8. SOIL FAUNA AND CEREAL CROPS*

K.B. ZWART† AND L. BRUSSAARD‡
†Institute for Soil Fertility, Department of Soil Biology, PO Box 30003, 9750 RA Haren, The Netherlands; ‡Institute for Soil Fertility, Haren, and Agricultural University, Department of Soil Science and Geology, PO Box 37, 6700 AA Wageningen, The Netherlands

INTRODUCTION

Cereals, in particular winter wheat and spring barley, are important crops in Dutch arable farming. Arable production in The Netherlands is among the most intensive in the world as a result of several environmental conditions and husbandry practices. Firstly, the natural soil fertility in The Netherlands is high, especially on reclaimed marine soils. Secondly, the use of large amounts of artificial fertilizers and animal manure by the farmers, prevents any deficiency of the basic nutrients during crop growth. Thirdly, the extensive use of chemicals suppresses weeds and pests. And finally, a good soil structure is created and maintained by intensive tillage.

During the last 10–15 years, the negative aspects related with this high production have begun to attract more attention. Several areas in The Netherlands are facing environmental problems due to: (i) contamination of groundwater by nitrate, originating from artificial fertilizers or animal manure; (ii) contamination of groundwater with agrochemicals; and (iii) deterioration of soil structure due to the use of heavy machinery. Apart from causing environmental problems, this so-called conventional farming (CF) is associated with high costs of agrochemicals and machinery, constituting a high demand for energy. Vereijken (1986) proposed integrated farming (IF) as a new way to overcome many problems associated with CF. In integrated farming, reduction of input in terms of artificial fertilizers, agrochemicals and soil tillage will result in lower crop production, but in economic terms this will, to a greater or lesser extent, be offset by lower costs (Vereijken 1989). A cost-effective and long-term environmentally sound arable farming may stimulate farmers to change farm management.

For integrated farming to become successful, basic knowledge about the mechanisms involved in the functioning of the soil-crop ecosystem is needed (Brussaard *et al.* 1988). The objective of the Dutch Programme on

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Soil Ecology of Arable Farming Systems is to obtain such knowledge with respect to: (i) matching of nutrient supply by the soil with nutrient demand by crops; and (ii) enhancement of the contribution of soil organisms to soil structure formation (Brussaard *et al.* 1988). Research within this programme is performed at laboratory and field level. Field research is carried out at the experimental farm Lovinkhoeve in the north-east Polder, which was reclaimed in 1942. The soil is a marine silt loam, with a pH-KCl of 7·5, an organic matter (OM) content of 2·3–2·8% and a total nitrogen (N) content of 0·09–0·14%, both depending on the history of the various trial fields. The annual rainfall is 650–800 mm. The trial includes three different types of management: (i) CF, (ii) IF (both since 1985); and (iii) IF with minimum tillage (since 1986). The third management system will not be discussed here. The site and farm management characteristics of CF and IF were described in detail by Kooistra, Lebbink & Brussaard (1989) and are summarized for winter wheat in Table 8.1. Field studies include collection of data on:

1 biological characteristics;
  (a) biomass of micro-organisms (bacteria and fungi),
  (b) biomass of fauna (protozoa, nematodes, collembola, mites, enchytraeids, earthworms and ground beetle larvae);
2 chemical/physical characteristics;
  (a) soil organic matter, total N, mineral N, N mineralization or immobilization,
  (b) total C and N input,
  (c) description of macropore structure of the soil,
  (d) quantification of soil macro- and microporosity, aggregate size distribution and aggregate stability.

Laboratory studies include:

1 studies on the effects of biotic and abiotic factors on the dynamics of the soil biota, related to the C and N turnover;
2 assessment of the impact of microflora and fauna interactions on C and N flows;
3 studies on the effects of enchytraeids and earthworms on soil structure.

