorded populations. Because of the great differences in efficiency between the various extraction methods it is not profitable to speculate about causes of possible differences in population densities.

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TABLE 1. Population density (thousands/m.<sup>2</sup>) and number of species of Acari and Collembola in grassland soils. (Number of species in parentheses.)

Author	Habitat	Acari	Collembola	Total
Salt <i>et al</i>	old pasture	232 (—)	66 (25)	298 (—)
Macfadyen	<i>Molinia</i> fen	172 (52)	32 (21)	204 (73)
Hairston and Byers	old meadow	221 (87)	14 (20)	235 (107)
Haarlov	old pasture ("Level Pasture")	179 (161)	109 (32)	288 (193)
Wood	<i>Sesleria</i> (III)	153 (103)	25 (25)	178 (128)
	<i>Festuca-Agrostis</i> (IV)	152 (87)	73 (26)	225 (113)
	<i>Nardus</i> (V)	176 (90)	59 (25)	235 (115)
Weis-Fogh	old pasture ("Plain")	24 (83)	8 (16)	32 (99)
Sheals	old grassland	34 (36)	23 (18)	57 (54)
Wood	old pasture	33 (—)	26 (21)	59 (—)
Dhillon and Gibson	old pasture	32 (19)	26 (16)	58 (35)
Davis	reclaimed ironstone workings (1)	15 (43)	20 (23)	35 (66)
	old pasture (100)	18 (51)	18 (21)	36 (72)



Mean density of Acari and Collembola is probably meaningless in itself, and the figures quoted indicate that it may not even be useful for comparative purposes. In fact, a feature of most investigations on soil micro-arthropods is the great seasonal variation in population density in any particular site, with the result that fluctuations in density are more readily related than the mean to site conditions.

COMMUNITIES OF ACARA AND COLLEMBOLA IN GRASSLAND SOILS

Over 100 species are found in most grassland soils (Table 1), and whereas the variety of

Collembola (16-32 species) is fairly uniform, that of Acari (19-161 species) is not. Dhillon and Gibson (1962) compared the published lists of species from ten old grasslands in Britain, although in most cases the fauna was incompletely identified and there were unavoidable errors in identification. However they were able to show that the species composition of these apparently similar habitats was very variable, and of the 63 species of Collembola recorded, only five were recorded from seven or more of the ten fields and 40 were recorded from only one.

