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Succession of invertebrate populations in artificial soil made of sewage sludge and crushed bark

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The animal succession was investigated in test plots made of different mixtures of sewage sludge and crushed bark. Three kinds of sludge (digested, activated and limed) were compared with each other. A fresh mixture of digested sludge and bark was compared with a composted one, with each of the initial materials alone, and with a compost heap made of the same materials. All the materials were compared with cultivated field, garden grassland and forest soil.

Flying insects and the phoretic nematodes and mites transported by them colonized fresh mixtures in a few days and reproduced rapidly. Later they became less numerous. Collembola increased within some weeks and remained important throughout the succession. Oribatei immigrated into more aged materials. The community at the early stages of succession was typical of dung and related accumulations of easily decomposable matter. The succession was rapid at first but gradually slowed down, the community changing through a less specialized "compost stage" into a generalist soil fauna. However, even in the oldest test material the community differed considerably from that in the adjacent arable soil. Mesostigmata showed the highest and Collembola the lowest degree of specialization to different substrates.

Of the fresh mixtures, that with activated sludge showed the highest total biomass, and that with digested sludge the lowest. Digested and limed sludges proved to be harmful or toxic to lumbricids and enchytraeids. Composting was shown to accelerate the succession. The succession in a mixture of sludge and bark was more rapid than in either of the two components alone.

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1. Introduction

The continuous increase in the efficiency of waste water treatment in the developed countries has resulted in rapid growth of the supply of sewage sludge, which contains the solid materials and a considerable part of the nutrients present in sewage. So far, however, proper arrangements have not been made for utilizing this sludge; in recent years in Finland only ca. 30 % has been used. There is now a strong movement, supported by the authorities, to organize the recycling of sewage sludge either in agriculture, or in the establishment of parks and other green areas in urban regions (Latostenmaa 1976).

Another waste material available in large quantities in the northern countries is the bark produced by pulp mills (Isomäki 1974). In several experiments this bark has proved to promote the humification of sewage sludge, since these two materials complement each other well in respect of their C:N ratios and nutrient contents.

The biology of sewage treatment processes has been thoroughly investigated, including the animals involved (for a review, see Curds & Hawkes 1975). In contrast, little is known about the processes taking place in the sludge after it has left the treatment plant. The only reports published to date, with the exception of that of Lagerlöf & Andrén (1978), concern the effects on certain groups of organisms of sludge applied as fertilizer to cultivated soil (Höller 1959, Höller-Land 1959, Kreuz 1963, Hunt et al. 1973, Habicht 1975). These usually confirm what is generally known about the effects of manures (reviewed by Marshall 1977), but sludge has also been shown to possess some special characteristics (Höller 1959). There are a number of papers dealing with animal successions in composts made of various organic materials (survey of the literature, with special reference to sludge and sludge compost, published by Steen et al. 1976). As a material, sludge resembles animal droppings, which have been the subject of much ecological work (reviewed e.g. by Valiela 1969), but the latter are discrete, temporary microhabitats, ecologically different from compost or deposits of sludge, which have a more permanent nature.

The present paper reports the zoological results of a research project financed by the Finnish Academy. The microbiological part and the results of physical, chemical and productivity analyses will be dealt with elsewhere. A brief general report in Finnish was published recently (Huhta et al. 1978). The aim of the study was to investigate the biological processes occurring during the humification of different sludge materials, with particular reference to the use of sludge as artificial soil in landscape gardening.

2. Material and methods

A. Experimental design

Three kinds of sewage sludge were used for the experiments:

1. Digested sludge[1] from a biological-chemical treatment plant (Helsinki, Tali). The treatment is based on the activated sludge method, with simultaneous precipitation of phosphorus using ferrosulphate. Prior to use the sludge was dried to 20 % dry matter content (on drying beds in 1973—74, mechanically in 1975).
2. Activated sludge[1] (without digestion) from a biological-chemical plant (Hyvinkää, Martti). Ferrosulphate used for precipitation, and lime and ferric chloride for conditioning. Dried mechanically.
3. Limed sludge from a chemical plant (Lohja), lime amounting to ca. 50 % of dry substance. Machine-dried.

The crushed bark was pine bark (1974—75) and spruce bark (1977), received from the pulp mills of Kaukopää and Summa, respectively, which are owned by the Enso-Gutzeit Company.

The following study objects were established from these materials:

Symbol	Description
D	Test plots made of fresh digested sludge and pine bark (1:1 by volume).
A	Test plots made of fresh activated sludge and spruce bark.
L	Test plots made of fresh limed sludge and spruce bark.
C	Test plots made of digested sludge and pine bark after one year's composting.
H	Compost heap made of fresh digested sludge and pine bark.
DI	D inoculated with natural mull soil (5 % inoculum (volume) mixed with the topmost 5 cm of the test plots).
DS	D with sand added (ratio sludge: bark: sand 1:1:0.75 by volume).
CI	C inoculated with mull (cf. DI).
CS	C with sand (cf. DS).
B	Test plot made of bark only.
S	Test plot made of fresh digested sludge only.

The following control plots were established:

F	Plots on forest soil (birch stand) from which the inoculum was taken for DI and CI.
—	Plots on arable land surrounding the test plots, which was further divided into:
T	Land tilled before the experiment, but treated like the ordinary test plots during the study.
G	Garden grassland, untilled, with no treatment.

A and L were established in May 1977, the others in May-June 1975. The composting of the material for C, CI and CS was started in Sept. 1973 and June 1974 (two heaps, which were combined for the experiment). The fresh sludge for the experiments was taken as soon as possible after leaving the drying machine, and transported to the study site with lorries. The test materials were first thoroughly mixed with the aid of tractors. The experimental plots were established on a small parcel of field belonging to the Agricultural Research Centre, situated in Tikkurila, 20 km north of Helsinki (60°17'N, 25°05'E). Before application of the test materials, the topsoil (depth of tillage) was removed, and the surface of the mineral soil was levelled. The test materials were arranged in rectangles measuring ca. 3.5×4 m (depth ca. 25 cm), and separated from each other and from the surrounding intact soil with subsoil (fine sand) taken from the site. On these were marked out sample squares with an area of 3×3 m. This was also the area of the control plots F, T and G. In June 1977 the test materials DS and CS were removed

[1] The activated sludge technique is a biological process where the nutrients contained by the sewage are transformed into microbial biomass in aerated containers. The microbial cells flocculate together with fine suspended particles, sediment and form sludge, part of which is returned to the process. The other part is collected together with coarser solid material separated in the presedimentation, and excess water is removed. This is what we call 'activated sludge'. It includes phosphorus precipitated by adding chemicals to the aerated containers (simultaneous precipitation). Activated sludge is turned into 'digested sludge' by rotting for ca. 30 days (average) in anaerobic conditions in digestion tanks.

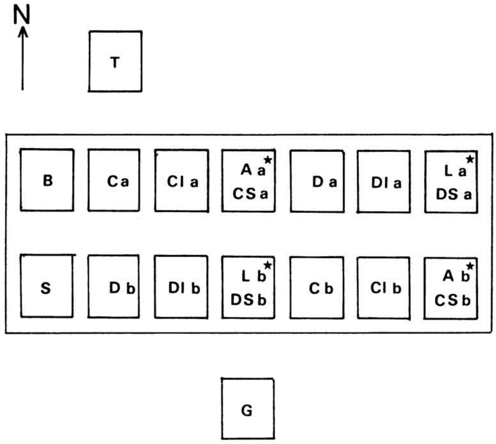


Fig. 1. Scheme of the experimental field at Tikkurila. For explanation of the abbreviations see p. 224. Asterisks = established in 1977.

and A and L were established on the same plots. The main test materials were thus represented by two replicate plots, a and b (Figs. 1 and 2).

A mixture of two lawn grasses, *Lolium multiflorum* (annual) and *Festura rubra* (perennial), was sown on each plot except F and G (ratio 3:1, 20 g/m²). The plots were watered at first, but only as much as was necessary for the initial development of the grasses. The amount of water received by each plot was estimated and added to the precipitation recorded.

The compost heaps were established in the area of the sewage treatment plant at Tali, Helsinki.

B. Results of preliminary investigations

A preliminary investigation was made (Uusitalo 1975) in order to obtain a general picture of the numbers and distribution of the different animal groups in the sludge soils and compost, and to test the efficiency of the extraction methods for sludge materials. The results can be briefly summarized as follows:

1. The horizontal distribution of populations is more or less aggregated. Logarithmic transformation of the data before statistical treatments is desirable (Elliot 1971). To reach an accuracy of ± 20 % in the population estimates at a probability of 0.95, a minimum of 10 sample units should be taken.
2. There are significant differences in the numbers of animals at different depths, thus at least two different horizons should be included in the samples.
3. The differences between the three extraction methods tested for nematodes were not significant, but on average more animals were recovered by the decantation—filtration method of Oostenbrink (1960) than by the elutriation method of Seinhorst (1956, 1962a) or the sugar-centrifugation technique (a modification developed at the Agricultural Research Centre, Finland).
4. For the extraction of Microarthropoda, the infrared high-gradient extractor of Lussenhop (1971) was superior to the hot rod apparatus of Valpas (1969), to the flotation method of Raw (1955), and to the standard dry funnel, the latter being the second most efficient equipment.
5. The wet funnel technique can be recommended for Enchytraeidae, but if the material is mixed with a mineral component, the result should be checked by Nielsen's (1955a) method.

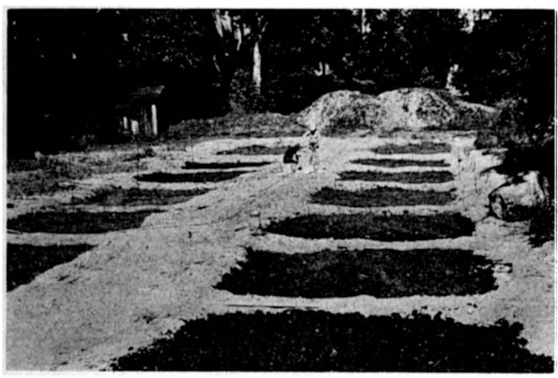


Fig. 2. The experimental field at Tikkurila on 23 June 1975.

C. Sampling and extraction

The main study objects were sampled at intervals of four to five weeks during the summer half of the year. The first samples were taken immediately after the plots had been established, and the second after an interval (June 1975) of only two weeks, in order to examine the early colonization of the materials. The control plots were sampled only three times a year, and samples for macroarthropods were taken less often than those for the other groups (usually twice a year).

The sampling was continued for three growing seasons, with the following exceptions: DS, CS and F were studied in the first year only. The sampling of H, DI and CI was stopped after the second year. Three additional samples for microarthropods and lumbricids were taken from A in 1978.

Samples were taken separately for nematodes, enchytraeids, microarthropods and macroarthropods. The macroarthropod samples consisted of 25 × 25 cm squares of the topmost 5 cm of soil, taken with a kind of spade with a straight, sharpened lower edge. The other groups were sampled with cylindrical steel corers, inside which were placed plastic rings with a height of 3 cm. The inner diameter of the rings was slightly wider than that of the cutting edge of the corer. The rings were kept in position by a detachable handle, fitting through holes in the walls of the corer. The handle was also used as a piston when the contents were pushed out through the upper end of the corer. The core was cut into pieces with a sharp knife inserted between the rings. Only the layers of 0—3 cm and 6—9 cm were kept for extraction, the rest was discarded. The area of the corer was 9.4 cm² for nematodes and microarthropods, and 25 cm² for enchytraeids.

Though the corers worked well in normal soil, some difficulties were encountered when samples were taken from fresh sludge. The sample often became compacted inside the corer, preventing the penetration of further material, so that the blocked corer only forced the soft soil aside. The sample obtained was usually acceptable (at least the lowest three rings were filled), but it was uncertain whether the contents of the rings exactly represented the corresponding depths *in situ*. The first samples from fresh plots were taken by simply filling the rings with the material with the aid of a spoon.

Each sample was composed of 10 units taken at random from the area of the test plots (10 units from a single plot, or 5 from each of the duplicates). To minimize the time of storage, samples were usually taken in two parts (5+5 units) at intervals of one week. Each unit was placed in a separate plastic bag and transported to the laboratory, where it was stored in a refrigerator and treated within one week.

The nematodes were extracted from the samples using the decantation-filtration technique of Oostenbrink (1960), as modified by Huhta & Koskenniemi (1975). From each homogenized initial unit (28 cm^3), a subsample of 1/6 was taken for extraction. When population densities were high, a further subsample for counting was taken after extraction.

The wet funnel method (O'Connor 1962) was used for the extraction of enchytraeids, Lussenhop's (1971) infrared high gradient extractor with some modifications for the microarthropods, and the large closed Tullgren funnels of Huhta (1972) for the macroarthropods. The lumbricids were also taken from the latter samples, because, due to limited resourccs and low numbers of worms, it was decided not to adopt a separate method for this group.

D. Counting, identification and estimation of biomasses

The following groups were identified to species level: Nematoda, Annelida, Araneae, Mesostigmata, Oribatei, Collembola, and adult Coleoptera. The determinations of Enchytraeidae were only qualitative (not all of the samples were checked), and detailed results concerning Oribatei and Coleoptera will be published later. Nematoda, and also Collembola in the first year, were identified only on every second sample unit. Unidentified samples (or specimens) were counted and measured under dissecting microscopes provided with ocular grids (cf. Huhta & Koskenniemi 1975). The biomasses were estimated in fresh weights, using different methods for each group.

Nematoda. Only adult nematodes were identified. Before identification the animals were fixed and prepared by the method of Seinhorst (1962a, 1966b). The classification is based on Andrassy (1976).

The average individual weights for unidentified specimens were obtained according to Andrassy (1956), by measuring 30 to 120 specimens from each of the size classes from 0.15 to 0.8 mm. A length-weight regression was calculated from these data, and estimated weights for each size class were derived from the formula obtained,

$$W = 0.49 \cdot L^{1.87} \quad (r = 0.975),$$

where W = weight in μg, and L = length in mm. Weights for identified adults were obtained either directly from Andrassy (1956), or by measuring. These are given in Appendix 1.

Enchytraeidae. 100 worms were taken from the preserved sample collected from test plots C in May 1977. Their lengths were measured, and their thickness at three points (1/4, middle, 3/4). Using the average density and the equation for body volume given by Abrahamsen (1973a), the fresh weight of each specimen was calculated, after which a length-weight regression was obtained:

$$W = 6.29 \cdot L^{1.83} \quad (r = 0.906)$$

The animals were identified living, but counted after preservation in alcohol.

Lumbricidae. The length-weight regressions given by Abrahamsen (1973b) were employed.

Mesostigmata. All adults and deutonymphs were identified; larvae and protonymphs were left undetermined, whether identification was possible or not. The average weights were obtained separately for males, females and deutonymphs in each species and in each size category of the unidentified specimens, using various methods:

1. Direct weighing was preferred for the abundant species.

A minimum of five living animals per species and stage were weighed with a microbalance to an accuracy of 0.1 μg.

2. Dry weighing with transformation to fresh weights was applied to common species for which insufficient living material was obtained. The animals weighed were taken from alcohol-preserved samples. Transformation was done by multiplying the dry weights by 2.0 (Uropodina), 2.5 (Gamasina with thick cuticle) or 3.0 (others). These coefficients are based on experiments where the same individuals were weighed alive and after preservation in alcohol.

3. Fresh weights were derived from the formula given by Persson & Lohm 1977:

$$W = 0.85(L^{2.09} \cdot l^{0.84} \cdot 10^{-6.44}), \text{ where}$$

L = length and l = width of idiosoma

When the weighed and calculated values were compared, systematic biases were found in the calculated weights, depending on the shapes of the animals. Therefore, the calculated values were corrected in some cases as follows:

Uropodina: correction	— 25 %
Dendrolaelaps spp:	— 20 %
Parasitus spp. adults:	+ 20 %
Parasitus spp. deutonymphs:	+ 50 %

4. The values of Persson & Lohm (1977) were used directly when these existed.

5. For the unidentified specimens, a length-weight regression was calculated using the lengths and weights (weighed or calculated) of deutonymphs of the 11 most abundant species in the material (these were thought to represent most accurately the larvae and protonymphs of the average fauna). The equation obtained was:

$$W = 268.12 \cdot L^{3.69} \quad (r = 0.99)$$

The exact weights are given in Appendix 3.

Collembola. All the specimens were identified whenever possible, and the numbers counted in size categories consisting of 0.1 mm intervals for specimens up to 1 mm and 0.2 mm intervals for larger ones. The biomasses were estimated with the length-dry weight regressions given by Tanaka (1970) and Petersen (1975). The regressions for species with similar shapes were used for species for which direct data were not available. The dry weights were transformed to fresh ones using the dry:fresh weight ratios of Petersen (1975). Detailed references are given in Appendix 2.

For unidentified samples, the average weights for each size category were calculated separately for each test plot, using the dominant species present.

Remaining groups. Average individual weights for adult Coleoptera were partly obtained from the data of Koskela & Hanski (1977), and partly estimated from shape-specific length-weight regressions. Dry weights were transformed to fresh ones by multiplying them by 2.0. The statistical calculations, however, were based on unidentified material, for which regressions given by Huhta & Koskenniemi (1975) were employed. These were also used for Araneae, Chilopoda, Prostigmata + Astigmata, Oribatei, coleopterous larvae, and dipterous larvae.

All the numbers and biomass values were transformed to units per square metre. All the figures given in this paper refer to the sum of the two sample horizons 0 to 3 and 6 to 9 cm (0 to 5 cm only for macroarthropods and lumbricids). If the change between the two depths is assumed to be linear, estimates for the topmost 9 cm can be obtained by multiplying the values given by 1.5. The numbers of animals occurring below the sample depth were not estimated. The estimates of the total biomass were obtained by simply summing the values of all the groups, though the sample depths were not identical. In some cases, when the macroarthropod samples were not taken in the same months as the main samples, the data of two successive months were combined to obtain an estimate of the total biomass.

The statistical calculations were performed on the summed figures from the two depths. The test plots were compared with each other and with the control plots using the analyses of variance on two or three dimensions (plot, time, duplicate). This was done separately for each year. The original figures were transformed logarithmically [ln (X+1)] before the calculations. Only samples taken simultaneously from the two test objects to be compared were included in the analyses, and the first samples from fresh material, which contained practically no animals, were also omitted. The results of the analyses are given in Appendix 5. The calculations were made with the aid of a computer at the Computer Centre of the University of Jyväskylä.

E. Other parameters measured

In addition to the zoological investigations, the following parameters were measured by the research team (Huhta et al. 1978):

Physical and chemical measurements. Precipitation, ambient temperature, soil temperature, water holding capacity, water content (percentage of weight and of WHC), water potential, percentage of aggregates, volume weight, pore volume, air volume, loss on ignition, pH, conductivity, base exchange capacity, contents of Ca (exchangeable), K (exchangeable), P (easily soluble), and Mg (exchangeable), total N (%), total P (%), C:N:P, redox potential, and contents of heavy metals (Pb, Cd, Zn and Ni) in soil and vegetation.

Microbiological parameters. Total numbers of bacteria (mesophiles, thermophiles), numbers of Clostridia, Streptomycetes, Protozoa, glucose-fermenting bacteria, length of fungal hyphae, numbers of ammonifying, denitrifying and nitrate-reducing bacteria, nitrification activity, numbers of indicators of hygienic status (faecal coliforms, faecal streptococci, *Clostridium perfringens*), oxygen consumption, dehydrogenase activity, and decomposition of cellulose.

Botanical studies. Species composition, net primary production.

The results of these investigations are presented briefly by Huhta et al. 1978.

3. Results

A. Numbers, biomass and species composition in the control soils (T, G and F)

Nematoda. The average annual densities of

Table 1. Yearly average numbers (ind./m²) of different groups in the control soils T, G and F.

	Tillage (T)			Garden grassland (G)			Forest (F)
	1975	1976	1977	1975	1976	1977	1975
Nematoda	1 350 000	810 000	1 320 000	940 000	970 000	1 930 000	1 670 000
Enchytraeidae	11 900	7 700	26 800	17 500	9 400	22 500	6 600
Lumbricidae	2	6	10	61	48	34	21
Collembola	14 000	19 500	23 100	28 400	25 300	39 100	26 500
Oribatei	3 300	12 700	38 400	12 900	18 300	12 900	30 100
Prostigmata + Astigmata	14 700	23 200	32 200	19 800	16 700	25 900	111 500
Mesostigmata	2 700	1 300	4 000	7 700	4 000	9 200	6 400
Chilopoda	5	25	63	30	3	18	65
Araneae	14	21	51	288	189	197	160
Coleopterous adults	40	88	342	288	192	336	161
Coleopterous larvae	93	83	197	1 253	496	646	528
Dipterous larvae	358	269	248	288	192	411	208

Table 2. Yearly average numbers of Nematoda (100 ind./m²) in the control soils (T, G, F).

	Tillage (T)			Garden grassland (G)			Forest (F)
	1975	1976	1977	1975	1976	1977	1975
Wilsonema sp.	–	–	17	28	–	34	14
Anaplectus sp.	227	–	17	64	96	43	69
Plectus sp.	–	–	17	74	11	26	180
Teratocephalinae sp.	–	–	–	–	–	17	–
Cephalobus persegnis	110	39	60	294	333	255	5
Eucephalobus oxyuroides	–	28	–	11	43	68	5
E. cf. striatus	–	21	9	–	–	–	–
Eucephalobus sp.	–	–	–	87	32	196	19
Acrobeles ciliatus	287	333	323	17	85	–	–
Acrobeloides cf. nanus	–	–	9	9	–	9	35
Panagrolaimus rigidus	43	7	51	21	46	–	9
Rhabditis oxycerca	–	18	–	–	–	9	–
Rhabditidae spp.	53	–	–	11	11	9	–
Bunonema reticulatum	–	21	–	19	11	9	–
Diplogasteridae spp.	–	–	–	–	–	26	–
Aphelenchoididae spp.	–	50	162	21	35	94	100
Tylenchinae spp.	181	103	68	111	135	519	68
Tylenchorchynchidae spp.	1064	641	1242	64	74	31	52
Pratylenchus sp.	113	362	–	162	138	153	9
Criconematidae sp.	–	–	–	351	–	–	–
Prismatolaimus cf. intermedius	–	–	–	–	–	–	5
Mononchus sp.	–	–	–	–	–	–	5
Prionchulus sp.	–	–	–	9	–	–	–
Dorylaimidae spp.	14	14	34	45	46	60	194
Undet. adults	78	85	43	132	121	94	45
Juveniles	11 322	6 393	11 155	8 202	8 519	17 671	15 878
Total	13 492	8 115	13 207	9 434	9 736	19 323	16 692

nematodes in the control soils ranged from less than one million to ca. 2 million/m² (Table 1), and the biomasses from ca. 100 to 200 mg/m². Their contribution to the total biomass was rather small (Fig. 3). The species present in the three sites were mainly the same, but they differed in their dominance relations (Table 2). The species composition was very similar in the tillage and the grassland, but the number of species was somewhat higher in the grassland soil. From the structure of the mouthparts, it may be concluded that the species of the arable soil feed mainly on plant liquids and/or fungal hyphae. *Acrobeles ciliatus* and species of Tylenchorchynchidae (mainly the genus *Tylenchorchynchus*) were very abundant in the tillage. The subfamily Tylenchidae and the genus *Pratylenchus* were numerous in both the tillage and the grassland, while *Cephalobus persegnis* was dominant only in the grassland.

Enchytraeidae. The numbers and biomass of enchytraeids fluctuated strongly, being lowest in the second year and highest in the third one (Table 1, Fig. 3). In all years, this group was considerably less abundant in the tillage than in the grassland soil. The number of species was relatively low in all the control sites (Table 3).

Lumbricidae. Together with enchytraeids, earthworms were the main component in the total biomass (Fig. 3). The numbers were very

Table 3. Species of Enchytraeidae present in the control soils.

	Tillage	Garden grassland	Forest
Fridericia bisetosa (Levinsen 1884)	+		
F. bulbosa (Rosa 1887)	+		+
F. ratzeli (Eisen 1872)		+	+
F. bulboides (Nielsen & Christensen 1959)	+		
Fridericia spp.	+	+	
Henlea verticulosa (Udekem 1854)	+		
Marionina diverticulata (Nurminen 1970)		+	

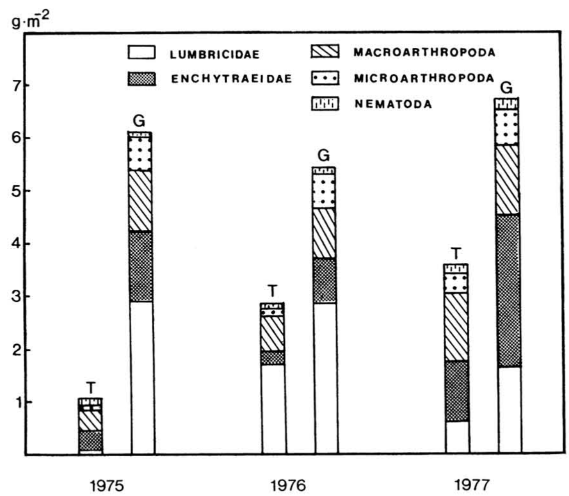


Fig. 3. Yearly average biomasses of soil animals in the control plots tillage (T) and garden grassland (G).

low in the tilled soil, but showed an increasing trend. It must be remembered that the sample depth (0 to 5 cm) reveals only part of the total population. The dominant species in the arable soils was *Lumbricus castaneus* (Sav.). Other species recorded were *Allolobophora caliginosa* (Sav.), *Dendrobaena octaedra* (Sav.), and *D. rubida* (Sav.).