Studies in the Dutch Research Programme are linked to earlier and ongoing studies on the ecology of arable soils performed in the Swedish Arable Land Project (e.g. Andrén *et al.* 1989b), the North American Detrital Food Web Project (e.g. Ingham *et al.* 1986), the North American Horse Shoe Bend studies (e.g. Hendrix *et al.* 1986) and the work of the Canadian group at Edmonton, Alberta (e.g. Rutherford & Juma 1989). The Dutch programme started in 1985 and the data presented in this paper relate to winter wheat in 1986. Since 1986 no extensive data on the soil

TABLE 8.1. Husbandry practices under conventional and integrated farming on the Lovinkhoeve site of a winter wheat crop in 1986. From Kooistra, Lebbink & Brussaard (1989)

Management	Conventional farming (CF)	Integrated farming (IF)
Tillage		
October	Plough	Fixed-tine cultivator
Depth	20 cm	12 cm/8 cm
Seed-bed	Spring-tine cultivator	Spring-tine cultivator
Depth	Superficial	Superficial
Fertilizer		
N	200 kg/ha*	155 kg/ha*
Crop protection		
Weed control	Mainly chemical	Mainly mechanical
Pest control	Recommended dosages of pesticides (EPIPRE system)	Less pesticides
	Soil fumigation after harvest	No soil fumigation

* Including mineral N amount in the soil (0–100 cm) in early spring.

fauna of cereal crops have been collected with the exception for winter wheat in 1990. These 1990 data, however, have not been completely analysed and will not be discussed here.

The focus of this paper is on soil fauna as related to C and N dynamics and to soil structure under cereals. Soil microflora will also be discussed. The paper is not meant to be a comprehensive review of the subject. Ample reference, however, will be made to the above-mentioned projects and other relevant literature.

SOIL BIOTA AND CARBON AND NITROGEN DYNAMICS

Matching of the nutrient supply by the soil and the nutrient demand by plants requires knowledge of the kinetics of biological processes such as decomposition of organic matter and mineralization, especially when organic nutrient sources are important, as is the case in integrated farming (IF). Therefore, factors that determine decomposition and mineralization receive particular attention in the Dutch Programme, in which the situation in conventional farming (CF) is compared with IF.

The role of soil fauna in mineralization

Mineralization is the process by which dead organic matter (DOM) is converted from labile complex biopolymers into stable simple mineral elements. Simultaneously, complex humic compounds are formed (stabilized DOM). Physical, chemical and especially biological factors play an important role in this process. The importance of the soil fauna for the decomposition of organic matter and the release of nutrients is dealt with in recent synthesis and review papers, e.g. Anderson (1988), Crossley, Coleman & Hendrix (1989) and Verhoef & Brussaard (1990). In arable land, labile DOM originates from several sources: crop residues, decaying roots from (previous) crops, decaying micro-organisms, root exudates, animal manure, green manure, etc. The estimated labile DOM input at CF and IF at the Lovinkhoeve site associated with winter wheat cropping, is given in Table 8.2. Besides labile DOM, arable soil contains a large pool of previously stabilized DOM (Table 8.2), which, although slowly degradable, may be just as important as the labile DOM, in view of its total mass. DOM is mineralized by a range of organisms, which are connected in detritus-based food webs. In such below-ground food webs, the organisms are grouped functionally into different trophic levels related to their main food source and life history characteristics, rather than taxonomically. Moore & De Ruiter (1990) have described the webs for CF and IF, respectively, at the Lovinkhoeve site. Figure 8.1 shows the food web for IF.

Figures 8.2 and 8.3 show the food webs as described for agro-ecosystems

TABLE 8.2. Input of organic matter immediately prior to and during growth of winter wheat on the Lovinkhoeve site, under conventional and integrated farming in 1986 (kg/ha)

Input	Conventional farming (CF)	Integrated farming (IF)
Previous crop*	500	4500
Exudation from wheat†	1940	1900
Degradation of SDOM‡	1370	1750
Total	3810	8150
Total carbon (50%)	1905	4075

* Sugar beet, input was different for CF and IF: on CF roots only; on IF roots and leaves were ploughed into the soil.