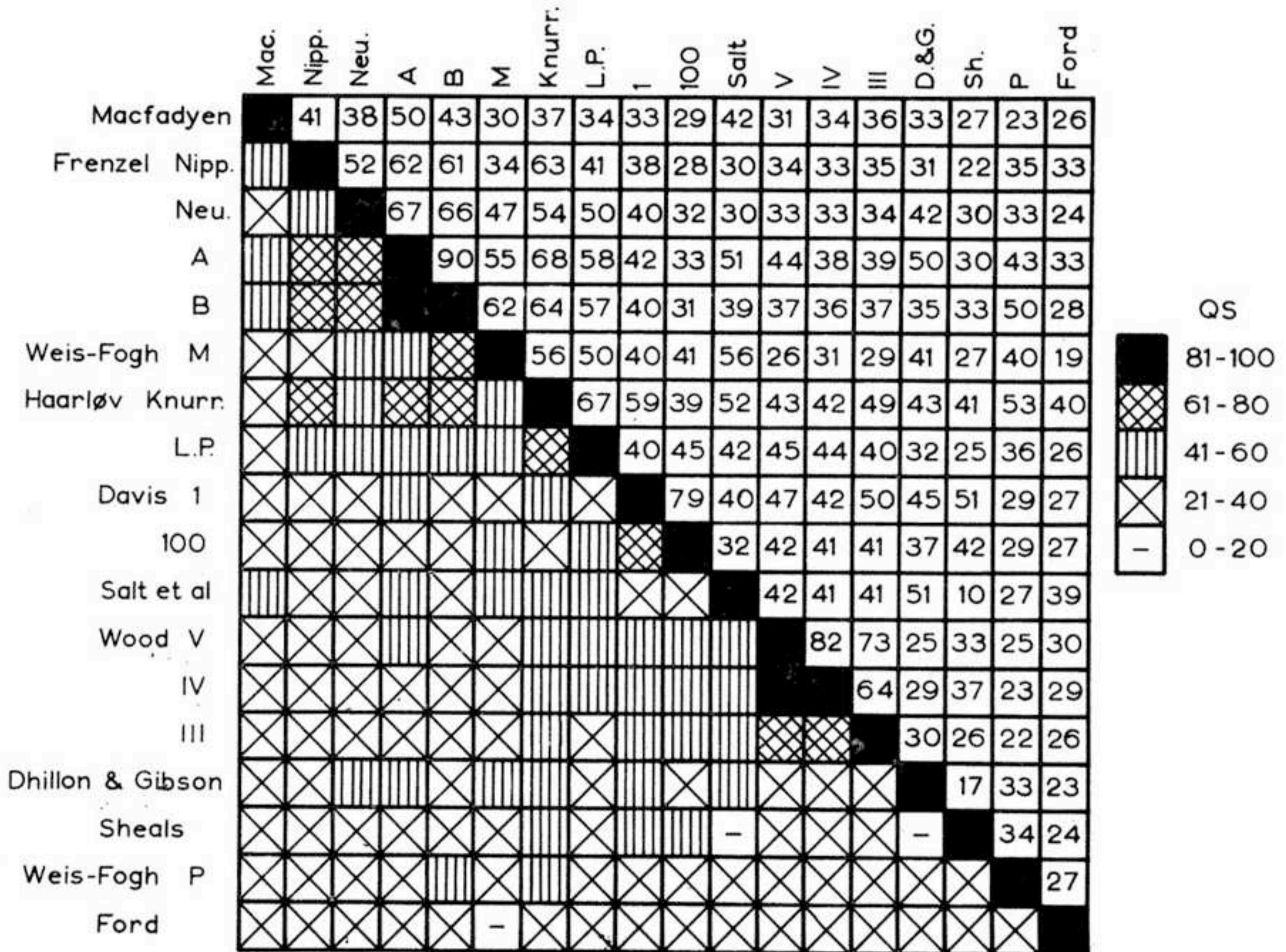


FIGURE 1. Comparison of species-composition of Collembola in various grassland soils. For explanation see text. Details of authors and habitats as in Table 1 with the addition of:—  
 Haarlov (1960)—LP: "Level Pasture" (see Table 1).  
 —Knurr: old pasture, north and south facing sides of ant mounds, Knurrevang. Brown earth, sandy loam.  
 Weis-Fogh (1948)—P: "Plain" (see Table 1).  
 —M: old meadow, "Meadow" and "Southern Meadow". Brown earth, sand.  
 Ford (1937)—Ungrazed *Bromus* grassland (tussock fauna only).  
 Frenzel (1936)—A: Hundsfeld, dry meadow, unmanured.  
 —B: Hundsfeld, dry meadow, manured.  
 —Neu: Neuhaus, moist meadow.  
 —Nipp: Nipperrn, wet Cyperaceae meadow. Poland, nr. Wroclaw (Breslau).



A comparison of the species of Acari and Collembola from several grassland soils in Britain and continental Europe is shown in Figs. 1 and 2. With one exception (Ford 1937) the comparison includes only those studies where identification of species was reliable and reasonably complete. For this reason the information on mites refers only to Mesostigmata and Cryptostigmata. The lists of species from each habitat were compared using Sorensen's (1948) quotient of similarity (QS) which is given by—

$$QS = \frac{2c}{a + b} \times 100$$

where, for any two habitats,  $c$  is the number of species common to both and  $a$  and  $b$  are the total number of species from each habitat. The figures obtained enable the habitats to be compared with each other in the form of a trellis diagram in which the habitats with the most similar faunas (highest QS values) are placed closest together.

The most obvious conclusion from the comparison of Collembola (Fig. 1) is that communities in different soils in the same locality (Frenzel's, Haarlov's, Davis's, and Wood's sites) are more similar (QS values of 52-90) than communities from different localities (QS values of 10-68). Excluding Weis-Fogh's site P, the Collembola communities of different grasslands in continental Europe (Frenzel's, Weis-Fogh's M and Haarlov's sites) show reasonable similarities to each other (mean QS = 54). There is less similarity among the Collembola of British grasslands (mean QS = 38), and in fact greater similarities are found between the very different sites studied by Davis and by Wood (mean QS between localities = 49) than between the four old agricultural grasslands (mean QS = 30) studied by Davis (site 100), Dhillon and Gibson, Sheals and Salt *et al.* It is perhaps surprising that the Collembola of Macfadyen's *Molinia* fen near Oxford have closest affinities with Frenzel's east European sites.

The comparison of Acari (Fig. 2) shows very clearly that the communities of different grassland soils in the same locality are very similar (QS values of 60-83), whereas there are few similarities between soils from different localities (QS values of 0-56). Similar conclusions may be drawn from Franz's (1963) com-

parisons of the oribatid mites in a variety of heathland and forest soils in Finland, Sweden and central Europe.