Collembola. The numbers and biomasses were higher in the grassland than in the tilled soil. The yearly average density in the tilled soil increased by ca. 65 %, and the biomass more than fourfold from 1975 to 1977. The highest density and biomass occurred in the grassland in 1977 (Table 1, Fig. 33). The species composition was fairly similar in the two sites, though there were differences in the proportions of the species, and the number of species was higher in the grassland (Table 4). *Tullbergia krausbaueri* and *Friesea mirabilis* were among the most abundant species in the tilled soil, while *Onychiurus armatus*, *Folsomia fimetaria* and *Isotoma notabilis* predominated in the grassland.

Oribatei. The average numbers of oribatids in the tilled soil increased ca. tenfold during the study period (Table 1). The change in the biomass was of the same order of magnitude. In the grassland soil the numbers did not fluctuate so greatly, the highest mean being recorded in 1976. In the third year the density of oribatids in the tillage exceeded that in the grassland, but their biomass still remained about half as high. The dominant species in the tillage were *Brachychthonius* sp., *Tectocepheus velatus* (Mich.) and *Oppia nova* (Oudms.). The most numerous species in the grassland were *Achipteria punctata* (Nic.), *T. velatus* and *Scheloribates confondatus* (Sell.), in 1977 also *Brachychthonius* sp.

Prostigmata and *Astigmata.* On average, the numbers and biomass of Prostigmatid mites were of the same order of magnitude in the tillage and in the grassland soil. In the tillage the numbers showed an increasing trend, but not the biomass. Prostigmata were very abundant in the forest site (Table 1).

Mesostigmata. The yearly average densities ranged from 1300 to 9200 /m^2, and the biomass from 6 to 180 mg/m^2. The numbers were clearly higher in the grassland than in the tillage (roughly 2 to 3-fold), and the difference in the biomass was even greater (2 to 20-fold). There was a strong increase of biomass in the tilled

Table 4. Yearly average numbers of Collembola (100 ind./m^2) in the control soils T and G.

	Tillage (T)			Garden grassland (G)		
	1975	1976	1977	1975	1976	1977
Hypogastrura manubrialis	32	14	1	6	1	2
H. denticulata	2	21	4	–	–	–
Willemia intermedia	–	–	1	–	–	–
Friesea mirabilis	9	25	53	–	6	1
Anurida granaria	–	–	–	2	3	–
Neanura muscorum	–	1	1	–	–	1
Onychiurus armatus	3	1	34	35	50	100
Tullbergia krausbaueri	114	104	81	18	27	40
T. affinis	–	–	–	–	–	2
T. quadrispina	–	–	5	16	15	29
Folsomia fimetaria	24	7	8	26	23	27
Isotomodes productus	–	–	1	2	8	38
Proisotoma minuta	9	3	7	6	4	9
Isotoma notabilis	2	–	6	76	74	100
I. viridis	–	8	9	15	3	2
I. propinqua	–	–	1	–	–	–
I. propinqua var. *pectinata*	–	–	1	–	3	–
I. tigrina	–	–	1	–	6	7
Isotomurus palustris	–	–	1	37	1	23
Lepidocyrtus sp.	–	6	11	3	5	5
L. lanuginosus	–	1	12	49	15	15
Dicyrtoma minuta	–	–	–	–	2	–
Sminthuridae spp.	4	6	–	5	6	4
Undet.	–	1	1	–	1	2
Total	140	195	231	284	253	391

soil from 1976 to 1977. Both the density and the biomass were lowest in the second year (Table 1, Fig. 33).

The tillage and the grassland differed sharply in the species composition. The dominant species in the tillage were *Dendrolaeleps foveolatus*, *Rhodacarellus silesiacus* and (in 1975 only) *Arctoseius cetratus*, all very small in size. The fauna of the grassland site was more varied, many species being dominant (Table 5).

Macroarthropoda. Araneae and Coleoptera (larvae and adults) were considerably more numerous in the grassland than in the tillage, while the numbers of Chilopoda and dipterous larvae were of the same order of magnitude (Table 1). The densities and biomasses of most groups were low in the tillage in the first year, but increased markedly in the following years, especially those of adult beetles. Dipterous larvae showed a decreasing trend in abundance, but an increasing one in biomass. The dominant

Table 5. Yearly average numbers of Mesostigmata (100 ind./m²) in the control soils T and G.

	Tillage (T)			Garden grassland (G)		
	1975	1976	1977	1975	1976	1977
Discourella modesta	—	1	—	6	3	11
Phaulocylliba orbicularis	—	—	1	1	—	4
Fuscuropoda marginata	—	—	1	—	—	—
Urosternella cf. foraminifera	—	—	1	—	—	—
Macrocheles merdarius	1	—	—	—	—	—
Ameroseius corbiculus	1	—	—	—	—	—
Proctolaelaps sp.	1	—	—	—	—	—
Cheiroseius borealis	—	—	—	1	—	—
Arctoseius cetratus	7	1	—	—	—	1
Rhodacarus coronatus	1	1	3	14	10	8
Rhodacarellus silesiacus	1	1	11	—	—	1
Dendrolaelaps zwoelferi	2	—	—	—	—	—
D. foveolatus	3	7	6	—	2	—
D. arvicolus	—	—	1	—	—	—
D. strenzkei	—	2	1	—	2	—
Dendrolaelaps spp.	—	—	—	—	—	1
Pergamasus suecicus	—	1	—	1	1	7
P. quisquiliarum	—	—	—	—	1	—
P. norvegicus	—	—	2	1	—	1
P. truncus	—	—	—	5	3	6
Pergamasus spp.	—	—	—	—	1	—
Parasitus cf. tichomirovi	—	—	1	1	—	—
P. cf. kraepelini	—	—	—	3	1	3
Parasitus spp.	—	—	—	1	—	—
Veigaia kochi	—	—	—	1	—	1
V. nemorensis	—	1	3	18	3	17
V. cf. exigua	—	—	—	4	1	4
V. cervus	—	—	—	—	—	1

Table 6. Yearly average numbers of Araneae (ind./m²) in arable soil (tillage T and grassland G pooled).

	1975	1976	1977
Dicymbium nigrum	6	4	2
Oedothorax apicatus	—	1	—
Tiso vagans	2	—	—
Tapinocyba pallens	1	2	3
Micrargus subaequalis	—	1	—
Erigonella hiemalis	18	22	10
Savignia frontata	1	2	2
Diplocephalus latifrons	2	3	3
Erigone dentipalpis	2	2	4
E. atra	—	2	1
Meioneta rurestris	2	1	—
Centromerita bicolor	2	1	2
Bathyphantes parvulus	—	—	1
Bolyphantes index	—	—	1
Lepthyphantes mengei	—	—	1
Total adults	36	40	30

species of spiders were *Erigonella hiemalis*, *Diplocephalus latifrons*, *Dicymbium nigrum* and *Erigone dentipalpis* (Table 6). All except *E. dentipalpis* were more numerous in the grassland than in the tillage.

Total biomass of animals. The untreated test plot on grassland soil can be considered to show the natural "backround" variations in the soil animal populations. The total biomass of soil animals in G was lowest in 1976 and highest in 1977. This pattern was especially evident in one group, Enchytraeidae, which is an important constituent in the biomass. The low numbers of enchytraeids in 1976 may be explained by the effect of severe frosts during the preceding winter (cf. Huhta in press). The high summer precipitation in 1977 probably contributed to the increase in the third year; enchytraeids are known to be sensitive to changes in soil moisture (Nielsen 1955b, O'Connor 1967, Abrahamsen 1972).

In the tillage the total biomass increased from year to year, as did also the biomasses of most of the individual groups. It has been shown by several investigations that populations of soil invertebrates are generally sparser in cultivated soils than in similar soils under permanent grass cover (Tischler 1955, Edwards & Lofty 1969, 1975, Karg 1961). Agricultural activity destroys the soil structure and stops the natural succession of the community at a pioneer stage.

When the test plot was sown for grass and left intact for three years, rapid development of soil populations was possible (Fig. 3).

B. Succession in uncomposted mixture of digested sludge and bark (D)

Nematoda. The nematodes were very numerous as early as one week after establishment of the plots, and increased towards the autumn (Fig. 4, Table 7). In the second year they were less abundant, but high densities were met again in May 1977. Both absolutely and relatively, the biomass was higher in D than in the control soils, especially in the first year (cf. Figs. 3 and Tables 2 and 7).

At first the dominant species changed very rapidly (Fig. 5, Table 7). *Pelodera cf. chitwoodi*, *Diploscapter coronata*, and species of Rhabditidae were among the first colonists. *Rhabditis oxycerca* became abundant in the first autumn, constituting ca. 50 % of the individuals in the second year, and 75 % in the third. In the older material the succession slowed down: from summer 1976 onwards the dominance relations remained practically unaltered. Nevertheless, even in the last year the species composition still differed considerably from that of the control soils.

Enchytraeidae. The first enchytraeids were met in autumn 1975, but the population remained very sparse until July 1977 (Table 8). Enchytraeids were thus one of the last groups in the succession, being the most dominant group in the biomass in the two last samples (Figs. 4 and 8). Even then their biomass did not reach the level prevailing in the control soils. The population consisted of a single species *Enchytraeus minutus* Nielsen & Christensen.

Collembola. In the first two samples (June 1975) only a few specimens of springtails were found, but after that their numbers increased rapidly, exceeding those in the control soils by the first autumn (Table 8). Their density decreased abruptly during the winter, but increased again during summer 1976. The highest numbers (146 500/m^2) were recorded in July 1976, when they were about fourfold the control densities. In the third year the numbers did not fluctuate so widely, but the mean density remained high. The course of the biomass was rather similar (Fig. 4). *Hypogastrura manubrialis* and *Proisotoma minuta* were the most numerous species in the first two years, and their occurrence showed distinct seasonal variation (Fig. 6). *P. minuta* had its highest density in the second

Table 7. Monthly average numbers of Nematoda (100 ind./m^2) in uncomposted mixture of digested sludge and bark (D). SE = standard error of the mean of 10 sample units.

	1975						1976					1977		
	VI	VI	VII	VIII	IX	X	V	VI	VII	VIII	IX	V	VII	IX
Cephalobus persegnis	–	–	–	–	–	13	–	–	–	–	48	–	–	–
Acrobeloides cf. nanus	–	–	–	38	191	13	23	–	14	223	96	13	64	102
Panagrolaimus rigidus	–	–	–	26	32	434	35	–	28	223	48	217	370	64
Pelodera cf. chitwoodi	326	915	32	–	–	–	12	128	–	–	–	–	–	–
Pelodera sp.	780	85	–	–	–	–	–	–	–	–	–	–	–	–
Rhabditis oxycerca	–	–	–	89	862	306	23	255	1106	766	1979	868	1914	2297
R. cf. inermis	28	–	64	–	–	–	–	–	–	–	–	–	–	–
Rhabditidae spp.	–	85	160	26	32	77	–	–	–	–	–	–	13	–
Diploscapter coronata	–	21	64	740	160	38	–	–	–	–	–	–	64	–
Butlerius cf. filicaudatus	–	–	–	–	64	13	–	–	–	–	–	–	–	–
Diplogasteridae spp.	–	64	–	32	–	–	–	–	–	–	–	–	13	–
Aphelenchoides bicaudatus	–	–	–	–	383	1544	–	43	–	64	–	13	51	13
Aphelenchoididae spp.	–	–	32	1148	926	1123	476	85	113	447	367	217	89	102
Tylenchinae spp.	–	–	–	–	–	191	46	–	128	32	–	–	–	13
Tylenchorchynchidae spp.	–	–	–	–	–	–	–	–	–	–	–	13	51	64
Undet. adults				13	–	13	–	–	–	–	–	–	38	13
Juveniles	23 400	32 900	41 400	78 200	92 600	67 000	42 100	22 800	32 300	37 800	16 200	55 300	48 500	29 400
Total	24 500	34 000	41 800	80 300	95 200	73 700	42 700	23 400	33 700	29 500	18 700	56 600	51 200	32 000
SE	5 900	4 500	6 500	8 200	11 200	10 600	3 600	4 700	7 300	6 000	3 900	11 200	5 700	4 100

Table 8. Numbers of Collembola and Enchytraeidae (100 ind./m²) in uncomposted mixture of digested sludge and bark (D). × = no sample. The numbers are the means of ten sample units (means of five units for individual species in 1975).

	1975						1976					1977				
	VI	VI	VII	VIII	IX	X	V	VI	VII	VIII	IX	V	VI	VII	VIII	IX
Hypogastrura manubrialis	4	2	315	211	172	87	21	151	313	32	9	80	118	36	21	31
H. denticulata	–	–	–	2	–	2	–	1	5	26	14	102	81	98	134	66
Willemia intermedia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7	–
Friesea mirabilis	–	–	–	–	–	–	–	–	–	–	–	4	–	23	20	67
Pseudachorutes subcrassus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–
Neanura muscorum	2	–	–	–	–	–	–	–	–	–	–	–	2	2	3	1
Tullbergia krausbaueri	–	–	–	–	–	–	2	–	–	–	1	–	–	–	10	–
Folsomia quadrioculata	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–
F. fimetaria	–	–	–	–	–	–	–	–	–	33	6	2	12	4	9	42
Isotomiella minor	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Proisotoma minuta	–	–	6	13	294	719	47	104	1084	653	283	54	204	489	496	302
Isotoma notabilis	–	–	–	–	–	–	–	–	–	–	–	–	–	2	4	6
I. viridis	–	–	2	6	2	–	–	12	31	105	97	3	34	13	15	12
I. propinqua var. pectinata	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	–
I. tigrina	–	–	15	9	115	113	–	–	2	1	1	–	1	–	3	10
Isotomurus palustris	–	–	–	–	–	–	–	–	–	–	1	–	1	5	6	34
Entomobrya nivalis	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
Lepidocyrtus sp.	–	–	–	15	23	28	10	4	26	204	41	6	342	54	40	26
L. lanuginosus	–	–	–	–	–	–	–	1	–	–	–	–	1	5	–	–
Sminthurinus elegans	–	–	–	–	–	2	–	–	–	1	–	1	–	–	–	–
Bourletiella hortensis	–	–	–	–	–	–	1	1	1	–	–	–	–	–	–	–
Sminthuridae spp.	–	–	–	–	–	–	3	5	2	1	–	10	3	–	–	–
Undet.	–	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–
Collembola total	7	9	312	205	861	856	84	279	1465	1056	453	267	799	736	771	597
SE	4	6	115	58	273	127	25	95	160	126	89	72	547	142	155	139
Enchytraeidae	x	x	0	0	22	4	2	0	1	1	1	7	10	66	155	95
SE					21	2						3	8	38	64	53

year, and the peak in the total numbers in 1976 was mainly due to this species. *Isotoma tigrina* also increased considerably in the first year, and so did *I. viridis* and *Lepidocyrtus* sp. in the second year. Being large species, they made an important contribution to the total biomass of springtails.

The succession in the community of Collembola was relatively slow compared with that of Nematoda and Mesostigmata. *P. minuta* still predominated in 1977. The population of *H. manubrialis* diminished, and that of *H. denticulata* increased up to the third year (Fig. 6).

The number of species showed an increasing trend but only a few species were dominant. Although many of the species were the same, the composition of the community differed considerably from that of the control soils even in the third year.

Oribatei. Oribatids occurred in the test plots only occasionally (Table 9). Several species were recorded in the first sample, but this may have been due to contamination by grassland soil when the material was mixed (the bark was stored on garden grassland before use). *Oppia subpectinata* (Oudms), and *O. nova* (Oudms) were recorded later.

Prostigmata and *Astigmata.* These groups were most numerous in the last study year. The peak density was very high (ca. 400 000/m²), but because of their small size their biomass remained rather low. However, the values exceeded those of arable soil right from the first year (Table 9, Fig. 4).

Mesostigmata. Mesostigmatid mites were the second group of animals in the succession. Their numbers increased within two weeks, and the peak density was recorded in autumn 1975 (ca. 35 000/m², 4.5-fold the average of that year for G). The numbers dropped during the winter and compared with arable soil they were still

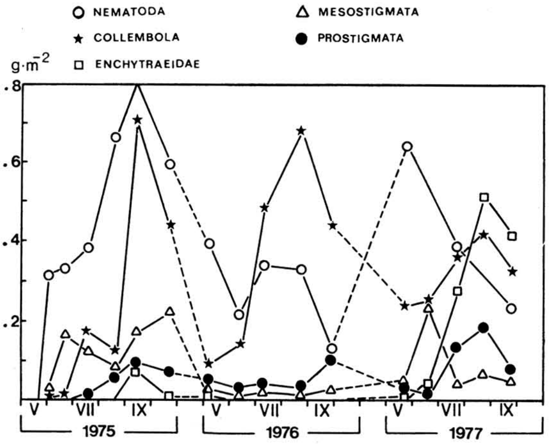


Fig. 4. Biomasses of different animal groups in uncomposted mixture of digested sludge and bark (D).

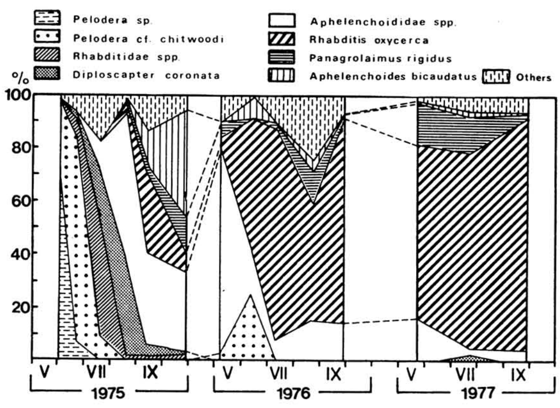


Fig. 5. Relative numbers of Nematoda in uncomposted mixture of digested sludge and bark (D).

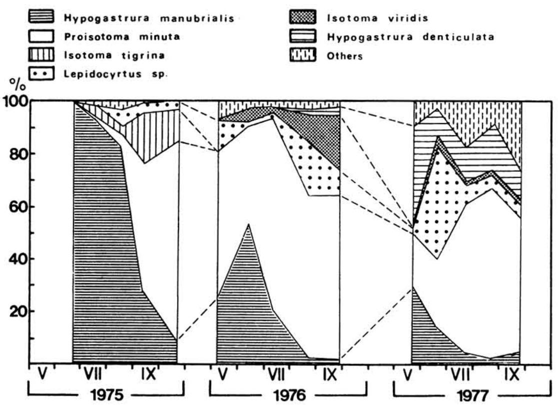


Fig. 6. Relative numbers of Collembola in uncomposted mixture of digested sludge and bark (D).

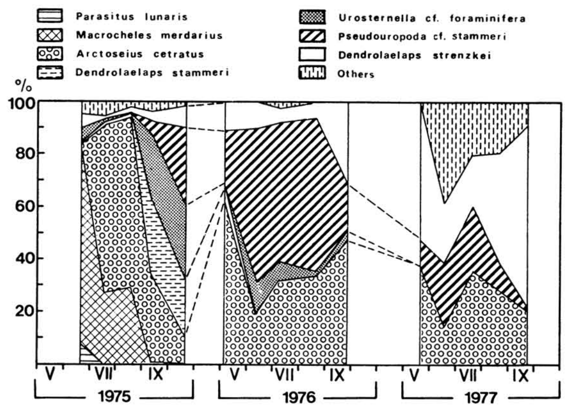


Fig. 7. Relative numbers of Mesostigmata in uncomposted mixture of digested sludge and bark (D).

high in 1976 but 'normal' in 1977 (Table 9). The course of the biomass was similar, but the values were lower than for the controls because the average size of the species was smaller (Fig. 4). The peak in June 1977 was caused by *Parasitus cf. tichomirovi* migrating from the adjacent test plots A and L (See p. 239).

The first abundant species in the succession was *Macrocheles merdarius*, but its population disappeared before the first winter. The second species, *Arctoseius cetratus*, persisted, though gradually diminishing. In autumn 1975 three further species reached densities over 5000/m².

The population of *Dendrolaelaps stammeri* was very transitory, while *Pseudouropoda cf. stammeri* was still present in the third year. *Dendrolaelaps strenzkei* gradually attained the most dominant position (Table 9, Fig. 7). The picture was similar as regards the biomasses, except that the proportion of the large-sized species of the genus *Parasitus* was more prominent.

Lumbricidae. Only a few specimens of *Lumbricus castaneus* were found, the first in August 1976. Nevertheless, in two samples their contribution to the total biomass was considerable (Fig. 8).

Table 9. Numbers of Acari (100 ind./m²) in uncomposted mixture of digested sludge and bark (D).

	1975						1976					1977				
	VI	VI	VII	VIII	IX	X	V	VI	VII	VIII	IX	V	VI	VII	VIII	IX
Phaulocylliba orbicularis	—	—	—	—	—	1	—	—	—	—	1	—	—	—	1	2
Urosternella cf. foraminifera	—	5	1	—	59	94	—	9	4	1	2	—	—	—	—	—
Pseudouropoda cf. stammeri	—	—	—	—	12	101	11	47	28	51	13	10	12	16	6	1
P. breviunguiculata	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Alliphis siculus	—	—	—	1	3	1	—	—	—	—	—	—	—	—	2	1
Macrocheles merdarius	1	68	37	27	2	1	—	—	—	—	—	—	—	—	—	—
Arctoseius cetratus	—	3	86	61	79	34	33	15	18	29	34	35	4	17	15	16
Halolaelaps sexclavatus	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—
H. punctulatus	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—	—
Zercon zelawaiensis	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dendrolaelaps zwoelferi	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
D. stammeri	—	—	1	1	69	74	2	—	—	—	—	—	—	—	—	—
D. arvicolus	—	—	1	—	—	—	—	—	1	—	—	—	—	3	3	1
D. strenzkei	—	5	1	2	9	30	6	9	3	5	21	46	6	9	23	54
Dendrolaelaps spp.	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	1
Pergamasus norvegicus	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
P. truncus	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—
Parasitus lunaris	—	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P. cf. tichomirovi	—	—	—	—	—	—	—	—	—	—	—	—	23	1	1	—
P. cf. remberti	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
P. cf. nolli	—	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—
P. cf. fimetorum	—	2	2	1	2	—	—	—	—	—	—	—	2	—	1	—
Veigaia nemorensis	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Gamasina sp.	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—
Undet. larvae and nymphs	9	41	45	20	94	12	—	22	5	10	3	15	13	19	18	6
Mesostigmata total	12	133	179	113	333	348	52	101	61	96	74	107	65	66	72	83
SE	4	34	46	21	89	96	17	24	12	34	18	28	8	12	12	19
Oribatei	0	0	0	0	0	6	0	10	0	0	0	0	1	2	1	1
Prostigmata + Astigmata	9	16	169	779	1530	778	358	156	337	294	2241	227	312	4013	3900	1770
SE	3	6	66	429	825	170	147	71	108	96	1782	58	88	1853	1527	976

Table 10. Numbers of Lumbricidae and Macroarthropoda (ind./m² ± SE) in uncomposted mixture of digested sludge and bark (D).

	1975		1976		1977	
	VIII	X	VI	VIII	V	VIII
Lumbricidae	0	0	0	2	4	2
Chilopoda	2	6	10	40	10	37
Araneae	72 ± 15	102 ± 51	51 ± 18	173 ± 96	261 ± 66	75 ± 29
Coleopterous adults	1485 ± 421	3992 ±1479	667 ± 310	910 ± 128	344 ± 65	298 ± 33
Coleopterous larvae	702 ± 158	157 ± 22	557 ± 62	546 ± 73	483 ± 40	302 ± 32
Dipterous larvae	858 ± 75	733 ± 115	150 ± 26	523 ± 93	330 ± 114	126 ± 29

Macroarthropoda. The average numbers of Araneae increased from year to year, but there were great differences between individual samples. The dominant species were *Erigone dentipalpis*, *E. atra*, and *Oedothorax apicatus*. No clear succession could be observed (Table 11).

The density and biomass of adult Coleoptera grew high in the first year, the values being many times as great as those in the control soils (Table 10, Fig. 8). Beetles are probably among the first colonizers of fresh sludge materials, as they are, for example, in cow droppings (Koskela 1972), but samples were not taken before August 1975. By May 1977 the numbers had decreased to about the control level. The species of Coleoptera occurring abundantly in the

Table 11. Numbers of Araneae (ind./m²) in uncomposted mixture of digested sludge and bark. Combined data from test plots D and DI.