† Assumed to be 10% of primary production (Woldendorp 1981).

‡ Degradation of SDOM (stable dead organic matter) assumed to be 2% per year (Kortleven 1963); CF < IF, because of slightly higher organic matter content in the IF plots.

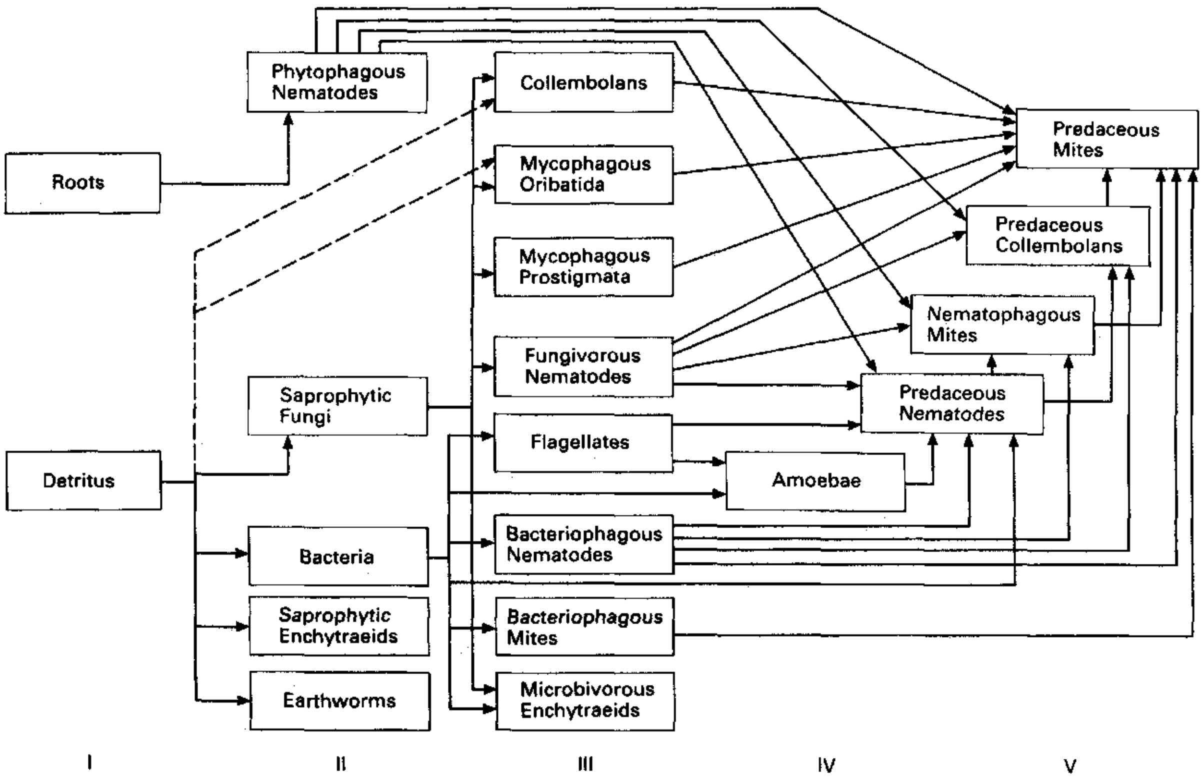


FIG. 8.1. Subterranean food webs for the Lovinkhoeve site under winter wheat with integrated farming. The roman numerals refer to trophic levels. Dashed vectors indicate potential feeding relationships, which have not been quantified. After Moore & De Ruiter (1990).