These comparisons of Acari and Collembola in 18 different grassland soils involved over 500 species. Very few occurred in more than 12 sites and among these were *Tullbergia krausbaueri* (Börn), *Folsomia quadrioculata* (Tullb.), *Isotoma viridis* Bourl. (Collembola), *Rhodacarus roseus* Oudms. (Mesostigmata), *Tectocephus velatus* (Mich.), *Minunthozetes semirufus* (C.L.K.) and *Punctoribates punctum* (C.L.K.) (Cryptostigmata). The majority (more than 90% of the total) might appear to be distributed by chance and to substantiate Haarlov's (1960) suggestion that microarthropod communities may be made up of species derived from the species-complex in the immediate surroundings (in a geographical sense), and that the species-composition of a particular habitat may be quite different from that of similar habitats in different localities. However, as Davis (1963) expressed it, the essence of community ecology rests on the "conviction that the presence and relative abundance of a number of species in a circumscribed area means more than that each of them happens to be there separately". Thus the occurrence of a particular group of species in a number of habitats would lead one to expect that the habitats in question had certain properties in common. For example the *Zygoribatula exelis* (Nic.)—*Eremeus oblongus* C.L.K. community of dry mosses, is of fairly constant species-composition in such widely-separated areas as northern England (Wood 1963), Germany (Strenzke 1952; Knülle 1957) and Austria (Pschorn-Walcher and Gunhold 1957). In more complex environments, such as grassland soils, the pattern (if it exists) is less obvious and the factors determining the occurrence of species are so little understood that more often than not what appears to be a uniform habitat as regards vegetation, soil type and various physical and chemical properties of the soil, may consist of a number of distinct habitats as far as the small soil arthropods are concerned. The environment of these animals consists of the network of soil cavities and the 'jungle' of root hairs and fungal hyphae, and it is unlikely that this environment can be adequately described in terms of soil type, vegetation or by quantitative measurements of soil properties such as pore space and organic matter. The lack of adequate descriptions of



		A	B	Neu.	Nipp.	V	IV	III	Mac.	1	100	L.P.	Knurr.	Sh.	M	P	D.&G.	Ford
Frenzel	A	73	56	43	24	23	31	33	15	12	25	14	13	20	26	10	8	
	B		52	36	23	20	26	36	16	13	19	12	11	28	26	7	12	
	Neu.			35	27	27	24	27	12	14	15	14	15	28	14	6	6	
	Nipp.				30	22	26	25	6	17	9	10	12	12	11	8	17	
Wood	V					83	61	34	21	29	17	21	31	16	13	15	13	
	IV						65	36	23	24	20	23	25	27	9	17	12	
	III							34	23	29	23	26	25	31	12	13	16	
Macfadyen									19	23	26	31	12	34	13	3	9	
Davis	1									62	12	17	29	26	23	32	15	
	100										23	23	26	30	21	37	10	
Haarløv	L.P.											69	26	23	30	9	4	
	Knurr.												22	15	36	17	13	
	Sheals													17	9	24	15	
Weis-Fogh	M														28	5	31	
	P															0	17	
Dhillon & Gibson																	6	
Ford																		

FIGURE 2. Comparison of species—composition of Acari (Mesostigmata and Cryptostigmata only) in various grassland soils. For explanation see text, Table 1 and Fig. 1.

these animals' environments may go a long way towards accounting for such apparent anomalies as an old pasture in Northamptonshire (Davis' site 100) having proportionately as many or more species of Collembola in common with each of three very different moorland soils (Wood's sites III, IV and V) as it has with three other old grassland soils in Britain (Salt's, Sheals' and Dhillon and Gibson's sites).

#### ROLE OF ACARI AND COLLEMBOLA IN SOIL PROCESSES

The significance of mites and Collembola in the life of the soil can be considered only in

relation to total animal activity. Of the many aspects of this subject, only two will be considered here: the pedological significance and contribution to total soil metabolism of these two groups.

#### Pedological significance

Interest in the pedological significance of soil animals was increased by Kubiena's (1943, 1953) studies of thin soil sections from different humus forms, which led him to state (Kubiena 1955) that the progress of humification (i.e. decomposition of organic matter) moved parallel with the accumulation of animal



excrement in the soil. A recent classification of grassland humus forms (Barratt 1964) indicates that soil animals play an important role in determining the characteristic features of their micro-fabrics. Edwards and Heath (1963) demonstrated, by a series of exclusion experiments, that there was no breakdown of litter in the absence of soil animals. Their experiments showed that earthworms removed litter three times faster than other invertebrates, the most important of which appeared to be Collembola, Enchytraeidae and Diptera larvae. Oribatids, although numerically abundant did not appear to be important in the breakdown of litter.