	1975		1976		1977	
	VIII	X	VI	VIII	V	VIII
Robertus arundineti	–	–	–	–	–	2
Pachygnatha degeeri	–	–	–	1	–	–
Dicymbium nigrum	–	1	–	–	–	2
Oedothorax apicatus	3	1	–	6	–	6
Silometopus reussi	1	–	–	–	6	3
Tiso vagans	–	–	–	1	–	2
Tapinocyba pallens	–	–	–	–	2	–
Micrargus subaequalis	–	–	1	–	–	–
Erigonella hiemalis	–	1	–	4	2	–
Savignia frontata	–	1	2	2	2	–
Diplocephalus latifrons	–	–	1	1	–	–
Erigone dentipalpis	1	4	2	10	18	13
E. atra	1	3	–	9	8	3
Ostearius melanopygius	–	–	–	1	–	–
Meioneta rurestris	–	–	1	3	–	–
Centromerus sylvaticus	–	–	–	1	–	–
Centromerita bicolor	–	2	–	–	–	2
Tapinopa longidens	–	–	–	1	–	–
Total adults	6	13	6	40	37	32

early stages of succession were mostly members of the family Staphylinidae, the most abundant of these being *Trogophloeus pusillus*.

Unlike the adults, the larvae of Coleoptera showed no clear trends in total numbers or biomass. The average values were on the level of the control soils. Dipterous larvae were abundant in the first year but decreased in the following years. Chilopoda showed a weak increasing trend (Table 10, Fig. 8).

Total biomass. The total biomass of soil animals increased rapidly, attaining its maximum in the first autumn (Fig. 8). The bulk consisted of adult Coleoptera (41 %), Nematoda (20 %) and dipterous larvae (17 %). Collembola, though already numerous in the first year, made their greatest contribution (24 %) in the second. The total biomass was very low in the early summer of 1976, probably due to the severe winter (cf.p. 230) and flooding in the spring. Prostigmata and Enchytraeidae were the last groups to form dense populations. Although most groups reached numbers many times as great as in the control soils, at least during a limited period, the total biomass of soil animals remained low, at most 50 % of the average in the grassland. This was because of the absence or low densities of Lumbricidae and Enchytraeidae, which constituted the bulk of the biomass in the arable soils.

C. Succession in uncomposted mixtures of activated sludge + bark (A), and limed sludge + bark (L)

Nematoda. The nematodes became more abundant in the activated sludge than in L or D, and reached their peak numbers earlier (Fig. 9). In L, the maximum biomass occurred at the same time as in A, and was of the same magnitude as in D. Towards the autumn, the biomasses in A and L decreased to the same level as in D of corresponding age. The average densities and biomasses were many times as great as in the arable soils.

The species succession proceeded rapidly, following a pattern similar to that in D. The species present were mainly the same, but there were differences in relative abundances (Table 12). Many species appeared after the same lapse of time in all the materials. *Diploscapter coronata* and *Rhabditis oxycerca* were more abundant in A than in D and L. The proportion of the family Diplogasteridae was fairly high in L in comparison with A and D.

Enchytraeidae. Enchytraeids propagated very rapidly in the mixture of activated sludge (A). After three months their density and biomass (ca. 11 g/m²) exceeded that in any other

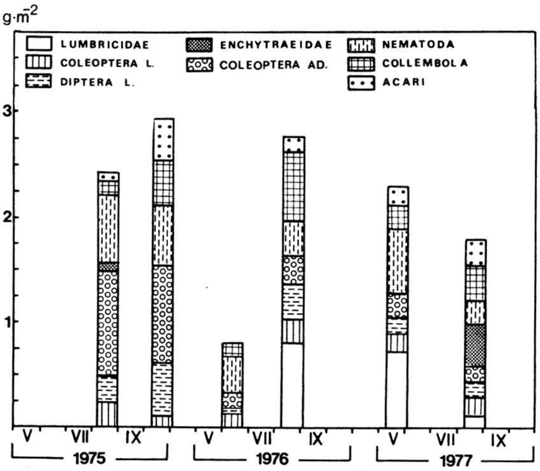
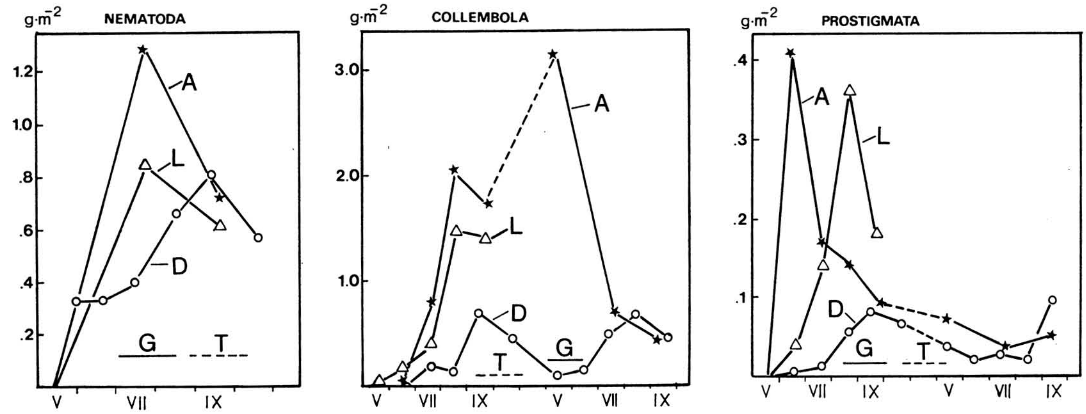


Fig. 8. Total biomass of soil animals in uncomposted mixture of digested sludge and bark (D).



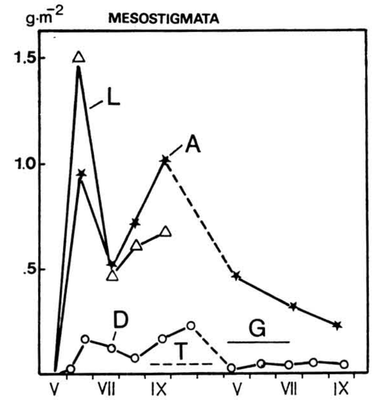


Fig. 9. Biomasses of different animal groups in uncomposted mixtures of activated (A), limed (L) and digested (D) sludge and bark (A and L in 1977, D in 1975). Average levels in the control soils (T = tilled soil, G = grassland) indicated by horizontal lines.

Table 12. Numbers of Nematoda (100 ind./m²) in mixtures of activated sludge and bark (A), and limed sludge and bark (L), in 1977.

	A			L		
	V	VII	IX	V	VII	IX
Cephalobus persegnis	–	–	13	–	–	–
Panagrolaimus rigidus	–	383	13	–	115	–
Pelodera cf. chitwoodi	–	89	–	–	–	–
Rhabditis oxycerca	–	3062	5053	–	893	3586
Rhabditidae spp.	13	–	–	–	–	–
Diploscapter coronata	–	8345	268	–	2310	370
Butlerius cf. filicaudatus	–	102	179	–	–	–
Diplogasteridae spp.	–	370	281	26	3381	1569
Aphelenchoides bicaudatus	–	931	310	–	13	383
Aphelenchoididae spp.	–	549	128	13	778	166
Tylenchinae sp.	–	408	931	–	13	–
Tylenchida spp.	–	–	–	–	–	459
Dorylaimidae spp.	–	–	26	–	–	51
Undet. adults	–	179	–	–	13	–
Juveniles	3 000	2 095	1 140	7 000	148 000	119 000
Total	3 000	224 000	121 300	7 000	155 600	125 600
SE	2 000	41 600	29 600	2 600	17 400	30 600

material at any time (Table 13). There was thus a striking difference from D, in which the population did not increase until the third summer. Enchytraeids were still abundant in A in the following year. Numerous worms were found in the microarthropod samples, though the extraction method used is inadequate for this group. E.g. in May 1978 ca. 150 000/m² were counted.

In the limed sludge (L), enchytraeids remained sparse in comparison with the population in A, but exceeded the level in the control soils and in D of corresponding age.

The only species recorded in A, L and D was *Enchytraeus minutus*.

Collembola. The numbers of springtails remained low for the first month, but after that they increased explosively, reaching their maximum in August (Table 13). During the next year the density decreased fairly rapidly: 331 000 specimens/m² in May, 74 000 in July, and 50 000

Table 13. Numbers of Collembola and Enchytraeidae (100 ind./m²) in mixtures of activated sludge and bark (A) and limed sludge and bark (L) in 1977. x = no sample.

	A					L				
	V	VI	VII	VIII	IX	V	VI	VII	VIII	IX
Hypogastrura manubrialis	2	34	403	306	83	6	266	236	251	154
H. denticulata	–	–	123	193	63	–	–	34	157	77
Willemia intermedia	–	–	–	1	–	–	–	–	1	–
Friesea mirabilis	–	1	–	–	20	–	–	–	–	–
Neanura muscorum	–	–	9	15	7	–	–	–	9	2
Tullbergia krausbaeri	–	–	23	1	1	–	5	1	2	–
Folsomia fimetaria	5	–	–	–	–	–	–	–	28	–
Proisotoma minuta	11	7	927	5194	4250	2	3	511	1667	5108
Isotoma notabilis	–	–	–	–	1	–	–	–	15	–
I. viridis	–	–	–	55	21	–	1	–	10	7
I. tigrina	–	–	14	40	37	–	–	6	119	38
Isotomurus palustris	–	–	–	–	2	–	–	–	–	1
Lepidocyrtus sp.	–	7	266	234	82	2	39	273	327	145
Sminthuridae spp.	–	–	–	–	–	1	–	–	–	–
Undet.	–	–	–	–	–	–	1	–	–	–
Collembola total	18	49	1765	6039	4567	11	315	1061	2586	5532
SE	12	14	377	1300	1126	5	218	380	303	880
Enchytraeidae	x	x.	587	3272	2009	x	x	16	294	198
SE			236	2057	874			7	128	157

in September 1978. The maximum biomass was reached in May 1978, after which a rapid decline took place (Fig. 9). The peak biomass in L (first year) was ca. 25 % lower than that in A, but more than twice as great as in D of the same age.

The succession of the springtail community was almost identical in A and L, and very similar to that in D, in spite of great quantitative differences. Some species established dense populations earlier than in D (*Isotoma viridis*, *Lepidocyrtus* sp., *Hypogastrura denticulata*). The dominance of *Proisotoma minuta* grew to 93 % in A, the high total numbers being mainly due to this species (Table 13, Fig. 10).

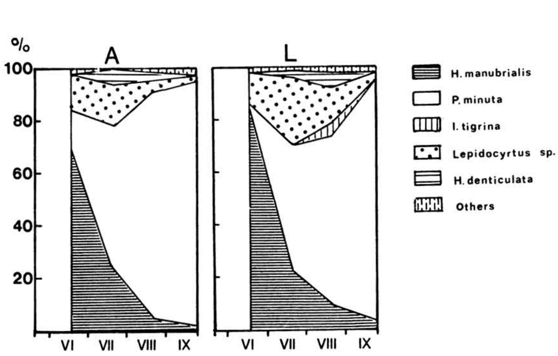


Fig. 10. Relative numbers of Collembola in uncomposted mixtures of activated (A) and limed (L) sludge and bark.

Oribatei. In the first year oribatid mites were found only sporadically, and their biomass remained negligible.

In 1978 a rapid increase took place in A (Table 14), so that by the autumn they had built up a considerable biomass: 433 mg/m² in May, 604 mg in July, and 1600 mg in September. The last record was higher than in any other plot, including the controls, and of the same magnitude as the average biomasses of Oribatei in spruce forests (Huhta & Koskenniemi 1975), which are the optimum habitat of this group. The high biomass in 1978 was attributable primarily to *Oppia nitens*, and secondarily to *O. nova*.

Prostigmata and *Astigmata*. Unlike the situation in D, there was a rapid flush of Prostigmata + Astigmata in A and L. In A the peak was reached only five weeks after establishment, and later the values decreased sharply. In L the biomass grew more slowly, but the trend was similar. The highest biomasses in A and L were

Table 14. Numbers of Acari (100 ind./m²) in mixtures of activated sludge and bark (A) and limed sludge and bark (L).

	A								L				
	1977					1978			1977				
	V	VI	VII	VIII	IX	V	VII	IX	V	VI	VII	VIII	IX
Phaulocylliba orbicularis	—	—	38	36	36	43	30	29	—	12	27	74	99
Fuscuropoda marginata	—	—	—	—	—	—	—	—	—	—	—	—	2
Prodinychus fimicolus	—	—	—	—	—	—	—	—	1	—	8	—	—
Uroobovella cf. varians	—	—	—	—	—	—	—	—	—	—	—	—	5
Urosternella cf. foraminifera	—	—	—	—	—	10	1	—	—	—	—	—	4
Pseudouropoda cf. stammeri	—	2	—	12	7	88	10	7	—	—	12	1	19
P. breviunguiculata	—	—	—	—	—	—	—	1	—	—	—	—	—
Alliphis siculus	1	5	—	—	—	1	—	—	—	12	—	3	—
Macrocheles insignitus	—	—	54	268	116	—	—	—	—	—	1	48	24
M. merdarius	—	1	16	1	—	—	—	—	—	1	12	3	—
M. rotundiscutis	—	—	—	3	—	—	—	—	—	—	—	1	—
M. glaber	—	9	—	1	1	1	1	—	—	4	2	4	—
Ololaelaps placentula	—	—	—	—	—	—	1	—	—	—	—	—	—
Hypoaspis krameri	—	—	—	1	—	—	—	—	—	—	1	—	6
H. aculeifer	—	—	—	—	—	—	1	—	—	—	—	—	—
Ameroseius corbiculus	—	—	—	—	—	—	1	—	—	—	—	—	—
Proctolaelaps pygmaeus	—	—	—	—	—	—	2	—	—	—	—	—	—
Iphidozercon gibbus	—	—	—	—	—	—	—	—	—	—	—	1	—
I. corticalis	—	—	—	—	—	—	—	—	—	—	—	60	1
Arctoseius cetratus	—	1	13	52	50	15	—	—	—	9	11	39	60
Saprosecans baloghi ?	—	—	—	—	—	—	—	1	—	—	—	—	2
Halolaelaps sexclavatus	—	223	15	—	—	—	—	—	—	4	7	—	—
H. punctulatus	—	—	4	1	—	1	—	—	—	—	2	2	—
Rhodacarellus silesiacus	—	1	—	—	—	—	—	—	—	—	—	—	—
Dendrolaelaps undulatus	—	—	—	—	—	1	—	—	—	—	—	—	2
D. punctatosimilis	—	21	153	27	2	—	—	—	—	26	11	4	4
D. arvicolus	—	—	—	—	—	39	27	29	—	—	—	—	—
Dendrolaelaps n. sp.	—	—	—	34	599	91	60	21	—	—	—	2	44
D. strenzkei	—	1	2	6	3	1	—	3	—	7	1	4	2
Dendrolaelaps sp.	—	—	—	—	—	—	—	—	1	1	—	—	4
Pergamasus quisquiliarum	—	—	—	—	2	—	—	—	—	—	—	—	—
Saprogamasus gracilis	—	—	2	2	—	—	—	—	—	—	12	6	1
Parasitus lunaris	—	3	4	—	—	—	—	—	—	18	4	1	1
P. cf. tichomirovi	—	68	6	—	—	2	5	1	—	90	3	—	—
P. coleoptratorum	—	—	—	—	1	—	—	—	—	—	—	—	—
P. cf. fimetorum	—	14	1	2	—	1	2	—	—	37	9	7	—
Undet. larvae and nymphs	2	109	172	129	115	17	45	7	—	196	122	79	59
Mesostigmata total	3	459	482	577	933	309	184	102	2	417	245	342	340
SE	3	119	191	68	159	73	61	12	2	59	34	30	40
Oribatei	0	3	7	6	18	118	209	565	0	0	2	1	6
SE						70	53	124					
Prostigmata + Astigmata	28	6585	1539	1374	560	292	202	350	17	354	1886	1900	2725
SE	11	2162	494	575	140	105	26	46	4	145	303	634	850

four- to fivefold the first-year maximum in D, and differed even more widely from those in the control soils (Fig. 9, Table 14). The strong peak in the biomass in L was absent in the numbers.

Mesostigmata. Similarly to many other groups, mesostigmatid mites were clearly more abundant in both A and L than in D. The populations formed very rapidly. In June, the numbers were of the same magnitude in the two materials, while later the density was roughly twice as great in A. The average size of the individuals was greater in L, so that the mean biomass was about the same (Fig. 9, Table 14). In the second year the numbers and biomass decreased in A, but were still several times as high as in D of corresponding age.

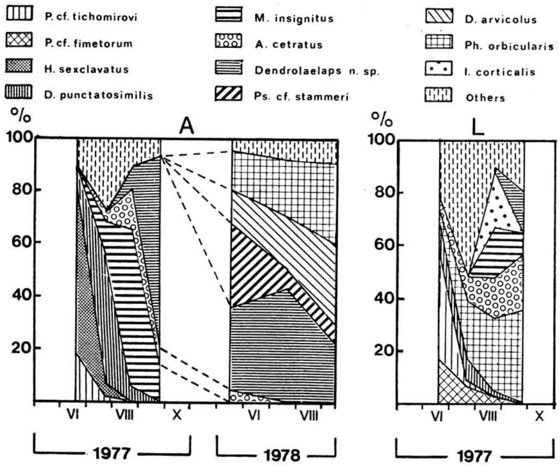


Fig. 11. Relative numbers of Mesostigmata in uncomposted mixtures of activated (A) and limed (L) sludge and bark (in 1977).

The mesostigmatid community differed considerably between the three materials. Many of the dominant species in A were practically absent from D, e.g. *Halolaelaps sexclavatus* and *Parasitus cf. tichomirovi* (two of the first species in the succession), and *Dendrolaelaps punctatosimilis*, *Macrocheles insignitus* and *Dendrolaelaps* sp., all very numerous in A in late summer and autumn 1977. Only some less abundant (though not infrequent) species were common to both materials (Fig. 11, Table 14). The community in the limed sludge was much more similar to that in A than in D. *H.sexclavatus*, *D. punctatosimilis*, *M. insignitus* and *Dendrolaelaps sp.* were less numerous in L, while the species of *Parasitus* were more abundant. *Iphidozercon corticalis* was present only in L. The individuals in L were more evenly distributed among the different species, the diversity thus being high.

The only species retaining its dominant position in A through the second year (although rapidly decreasing) was *Dendrolaelaps* sp. The new dominants also occurred in other test materials: *Pseudouropoda cf. stammeri* was shared with D and H, *Dendrolaelaps arvicolus* and *Phaulocylliba orbicularis* with B.

Lumbricidae. No earthworms were found in L. Unlike L and D, the activated sludge already had a population of *L. castaneus* in the first autumn. In addition, a mature *L. rubellus* was found as early as August. The numbers remained rather low through the following year (8/m^2 in May, 21 in July, and 16 in Sept. 1978; biomass 170, 340 and 1700 mg/m^2, respectively). Three species were identified in Sept. 1978: *L. castaneus*, *A. caliginosa* and *D. octaedra*.

Macroarthropoda. In the only sample taken (Sept. 1977), adult Coleoptera were very numerous in the activated sludge, their numbers and biomass being many times as great as in all the other test materials. *Trogoploeus pusillus* contributed 87 % of the specimens (the most abundant species in D also), but several other species showed high densities as well. Despite quantitative differences, the species composition was very similar in A, L and D. The density of Coleoptera was almost equal in L and D. The mass occurrence of Staphylinidae continued in May 1978, but during the second summer their numbers decreased rapidly.

Araneae, Chilopoda and dipterous larvae were more numerous in A than in D, while the numbers of larval Coleoptera were equal. Dipterous larvae were most abundant in the limed sludge (Table 15). The spider community was very similar in A, L and D (Tables 11 and 16).

Total biomass. The total biomass of soil animals was very different in the three materials (A, L, D) at the same age (Fig. 12). The value was about twice as high in the limed sludge as in the digested sludge, and the biomass of the activated sludge was roughly 3.5-fold that in L, and 7-fold that in D. Many individual groups showed similar differences. Enchytraeids and adult Coleoptera were the main constituents in the total biomass of A.

Table 15. Numbers of Lumbricidae and Macroarthropoda (ind./m^2 ± SE) in mixtures of activated sludge and bark (A), and limed sludge and bark (L) in 1977.

	A IX	L IX
Lumbricidae	10	0
Chilopoda	32	5
Araneae	139 ± 26	166 ± 35
Coleopterous adults	20950 ± 5880	1622 ± 278
Coleopterous larvae	269 ± 50	160 ± 21
Dipterous larvae	958 ± 133	1707 ± 371

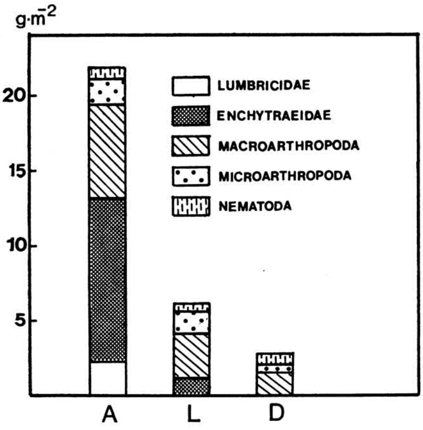


Fig. 12. Total biomasses of soil animals in uncomposted mixtures of activated (A), limed (L) and digested (D) sludge and bark in the first autumn (Sept. 1977 in A and L, mean of Aug. and Oct. 1975 in D).

Table 16. Numbers of Araneae (ind./m^2) in mixtures of activated sludge and bark (A), and limed sludge and bark (L), in September 1977.

	A	L
Walckenaera vigilax	2	—
Dicymbium nigrum	—	2
Oedothorax apicatus	10	18
Silometopus reussi	5	—
Troxochrus scabriculus	—	2
Savignia frontata	2	—
Erigone dentipalpis	22	46
E. atra	—	3
Diplostyla concolor	—	2
Allomengea scopigera	—	2
Centromerita bicolor	3	5
Total adults	43	78

D. Succession in digested sludge alone (S)

Nematoda. The density of nematodes increased rapidly. After ca. two months the numbers were slightly higher, and the biomass almost twice as high as in the mixture of sludge and bark (D). In the first autumn, the numbers and biomass were many times as great as those in most other test materials (Fig. 13). In contrast to their behaviour in D, the nematodes continued to increase in the second year. The maximum biomass, ca. threefold the maximum in D, was attained in autumn 1976, and in spring and summer 1977. The contribution of Nematoda to the total biomass was considerable throughout the study period.

The succession in the nematode community was different from that in all the other materials (Table 17, Fig. 14). The populations of different species formed more slowly than in the mixture of sludge and bark (D), and some of the pioneer species (*Pelodera cf. chitwoodi*, *Rhabditis* sp. s.l.)

Table 17. Numbers of Nematoda (100 ind./m^2) in digested sludge (S).

	1975				1976			1977		
	VI	VI	VIII	X	V	VIII	IX	V	VII	IX
Acrobeloides cf. nanus		—	—	—	—	—	—	38	26	191
Panagrolaimus rigidus		—	—	26	64	102	89	204	166	176
Pelodera cf. chitwoodi		112	38	—	—	—	—	51	—	—
Pelodera sp.		—	89	—	—	—	—	64	—	—
Rhabditis oxycerca		—	—	—	—	—	—	191	38	26
R. cf. inermis		—	13	—	—	—	—	—	—	—
Rhabditidae spp.		—	64	—	—	—	—	—	89	140
Diploscapter coronata		—	587	13	—	—	—	—	—	—
Diplogasteridae spp.		48	26	217	—	—	—	—	—	—
Aphelenchoides bicaudatus		—	13	—	—	—	—	—	—	—
Aphelenchoididae spp.		—	—	—	—	—	102	498	625	651
Tylenchorchynchidae spp.		—	—	—	—	—	—	—	13	4
Juveniles	6400	24800	86500	108500	76900	104700	104700	130700	168400	135400
Total	6400	24900	87400	108800	76900	104800	104900	131800	169300	136600
SE	3900	14900	16900	10900	12900	24800	26600	36200	108700	31200

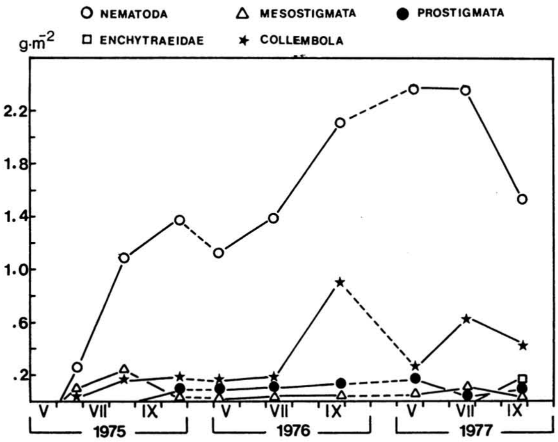


Fig. 13. Biomasses of different animal groups in digested sludge alone (S).

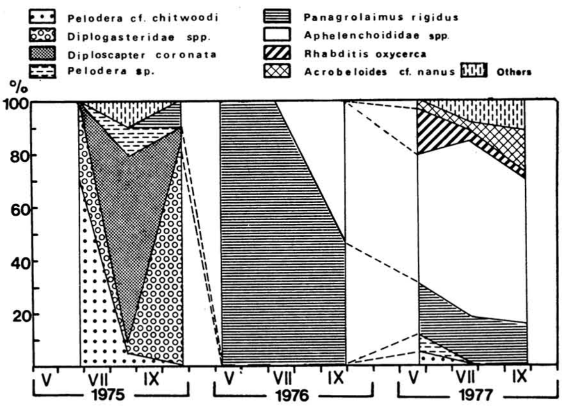


Fig. 14. Relative numbers of Nematoda in digested sludge alone (S).