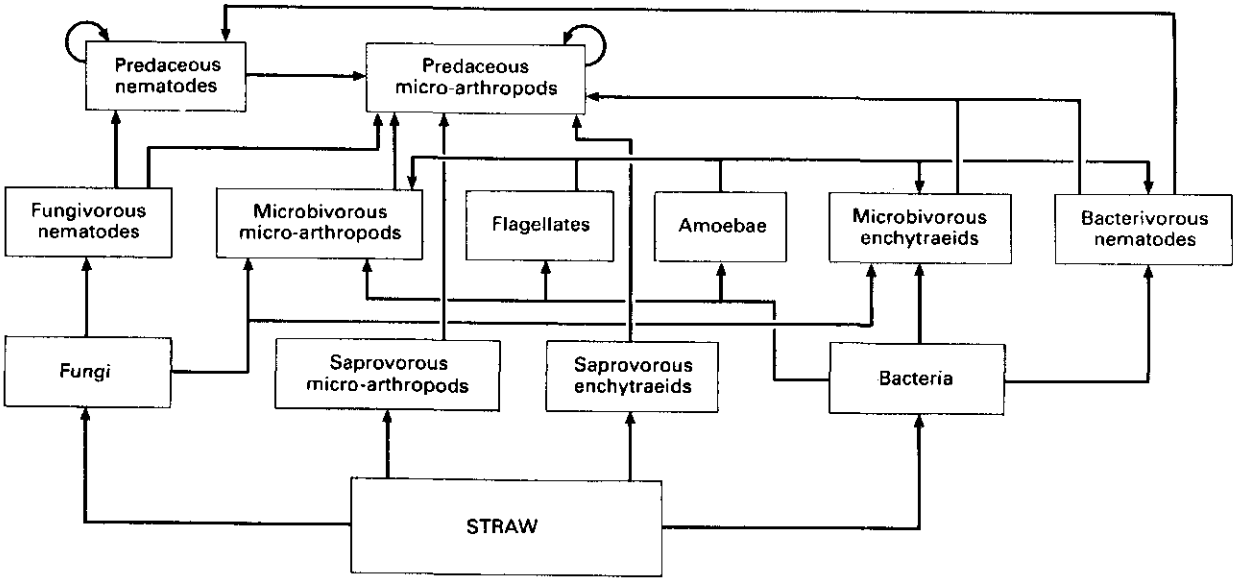


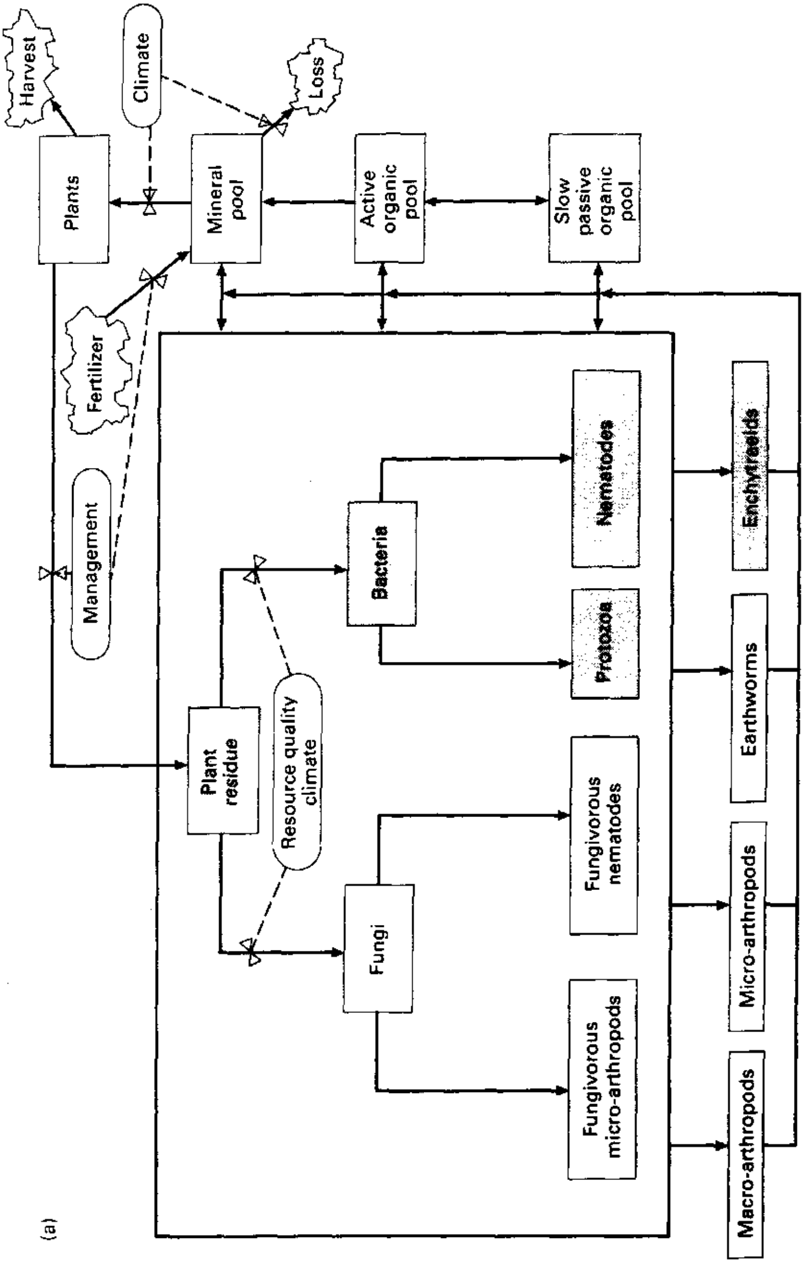
FIG. 8.2. Conceptual subterranean food web of decomposing barley-straw litter during decomposition. From Andrén, Paustian & Rosswall (1988).

in Sweden (Andrén, Paustian & Rosswall 1988) and North America (Hendrix *et al.* 1986, 1987). The role of different trophic levels of such a food web in mineralization is schematically presented in Fig. 8.4. In each degradation step, organic matter (OM) is converted into newly formed biomass, partly digested OM and mineral elements. The amount of mineral elements released by functional groups determines their impact on *direct* mineralization. The amount of newly formed biomass and partly decomposed OM determines their impact on *indirect* mineralization, since newly formed biomass may be further consumed (*i.e.* mineralized) by higher trophic levels, while the partly decomposed OM returns to the DOM pool and re-enters the process. Organisms of a functional group also have an *indirect* effect on mineralization if they affect the decomposition rates of lower trophic levels. The quantities and proportions of biomass, released OM and minerals produced vary widely among the functional groups within the trophic levels. Therefore, the role of different groups will show wide variation. The relative importance of organisms in mineralization will generally depend on their biomass (C and N pool), their population turnover rate and their assimilation efficiency (C and N fluxes).

The average biomass of several functional groups during the growing season of winter wheat under CF and IF on the Lovinkhoeve site is given in Table 8.3. Microbial biomass forms by far the largest pool under winter wheat, followed by earthworms (IF only), protozoa, micro-arthropods and enchytraeids. Within the microbial biomass, fungi are of minor importance. The irregular distribution of earthworms has not resulted from different management systems, but rather from the history of the fields. The polder where the Lovinkhoeve site is located, was reclaimed from the sea almost

TABLE 8.3. Average biomass (kg C/ha) in the top 25 cm of soil under winter wheat on the Lovinkhoeve site under conventional and integrated farming during the 1986 growing season

Organisms	Conventional farming (CF)	Integrated farming (IF)
Bacteria	339·80	436·70
Fungi	16·20	24·70
Protozoa	10·00	13·00
Nematodes	0·48	1·20
Micro-arthropods	0·79	0·64
Macro-arthropod larvae	0·30	0·00
Enchytraeids	0·78	0·55
Earthworms	0·00	15·00
Total biomass C	368·35	491·81