The role of soil animals in litter breakdown and the development of humus forms may be clearly seen by comparing three moorland soils in northern England. Their pedological features were studied by Barratt (1960) and their fauna by Wood (1963). The soils are: a mull-like rendzina developed from limestone and found under *Sesleria caerulea* (L.), a brown earth of low base status developed from heavy textured, shaley drift and found under *Festuca-Agrostis*, and a gleyed, weakly podsollic brown earth developed from similar drift material and found under *Nardus* grassland. These are sites III, IV and V respectively in Table 1 and Figs. 1 and 2. The activities of soil fauna may be considered in relation to the different processes influencing the fate of plant material:

1. Accumulation of litter
2. Comminution of litter
3. Incorporation with mineral soil—
  - (a) mechanical incorporation
  - (b) chemical incorporation involving the formation of "clay-humus complexes".

The mull-like rendzina is a shallow (8cm.), black, A/C soil developed on Carboniferous limestone. There is no surface accumulation of litter, and initial comminution of the dense *Sesleria* tussocks appears to be due to the dense population (about 3,000/m.<sup>2</sup>) of snails (five species, the most abundant of which is *Lauria cylindracea* da Costa) which feed principally at the soil surface and in the base of the tussocks. These snails skeletonise the plant material and produce a mass of fine, black excrement. Further comminution of vegetable debris and its thorough incorporation with mineral material (calcite) can be largely attributed to woodlice, (*Oniscus asellus* L.) aided by a small,

specialised earthworm fauna (*Lumbricus festivus* (Sav.) and *Allolobophora chlorotica* (Sav.)). The effectiveness of woodlice in comminuting plant material and incorporating it with mineral soil is evident from laboratory cultures where these animals rapidly convert a loose mixture of soil and plant litter into a mass of cylindrical droppings. Under field conditions factors such as high rainfall and the activities of earthworms are probably responsible for the rapid breakdown of this excrement. The absence of clay minerals from limestone weathering precludes the formation of clay-humus complexes, and the humus fabric has the appearance of a mull-like rendzina moder.

The brown earth and the podsollic brown earth are developed on heavy-textured, non-calcareous, shaley drift (30-70 cm. deep), and have acid (pH 3.5-4.8) surface horizons. There is no accumulation of litter in the brown earth, although there is a distinct organic-rich A<sub>1</sub> horizon. Comminution of plant material is largely caused by insect larvae, living predominantly in the A<sub>1</sub> horizon, and earthworms (about 300/m.<sup>2</sup>). The fabric of the A<sub>1</sub> horizon is a mull-like moder of which the dominant constituents are the excrement of insect larvae, particularly that of larvae of Bibionidae (*Bibio lepidus* Loew: > 3,000/m.<sup>2</sup>) in which organic and mineral material are mixed. Surface-active earthworms, of which the most abundant are *Eisenia rosea* (Sav.) and *Allolobophora caliginosa* (Sav.), give a superficial mull-like appearance to this horizon, and the predominantly coprolitic nature of the fabric is evident only in microscopic preparations. The workings of *Lumbricus terrestris* L. and to some extent *A. caliginosa* are evident in the A<sub>2</sub> and B horizons of the soil where the fabric has the appearance of a weak mull humus.

The accumulation of dead and partly decomposed plant material in distinct L, F and H layers in the gleyed podsollic brown earth can be related to the absence of effective comminuting agents such as earthworms (< 35/m.<sup>2</sup>) and saprophagous or phytophagous Diptera larvae. The L layer has a raw humus fabric consisting almost entirely of undecomposed *Nardus* litter with abundant fungal hyphae and little animal excrement. Partly decomposed plant material is the dominant constituent in the F layer, but there is some comminution and in microscopic preparations, excrement of micro-arthropods is evident. In



the H layer decomposition is more complete and the excrement of micro-arthropods less distinct, possibly because of their destruction by enchytraeids and Diptera larvae, although there is no apparent incorporation of organic and mineral material. The fabrics in the H and F layers are coarse (silica) moder and fine (silica) moder respectively.