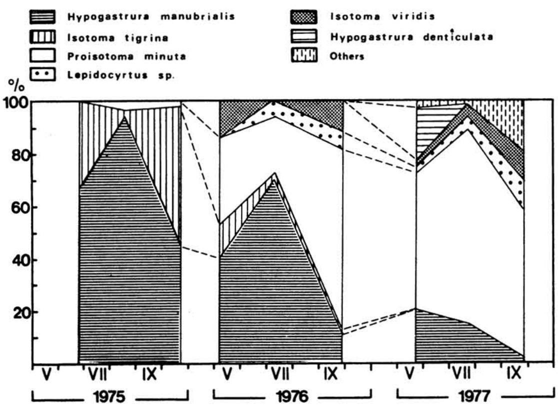


Fig. 15. Relative numbers of Collembola in digested sludge alone (S).

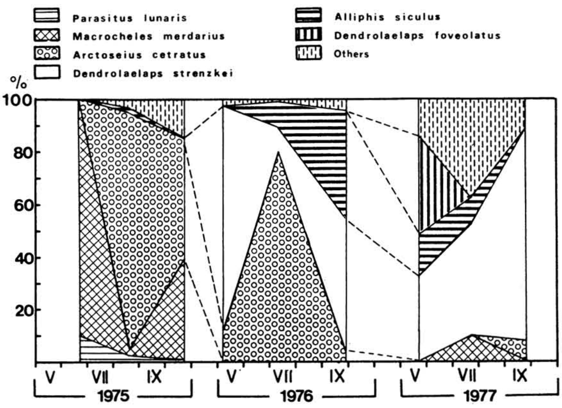


Fig. 16. Relative numbers of Mesostigmata in digested sludge alone (S).

persisted longer. *Panagrolaimus rigidus* was very dominant in the second summer, and *Rhabditis oxycerca* did not become abundant until 1977. The number of species was low in comparison with that in the other materials.

Enchytraeidae. The numbers of enchytraeids remained negligible throughout the study period.

Collembola. The rise in the numbers of springtails was later than in the sludge mixed with bark. The increase was smooth, and the maximum was not reached until autumn 1976 (Fig. 13, Table 18). The maximum was of the same order of magnitude as in D, though it took place somewhat later. The dominant species were the same as in D, but the succession was slower. Many species achieved dominance later in S than in D, and the number of species was lower in S. The peak biomass in 1976 consisted mainly of *Isotoma viridis* and *Proisotoma minuta* (Fig. 15, Table 18).

Oribatei. Only occasional records were made (Table 19).

Prostigmata and *Astigmata.* The density and biomass of prostigmatid mites grew slowly from

Table 18. Numbers of Collembola and Enchytraeidae (100 ind./m²) in digested sludge (S). × = no sample. The numbers are the means of ten sample units (means of five units for individual Collembola species in 1975).

	1975				1976			1977		
	VI	VI	VIII	X	V	VII	IX	V	VII	IX
Hypogastrura manubrialis	—	4	243	45	6	229	176	69	204	16
H. denticulata	—	—	—	—	—	—	—	67	1	3
Friesea mirabilis	—	—	—	—	—	—	—	1	—	3
Neanura muscorum	—	—	—	—	—	—	4	3	11	1
Folsomia quadrioculata	—	—	—	2	—	—	—	—	—	—
Proisotoma minuta	—	—	6	—	5	70	1208	179	1038	398
Isotoma notabilis	—	—	—	—	—	—	—	1	—	—
I. viridis	—	—	—	—	2	1	217	9	61	74
I. tigrina	—	2	6	53	2	7	10	2	4	12
Isotomurus palustris	—	—	—	—	—	—	2	—	9	113
Willowsia buski	—	—	2	—	—	—	—	—	—	—
Lepidocyrtus sp.	—	—	—	—	—	18	121	5	56	74
L. lanuginosus	—	—	—	—	—	—	—	1	4	—
Sminthurinus elegans	—	—	—	—	—	—	—	—	—	1
Sminthuridae spp.	—	—	—	—	—	2	3	4	7	13
Undet.	—	—	—	—	—	1	1	1	—	—
Collembola total	0	14	251	152	15	327	1746	342	1395	708
SE		8	64	30	4	115	269	63	239	174
Enchytraeidae	x	0	0	3	0	1	1	0	0	2

Table 19. Numbers of Acari (100 ind./m²) in digested sludge (S).

	1975				1976			1977		
	VI	VI	VIII	X	V	VII	IX	V	VII	IX
Phaulocylliba orbicularis		—	—	—	—	1	—	2	—	—
Prodinychus fimicolus		—	1	—	—	—	—	—	—	—
Urosternella cf. foraminifera		—	—	—	—	1	1	—	—	—
Pseudouropoda cf. stammeri		—	1	—	—	—	—	1	—	—
P. breviunguiculata		—	—	—	—	—	—	1	—	—
Uropodina sp.		—	—	—	—	—	1	—	—	—
Alliphis siculus		—	—	—	—	10	15	6	2	—
Macrocheles merdarius		45	6	10	—	—	—	—	2	—
Arctoseius cetratus		—	227	12	3	83	1	—	—	2
Halolaelaps punctulatus		—	—	2	—	—	—	—	—	—
Dendrolaelaps foveolatus		—	—	—	—	—	—	14	—	—
D. arvicolus		—	—	—	—	—	—	1	—	1
D. strenzkei		—	—	—	22	9	19	12	9	19
Dendrolaelaps sp.		—	—	—	—	—	—	—	1	—
Parasitus lunaris		5	6	—	—	—	—	—	—	—
P. cf. tichomirovi		—	—	—	—	—	—	—	1	—
P. cf. remberti		—	—	—	—	—	—	—	—	1
P. cf. fimetorum		1	8	—	—	1	—	—	—	—
P. cf. kraepelini		—	—	—	—	—	—	—	3	—
Parasitus sp.		—	—	1	—	—	—	—	—	—
Veigaia nemorensis		—	—	—	—	—	—	—	3	—
Undet. larvae and nymphs		62	82	12	—	49	2	1	12	5
Mesostigmata total	0	112	386	28	26	153	39	38	33	29
SE		40	62	11	13	40	9	15	11	7
Oribatei	0	0	3	2	0	0	1	0	0	0
Prostigmata + Astigmata	0	32	86	692	63	1441	2644	3505	686	431
SE		25	12	233	20	351	767	1986	118	123

year to year (Fig. 13, Table 19). As in D, the highest values were recorded in the third year, but a rapid decrease took place from spring to autumn. The biomass remained low.

Mesostigmata. Both the density and the biomass of Mesostigmata remained lower than in D, except in three samples: June 1975, when *Macrocheles merdarius* was very abundant, and Aug. 1975 and July 1976, when the dominance of *Arctoseius cetratus* was marked. The sludge showed lower species diversity than the sludge mixed with bark, many of the species dominant in D being absent from S. The most numerous species in S also occurred in D, and in the same sequence (Fig. 16, Table 19).

Macroarthropoda. The numbers and biomasses of the different groups of macroarthropods were generally lower than in D. The successional trends were less clear; e.g. the peak of adult beetles was almost lacking. Coleopterous larvae, Araneae and Chilopoda were most abundant in the third year (Table 20). The species of Coleoptera and Araneae present in S also occurred in D, but the number of species was lower in S (Table 21).

Table 20. Numbers of Lumbricidae and Macroarthropoda (ind./m^2 ± SE) in digested sludge (S).

	1975	1976		1977	
	IX	V	IX	VI	VIII
Lumbricidae	0	0	0	3	0
Chilopoda	0	0	0	3	11
Araneae	38±15	13± 4	88±22	141±33	82±26
Coleopterous adults	227±34	102±20	178±35	80±15	179±25
Coleopterous larvae	75±14	0	46±10	712±86	371±62
Dipterous larvae	298±62	166±23	426±94	83±14	104±22

Table 21. Numbers of Araneae (ind./m^2) in digested sludge (S).

	1975	1976		1977	
	IX	V	IX	VI	VIII
Oedothorax apicatus	2	–	6	–	–
Silometopus reussi	–	2	2	–	–
Tiso vagans	2	–	–	–	–
Erigonella hiemalis	–	2	–	–	–
Savignia frontata	–	–	5	–	–
Erigone dentipalpis	2	–	22	8	2
E. atra	3	5	1	–	2
Centromerita bicolor	–	–	2	–	–
Diplostyla concolor	–	–	2	–	–
Total adults	8	8	46	8	3

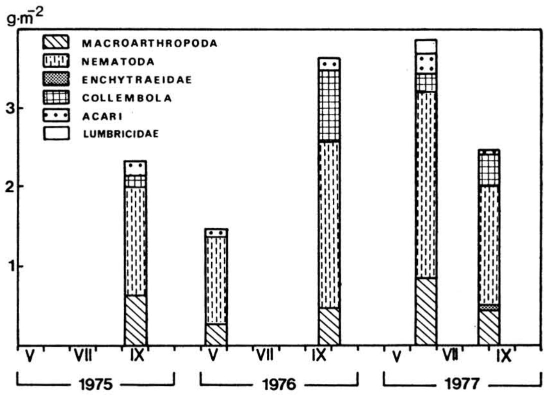


Fig. 17. Total biomass of soil animals in digested sludge alone (S).

Total biomass. Similarly to the biomass of many individual groups, the total biomass of soil animals developed relatively slowly in S. The highest values were recorded in autumn 1976 and early summer 1977. Due to their abundance and the low numbers of most other groups, nematodes occupied a very dominant position in the total biomass. The proportion of Collembola was also high in the second autumn. Compared with that in D, the total biomass in S was lower in the first year, but higher from autumn 1976 onwards (Fig. 17).

E. Succession in crushed bark alone (B)

Nematoda. During the whole study period nematodes were less abundant than in the sludge (S) or the sludge-bark mixture (D). The maximum density was recorded in autumn 1975, and the maximum biomass in spring 1977. Both the numbers and the biomass were on the same level as in the arable soils, and showed only slight fluctuation (Fig. 18). The proportion of nematodes in the total biomass remained low.

The family Diplogasteridae was initially numerous, but decreased rapidly. Some species abundant in the sludge materials were absent from the bark. *Rhabditis oxycerca* dominated in the two first years, but was less numerous in 1977. A species belonging to the family Dorylaimidae, absent from other test plots, became

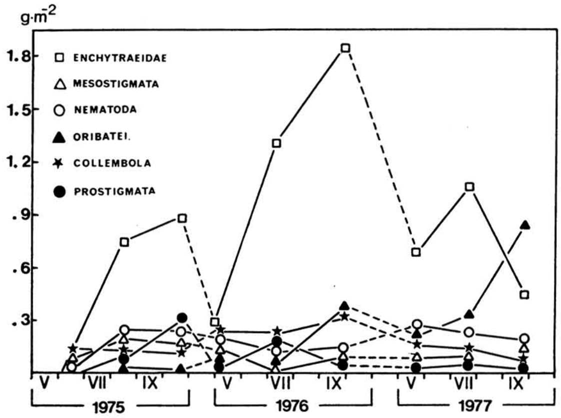


Fig. 18. Biomasses of different animal groups in crushed bark alone (B).

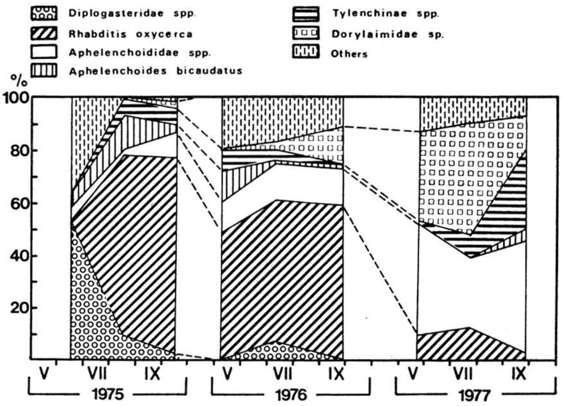


Fig. 19. Relative numbers of Nematoda in crushed bark alone (B).

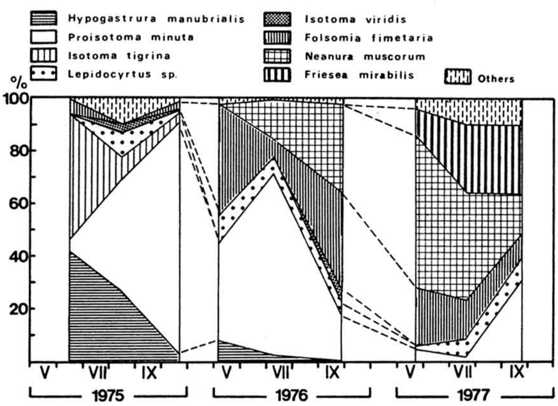


Fig. 20. Relative numbers of Collembola in crushed bark alone (B).

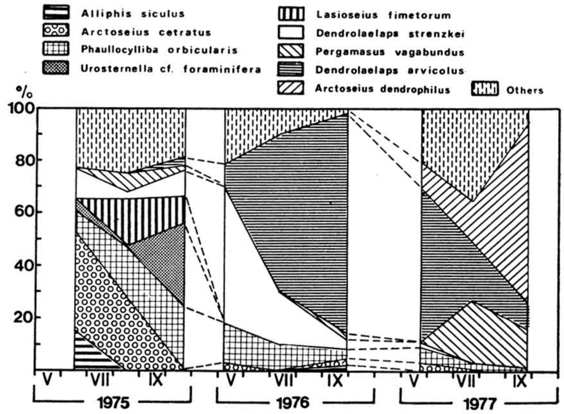


Fig. 21. Relative numbers of Mesostigmata in crushed bark alone (B).

dominant in autumn 1976 and spring 1977. The same behaviour was shown by the family Aphelenchoididae (Table 22, Fig 19).

Enchytraeidae. The enchytraeid populations established themselves rapidly and attained considerable density within a few months (Fig. 18, Table 23). They decreased sharply during winter 1975—76 (for conditions in the winter, see p. 230), but increased rapidly towards the second autumn, contrary to their behaviour in all the other study plots. Their numbers decreased in the third year, reaching the level of D in the last samples. Comparison with the yearly averages for the grassland soil (G) shows that enchytraeids were more abundant in B in 1976, but less abundant in 1975 and 1977, especially in the latter year. Their proportion in the total biomass of B was considerable. The main species (*Enchytraeus minutus*) was shared with the sludge materials, but *Fridericia bulboides* was recorded in B alone.

Collembola. The density and biomass of Collembola fluctuated less sharply and remained at a lower level than in D. The highest density was not more than half of that in D. The initial growth of the populations was rather slow. The highest biomass was recorded in 1976, after which a decreasing trend can be seen (Fig. 18, Table 23).

In the first year the dominant species were

Table 22. Numbers of Nematoda (100 ind./m²) in crushed bark (B).

	1975			1976			1977		
	VI	VIII	X	V	VII	IX	V	VII	IX
Anaplectus sp.	—	—	—	—	64	—	26	64	51
Plectus sp.	—	13	—	—	—	—	13	—	13
Cephalobus persegnis	18	—	28	—	—	38	—	—	—
Eucephalobus oxyuroides	91	—	28	14	13	64	—	26	—
E. cf. striatus	—	—	—	—	64	—	13	—	—
Acrobeles ciliatus	18	—	—	—	—	—	—	—	—
Acrobeloides cf. nanus	18	—	—	—	—	—	—	—	—
Panagrolaimus rigidus	—	13	14	14	—	38	—	—	—
Rhabditis oxycerca	—	2131	2667	170	970	1480	115	128	38
Bunonema reticulatum	—	—	—	—	26	102	—	—	—
Butlerius cf. filicaudatus	—	13	14	14	89	26	38	13	—
Diplogasteridae spp.	201	268	71	—	77	—	—	—	—
Aphelenchoides bicaudatus	18	383	113	43	13	—	—	—	51
Aphelenchoididae spp.	18	64	312	43	280	345	549	293	574
Tylenchinae spp.	—	191	255	28	64	—	13	102	408
Tylenchorchynchidae spp.	—	—	—	—	26	102	—	—	—
Dorylaimidae sp. 1.	—	—	—	14	51	38	64	13	26
Dorylaimidae sp. 2.	—	—	57	—	51	370	434	459	153
Undet. adults	—	—	—	14	26	26	13	—	13
Juveniles	4 500	29 300	30 700	8 900	10 900	11 000	14 300	23 200	24 500
Total	4 800	32 400	34 300	9 200	12 700	13 600	15 600	24 300	25 800
SE	900	6 000	8 900	1 800	3 700	2 000	2 400	3 100	4 200

Table 23. Numbers of Collembola and Enchytraeidae (100 ind./m²) in crushed bark (B). x = no sample. The numbers are the means of ten sample units (means of five units for individual Collembola species in 1975).

	1975			1976			1977		
	VI	VIII	X	V	VII	IX	V	VII	IX
Hypogastrura manubrialis	17	19	13	10	17	5	2	—	1
H. denticulata	—	—	—	—	—	1	—	—	4
Friesea mirabilis	—	—	—	2	6	9	14	34	24
Pseudachorutes subcrassus	—	—	—	—	3	—	—	—	—
Neanura muscorum	—	—	—	—	103	134	84	55	13
Tullbergia krausbaueri	—	2	—	—	—	—	—	12	4
T. quadrispina	—	—	—	—	—	—	—	—	1
Folsomia quadrioculata	—	2	—	—	—	—	—	—	—
F. fimetaria	2	—	13	51	35	146	32	18	8
Proisotoma minuta	2	30	368	44	149	67	7	3	27
Isotoma notabilis	—	—	—	—	—	—	—	1	—
I. viridis	—	2	2	—	3	11	2	—	—
I. tigrina	19	6	11	—	—	—	1	—	—
Isotomurus palustris	—	—	2	—	—	—	—	—	—
Lepidocyrtus sp.	—	6	4	12	22	17	1	9	7
L. lanuginosus	—	—	—	—	—	1	—	—	—
Sminthurinus elegans	—	—	—	—	—	—	1	—	—
Sminthuridae spp.	—	—	—	—	—	2	—	—	—
Undet.	—	4	2	—	—	3	2	—	—
Collembola total	44	79	445	119	608	396	146	132	88
SE	17	17	89	58	171	72	22	29	13
Enchytraeidae	x	311	458	99	530	659	191	334	127
SE		98	101	20	169	76	25	54	19

Table 24. Numbers of Acari (100 ind./m²) in crushed bark (B).

	1975			1976			1977		
	VI	VIII	X	V	VII	IX	V	VII	IX
Phaulocylliba orbicularis	2	6	14	5	1	2	3	1	1
Phyllodinychus septentrionalis	–	–	–	–	–	–	1	1	4
Urosternella cf. foraminifera	1	–	19	–	–	1	–	–	–
Pseudouropoda cf. stammeri	1	–	2	–	–	–	–	–	–
P. vinicolora	–	1	–	–	–	–	–	–	–
Alliphis siculus	4	–	–	–	–	1	–	–	–
Eviphis ostrinus	–	2	1	–	–	–	2	3	1
Lasioseius fimetorum	–	6	6	–	–	–	–	–	–
Iphidozercon gibbus	–	–	2	–	–	–	–	–	–
I. minutus	–	–	–	–	–	1	–	1	–
Arctoseius dendrophilus	–	–	–	1	–	–	5	5	53
A. cetratus	10	9	–	1	–	–	–	–	–
Rhodacarellus silesiacus	–	–	–	–	–	–	1	–	–
Dendrolaelaps zwoelferi	–	2	–	1	–	–	–	–	–
D. foveolatus	–	–	–	–	–	–	1	–	–
D. punctatosimilis	–	–	–	3	1	–	–	1	–
D. arvicolus	–	–	2	3	6	43	26	7	7
D. strenzkei	3	1	6	17	2	2	1	–	–
Dendrolaelaps sp.	1	2	–	1	–	–	–	–	–
Pergamasus norvegicus	–	–	–	–	–	–	–	1	–
P. truncus	–	–	–	–	–	–	–	2	–
P. vagabundus	–	2	1	–	–	1	–	7	10
Pergamasus sp.	–	–	–	–	–	–	1	–	–
Parasitus cf. consanguineus	1	–	3	–	–	–	–	–	–
P. cf. distinctus	2	–	1	–	–	–	–	–	–
P. cf. kraepelini	–	–	–	–	–	–	2	–	1
Veigaia nemorensis	–	1	–	–	–	–	–	–	–
Undet. larvae and nymphs	13	11	5	–	12	14	7	27	10
Mesostigmata total	39	43	64	33	22	65	51	57	83
SE	9	10	13	6	5	12	6	10	20
Oribatei	3	7	13	16	23	118	85	275	571
SE							20	96	122
Prostigmata + Astigmata	56	381	1630	429	1241	575	428	498	219
SE	13	95	375	86	403	84	236	88	28

the same in B and D, but in the second and third year, especially the latter, the communities differentiated. Some species became more abundant in B (*Folsomia fimetaria, Friesea mirabilis, Neanura muscorum*), while some species that were numerous in the sludge materials were of minor importance in B (*Isotoma viridis, Hypogastrura* spp.). Most of the species were common to B and D, but there were fewer species in B (Fig. 20, Table 23).

Oribatei. The numbers of oribatids were low at first but began to increase rapidly in autumn 1976. The highest values were recorded in the third autumn, when the biomass was many times as great as in the control plots T and G (Fig. 18). The difference in the densities was smaller. *Tectocepheus velatus* (Mich.) and *Oppia nitens* (C. L. Koch) were among the dominant species throughout the study period, their proportions changing gradually in favour of the latter. Other dominants were *Suctobelba subcornigera* Forssl. in 1975, and *O. nova* (Oudms.) in 1976—77.

Prostigmata and *Astigmata.* The numbers and biomass were highest in autumn 1975, when they exceeded those of D (the biomass many times as great). In the following years both the density and the biomass showed decreasing trends (Fig. 18, Table 24), the values being equal to those of the arable soils in 1977.

Mesostigmata. The strong peaks observed in the populations of the fresh mixtures of sludge and bark were practically absent. The annual means for the density and biomass values changed within narrow limits. In autumn 1977 the biomass of Mesostigmata exceeded that in D.

The numbers of individuals were divided fairly evenly among several species. Some of the species were shared with D (*Arctoseius cetratus, Dendrolaelaps strenzkei*), but some were found only in B (*A. dendrophilus, D. arvicolus, Pergamasus vagabundus*). The latter did not become abundant until the second or third year (Table 24, Fig. 21).

Lumbricidae. Sparse populations of *L. castaneus* and *A. caliginosa* were present in autumn 1977. Before that only two specimens of earthworms were found.

Macroarthropoda. The numbers and biomasses of most groups of macroarthropods were lower than in D. Dipterous larvae were the only group showing higher densities in B (Sept. 1975). Coleopterous adults and dipterous larvae were most numerous in the early stages. The populations of Araneae and larval Coleoptera showed no clear trends (Table 25). As with Mesostigmata, many species of Coleoptera were at first common to B and D, but their densities were much lower in B. *E. dentipalpis* and *Walckenaera fugax* were the only species of Araneae recorded.

Total biomass. Apart from being much higher in June 1977, the course of the total biomass of soil animals was very similar to that in S (cf. Figs. 17 and 22). However, the contributions of

Table 25. Numbers of Lumbricidae and Macroarthropoda (ind./m^2 $\pm$ SE) in crushed bark (B).

	1975 IX	1976 V	1976 IX	1977 V	1977 VIII
Lumbricidae	2	0	0	2	8
Chilopoda	3	0	3	30	26
Araneae	6± 3	8± 3	13± 7	29±20	21±12
Coleopterous adults	499± 35	186± 52	293±33	125±17	146±26
Coleopterous larvae	155± 24	26± 15	67±14	232±38	54±12
Dipterous larvae	1200±129	765±186	152±38	114±21	70±18

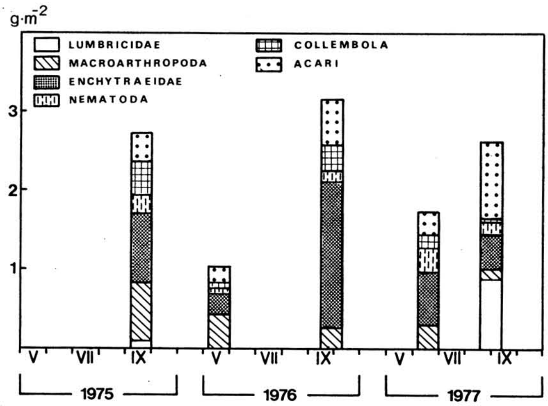


Fig. 22. Total biomass of soil animals in crushed bark alone (B).

the various animal groups were quite different, enchytraeids and mites predominating in the bark and nematodes in the sludge. The mixture of the two materials was intermediate between these and showed a more diverse fauna.

F. Succession in composted mixture of digested sludge and bark (C)

Nematoda. The numbers and biomass of nematodes were much lower in C than in the corresponding uncomposted mixture (D). In the first year the density was only ca. one fourth, and the biomass one fifth of that in D. The difference gradually became smaller, but in 1977 the biomass was still ca. twice as high in D. The numbers of nematodes were roughly on a level with those in arable soil (T and G) in the first two years, but considerably higher in 1977. The proportion of nematodes in the total biomass was about the same as in T and G, but much lower than in other sludge materials (Fig. 23).

The species of nematodes predominating in the fresh sludge materials in the early stages of succession were absent from the composted mixture (Fig. 24, Table 26). The succession of the community proceeded further than in the corresponding uncomposted mixture. *Rhabditis oxycerca* was dominant in the first year (ca. 60 %), but its proportion decreased rapidly, being only 3 % in 1976.

In D this species was still dominant in the third year. The number of abundant species was fairly high in the second year, *Panagrolaimus*

Table 26. Numbers of Nematoda (100 ind./m²) in composted mixture of digested sludge and bark (C).

	1975						1976					1977		
	VI	VI	VII	VIII	IX	X	V	VI	VII	VIII	IX	V	VII	IX
Plectus sp.	–	–	–	14	–	14	–	26	–	–	–	–	–	–
Cephalobus persegnis	–	–	–	28	32	14	115	51	26	–	472	791	383	651
Eucephalobus oxyuroides	–	–	–	–	–	–	–	–	–	–	26	–	–	–
Eucephalobus sp.	–	–	–	–	–	–	–	–	–	–	26	–	38	–
Acrobeles ciliatus	–	–	–	14	–	–	–	–	–	–	–	–	–	–
Acrobeloides cf. nanus	–	–	64	43	64	14	38	179	26	255	64	191	293	228
Panagrolaimus rigidus	–	–	–	113	128	57	255	255	179	32	204	574	–	26
Pelodera cf. chitwoodi	14	–	–	14	–	–	–	–	–	–	–	–	–	–
Rhabditis oxycerca	539	574	415	383	1245	596	–	26	–	–	26	38	13	38
Rhabditidae spp.	43	–	–	–	32	–	–	–	–	64	–	26	–	140
Diploscapter coronata	14	–	–	–	–	–	–	–	–	–	–	–	13	26
Butlerius cf. filicaudatus	–	–	64	14	160	14	–	–	–	–	64	–	–	153
Diplogasteridae spp.	–	–	–	–	–	28	–	–	–	–	38	–	–	–
Aphelenchoides bicaudatus	–	–	–	–	–	28	–	–	–	–	–	–	–	–
Aphelenchoididae spp.	14	43	223	43	128	440	179	306	281	160	460	370	498	115
Tylenchinae spp.	–	–	–	43	–	28	115	331	77	32	13	38	38	51
Tylenchorchynchidae spp.	–	–	–	298	1309	1007	26	–	–	32	26	–	–	–
Pratylenchus sp.	–	–	–	28	–	–	–	–	–	–	38	–	–	–
Dorylaimidae spp.	–	–	–	–	–	–	–	–	–	–	–	13	–	–
Undet. adults	–	–	–	–	–	57	–	–	–	–	13	26	51	–
Juveniles	9 900	11 400	14 600	8 700	11 400	16 700	4 200	6 600	9 800	26 500	17 000	29 800	54 200	19 100
Total	10 500	12 000	15 300	9 800	14 300	19 000	4 900	7 700	10 400	27 000	18 400	31 900	55 500	20 300
SE	1 800	1 600	2 300	1 600	1 600	2 600	500	1 400	1 500	5 200	5 600	12 400	5 300	2 500

Table 27. Numbers of Collembola and Enchytraeidae (100 ind./m²) in composted mixture of digested sludge and bark (C). The numbers are the means of ten sample units (means of five units for individual Collembola species in 1975).

	1975						1976					1977				
	VI	VI	VII	VIII	IX	X	V	VI	VII	VIII	IX	V	VI	VII	VIII	IX
Hypogastrura manubrialis	13	19	117	34	194	70	43	184	127	23	14	9	17	1	13	22
H. denticulata	–	–	–	11	9	2	–	–	18	46	83	56	152	80	103	221
Willemia intermedia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Friesea mirabilis	–	–	–	–	–	–	–	–	1	20	17	22	9	61	53	112
Neanura muscorum	–	–	–	–	–	–	–	–	–	–	1	–	–	1	1	–
Onychiurus armatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–
Tullbergia krausbaueri	–	–	–	–	4	–	2	2	15	57	201	192	231	1700	1153	1423
Folsomia fimetaria	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1
Proisotoma minuta	13	28	272	292	466	619	35	48	165	215	497	55	32	43	81	306
P. minima	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3
Isotoma notabilis	–	–	–	–	–	–	–	–	–	–	–	–	–	27	105	112
I. viridis	–	–	–	2	6	104	1	9	34	64	68	10	49	16	16	15
I. propinqua var. pectinata	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–
I. tigrina	2	–	2	34	111	100	–	–	1	18	–	3	–	–	1	6
Isotomurus palustris	–	–	–	–	–	55	–	–	–	–	–	–	–	–	–	83
Willowsia buski	–	–	–	4	–	–	–	–	–	–	–	–	–	–	–	–
Lepidocyrtus sp.	–	–	–	–	13	15	–	10	33	88	28	7	7	65	35	72
L. lanuginosus	–	–	–	–	–	–	–	–	2	–	2	1	–	–	9	4
Sminthurinus elegans	–	–	–	–	2	2	–	–	7	1	–	–	–	–	–	–
Sminthuridae spp.	–	–	–	–	2	–	9	–	12	1	–	10	–	–	–	–
Undet.	–	–	–	2	–	–	–	1	1	–	–	–	–	–	–	–
Collembola total	33	99	362	363	639	828	90	254	416	533	911	365	498	1996	1575	2383
SE	9	32	67	84	93	182	18	40	70	93	116	70	66	383	185	390
Enchytraeidae	447	860	922	585	408	311	108	113	264	204	237	547	334	512	796	1431
SE	71	161	148	145	106	41	24	26	54	42	55	119	89	103	261	349

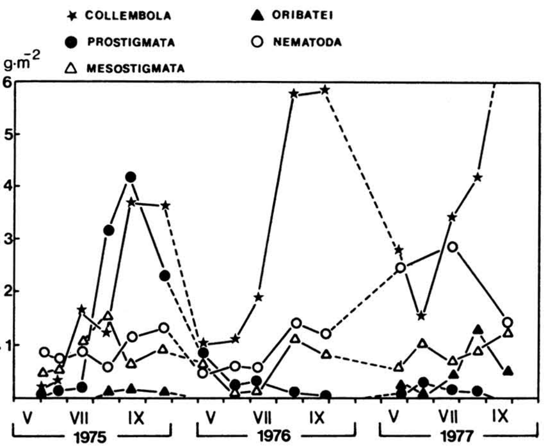


Fig. 23. Biomasses of different animal groups in composted mixture of digested sludge and bark (C).

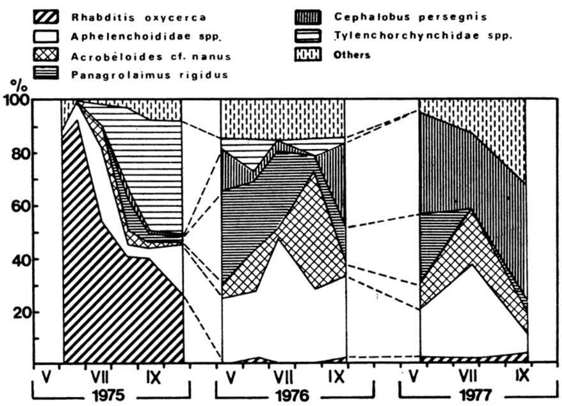


Fig. 24. Relative numbers of Nematoda in composted mixture of digested sludge and bark (C).

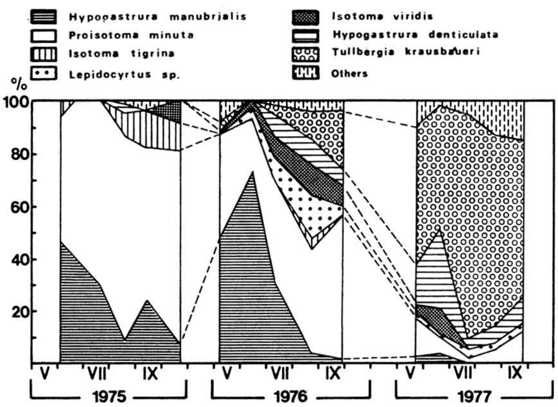


Fig. 25. Relative numbers of Collembola in composted mixture of digested sludge and bark (C).

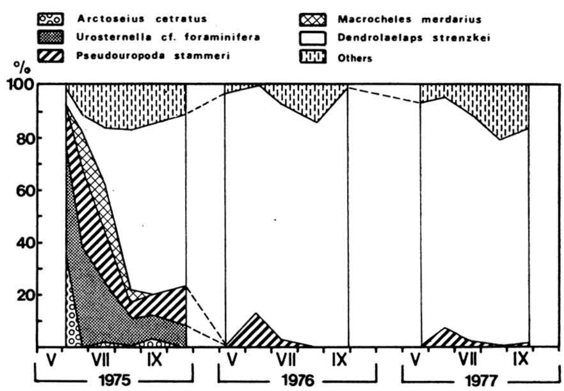


Fig. 26. Relative numbers of Mesostigmata in composted mixture of digested sludge and bark (C).

rigidus, *Acrobeloides cf. nanus* and the family Aphelenchoididae together forming ca. 70 % of the total density. *Cephalobus persegnis* became numerous in 1977. In the third year the species composition in C still differed considerably from that in T and G, especially the latter.

Enchytraeidae. The enchytraeids were already fairly abundant in the first sample (Fig. 27, Table 27). (They had colonized the compost heap in the preceding summer.) The biomass fluctuated within the same range as in the control plots T and G, but the density was much higher. As in the control soils, the numbers were lowest in 1976 (cf. p. 230). The density of enchytraeids and their contribution to the total biomass were many times as great as in the uncomposted mixture.

Enchytraeus minutus was recorded in all three years and, in addition, *Fridericia* sp. in 1976 and *Henlea verticulosa* in 1977.

Collembola. In the first two years of study the populations of springtails behaved in the same way as in the uncomposted mixture (D). The fluctuations were very similar (low density in spring, high in autumn; cf. Figs. 23 and 4), but the peak values in C were reached in the third year.

In 1977 the maximum density was higher than in the uncomposted mixture in the previous year, but the difference in the biomass was small (different species composition at time of peak biomass). Collembola were consistently more abundant in C than in the control plots T and G, the difference being greatest in 1977.

The succession of the springtail community was similar to that in the uncomposted material in the first two years. The same species dominated (*H. manubrialis*, *P. minuta*, *I. tigrina*, *I. viridis*, *Lepidocyrtus* sp.), and the species composition was almost identical (Tables 27 and 8, Figs. 25 and 6). From the second year onwards, certain species began to increase in C, and by the third year the structure of the community had changed completely, *Tullbergia krausbaueri* now predominating (Fig. 25). Besides the most abundant species, some others also established their populations earlier in C than in D, though some of them not until 1977 (*F. mirabilis*, *I. notabilis*).

Oribatei. The populations of Oribatei were sparse until the third year, and even then their numbers remained lower than in the control soils (T and G) or in the bark alone (B) (Table 28). *Oppia nova* was the chief dominant in all three years, *O. subpectinata* was the second in the first two years, giving place to *Tectocepheus velatus* and *O. nitens* in 1977.

Prostigmata and *Astigmata.* These mites were most abundant in the first year, when their

Table 28. Numbers of Acari (100 ind./m²) in composted mixture of digested sludge and bark (C).

	1975						1976					1977				
	VI	VI	VII	VIII	IX	X	V	VI	VII	VIII	IX	V	VI	VII	VIII	IX
Uropoda orbicularis	—	—	—	1	1	—	—	—	—	1	—	—	—	1	7	4
Uroobovella cf. varians	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Urosternella cf. foraminifera	13	18	14	13	7	9	—	—	—	—	—	—	—	—	—	—
Pseudouropoda stammeri	4	15	13	9	6	17	—	4	1	—	—	—	1	1	—	1
P. breviunguiculata	—	—	—	—	—	—	—	—	—	—	—	1	—	—	5	1
Uropodina sp.	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	—
Alliphis siculus	1	3	2	3	3	2	—	—	—	—	—	—	—	—	—	—
Eviphis ostrinus	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Macrocheles merdarius	—	4	12	7	—	—	—	—	—	—	—	—	—	—	—	—
Hypoaspis krameri	—	—	3	5	2	1	—	—	—	—	—	—	—	—	—	—
Lasioseius fimetorum	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Arctoseius cetratus	11	—	1	1	2	—	—	—	—	—	—	—	—	—	—	—
Dendrolaelaps stammeri	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—
D. punctatosimilis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
D. arvicolus	—	—	1	6	2	5	3	—	—	2	—	—	—	1	—	6
D. strenzkei	2	3	14	80	50	77	115	27	27	57	102	64	14	56	62	77
Pergamasus brevicornis	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
P. norvegicus	—	—	—	—	—	—	—	—	—	2	1	—	—	1	—	2
Parasitus lunaris	—	—	—	—	—	—	—	—	—	—	—	—	16	—	—	—
P. cf. tichomirovi	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—
P. cf. eta	—	—	—	—	—	—	—	—	1	1	—	—	—	1	—	—
P. cf. remberti	—	2	4	2	2	—	—	—	—	—	—	—	—	—	1	—
P. cf. nolli	—	—	1	1	1	—	—	—	—	—	—	—	—	—	—	—
P. cf. fimetorum	—	—	—	2	—	—	1	—	—	1	—	1	1	—	1	—
Parasitus sp.	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
Gamasina sp.	—	—	—	—	—	1	—	—	—	—	—	—	—	1	1	—
Undet. larvae and nymphs	11	4	6	41	12	12	—	2	16	14	3	1	14	33	15	3
Mesostigmata total	41	51	71	172	88	128	119	33	46	80	106	70	46	98	94	96
SE	13	12	16	29	17	28	38	12	15	22	20	16	7	22	16	19
Oribatei	1	6	2	5	14	12	7	1	6	2	22	31	3	79	116	116
SE												6	2	24	24	32
Prostigmata + Astigmata	55	151	157	5696	9309	4539	1261	204	278	156	81	98	231	269	168	69
SE	15	22	22	919	891	1069	316	77	74	34	15	22	97	52	50	13

Table 29. Numbers of Lumbricidae and Macroarthropoda (ind./m² ± SE) in composted mixture of digested sludge and bark (C).

	1975			1976		1977	
	VI	VII	X	VI	VIII	V	VIII
Lumbricidae	2	0	0	0	3	8	19
Chilopoda	2	0	0	20	3	80	40
Araneae	0	5 ± 3	16 ± 5	30 ± 10	147 ± 44	96 ± 20	53 ± 13
Coleopterous adults	53 ± 10	99 ± 29	157 ± 30	109 ± 31	358 ± 41	317 ± 60	293 ± 71
Coleopterous larvae	229 ± 27	176 ± 45	187 ± 35	418 ± 117	453 ± 69	1157 ± 179	302 ± 91
Dipterous larvae	195 ± 30	221 ± 39	205 ± 36	56 ± 12	350 ± 78	155 ± 42	104 ± 38

density grew extremely high (up to 930 000 /m²) and their biomass exceeded that of all other groups except enchytraeids (Fig. 23, Table 28). In the following years their numbers decreased to the control level (1976) or even below (1977).

Mesostigmata. In the first year the numbers and biomass of Mesostigmata were about half as high as in the uncomposted mixture (D), while in the next two years the average values were on the same level (Fig. 23).

In the first year the dominant species were the same as in D in the middle stages of succession. *Arctoseius cetratus* and *Urosternella cf. foraminifera* persisted only until the following winter, and *Pseudouropoda cf. stammeri* was also sparse in 1976 and 1977. The specimens of *Macrocheles merdarius* may have migrated from the adjacent fresh materials, as did those of *Parasitus* spp. in the third year. *Dendrolaelaps strenzkei* was strongly dominant from Aug. 1975 onwards (Table 28, Fig. 26). The composition of the mesostigmatid community remained practically unchanged during the last two years, although it was still almost completely different from that of the control soils (T and G). Succession proceeded further than in the uncomposted mixture.

Lumbricidae. The numbers of earthworms remained very low until the third summer. In August 1977 a moderate population of *Lumbricus castaneus* was present, and *Allolobophora caliginosa* was also recorded. At that time, the proportion of *Lumbricidae* in the total biomass was considerable (Fig. 27, Table 29).

Macroarthropoda. Populations of macroarthropods were present from the beginning, but the numbers were low. Both the densities of the different groups and the total macroarthropod biomass were higher in 1976 and 1977. With the exception of larval Coleoptera in 1977, the macroarthropods were considerably less abundant than in D, especially at the beginning of succession. In 1975 the numbers in the composted mixture were smaller than in the grassland soil, but the differences diminished towards the end of the study (higher values were even obtained in C). In summary, the composted mixture of sludge and bark showed slow establishment of the soil fauna, contrasting with the fresh mixture, which had a rapid flush of saprophagous species. The species of Coleoptera abundant in the fresh materials were almost absent from C. The spider species found in C were shared with D, though the number of species was lower, especially at the beginning (Table 30).

Total biomass. The first important animal groups in the succession of the composted material were Enchytraeidae, Prostigmata and

Table 30. Numbers of Araneae (ind./m²) in composted mixture of digested sludge and bark. Combined data from test plots C and CI.

	1975		1976		1977	
	VII	X	VI	VIII	V	VIII
Walckenaera vigilax	–	–	–	–	2	–
Dicymbium nigrum	–	–	–	4	3	–
Oedothorax apicatus	1	2	–	2	–	–
Silometopus reussi	–	–	–	2	2	–
Cnephalocotes obscurus	–	–	–	–	2	–
Erigonella hiemalis	–	–	–	1	–	–
Savignia frontata	–	–	–	2	2	–
Diplocephalus latifrons	–	–	–	1	–	–
Erigone dentipalpis	–	–	2	19	29	13
E. atra	–	1	–	5	13	–
Meioneta rurestris	2	–	–	2	–	–
Centromerita bicolor	–	2	–	1	–	2
Total adults	3	5	2	38	51	16

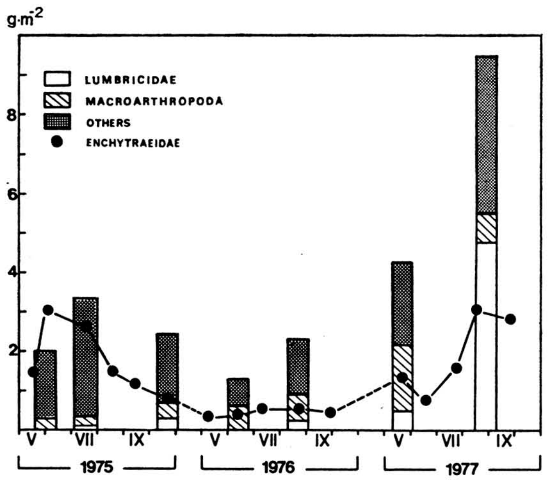


Fig. 27. Total biomass of soil animals and biomass of Enchytraeidae in composted mixture of digested sludge and bark (C).

Collembola. The contribution of the enchytraeids to the total faunal biomass was high, and so was that of earthworms in the last samples. Collembola and adult Coleoptera were also relatively important in 1976.

At the beginning the total biomass of soil animals in C was higher than in the uncomposted material, because the populations had become established during the composting. In Oct. 1975 and in 1976, the total biomass was almost identical in C and D, but in 1977 a considerable increase was observed in C, which was mainly due to the high densities of Enchytraeidae and Lumbricidae (Fig. 27). The peak biomass in autumn 1977 was ca. 3-fold that in the tillage (T), and 1.5-fold that in the grassland soil (G).

G. Succession in compost heap made of digested sludge and crushed bark (H)

The compost heap was too small for proper composting, but the temperature in the heart of a true compost heap is too high for animal life (more than 50°C). Thus the results can be considered valid for the outer layer of a good compost heap.

Nematoda. The numbers and biomass of nematodes increased rapidly at first, even more rapidly than in the mixture applied directly to the soil (D), but they decreased before the winter and remained low in the second summer (Fig. 28). The species composition was similar to that in D, and so was its succession, with some exceptions: *Pelodera* spp. were absent from H, and *D. coronata* and *Acrobeloides cf. nanus* were more abundant (Fig. 29, Table 31).

Table 31. Numbers of Nematoda (100 ind./m²) in compost heap made of digested sludge and bark (H).

	1975				1976		
	VII	VII	IX	X	VI	VIII	IX
Acrobeloides cf. nanus	–	41	1532	64	–	13	–
Panagrolaimus rigidus	–	–	–	–	13	13	–
Rhabditis oxycerca	–	–	85	–	–	217	153
Rhabditidae spp.	64	–	43	13	–	–	–
Diploscapter coronata	–	5074	423	–	–	–	–
Butlerius cf. filicaudatus	–	16	–	–	–	–	–
Diplogasteridae spp.	–	48	–	–	–	–	–
Aphelenchoides bicaudatus	–	16	–	38	–	–	–
Aphelenchoididae spp.	–	16	128	140	140	26	13
Undet. adults	–	176	–	–	–	–	–
Juveniles	800	135 000	92 500	15 500	2 100	6 400	7 500
Total	800	140 300	94 700	15 800	2 200	6 600	7 700
SE	200	33 600	66 300	9 800	1 000	1 900	1 900

Enchytraeidae. Only a few specimens were found, and the biomass remained as low as in D. This contrasts with the high numbers in the compost used for test plot C (p. 249).

Table 32. Numbers of Collembola and Enchytraeidae (100 ind./m²) in compost heap made of digested sludge and bark (H). x = no sample. The numbers are the means of ten sample units (means of five units for individual Collembola species in 1975).

	1975					1976		
	VI	VII	VIII	IX	X	VI	VIII	IX
Hypogastrura manubrialis	–	–	9	–	228	358	3	6
H. denticulata	–	–	–	–	–	–	–	1
Folsomia fimetaria	–	–	–	–	–	–	1	–
Proisotoma minuta	–	–	–	–	162	86	30	37
Isotoma viridis	–	–	–	–	–	–	1	2
Sinella coeca	–	–	–	–	–	–	–	17
Willowsia buski	–	2	23	6	4	2	4	4
Lepidocyrtus sp.	–	–	–	–	–	2	7	10
Undet.	–	–	–	2	–	–	3	–
Collembola total	0	2	94	30	477	448	49	77
SE		2	38	9	105	92	8	12
Enchytraeidae	x	0	0	0	7	2	1	1

Collembola. The populations increased more slowly than in D and were generally smaller (Table 32, Fig. 28). In the second year the numbers of springtails were very low, although high in D. The species succession proceeded slowly and the number of species remained low (Table 32, Fig. 30). Two species almost lacking in other test materials occurred frequently in H (*Willowsia buski*, a pioneer species, and *Sinella coeca* in autumn 1976). Most of the other species were shared with the other fresh sludge materials.

Oribatei. The oribatid populations propagated much more rapidly in H than in D. The increase was especially steep in the second autumn, though the biomass did not reach the level of the grassland soil (Fig. 28). *Oppia nitens* dominated in both years, followed by *O. nova* in 1976.

Prostigmata and *Astigmata*. The numbers of this combined group were on the same level as in D, but the maxima occurred in the first year, the values for 1976 being much lower (Fig. 28, Table 33).

Mesostigmata. The average density and biomass were higher than in D, the biomass being roughly two to three times as great. The decrease from 1975 to 1976 was smaller than in D. The species succession was very similar to that in D. This was the only test object with high densities of *Parasitus cf. nolli*, *Dendrolaelaps punctum* and *Prodinychus fimicolus* (Table 33, Fig. 31).

Lumbricidae. A population of *Eisenia foetida* (Sav.) occurred in the compost heap from the first summer onwards. Its contribution to the total biomass was considerable in the second autumn (Fig. 32), though the density was still low (Table 34).

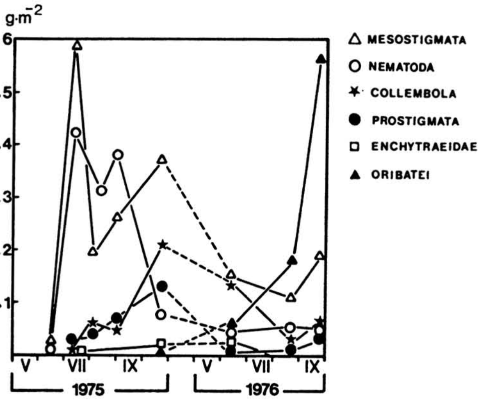


Fig. 28. Biomasses of different animal groups in the compost heap (H) made of digested sludge and bark.

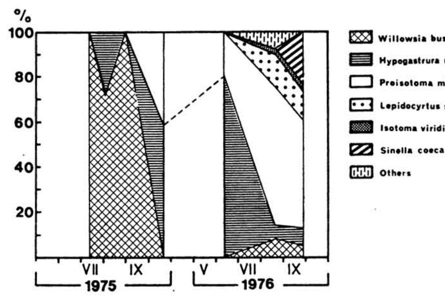


Fig. 30. Relative numbers of Collembola in the compost heap (H) made of digested sludge and bark.