These three soils occur within a distance of 250 yd. That they have very similar population densities of micro-arthropods and of Enchytraeidae suggests that when other invertebrates are abundant, as in the mull-like rendzina and the brown earth, these groups of animals (the meso-fauna) have little pedological significance. The three processes, enumerated above, influencing the fate of plant material may now be considered in the light of our knowledge of the fauna of these three soils. In the absence of comminution and incorporation, litter accumulation leads to raw humus formation (L layer, gleyed podsol brown earth); accumulation and comminution without incorporation leads to moder formation (F and H layers, gleyed podsol brown earth); comminution and mechanical incorporation produce mull-like moder fabrics (mull-like rendzina and A<sub>1</sub> horizon of the brown earth) and, with chemical incorporation, lead to mull formation.

#### *Contribution to total soil metabolism*

The pedological approach emphasises morphological aspects of the effects of soil animals on soil; and, of the many hundreds of species of invertebrates present in most soils, only a few are of direct pedological significance. Another approach to assessing the significance of a particular species or group of soil animals is to study its position in the "food web", thus assessing in a qualitative way its contribution to the circulation of nutrients through the soil. No such food web has been constructed for soil animals, but Brauns (1954) has shown how complex such relationships are among Diptera larvae in forest litter. Macfadyen (1963) has attempted to overcome these complexities by estimating the flow of energy at various trophic levels in a grazed meadow. He estimates that about 80-90 per cent. of the total soil metabolism stems from micro-organisms (bacteria, protozoa, etc.) and the remaining 10-20 per cent. from soil animals, of which the small decomposers (Acari, Collembola, Enchytraeidae, Nematoda) contribute two

fifths, that is, less than 10 per cent. of the total. However, he (1961, 1963) suggests that the activities of these small arthropods may have indirect effects on the total soil metabolism far greater than the direct effects of their own metabolic rates. This could arise through stimulation of microbial activity by means of distribution of spores, elimination of mycostasis and bacteriostasis and the encouragement of microbial growth by grazing on senescent colonies. If this hypothesis is true, the effect of insecticides in inducing quantitative and qualitative changes in soil fauna is likely to be reflected in changes in soil fertility. On the one hand the marked reduction in saprophagous micro-arthropods after the application of certain insecticides, such as BHC (Sheals 1956), could result in a decrease in total soil metabolism and the locking up of energy in the form of undecomposed plant debris. On the other hand, certain saprophagous micro-arthropods, such as Collembola (Satchell 1955; Sheals 1956) are not affected by DDT, whereas predaceous arthropods such as Mesostigmata and various Coleoptera are killed and the significant increase in Collembola populations following applications of DDT (Sheals 1956) could result in an increase in energy flow and liberation of nutrients.

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## NOTES:

Salt, Hollick, Raw and Brian (1948): mean of 8 samples (Nov. only) (numbers 12-20), 12 in. deep; flotation extraction 0.1 mm. mesh. Cambridge, England. Brown earth, clay loam.

Macfadyen (1952): mean of 120 samples, 5 cm. deep, corrected to depth of 15 cm. from Macfadyen's date; Tullgren funnel extraction. Oxford, England. Organic peat.

Hairston and Byers (1954): mean of 35 samples, 8.5 in. deep; Tullgren funnel extraction. Southern Michigan, U.S.A. Brown earth, sandy loam.

Haarlov (1960): mean of 26 samples, 6 cm. deep; Tullgren funnel extraction. Denmark. Brown earth, sandy loam.

Wood (1963): means of 20 samples, 8 cm. deep (III), or 12 cm. deep (IV and V); Tullgren funnel extraction. Yorkshire, England; III—mull-like rendzina, organic loamy sand; IV—brown earth, silty clay loam; V—podsolc brown earth; organic layered mor.

Weis-Fogh (1948): mean of 270 samples, 5 cm. deep, plots I to VII only; Berlese funnel extraction. Denmark. Brown earth, sand.

Sheals (1957): mean of 40 samples, 6 in. deep; flotation extraction, 0.15 mm. mesh. Glasgow, Scotland. Brown earth, clay loam.

Wood (unpub.): mean of 42 samples, 9 in. deep; flotation extraction, 0.15 mm. mesh. Northumberland, England. Brown earth, clay loam.

Dhillon and Gibson (1962): mean of 90 samples 6 in. deep; Tullgren funnel extraction. Leeds, England. Brown earth, sandy loam.

Davis (1963): means of 36 samples, 3 in. deep corrected to depth of 9 in. from Davis' data; flotation extraction, 0.15 mm. mesh. Northamptonshire, England. Brown earth, sandy clay.