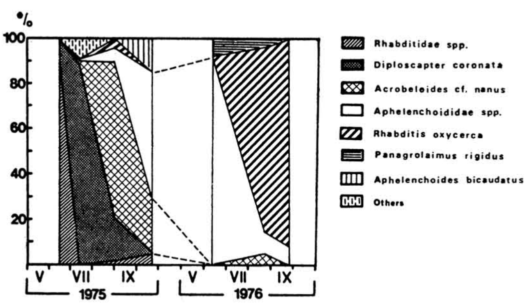


Fig. 29. Relative numbers of Nematoda in the compost heap (H) made of digested sludge and bark.

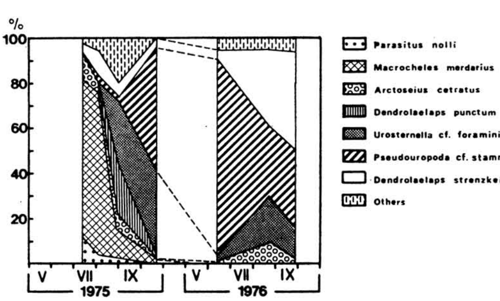


Fig. 31. Relative numbers of Mesostigmata in the compost heap (H) made of digested sludge and bark.

Table 33. Numbers of Acari (100 ind./m²) in compost heap made of digested sludge and bark (H).

	1975					1976		
	VI	VII	VIII	IX	X	VI	VIII	IX
Prodinychus fimicolus	—	—	2	12	1	—	1	—
Uroobovella cf. varians	—	—	2	9	7	—	—	—
Urosternella cf. foraminifera	—	—	—	49	174	5	28	36
Pseudouropoda stammeri	—	—	3	2	240	136	40	96
Uropodina sp.	—	—	1	—	—	—	—	1
Macrocheles merdarius	—	242	94	22	3	—	—	—
M. mammifer	—	—	—	1	—	—	—	—
Hypoaspis krameri	—	—	—	—	1	—	—	—
Arctoseius cetratus	—	44	7	10	1	2	12	6
Dendrolaelaps zwoelferi	—	—	—	—	—	—	4	7
D. strenzkei	—	11	15	10	13	7	45	120
D. punctum	—	—	—	40	—	—	—	—
Parasitus cf. tichomirovi	—	—	—	—	—	1	—	—
P. cf. remberti	—	—	—	—	—	—	—	3
P. cf. nolli	—	45	5	6	—	—	—	—
P. cf. fimetorum	—	12	—	12	—	3	—	—
Gamasina sp.	—	—	—	—	—	—	1	—
Undet. larvae and nymphs	—	35	20	23	6	7	16	10
Mesostigmata total	0	387	150	196	447	163	147	280
SE		47	24	31	69	42	29	29
Oribatei	0	0	0	0	1	0	60	177
Prostigmata + Astigmata	0	112	252	984	2044	81	254	668
SE		37	72	247	270	15	57	169

Macroarthropoda. The succession of macroarthropods resembled that in D; adult Coleoptera and larval Diptera showed high densities in 1975, although less numerous than in D (Table 34).

Spiders were more abundant in the heap than in the test plots, but their numbers fluctuated widely. Most of the spider species also occurred in the soil-applied materials (Table 35), but not *Ostearius melanopygius*, which was abundant in H. The composition of the beetle community differed markedly from that in the test plots.

Total biomass. The total biomass of soil animals was lower than in D in the first year, and of about the same magnitude in 1976. It fluctuated less widely than in D (Fig. 32).

Table 34. Numbers of Lumbricidae and Macroarthropoda (ind./m²±SE) in compost heap made of digested sludge and bark (H).

	1975		1976	
	VIII	X	VI	IX
Lumbricidae	2	0	3	5
Chilopoda	0	0	2	2
Araneae	18± 7	228± 53	75±11	245±52
Coleopterous adults	262±39	1413±460	173±24	136±15
Coleopterous larvae	74±10	54± 19	13± 5	13± 5
Dipterous larvae	74±49	595±149	64±14	24±10

Table 35. Numbers of Araneae (ind./m²) in compost heap made of digested sludge and bark (H).

	1975		1976	
	VIII	X	V	IX
Robertus arundineti	—	—	2	3
Silometopus reussi	—	2	11	50
Savignia frontata	—	2	8	50
Erigone dentipalpis	—	3	2	2
E. atra	—	18	3	13
Ostearius melanopygius	3	32	—	5
Porrhomma convexum	—	—	2	—
Meioneta rurestris	—	2	—	6
Total adults	3	58	27	128

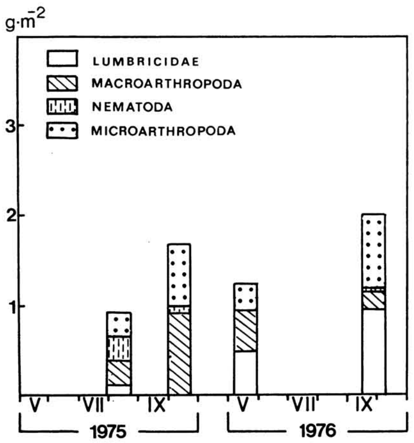


Fig. 32. Total biomass of soil animals in the compost heap (H) made of digested sludge and bark.

H. Differences between replicates of the same test materials

Populations of soil animals could not be established in the test materials by inoculation with mull soil (test plots DI and CI). In some cases, statistical tests showed significant differences in the densities or biomasses between the inoculated and non-inoculated plots (Appendix 5), but further analyses did not reveal any species whose populations could have originated from animals introduced in the inoculum. In addition to the soil inoculum, two species of earthworms were introduced into the test plots: *Allolobophora caliginosa* in CI, and *A. caliginosa* and *Eisenia foetida* in DI. No specimens of these species were later recovered from the plots. Even a composted mixture of sludge and bark probably differs so much from forest soil that it is unlikely to have any species in common. As inoculation was not performed on other kinds of sludge, the role played by the toxic qualities of the digested sludge remained uncertain (see pp. 262—263). The method of P. Augustin Hessing for composting dung makes use of populations existing in old compost by applying fresh dung on older deposits at proper intervals (Mrohs 1961).

The proportion of organic material in the soil is known to be one of the environmental variables affecting soil animals. In some cases there were differences in numbers or biomasses between the main test plots D and C and their counterparts with added sand (DS and CS). However, at the same time there were also differences between the two identical replicates, especially in the fresh mixtures. A species-level analysis showed that the populations did not arise simultaneously in all the replicates: at a certain moment a species could be abundant in one replicate and absent from the other, while at the next sampling the situation could be totally different. Accidental factors in the dispersal of the species and the 'priority effect' connected with interspecific competition may play roles in the colonization of small transitory microhabitats like carrion or dung (Costa 1969, Hanski & Kuusela 1977). In spite of the fairly large area of the test plots in the present case, the effect of these factors cannot be excluded. Another possible explanation of the differences is the different exposure of the plots. The experimental field was bordered by trees on the southern and western sides, so that more light reached the northern row of plots (Fig. 1). Mohr (1943) and Koskela (1972) have shown that the insect communities of cow droppings are markedly different in open terrain and in forest. The mass occurrence of Staphylinidae in the fresh mixtures of sludge and bark, including the dominant species *Trogophloeus pusillus*, was clearly concentrated in the shadier replicates. However, the uropodid mite *Pseudouropoda cf. stammeri*, which was observed to be transported by several species of beetles, including *T. pusillus*, colonized the northern test plots first. This observation emphasizes the importance of environmental factors as opposed to mere chance, at least as far as the abundant species are concerned.

I. Correlation of animal populations with physical, chemical and microbiological parameters

The relations of the zoological data with the other parameters measured (see p. 227) were examined with the aid of factor analysis (varimax rotation) and canonical correlation analysis (Cooley & Lohnes 1971). The zoological parameters used for the analyses were the biomasses of the most abundant species of Nematoda, Collembola and Mesostigmata, and the group totals of Enchytraeidae, Prostigmata + Astigmata and Oribatei. Groups of variables giving too high correlations with each other were reduced till only one variable per group remained. *Halolaelaps sexclavatus* was the only animal species dropped. Other parameters dropped were exchangeable Ca, C %, volume weight, water space and air space at WHC. For parameters measured only once a year, the measurements were regarded as valid for the whole year. After several trials, only data for the test plots D, A, L, S, B and C were included, so that the data were reduced to 78 observations.

In the factor analysis, the zoological variables were generally not weighted in the same factors as the other parameters (Table 36). The animal species were mainly weighted in four factors. The first of them (Factor 1) is mainly loaded for species with peak occurrences in the activated sludge (A) in autumn 1977. Factor 4 shows a group of species abundant in D in the first autumn, while Factor 3 has loadings for species of stabilized mixtures and for the age of the material. In Factor 5 two species of Mesostigmata typical of the "dung complex" are grouped with chemical and microbiological variables attaining peak values in the fresh mixtures A and L.

The canonical analysis revealed pairs of canonical variables with high correlations. These seemed to be informative up to the sixth pair.

The first pair of variables contains a group of species showing their highest densities in A, L, or both. These can be explained by a group of variables indicating high nutrient content, pH, moisture and biological activity (Table 37). The second pair is less distinct, the cor-

Table 36. The most prominent variables and their factor loadings in the varimax solution for eight factors, arranged in order of decreasing absolute values. N = Nematoda, C = Collembola, M = Mesostigmata.

Factor 1.	
P. minuta (C)	.93
M. insignitus (M)	.81
Dendrolaelaps sp. (M)	.76
Ph. orbicularis (M)	.76
Rh. oxycerca (N)	.64
Enchytraeidae total	.60
Lepidocyrtus sp. (C)	.56
Factor 2.	
Physical and microbiological variables.	
Factor 3.	
F. mirabilis (C)	−.86
T. krausbaueri (C)	−.81
I. notabilis (C)	−.77
C. persegnis (N)	−.66
H. denticulata (C)	−.65
Age	−.51
A. cf. nanus (N)	−.47
D. strenzkei (M)	−.45
Factor 4.	
D. stammeri (M)	−.95
U. cf. foraminifera (M)	−.94
I. tigrina (C)	−.76
A. bicaudatus (N)	−.74
Ps. cf. stammeri (M)	−.68
Aphelenchoidinae (N)	−.55
Factor 5.	
pH	.76
Mg exchangeable	.75
Dehydrogenase activity	.73
O_2 consumption	.73
P. cf. tichomirovi (M)	.72
P. cf. fimetorum (M)	.67
P easily soluble	.60
Streptococcus faecalis	.55
Ammonification	.50
Factor 6.	
D. punctatosimilis (M)	.82
D. coronata (N)	.74
Precipitation	.61
Lepidocyrtus sp. (C)	.60
Ph. orbicularis (M)	.51
Diplogasteroidae (N)	.50
Factor 7.	
Physical and microbiological variables.	
Factor 8.	
M. merdarius (M)	.70
Escherichia coli	.64
Age	−.56
Decomposition	.56
P. cf. chitwoodi (N)	.53
Nitrate reduction	.53
Viable bacteria 24°C	.52

Table 37. Canonical variable correlations of the most prominent original variables in each of the six most significant pairs of canonical variables. r_c = canonical correlation coefficient, N = Nematoda, C = Collembola, M = Mesostigmata.

Predictor set		Criterion set	
1. r_c = 0.999			
Mg exchangeable	.68	*Ph. orbicularis* (M)	.73
pH	.55	*Lepidocyrtus* sp. (C)	.68
O_2 consumption	.51	*D. punctatosimilis* (M)	.59
Dehydrogenase activity	.47	*P. minuta* (C)	.56
Water % WHC	.47	*M. insignitus* (M)	.55
P easily soluble	.46	*Rh. oxycerca* (N)	.47
		D. coronata (N)	.47
		Diplogasteroidea (N)	.46
2. r_c = 0.994			
Escherichia coli	.46	*D. stammeri* (M)	.33
Ammonification	.33	*I. tigrina* (C)	.32
Decomposition	.28	*Ph. orbicularis* (M)	−.31
Viable bact. 24°C	.28	*M. insignitus* (M)	−.30
O_2 consumption	.28	Aphelenchoidinae (N)	.28
N %	.27	*P. cf. fimetorum* (M)	.28
3. r_c = 0.994			
Net primary prod.	.58	*F. mirabilis* (C)	.66
Age	.46	*T. krausbaueri* (C)	.66
Fungal hyphae	.46	*C. persegnis* (N)	.57
Conductivity	−.41	*I. notabilis* (C)	.56
K exchangeable	.39	*D. strenzkei* (M)	.46
		A. cf. nanus (N)	.46
4. r_c = 0.978			
Viable bact. 24°C	.41	*U. cf. foraminifera* (M)	−.44
Glucose fermentation	.36	*D. stammeri* (M)	−.37
		I. tigrina (C)	−.33
5. r_c = 0.971			
Exchange capacity	−.51	*M. merdarius* (M)	.37
Escherichia coli	.42	*P. rigidus* (N)	−.34
P easily soluble	.38	*H. manubrialis* (C)	.32
Age	−.37	*P. cf. fimetorum* (M)	.31
Nitrate reduction	.36		
6. r_c = 0.969			
Decomposition	−.44	Enchytraeidae total	−.47
K exchangeable	−.41	*H. denticulata* (C)	−.39
Pore volume	.40	*I. viridis* (C)	.33
Viable bact. 47°C	−.33	*C. persimilis* (N)	−.27
N %	−.32		

relations of the original variables with the canonical variables being low. It contains some species either frequent or absent (negative correlations) in D in the first year. The third correlation could be termed a "stability" or "age" factor, the animal species included having their highest densities in the composted mixture (C) in the third year. These correlate positively with the age of the material, primary production, amount of fungal hyphae and low conductivity, all associated with an advanced degree of humification. The next pair combines numbers of bacteria and fermentation of glucose with a negative correlation to some autumn 1975 populations in D.

The 5th pair reveals three species abundant in and one absent from fresh sludge materials. These are combined with such factors as low age, low exchange capacity, high nutrient level and poor hygienic state (*E. coli*). The last canonical correlation shows a group of species frequent in C in 1977, but the parameters with which these are combined are not connected with the age of the material, as in correlation 3. The predictor set indicates properties of the composted sludge-bark mixture troughout the study period.

J. Culture experiments with earthworms

The suitability of sludge materials as the food and substrate of earthworms was tested in pot experiments with *Allolobophora caliginosa* and *Eisenia foetida*. The former species is the most common deep-burrower in arable soils in Finland, and the latter is specialized on composts and related habitats.

Plastic flower-pots were filled to one third with fine sand, and the material to be tested was added to ca. 2/3 of the volume. Five mature worms were placed in each pot, and prevented from escaping by covering the pot with polyethylene mesh or perforated plastic, and closing the hole in the bottom. Five replicates were used for each experiment (Edwards & Lofty 1972).

The pots were kept in temperatures roughly corresponding to the preferences of the species in nature (room temperature for *E. foetida*, ca. 15°C for *A. caliginosa*; Grant 1955). The temperatures were not controlled and fluctuated by a few degrees. After three months the contents of the pots were sieved and the worms and cocoons (many of them hatched) were picked out and counted.

The test materials S, D, DS, and C (see p. 224) were used for the first experiment, and deciduous litter as a control. The pots were covered with perforated plastic. *A. caliginosa* produced cocoons only in the control pots. In other materials the worms remained inactive and lost maturity. Many of them died and several were found in diapause (Table 38). *E. foetida* did rather well in the mixtures of sludge and bark, but the cocoon production was highest in the control pots. In the digested sludge alone most of the worms died.

Fresh sludge consumes much oxygen (Huhta et al. 1978), which may cause anaerobic conditions even in originally aerobic sludge. There are also reports indicating that the sulphates in sludge may be detrimental to many earthworm species (Marshall 1977).

In another experiment, fresh sludge from the sewage treatment plant at Tali (used for the present investigation) was compared with that from Rajasaari, processed by the same technique but without addition of ferrosulphate. A replicate set of pots was covered with polyethylene mesh, which allowed better aeration than perforated plastic. The results of this experiment suggested that the worms may do better in well-aerated sludge without Fe_2SO_4 (Table 38), but the evidence was not conclusive, and the poor result of the first experiment cannot

Table 38. Results of earthworm culture experiments 1 and 2. For symbols of the test materials, see p. 224.

	A. caliginosa Surviving worms	*A. caliginosa* Cocoons laid	*E. foetida* Surviving worms	*E. foetida* Cocoons laid
Experiment 1. 7 June – 12 Sept. 1975				
Fresh sludge (S)	11	–	3	3
Fresh mixture (D)	17	–	20	87
Fresh mixture with sand (DS)	21	–	20	64
Composted mixture (C)	8	–	22	62
Deciduous litter	22	22	23	116
Experiment 2. 7 Oct. 1975 – 6 Jan. 1976				
Sludge with Fe_2SO_4				
Good aeration	24	2	12	26
Poor aeration	19	–	0	20
Sludge without Fe_2SO_4				
Good aeration	24	–	23	59

be fully explained by these two factors.

The content of heavy metals in the sludge from the sewage treatment plant at Tali is rather high; 680 ppm Cu and 2500 ppm Zn have been measured (Vesihallitus 1976). These metals have been reported to be poisonous to earthworms in concentrations of 85 ppm Cu (van Rhee 1963), 260 to 360 ppm Cu (Nielson 1951) and 1100 ppm Zn (van Rhee 1975). The third experiment was designed to compare sludge from Tali with that from Mikkeli, treated similarly but containing only 200 ppm Cu and 670 ppm Zn (Vesihallitus 1976). The results of the experiment were poor, probably for technical reasons, and the worms laid few eggs even in the control pots with herbaceous compost. However, the worms did no better in the sludge from Mikkeli than in that from Tali.

In the fourth experiment, the test materials D, A, L and C were compared with each other and with deciduous litter. (A, L and C were taken directly from the test plots, and for D a new mixture was made of fresh sludge and bark.) A layer of garden soil was placed in the pots between the sand and the test material, so that the worms were not obliged to be in direct contact with the sludge. The results differed considerably from those of the previous experiments (Table 39). Both species of worms produced the highest numbers of cocoons in the pots containing digested sludge. For *E. foetida* the differences between D and all the other materials were highly significant, while *A. caliginosa* showed wide variation and the differences were not significant. In the other sludge materials *E. foetida* laid somewhat more eggs and *A. caliginosa* somewhat fewer than in the control pots (differences not significant).

At the end of the experiment the average weight of the worms was generally lower in the sludge materials than in the control, especially in the limed sludge, which also showed the lowest egg production. Many of the individuals of *A. caliginosa* were found in diapause or poor condition in D, L and C, but not in A or in the control.

Table 39. Results of earthworm culture experiment 4 (31 May – 31 Aug. 1977). S = surviving worms, C = cocoons laid, W = average dry weight (mg/specimen) at end of experiment.

	A. caliginosa			*E. foetida*		
	S	C	W	S	C	W
Fresh digested sludge + bark (D)	25	80	217	25	410	65
Fresh activated sludge + bark (A)	25	28	210	21	165	53
Fresh limed sludge + bark (L)	23	22	108	24	126	40
Old digested sludge + bark (C)	25	23	165	24	158	52
Deciduous litter	25	31	249	24	116	58

4. Discussion

A. Colonization of the test materials by animals

To discover whether the animal populations found in the sludge materials originate from the sewage treatment plant, fresh digested sludge was taken for examination immediately after leaving the drying machine. If it was extracted at once, no animals were encountered, but after one weeks's incubation in the laboratory at room temperature, considerable numbers of nematodes were found. *Rhabditis cf. inermis*, *Pelodera cf. chitwoodi*, *Diploscapter coronata* and Diplogasteridae spp. could be identified among the adult specimens. The same species were among the early inhabitants in the test plots. In the activated sludge juvenile nematodes were already present when the test plots were established. No oligochaetes or arthropods were extracted from the digested sludge even after incubation.

The fauna involved in sewage treatment processes has been investigated in some detail. The percolating filters used in certain techniques harbour a considerable variety of saprophagous populations (Curds and Hawkes 1975). They are even considered to be of economic importance, since they eat the microbial film that might otherwise block the filter pores (Solbé 1975). In the activated sludge process, however, the nematodes are the only metazoan group besides Rotatoria that occur regularly, and even these are not as numerous as in the filters (Schiemer 1975). They are also found when there is an oxygen deficiency. Our experiment indicated that the eggs of some species retain their viability through the digestion phase, but it is also possible that the founders of the populations entered the sludge in the drying machine.

With the exception of these nematodes, the animals inhabiting the test materials all originate from the surroundings. A wide variety of invertebrates are capable of rapid colonization of animal excreta and related materials. Flying insects, mostly Coleoptera and Diptera, appear within a few hours (Mohr 1943, Valiela 1974). Many wingless animals are able to reach new resources by means of phoresy. Nematodes, Rhabditidae in particular, are known to be transported by insects (Weingärtner 1951, Kühnelt 1950: 63, Calaway 1963). Černova (1977) reports that Drosophilidae transporting nematodes are among the first animals appearing in fresh horse droppings. Phoresy is also a normal, in some cases even an obligatory phase in the life cycle of many mites, especially of those specialized to saprobic environments. Most of the species of Mesostigmata found in the test plots have been reported to be phoretic, or belong to genera in which phoresy is widespread (Costa 1969, Karg 1971, Lindqvist 1975, Binns 1976).

Mites were commonly found attached to insects sampled from the test plots. Hypopi of Astigmata were especially common, as well as wandering deutonymphs of *Pseudouropoda cf. stammeri*, which was recorded from several species of Coleoptera belonging to different families. The dung beetle *Aphodius fimetarius* was sometimes found to carry dozens of specimens.

Nematoda and Collembola may also be carried by air currents (Freeman 1952, Orr & Newton 1971), but the role of aeolian transport in the colonization of new substrates is not known. Most of the species of springtails found in the test materials also occurred in the adjacent arable soil, so that terrestrial dispersal can be regarded as more probable. Nematodes, mites and springtails are able to migrate in search of fresh decomposable material, at least over short distances (Weingärntner 1951, Höller 1959, Höller-Land 1959, Černova 1970). Mrohs (1961) showed that under certain conditions individuals of *Eisenia foetida* travel distances of ca. 40 m from the compost inhabited by the population. Spiders migrate over the ground, but aerial dispersal is also common, occurring in many of the species in our material (Bristowe 1939: 192, Duffey 1956). The spiders found in the sludge plots also occurred in the control plots.

B. Characterization of the animal community of the test materials

In the biological succession in the sludge materials, nematodes, Mesostigmata, adult Coleoptera and dipterous larvae can be regarded as typical inhabitants of the early stages, while enchytraeids and Oribatei attain an important position in aged materials. Differences occur, however, between the different kinds of sludge, enchytraeids becoming numerous fairly early in activated sludge. Composting seems to accelerate arrival of the "late" groups. Springtails are important throughout the succession except in the very first weeks. The proportion of Collembola in the total biomass was higher in the sludge materials than in the control plots, or in forest and grassland soils in general (e.g. Huhta & Koskenniemi 1975). High densities of springtails and enchytraeids in sludge compost were also recorded by Lagerlöf & Andrén (1978).

The species found in the sludge materials can be arbitrarily divided into categories according to their main period of occurrence in the course of the succession:

1) *Species of the early stages of succession*, almost entirely confined to the first year. If needed, this group can be further divided into two subgroups, the first one showing peak densities in the first to the third month, the other in the third to the fifth month. (The phenology of the species should not be confused with the successional changes, but the primary colonizers generally reproduce independently of the season, see Černova 1977.) This group includes the following species:

Nematoda:	Mesostigmata:	
Pelodera cf. chitwoodi	*Macrocheles* spp.	
Pelodera sp.	*Parasitus* spp.	
Rhabditis cf. inermis	*Iphidozercon corticalis*	(L)
Diploscapter coronata	*Hypoaspis sexclavatus*	(A)
Diplogasteridae spp.	*Dendrolaelaps stammeri*	(D)
	D. punctum	(H)
Collembola:	*D. punctatosimilis*	(A)
Isotoma tigrina	*Saprogamasus gracilis*	
Willowsia buski (H only)	*Prodinychus fimicolus*	

This category thus contains several species of Nematoda and Mesostigmata but only two Collembola. The species of Nematoda are the same as those recorded from fresh digested sludge after incubation, and they have also been reported from sewage sludges by previous authors (Peters 1930, Chang & Kabler 1962). All the members of this group are more or less rare in normal soils, and occur frequently in dung, compost and related easily decomposable organic materials (Karg 1968 a, 1971, Schiemer 1975, Černova 1977). Representatives of the genera *Macrocheles* and *Parasitus* are especially abundant in fresh dung and dung compost (could be grouped in 1 a), while the *Dendrolaelaps* spp. prefer substrates in a more advanced state of decay (Karg 1968 b).

According to Weingärtner (1951), no special community of compost nematodes can be defined, the species of compost heaps comprising dung species on the one hand, and species of decomposing vegetable material on the other. The nematode communities in dung are somewhat different and depend on the age of the excreta.

The nematode and mesostigmatid species of this group were practically absent from the control plots, but the springtail *I. tigrina* occurred there.

2) *Species of early and medium stages of succession.* These also appeared in the fresh sludge materials during the first summer, but they persisted for a longer period. In the composted mixture (C) many of them were found regularly in 1975, but in 1977 only occasionally (Nematoda and Mesostigmata) or in reduced numbers (Collembola). In D their occurrence still continued in the third year. These include:

Nematoda:
Rhabditis oxycerca

Collembola:
Hypogastrura manubrialis
Proisotoma minuta
Isotoma viridis
Lepidocyrtus sp.

Mesostigmata:
Urosternella cf. foraminifera
Pseudouropoda cf. stammeri
Arctoseius cetratus
Alliphis siculus
Dendrolaelaps sp.

As regards habitat preferences, this group is more heterogeneous than the first one. *A. siculus* was defined as eurytopic by Karg (1968 b), while *A. cetratus* occurs in forests, arable soils and strongly decayed composts. *Ps. cf. stammeri* inhabits decaying plant remains and dung (Ghilarov 1977). The collembolan species have been reported to occur in heaps of manure (Franz 1950, Mrohs 1958), dung compost (Černova 1963 a, b), sludge heaps and compost (Höller-Land 1959), and trash compost (Łosinski 1972), but also outside these habitats, being most abundant in fertile soils near human settlements (Linnaniemi 1912, Gisin 1943, 1960, Stach 1947, 1949, Franz 1950). In forest soils they are rare or absent. According to Bödvarsson (1961), *H. manubrialis* is the most numerous species in dung heaps.

3. *Species of the medium and late stages of succession* were most abundant in the composted material (C) in the second and third year, but also occurred regularly in D.

Nematoda:
Acrobeloides cf. nanus
Aphelenchoididae spp.
Cephalobus persegnis (C)

Mesostigmata:
Dendrolaelaps strenzkei

Collembola:
Tullbergia krausbaueri
Hypogastrura denticulata
Isotoma notabilis
Friesea mirabilis

According to Nielsen (1949), the species of Cephalobidae occur in fertile mull (*C. persegnis*) and arable soils (*A. cf. nanus*). *D. strenzkei* was placed by Karg (1968a) in the same group as *A. cetratus*. *I. krausbaueri*, *F. mirabilis* and *I. notabilis* probably occur more frequently in normal soils than in dung or sludge materials (Černova 1963 a, b, Franz 1950). *H. denticulata* is common in cow and horse droppings (Thome & Desière 1975), and also in decaying grassland herbage (Curry 1969). All the collembolan species had regular populations in test plots T or G or in both, while *D. strenzkei* was only occasionally found there.

In summary, the succession in the sludge materials was initially characterized by rapid invasion and reproduction of species specialized to exploit accumulations of easily decomposable organic matter. These kinds of substrates are usually patchy and transitory in character (e.g. animal droppings), and the adaptations required by successful colonizers include effective dispersal mechanisms (flying or phoretic), rapid reproduction (often parthenogenesis), and short generation turnover (Mohr 1943, Costa 1969, Lindqvist 1975, Košir 1975). The species of this group have been shown to tolerate higher concentrations of such gases as CO_2, NH_2 and H_2S, produced by microbial activity in these environments, than do related species of normal soils (Moursi 1962).

Gradually these pioneer species were replaced by "generalists", some of which are typical inhabitants of normal soils, while others live in many different kinds of substrates. Most of the "specialists" were found in the groups Nematoda and Mesostigmata.

In Coleoptera, most of the saprophagous and very abundant predacious species were among the first colonizers, while generalistic predators were present throughout the succession.

This pattern of succession conforms closely with that described by several authors from dung, compost and related substrates (Stöckli 1943, 1964, Franz 1953, Mrohs 1958, 1961, Černova 1963 a, b, 1970, 1971, Koskela 1972, Koskela & Hanski 1977, Alejnikova et al. 1975, Lagerlöf & Andrén 1978). Černova (1977) divides the microarthropod community in decomposing organic materials into three main groups or complexes of species. The first of them can be termed the "pioneer", "phoretic" or "dung complex", and contains species with phoretic modes of dispersal. This subcommunity is strongly developed in dung and other saprobic environments rich in nitrogen, less prominent in herbaceous composts and practically absent from forest litter. This is followed by the "compost-litter complex", which is gradually replaced by the "soil complex". The composition of the community at the first stages of succession is strongly dependent on the nature of the decomposing matter, while later the communities in substrates of different origin become more and more similar. The mesostigmatid genera *Macrocheles* and *Parasitus* together with phoretic Prostigmata and Astigmata are typical of the first complex, while the second one includes several species of Collembola and the "*Oppia* complex" of Oribatei. The dominant species change rapidly at first but gradually the succession slows down.

Bark alone (B) is poor in nitrogen and cannot be termed "easily decomposable organic matter". Consequently, the animal succession in it differed markedly from that in the other test materials. In the first year, most of the species found in B were also found in the sludge plots, but their populations were sparse in B, as if the whole community were composed of marginal individuals of the sludge populations. Only from the second summer onwards did the bark plots harbour populations of species not recorded from other test materials. The occurrence of Coleoptera was exceptional, the "final" species being present right from the first year. This pattern can most probably be explained by the modes of dispersal of the species. Flying insects can easily attain their proper microhabitats, but since phoresy is exceptional among the litter species that find a suitable substrate in bark (e.g. only one phoretic species reported in Oribatei; Woolley 1969), these must rely on dispersal by land. The isolating sand around the test plots formed a barrier that probably further retarded initial colonization. As far as can be concluded from the literature records, the mesostigmatid species of the bark plot originate from forest litter and decaying wood (Karg 1968 a). However, two dominant species, *Dendrolaelaps arvicolus* and *Phaulocylliba orbicularis*, were also found in test plot A in the second year. According to Karg (1968 b), *Ph. orbicularis* is eurytopic. Even the "bark fauna" included some phoretic species (e.g. *Eviphis ostrinus*).

The oldest sludge material examined was the composted mixture of digested sludge and bark (C) in the third summer. Having undergone the longest succession, its animal community should show the greatest resemblance to "normal" soil. Comparison with the other sludge plots showed that this was true, but there were still great differences from the adjacent control plots (T and G). The differences were greatest in the nematode and mesostigmatid communities (Table 39). Two of the dominant species of Mesostigmata do also occur in arable and grassland soils (Karg 1961, 1967), but in our control plots they were scarce. The springtail community was most similar to that in arable soil. The species were mainly the same, and there were only differences in their relative abundances. According to Höller-Land (1962) and Kreuz (1963), there are no springtail species that are specialized to dung, compost or sludge, but certain soil species can develop higher population densities in these materials than in normal soils. Fertilizing arable soils with sludge or manure benefits the soil species found in our test plots.

Collembola showed little differentiation between different kinds of sludge: the first-year communities in test plots D, A and L were practically identical, as can be demonstrated by the index of diversity overlap R_0 (Table 40). In contrast, the mesostigmatid community of the activated sludge (A) differed sharply from that of digested sludge (D), and was also dis-

Table 40. Values of diversity overlap R_0 (see Horn 1966) in paired comparisons of different test plots. The calculations are each based on pooled data for one year. For symbols of the test plots, see p. 244.

	Nematoda	Collembola	Mesostigmata
D/T+G 1977	0.208	0.447	0.486
C/T+G 1977	0.478	0.798	0.510
D/C 1977	0.415	0.582	0.666
D 1975/A 1977	0.760	0.927	0.314
A/L 1977	0.839	0.989	0.751

similar from that in L. As the mesostigmatids showed similar species composition in test plots D in 1975 and 1976, test plots C in 1975, the compost heap H in 1975 and the compost heap containing the material of C in 1974, the difference between A and D cannot be explained by different weather conditions (year) or surroundings (heap at Tali, test plots at Tikkurila), but only by the quality of the materials. Mesostigmata are thus valuable as indicators of the nature of the substrate, a characteristic less obviously seen in Nematoda, and not at all in Collembola. Karg (1968a) considered the mesostigmatids, especially those occurring in average frequencies, to be good indicators of soil properties, and arranged 151 species in categories according to their preferred substrates. As many of the species placed by him in the same category differed in their occurrence between the different sludges, Mesostigmata may have even greater indicator value than he realized. The position of different groups and species in the successional sequence should be remembered here (Černova 1977): many Mesostigmata belong to the "pioneer complex", which is strongly influenced by the quality of the substrate, while Collembola are members of the less differentiated secondary complex. Nevertheless, the dominance relations of Collembola change during the course of decomposition, and Mrohs (1961) regards springtails as good indicators of the stage of decay of the compost material.

C. Comparison of the test materials

Of the different materials examined, the mixture of activated sludge and bark (A) proved to be the most favourable substrate for animal life. The populations developed rapidly, most groups attaining densities and biomasses considerably higher than those in the other two fresh mixtures (D and L) (Fig. 9). The total faunal biomass in A in the first autumn was sevenfold that in the mixture of digested sludge (D) of corresponding age (Fig. 12). The digested sludge was least favourable for animals, the limed sludge (L) being intermediate between these two extremes.

Although the above conclusion holds for many groups and species, two of them deserve special attention: Enchytraeidae and Lumbricidae. Both of them were practically absent from D and L in the first year, while a dense population of enchytraeids developed in the activated sludge mixture within two months, earthworms also approaching a moderate density towards the autumn. Because of the great size of the individuals, these groups make a substantial contribution to the biomass. The considerable differences between the three materials are thus largely attributable to enchytraeids and lumbricids. Four species of Lumbricidae were recorded, while the bulk of the enchytraeid biomass was attributable to *Enchytraeus minutus* alone.

The changes in the community of Mesostigmata offer evidence that the succession in the activated sludge started from an earlier stage and proceeded more rapidly than that in the digested sludge (cf. Figs. 7 and 11). The initial communities had no dominants in common, but later some of the early dominants of D also colonized A (*Macrocheles* spp., *Arctoseius cetratus*, *Pseudouropoda cf. stammeri*). In the second year these species decreased considerably in numbers (*Ps. cf. stammeri*) or disappeared altogether (*Macrocheles spp.*, *A. cetratus*) in A, while in D two of them were still dominant in the third year. The different initial situation is explained by the fact that activated sludge is "fresher", containing more decomposable matter than digested sludge, which undergoes considerable changes during the digestion; e.g. it loses a considerable part of its carbon. The rapid change in A is explained by the abundance of organisms and high biological activity, but the activity itself is only partly explained by the less advanced humification.

The field results together with the culturing experiments (pp. 257—258) indicate that digested and limed sludges, especially if fresh but even after composting, are harmful or even poisonous to Lumbricidae. *Eisenia foetida* is less susceptible to the toxic effects than *Allolobophora caliginosa*. In limed sludge, the unnaturally high content of calcium may be the prime reason for the toxicity. In the digested sludge, none of the factors examined, anaerobic conditions, content of ferrosulphate and content of heavy metals, could explain the toxicity, or at least none of them alone. On the other hand, in the experiment in which the worms were not obliged to live in the sludge itself, but could inhabit the soil beneath it, digested sludge seemed to be even more favourable than activated or limed sludge, or deciduous litter.

Mitchell et al. (1977) also recently reported that anaerobic sewage sludges are evidently toxic to lumbricids and enchytraeids. Two of the three anaerobic sludges tested were initially extremely poisonous, whereas the worms (*E. foetida*, *L. terrestris*) devoured aerobic sludge without any observable harm. When the anaerobic sludge was spread in a thin layer (2—3 cm) on a mineral substrate in aerobic conditions, it lost its toxicity within 2 months, while sludge kept in closed plastic bags retained its toxicity. In our case, the depth of the sludge layer was ca. 25 cm and the materials seemed to retain some toxicity during the whole study period. Even the composted mixture (C) did not show a noteworthy increase in lumbricid populations until the third summer.

Höller (1959) and Höller-Land (1959) have published results on mites and springtails that are consistent with the present observations. Sludge stored in heaps for one winter and then applied to soil had a favourable effect on springtails but was unfavourable for mites. Domestic animal manure increased mite populations as well. The sludge itself was poisonous and the animals avoided the immediate vicinity of sludge lumps in the soil. The authors did not report what kind of sludge they used.

Höller-Land (1959) and Mrohs (1961) suggest that the high nitrogen content may explain the toxicity of sludge materials. The content of N in our test plots D and S was in fact higher (1.8 and 2.2 %, respectively) than in A and L (1.4 %, 0.8 %), though lower than in the sludge examined by Höller-Land (4 %). Kreuz (1963) and Bruce (1969) claim that sludge is not poisonous to arthropods.

According to Hunt et al. (1973), communal sewage sludge compost is toxic to some plant parasitic nematodes, but not to species of the genera *Cephalobus* or *Rhabditis*. The literature records are difficult to evaluate because the descriptions of the sludge materials are insufficient.

Mrohs (1961) obtained similar results with domestic animal manure. Composting manure, especially if treated by Hessing's method, harboured a luxuriant animal community, while manure stored in anaerobic conditions (compact stacks) showed very poor development of populations, not only during storage but even after removal to an aerobic environment.

Curry (1976) showed that fresh, semiliquid cattle and pig manure is toxic to earthworms, in pot experiments as well as after heavy application in the field. Similarly to sludge, manure gradually loses its toxicity, but retains it for a long period if kept in closed vessels. Thome & Desière (1975) reported that fresh cow and horse droppings are also unfavourable to Collembola: the first individuals do not invade the droppings before they have aged for 10 (cow) to 20 (horse) days. Curry (1976) tested the toxicity to earthworms of some substances present in cattle manure. Among the toxic substances were NH_4CO_3, benzoic acid and Na_2S in high concentrations.

Composting was shown to accelerate the succession of the animal community, as well as the disappearance of the toxic properties of digested sludge. This conforms with the observations of Höller (1959) and Höller-Land (1959). Enchytraeids were present in the composted mixture right from the beginning (Fig. 33), and oribatids, almost lacking in the uncomposted mixture (D), began to increase in numbers (in the third year in C, in the second year in H). Lagerlöf & Andrén (1978) found that enchytraeids were very abundant in compost made of sludge and bark or of sludge and trash, but digested sludge alone was also densely populated by enchytraeids. The flush in the numbers of nematodes and springtails passed more rapidly in the compost heap than in the test plots made of fresh mixture (D). Nevertheless, the total biomass of soil animals remained on the same level as in D until the third year (Fig. 33). Many animal species typical of the first stages of succession in the fresh mixtures were lacking in the composted one. Several species of Mesostigmata and Nematoda that disappeared from the test plots C before the second summer persisted in D during the whole study period. The succession in the composted material thus proceeded to a further stage in comparison with the uncomposted one, the community becoming more similar to that in the control soils (see also pp. 247—251).

Although the fresh mixture of digested sludge and bark cannot be considered especially favourable to soil animals, at least when compared with the activated sludge (A), the test material D proved to be clearly more favourable than either of the initial materials alone. In S and B most animal groups were less abundant than in D, and the flush typical of the fresh mixture was lacking or took place later (Fig. 33). The changes in the proportions of species were most rapid in the mixed material

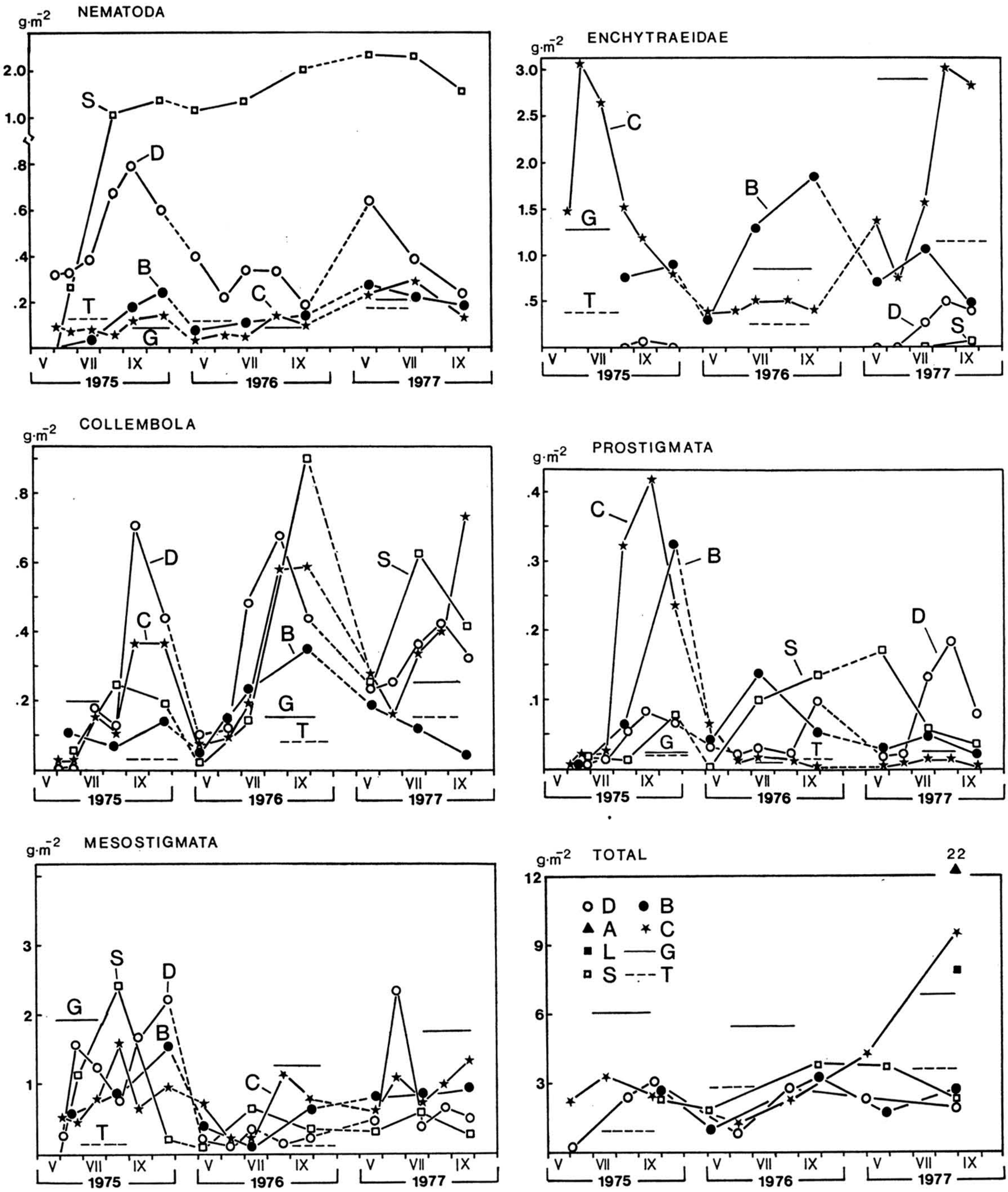


Fig. 33. Biomasses of different animal groups and their total biomass in different test materials. Average annual levels in the control soils indicated by horizontal lines. For explanation of the abbreviations see p. 224.

(cf. Figs. 5—7, 14—16, and 19—21). Certain groups were very abundant in the pure materials: Nematoda in the sludge (Fig. 33), Enchytraeidae in the bark (Fig. 33), and in consequence the total biomass was of the same order of magnitude in D, S and B. The physical and chemical properties of crushed bark are comparable to those of coniferous forest litter, and the preponderance of Enchytraeidae and Oribatei was therefore to be expected. Fungal hyphae form an important part of their diet (e.g. O'Connor 1967, Dash et al. 1972, Hartenstein 1962, Luxton 1972), and test plot B was especially rich in hyphae (Sundman & Sivelä 1978). Judged from their mouthparts (e.g. Twinn 1974), the nematodes occurring in the fresh sludge were mainly bacterial feeders. Bacteria were abundant in all the sludge materials.

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References

Abrahamsen, G. 1972: Ecological study of Enchytraeidae (Oligochaeta) in Norwegian coniferous forest soils. — Pedobiologia 12:26—82.

—»— 1973 a: Studies on body-volume, body-surface area, density and live weight of Enchytraeidae (Oligochaeta). — Pedobiologia 13:6—15.

—»— 1973 b: Biomass and body-surface area of populations of Enchytraeidae and Lumbricidae (Oligochaeta) in Norwegian coniferous forest soils. — Pedobiologia 13:28—39.

Alejnikova, M. M., Artemjeva, T. I., Borisovič, T. M., Gatilova, F. G., Samosova, S. M., Utrobina, N. M. & Šitova, L. I. 1975: Sukzession des Mikroben- und Kleintierbesatzes und ihre Zusammenhänge mit biochemischen Vorgängen während der Mistrotte im Boden. — Pedobiologia 15:81—97.

Andrassy, I. 1956: Die Rauminhalts- und Gewichtsbestimmung der Fadenwürmer (Nematoden). — Acta Zool. Acad. Sci. Hung. 11:1—15.

—»— 1976: Evolution as a basis for the systematization of nematodes. — 288 pp. Budapest.

Binns, E. S. 1976: Notes on the biology of Arctoseius cetratus (Sellnick) (Mesostigmata: Ascidae). — Acarologia 18:577—582.

Bristowe, W. S. 1939: The comity of spiders. I. — 228 pp. London.

Bruce, A. M. 1969: Percolating filters. — Process Biochem. 4:19—23.

Bödvarsson, H. 1961: Beitrag zur Kenntnis des südschwedischen bodenlebenden Collembolen. — Opuscula Entomol. 26: 178—198.

Calaway, W. T. 1963: Nematodes in wastewater treatment. — J. Water Poll. Control Fed. 35: 1006—1016.

Černova, N. M. (Чернова, Н. М.) 1963 a: Динамика численности коллембол (Collembola, Insecta) в компостах из листового опада. (Summary: Dynamics of Collembola population (Collembola, Insecta) in composts of fallen leaves). — Zool. Žurnal 42:1370—1382.

—»— 1963 b: Зоопогические процессы при созревании торфонавозного компоста. (Summary: Zoological processes during the maturing of peat manure compost). — Pochvovedenie 9:95—102.

—»— 1970: Gesetzmässigkeiten der Verteilung der Mikroarthropoden in Komposthaufen. — Pedobiologia 10:365—372.

—»— 1971: Dynamik der Tierbevölkerung bei der Mistzersetzung im Boden. — IV. Colloq. Pedo-

biol.: 371—378.
—»— 1977: Екологические сукцессии при разложении растительных остатков. 200 pp. Izdatelstvo "Nauka", Moscow.
Chang, S. L. & Kabler, P. W. 1962: Free-living nematodes in aerobic treatment plant effluent. — J. Water Poll. Control Fed. 34: 1256—1261.
Cooley W. W. & Lohnes, P. R. 1971: Multivariate data analysis. — 364 pp. Wiley & Sons, New York.
Costa, M. 1969: The association between mesostigmatid mites and coprid beetles. — Acarologia 11: 411—428.
Curds, C. R. & Hawkes, H. A. (eds.) 1975: Ecological aspects of used-water treatment. Vol. 1. The organisms and their ecology. — 414 pp. London.
Curry, J. P. 1969: The decomposition of organic material in soil. II. The fauna of decaying grassland herbage. — Soil Biol. Biochem. 1:259—266.
—»— 1976: Some effects of animal manures on earthworms in grassland. — Pedobiologia 16:425—438.
Dash, M. C. & Cragg, J. B. 1972: Selection of microfungi by Enchytraeidae (Oligochaeta) and other members of the soil fauna. — Pedobiologia 12: 282—286.
Duffey, E. 1956: Aerial dispersal in a known spider population. — J. Animal Ecol. 25: 85—111.
Edwards, C. A. & Lofty, J. R. 1969: The influence of agricultural practice on soil microarthropod populations. — In: Sheals, J. G. (ed.), The Soil Ecosystem. Systematic Assoc. Publ. 8:237—247.
—»— 1972: Biology of earthworms. — 283 pp. London.
—»— 1975: The influence of cultivations on soil animal populations. — In: Vaněk, J. (ed.), Progress in Soil Zoology: 399—406. Prague.
Elliot, J. M. 1971: Some methods for the statistical analysis of samples of benthic invertebrates. — Freshwater Biol. Assoc. Scient. Publ. 25:1—144.
Franz, H. 1950: Neue Forschungen über die Rotteprozess von Stallmist und Kompost. — 114 pp. Wien.
—»— 1953: Der Einfluss verschiedener Düngungsmassnahmen auf die Bodenfauna. — Allgem. Pflanzensoc. 11:1—50.
Freeman, J. A. 1952: Occurrence of Collembola in the air. — Proc. R. Entomol. Soc. London (A) 27:28.
Ghilarov, M. S. (Гиляров, М. С.) (ed.) 1977: Определитель обитающих в почве клещей. Mesostigmata. — 718 pp. Izdatelstvo 'Nauka', Leningrad.
Gisin, H. 1943: Ökologie und Lebensgemeinschaften der Collembolen im schweizerischen Excursionsgebiet Basels. — Rev. Suisse Zool. 50:131—224.
—»— 1960: Collembolenfauna Europas. — 312 pp. Genève.
Grant, W. C. 1955: Temperature relationships in the megascolecid earthworm Pheretima hupeiensis in the eastern United States. — Ecology 36: 412—417.
Habicht, W. A., Jr. 1975: The nematicidal effects of varied rates of raw and composted sewage sludge as soil organic amendments on a root-knot nematode. — Plant Disease Reporter 59:631—634.
Hanski, I. & Kuusela, S. 1977: An experiment on competition and diversity in the carrion fly community. — Ann. Entomol. Fennici 43: 108—115.
Hartenstein, R. 1962: Soil Oribatei. I. Feeding specificity among forest soil Oribatei (Acarina). — Ann. Entomol. Soc. Amer. 55:202—206.
Huhta, V. 1972: Efficiency of different dry funnel techniques in extracting Arthropoda from raw humus forest soil. — Ann. Zool. Fennici 9: 42—48.
—»— (in press): Mortality in Enchytraeid and Lumbricid populations caused by hard frosts. — Proc. Symp. 'Adaptations of animals to winter conditions', Moscow 1978.
Huhta, V. & Koskenniemi, A. 1975: Numbers, biomass and community respiration of soil invertebrates in spruce forests at two latitudes in Finland. — Ann. Zool. Fennici 12: 164—182.
Huhta, V., Sundman, V., Ikonen, E., Sivelä, S., Wartiovaara, T. & Vilkamaa, P. 1978: Jäteliete-kuorirouhe-seosten maatumisen biologia. — Jyväskylän yliopiston biologian laitoksen tiedonantoja 11:1—124.
Hunt, P. G., Hortenstine, C. C. & Smart, G. C. Jr. 1973: Responses of plant parasitic and saprophytic nematode populations to composted municipal refuse. — J. Environ. Quality 2:264—266.
Höller, G. 1959: Die Wirkung der Klärschlammrotte auf die Bodenmilben. — Zeitschr. Angew. Entomol. 44: 405—424.
Höller-Land, G. 1959: Über die Besiedlung des Bodens mit Collembolen bei Düngung mit verschieden behandeltem Klärschlamm. — Zeitschr. Angew. Entomol. 44:425—444.
—»— 1962: Die Abhängigkeit der bodenbewohnenden Collembolen von Düngung und anderen Standortfaktoren unter Dikopshofer Verhältnissen. — Monogr. Angew. Entomol. 18:80—120.
Isomäki, O. 1974: Sahateollisuuden kuorintajätteiden käyttömahdollisuudet. (Summary: Using possibilities of barking waste in sawmill industry. Specially using as a soil improver and substrate for plants). — Acta Forest. Fenn. 140:1—81.
Karg, W. 1961: Ökologische Untersuchungen von edaphischen Gamasiden (Acarina, Parasitiformes). 1. Teil. — Pedobiologia 1:53—74.
—»— 1967: Synökologische Untersuchungen von Bodenmilben aus forstwirtschaftlich und landwirtschaftlich genutzten Böden. — Pedobiologia 7: 198—214.
—»— 1968 a: Bodenbiologische Untersuchungen über die Eignung von Milben, insbesondere von parasitiformen Raubmilben, als Indikatoren. — Pedobiologia 8: 30—39.
—»— 1968 b: Ökologische Untersuchungen an Milben aus Komposterden im Freiland und unter Glas besonders im Hinblick auf die Uroobovella marginata C. L. Koch. — Archiv für Pflanzenschutz 4:98—122.
—»— 1971: Acari (Acarina), Milben. Unterordnung Anactinochaeta (Parasitiformes). Die freilebenden Gamasina (Gamasides), Raubmilben. — Tierwelt Deutschlands 59:1—475.
Košir, M. 1975: Ernährung und Entwicklung von Pygmephorus mesembrinae und P. quadratus (Pygmephoridae, Tarsonemini, Acari) und Bemerkungen über drei weitere Arten. — Pedobiologia 15:313—329.

Koskela, H. 1972: Habitat selection of dung-inhabiting Staphylinids (Coleoptera) in relation to age of the dung. — Ann. Zool. Fennici 9:156—171.

Koskela, H. & Hanski, I. 1977: Structure and succession in a beetle community inhabiting cow dung. — Ann. Zool. Fennici 14:204—223.

Kreuz, E. 1963: Die Wirkung einer Klärschlammdüngung auf Sandboden unter besonderer Berücksichtigung der terricolen Mesofauna. — Zeitschr. Landeskultur 4 (1):59—72.

Kühnelt, W. 1950: Bodenbiologie. — 368 pp. Wien.

Lagerlöf, J. & Andrén, O. 1978: Markbiologiska undersökningar inom Laxåprojektet — Faunan i sopslamkompost samt inverkan av kompost på jordbruksmarkens fauna. (Soil biological investigations in the Laxå project). — Rapport från statens Naturvårdsverk 1978:1—43.

Latostenmaa, H. 1976: Jätevesilietteen hyödyntämisen perusteet. — YVY-tutkimus 21. 86 pp. Vesihallitus, Helsinki.

Lindquist, E. E. 1975: Associations between mites and other arthropods in forest floor habitats. — Canad. Entomol. 107:425—437.

Linnaniemi, W. M. 1912: Die Apterygotenfauna Finnlands. II. Spezieller Teil. — 359 pp. Helsingfors.

Łosinski, J. 1972: Wstępne obserwacje nad fauną Collembola w pryzmie Kompostowej. (Summary: First observations on the Collembola in a compost hill.) — Zesz. Nauk. Uniw. Nikolaja Kopernika Toruniu Nauki Mat.-Przyr. Biol. 14:37—58.

Lussenhop, J. 1971: A simplified canister-type soil arthropod extractor. — Pedobiologia 11:40—45.

Luxton, M. 1972: Studies on the oribatid mites of a Danish beech wood soil. — Pedobiologia 12: 434—463.

Marshall, V. G. 1977: Effects of manures and fertilizers on soil fauna: a review. — Commonwealth Bureau of Soils, Special Publ. 3:1—79.

Mitchell, M. J., Mulligan, R. M., Hartenstein, R. & Neuhauser, E. F. 1977: Conversion of sludges into "topsoils" by earthworms. — Compost Sci. 18:28—32.

Mohr, C. O. 1943: Cattle droppings as ecological units. — Ecol. Monographs 13:275—298.

Moursi, A. 1962: Lethal doses of CO_2, N_2, NH_3 and H_2S for soil Arthropoda. — Pedobiologia 2:9—14.

Mrohs, E. 1958: Die Collembolen des Flachmistkompostes. — Zeitschr. Angew. Entomol. 42:316—333.

—»— 1961: Die Tierbesiedlung des Kompostes bei Zusatz verschiedener anorganischer Düngemittel im Flachkompostverfahren nach P. Augustin Hessing. — Zeitschr. Angew. Entomol. 42:345—376.

Nielsen, C. O. 1949: Studies on the soil microfauna. II. The soil inhabiting nematodes. — Natura Jutlandica 2:1—131.

—»— 1955a: A technique for extracting Enchytraeidae from soil samples. — In: Kevan, D. K. McE. (ed.), Soil Zoology: 365—372. London.

—»— 1955b: Studies on Enchytraeidae 5. Factors causing seasonal fluctuations in numbers. — Oikos 6:153—169.

Nielson, R. L. 1951: Effect of soil minerals on earthworms. — N. Z. J. Agric. 83:433—435.

O'Connor, F. B. 1967: The Enchytraeidae. — In: Burges, A. & Raw, F. (eds.), Soil Biology:213—258. London.

Oostenbrink, M. 1960: Estimating nematode populations by some selected methods. — In: Sasser, J. N. & Jenkins, W. R. (eds.), Nematology: 85—102.

Orr, C. C. & Newton, O. H. 1971: Distribution of nematodes by wind. — Plant Disease Reporter 55:61—63.

Persson, T. & Lohm, U. 1977: Energetical significance of the Annelids and Arthropods in a Swedish grassland soil. — Ecol. Bull. 23:1—211.

Peters, B. G. 1930: Some nematodes met with in a biological investigation of sewage. — Helminthology 8:165—184.

Petersen, H. 1975: Estimation of dry weight, fresh weight, and calorific content of various Collembolan species. — Pedobiologia 15:222—243.

Raw, F. 1955: A flotation extraction process for soil micro-arthropods. — In: Kevan, D. K. McE (ed.), Soil Zoology: 341—346. London.

Van Rhee, J. A. 1963: Earthworm activities and the breakdown of organic matter in agricultural soils. — In: Doeksen, J. & van der Drift, J. (eds.), Soil Organisms: 55—59, Amsterdam.

—»— 1975: Copper contamination effects on earthworms by disposal of pig waste in pastures. — In: Vaněk, J. (ed.), Progress in Soil Zoology: 451—458. Prague.

Schiemer, F. 1975: Nematoda. — In: Curds, C. R. & Hawkes, H. A. (eds.), Ecological aspects of used-water treatment, 1:269—288. London.

Seinhorst, J. W. 1956: The quantitative extraction of Nematodes from soil. — Nematologica 1:249—267.

—»— 1962a: Modifications of the elutriation method for extracting nematodes from soil. — Nematologica 8:117—128.

—»— 1962b: On the killing, fixation and transferring to glycerin of nematodes. — Nematologica 8: 29—32.

Solbé, J. F. de L. G. 1975: Annelida. — In: Curds, C. R. & Hawkes, H. A. (eds.), Ecological aspects of used-water treatment, 1:305—335. London.

Stach, J. 1947: The Apterygotan fauna of Poland in relation to the world-fauna of this group of insects. Family: Isotomidae. — 488 pp. Kraków.

—»— 1949: The Apterygotan fauna of Poland in relation to the world-fauna of this group of insects. — Families Neogastruridae and Brachystomellidae. — 341 pp. Kraków.

Steen, E., Torstensson, L., Wessen, B. & Åkerberg, C. 1976: Markorganismernas betydelse vid deponering och inkorponering av organiskt avfall, bl. a. rötslam och slamkompost. — Rapport från institutionen för mikrobiologi, Uppsala 6:1—41.

Stöckli, A. 1943: Bodenbiologische Studien. — Schweiz. Landw. Monatschr. 21:107—129.

Sundman, V. & Sivelä, S. 1978: A comment on the membrane filter technique for estimation of length of fungal hyphae in soil. — Soil Biol. Biochem. 10:399—401.

Tanaka, M. 1970: Ecological studies on communities of soil Collembola in Mt. Sobo, Southwest Japan. — Jap. J. Ecol. 20:102—110 .

Thome, J. P. & Desière, M. 1975: Evolution de la densité numérique des populations des Collemboles dans les excréments de Bovidés et d'Equidés. — Rev. Ecol. Biol. Sol. 12:627—641.

Tischler, W. 1955: Synökologie der Landtiere. — 414

pp. Stuttgart.
Twinn, D. C. 1974: Nematoda. — In: Dickinson, C. H. & Pugh, G. J. F. (eds.), Biology of plant litter decomposition. II: 421—465. London.
Uusitalo, M. 1975: Jätelietteen maaperäeläimistö. Suomen Akatemian ns. lieteprojektin metodinen esitutkimus. — Master's thesis, Univ. of Helsinki. 46 pp.
Valiela, I. 1969: The arthropod fauna of bovine dung in Central New York and sources on its natural history. — J. N. Y. Entomol. Soc. 77:210—220.
—»— 1974: Composition, food webs and population limitation in dung arthropod communities during invasion and succession. — Amer. Midland Naturalist 92:370—385.
Valpas, A. 1969: Hot rod technique, a modification of the dry funnel technique for extracting Collembola especially from frozen soil. — Ann. Zool. Fennici 6:269—274.
Vesihallitus 1976: Jätevesilietteen raskasmetalleista ja hygieenisistä määrityksistä Suomessa. (Summary: On heavy metals and hygienic determinations of waste water sludges in Finland.) — Vesihallituksen Tiedotus 112:1—135.
Weingärtner, I. 1951: Die Nematoden des Kompostes samt einer Neuordnung der Gattung Diplogasteridae. — Erlangung des Doktorgrades, Friedrich-Alexander Universität, Erlangen. 83 pp.
Woolley, T. A. 1969: A new and phoretic Oribatid mite. — Proc. Entomol. Soc. Washington 71:476—481.

Appendix 1—5

Appendix 1. List of species of Nematoda recorded during the investigation and average fresh weights (μg) of adult specimens.

Wilsonema sp.	0.02
Anaplectus sp.	1.20
Plectus sp.	1.20
Teratocephalinae sp.	0.02
Cephalobus persegnis Bastian 1865	0.29
Eucephalobus oxyuroides (De Man 1876), Steiner 1936	0.16
E. cf. striatus (Bastian 1865), Thorne 1937	0.16
Eucephalobus sp.	0.16
Acrobeles ciliatus Linstow 1877	0.64[1]
Acrobeloides cf. nanus (De Man 1880), Anderson 1967	0.13
Panagrolaimus rigidus (Schneider 1866), Thorne 1937	0.32
Pelodera cf. chitwoodi (Bassen 1940), Dougherty 1955	1.20
Pelodera sp.	0.84
Rhabditis cf. inermis (Schneider 1866), Oerley 1880	0.50
R. oxycerca De Man 1895	0.32
Rhabditidae spp.	0.50
Diploscapter coronata (Cobb 1893), Cobb 1913	0.12[1]
Bunonema reticulatum Richters 1905	0.05
Butlerius cf. filicaudatus Adam 1930	0.06
Diplogasteridae spp.	0.25
Aphelenchoides bicaudatus (Imamura 1931), Filipjev & Schuurmans Stekhoven 1941	0.05
Aphelenchoididae spp.	0.12
Tylenchinae spp.	0.19
Tylenchorchynchidae spp.	0.18
Pratylenchus sp.	0.19
Criconematidae sp.	0.35
Paratylenchus sp.	0.19
Prismatolaimus cf. intermedius (Bütschlii 1873), De Man 1880	0.14[1]
Mononchus sp.	12.70
Prionchulus sp.	12.70
Dorylaimidae sp. (1)	0.80
Dorylaimidae sp. (2)	0.88

[1] After Andrassy (1956)

Appendix 2. List of species of Collembola recorded during the investigation and the methods used for the biomass calculations.

Hypogastrura manubrialis (Tullberg)[1]
**H. denticulata* (Bagnall)[5]
Willemia intermedia (Mills)[3]
W. aspinata (Stach)[3]
Friesea mirabilis (Tullberg)[5]
Pseudachorutes subcrassus (Tullberg)[5]
Anurida granaria (Nicolet)[3]
Neanura muscorum (Templeton)[4]
Onychiurus armatus (Tullberg)[2]
Tullbergia krausbaueri (Börner)[2]
T. affinis Börner[6]
T. quadrispina (Börner)[6]
Folsomia quadrioculata (Tullberg)[2]
F. fimetaria (Linne)[7]
Isotomodes productus (Axelson)[7]
Isotomiella minor (Schäffer)[2]
Proisotoma minuta (Tullberg)[7]
P. minima (Absolon)[7]
Isotoma notabilis Schäffer[2]
I. viridis Bourlet[8]
I. propinqua Axelson[8]
**I. propinqua var. pectinata* (Stach)[8]
I. tigrina (Nicolet) Fjellberg[8]
Isotomurus palustris (Müller)[8]
Sinella coeca (Schött)[9]
Entomobrya nivalis (Linné)[9]
Willowsia buski (Lubbock)[9]
***Lepidocyrtus* sp.[10]
L. lanuginosus (Gmelin)[2]
Tomocerus vulgaris (Tullberg)[11]
Sminthurinus elegans (Fitch)[12]
Bourletiella hortensis (Fitch)[12]
Sminthurus viridis (Linne)[12]
Dicyrtoma minuta (O. Fabricius)[2]

[1] After Tanaka (1970)
[2] After Petersen (1975)
[3] Petersen's (1975) regression for *Onychiurus furcifer*
[4] Takana's (1970) regression for *Neanura* sp.
[5] Tanaka's regression for *H. manubrialis*
[6] Petersen's regression for *Tullbergia krausbaueri*
[7] Petersen's regression for *Folsomia quadrioculata*

[8] Petersen's regression for *Isotoma notabilis*
[9] Tanaka's regression for *Entomobryidae* exl. head
[10] Petersen's regression for *Lepidocyrtus lignorum*
[11] Petersen's regression for *Tomocerus flavescens*
[12] Petersen's regression for *Sminthurinus aureus*

*Not previously recorded from Finland
**Probably a new species (Szeptycki, personal communication)

Appendix 3. List of species of Mesostigmata recorded during the investigation, and average fresh weights (μg) of ♂♂, ♀♀ and deutonymphs. Unless otherwise indicated, the weights are based on length and width measurements.

	♂	♀	D
Trachytes aegrota (C.L.Koch 1841)	–	–	–
Discourella modesta Leonardi 1900	–	9.0	7.2
Phaulocylliba orbicularis (Müller 1776)	–	103[1]	46[1]
Fuscuropoda marginata (C.L.Koch 1839)	–	200	100
Prodinychus fimicolus Berl. 1903	–	–	13.5
Phyllodinychus septentrionalis (Trägårdh 1943)	–	14	9
Ph. cf. tetraphyllus (Berl. 1903)	–	–	–
Uroobovella cf. varians Hirschm. & Z-N. 1962	10[3]	12	8.3
Urosternella cf. foraminifera Berl. 1903	13.5	13.5[2]	9.3[2]
Pseudouropoda cf. stammeri (Hirschm. & Z-N. 1969)	8.2[2]	10.6[2]	6.9[2]
P. breviunguiculata Willmann 1949	20	27	17
P. vinicolora Vitzhum 1926	25	–	14
Eviphis ostrinus (Koch 1836)	–	20	–
Alliphis siculus (Oudemans 1905)	6.2[1]	10.4[1]	5.3[1]
Holostaspella ornata (Berl. 1904)	–	48	–
Macrocheles insignitus (Berl. 1918)	7.8[1]	19[1]	8
M. merdarius (Berl. 1889)	9.8[2]	18[2]	9
M. rotundiscutis Bregetova & Koroleva 1960	–	63	–
M. glaber (Müller 1860)	–	72[2]	–
M. mammifer (Berl. 1918)	–	84	43
Ololaelaps placentula (Berl. 1887)	–	65	–
Hypoaspis krameri (Can. 1881)	30	51	21
H. aculeifer (Can. 1883)	–	20	–
Amblyseius zwölferi Dosse 1954	–	–	–
Ameroseius corbiculus (Sowerby 1806)	–	19	–
Proctolaelaps pygmaeus (Müller 1860)	–	10	–
Proctolaelaps sp.	–	9	–
Lasioseius fimetorum Karg 1971	–	8	–
Cheiroseius borealis (Berl. 1904)	–	21	–
Iphidozercon gibbus Berl. 1903	–	9.2	–
I. corticalis Evans 1958	3.1	3.7	–
I. minutus (Halbert 1915)	1.9	2.9	1.8
Arctoseius dendrophilus Karg 1969	–	3.5	3.1
A. cetratus (Sellnick 1940)	2.2	4.4	1.9
Leioseius bicolor (Berl. 1918)	–	–	–
Saprosecans baloghi Karg 1964 (?)	–	10.0	7.0
Halolaelaps sexclavatus (Oud. 1902)	3.2	6.2	3.6[2]
H. punctulatus (Leitner 1946)	15	34	13[3]
Parazercon sarekensis Willmann 1939	–	6.7	–
Zercon zelawaiensis Sellnick 1944	–	13	–
Rhodacarus coronatus Berl. 1921	5.1	6.0	3.9
Rhodacarellus silesiacus Willm. 1935	–	2.2	1.8
Dendrolaelaps zwoelferi Hirschm. 1960	5.0	5.9	3.1
D. foveolatus (Leitner 1949)	2.8	4.0	2.7
D. stammeri Hirschm. 1960	2.6	3.8	2.5
D. undulatus Hirschm. 1960	–	17.0	–
D. punctatosimilis Hirschm. 1960	2.6[2]	4.2[2]	2.2[2]
D. arvicolus (Leitner 1949)	7.4	10.0	6.2
Dendrolaelaps n. sp. (cf. *arvicolus*)	7.4	10.0	6.2
D. strenzkei Hirschm. 1960	5.2[2]	6.2[2]	4.8[2]
D. punctum (Berl. 1904)	2.3	3.1	1.6
Dendrolaelaps sp.	13.6	17.6	–
Holoparasitus excipuliger (Berl. 1905)	62.5[3]	62.5[3]	–
Pergamasus suecicus (Trägårdh 1936)	8.0	10.0	6.9
P. quisquiliarum (G. & R. Can. 1882)	–	260	–
P. brevicornis Berl. 1903	–	225[3]	145
P. longicornis (Berl. 1905)	–	–	–
P. norvegicus (Berl. 1905)	300[3]	300[3]	100
P. truncus Schweizer 1961	15	20	12
P. vagabundus Karg 1968	40	53	43
Saprogamasus gracilis (Karg 1965)	7	8	6
Parasitus lunaris (Berl. 1882) (s. lato)	42	69[1]	56[1]
P. cf. tichomirovi Davydova 1971[4]	67[1]	111[1]	69
P. cf. consanguineus Oud. & Voigts 1904[4]	124	210	154
P. coleoptratorum (Linné 1758)	–	–	320
P. cf. distinctus (Berl. 1903)[4]	–	42	21
P. cf. remberti (Oud. 1912)[4]	23	40	23
P. cf. nolli Karg 1965[4]	11	20	13
P. cf. hyalinus (Willman 1949)[4]	–	32	22
P. cf. fimetorum (Berl. 1903)[4]	83[1]	127[1]	83[1]
P. cf. kraepelini (Berl. 1905)[4]	130	145	72
Paracarpais niveus (Wankel 1861)	–	–	–
Veigaia kochi (Trägårdh 1901)	–	225[3]	168[3]
V. nemorensis (C. L. Koch 1839)	–	42[3]	21
V. cf. exigua (Berl. 1917)[4]	–	8	5
V. cervus (Kramer 1876)	–	–	32

[1] Weighed living
[2] Weighed dry after preservation
[3] After Persson and Lohm 1977
[4] According to Athias-Henriot (personal communication) not identifiable before specific or generic revision

Appendix 4. List of species of Araneae recorded during the investigation.

Robertus arundineti (Cambr.)	*Diplocephalus latifrons* (Cambr.)
Pachygnatha degeeri Sundev.	*Erigone dentipalpis* (Wider)
Walckenaera dysderoides (Wider)	*E. atra* (Blackw.)
W. vigilax (Blackw.)	**Ostearius melanopygius* (Cambr.)
Dicymbium nigrum (Blackw.)	*Porrhomma convexum* (Westr.)
Oedothorax apicatus (Blackw.)	*Meioneta rurestris* (C.L.Koch)
Silometopus reussi (Thorell)	*Centromerus sylvaticus* (Cambr.)
Cnephalocotes obscurus (Blackw.)	*Centromerita bicolor* (Blackw.)
Tiso vagans (Blackw.)	*Diplostyla concolor* (Wider)
Troxochrus scabriculus (Westr.)	*Bathyphantes parvulus* (Wider)
Tapinocyba pallens (Cambr.)	*Tapinopa longidens* (Wider)
Micrargus subaequalis (Westr.)	*Bolyphantes index* (Thorell)
Erigonella hiemalis (Blackw.)	*Lepthyphantes mengei* Kulcz.
Savignia frontata Blackw.	*Allomengea scopigera* (Grube)

* Not previously recorded from Finland.

Appendix 5. Condensed results of the analyses of variance. Only significant differences in densities/m² presented. The differences in the biomasses generally showed the same or a lower level of significance. The test plot with the higher density is mentioned first. The asterisks denote the probability levels of 0.05(*), 0.01(**) and 0.001(***). [1]indicates that the experiment/season and/or experiment/duplicate interaction was at least as significant as the difference between the experiments. For symbols of the test plots see p. 224.

Nematoda
1975:
C/CS ***
D/C ***
DI/D **
H/D *[1]

1976:
D/C ***
D/B ***[1]
S/D ***
D/T ***
D/G ***
D/H ***

1977:
D/C **[1]
C/T ***
C/G *
D/B ***
S/D ***
D/T ***
D/G ***

Enchytraeidae

1975:
C/D ***
DS/D **
C/T ***
C/G ***
C/F ***

1976:
CI/C *
C/D ***
C/T *
C/G ***
B/D ***[1]
T/D ***[1]
G/D ***

1977:
C/D ***
C/G ***
B/D ***[1]
D/S ***[1]
T/D ***
G/D ***[1]

Collembola
1975:
C/G ***
C/F **

1976:
C/T **
B/D *
D/T **
D/S **[1]
D/H ***[1]

1977:
C/D ***
C/T ***
C/G ***
D/B ***
D/S **
D/T ***[1]
D/G ***

Prostigmata + Astigmata
1975:
C/D ***[1]
C/G ***
F/C ***
DI/D *

1976:
C/CI *[1]
C/G *[1]
D/B **[1]
D/G ***

1977:
D/C ***[1]
T/C ***
G/C **
B/D **[1]
D/T **[1]

Mesostigmata

1975:
D/C ***
C/T **
C/F **
D/DS***[1]
H/D **[1]

1976:
C/T ***
C/G **
D/T ***
H/D ***

1977:
D/S ***
D/T *
A/L ***

Araneae

1975:
D/C ***
G/C ***
F/C ***
D/B ***

1976:
D/B ***
D/T *
H/D *

1977:
D/B ***

Coleopterous adults

1975:
D/C ***
C/T *
G/C ***
D/H ***

1976:
D/C ***
C/T *
D/B ***
D/S ***
D/T ***
D/G **
D/H ***

1977:
D/B ***
D/S ***
A/L ***

Coleopterous larvae
1977:
C/D *[1]
C/T ***
D/B ***
L/D *
D/T ***

Dipterous larvae

1975:
CS/C **
D/C ***
D/DS **
B/D **
D/S **
D/H ***

1976:
D/C **
T/C *[1]
D/G *
D/H ***[1]

1977:
D/C *
T/C *
G/C ***
D/B **
D/S **
T/D *

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