(a)
Harvest
Climate
Loss
Plants
Mineral pool
Active organic pool
Slow passive organic pool
Fertilizer
Management
Plant residue
Resource quality climate
Bacteria
Fungi
Nematodes
Protozoa
Fungivorous nematodes
Fungivorous micro-arthropods
Enchytraeids
Earthworms
Micro-arthropods
Macro-arthropods

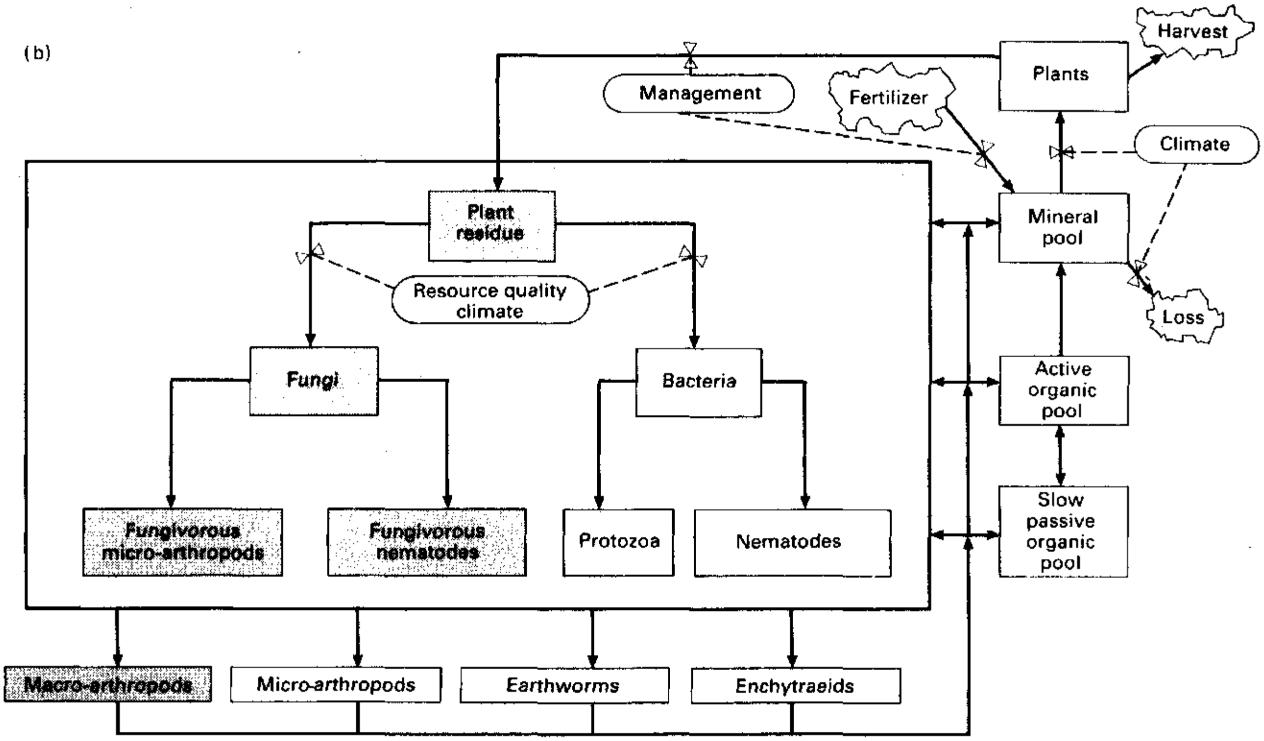


FIG. 8.3. Conceptual detritus based, subterranean food webs under conventional tillage (a) and no tillage (b) agro-ecosystems. Boxes = nutrient stores, 'clouds' = nutrient sources or sinks, arrows = nutrient transfer pathways, valve symbols on arrows indicate that nutrient transfers are influenced by factors connected by dotted lines. The shaded boxes denote the major nutrient pools. From Hendrix *et al.* (1987).

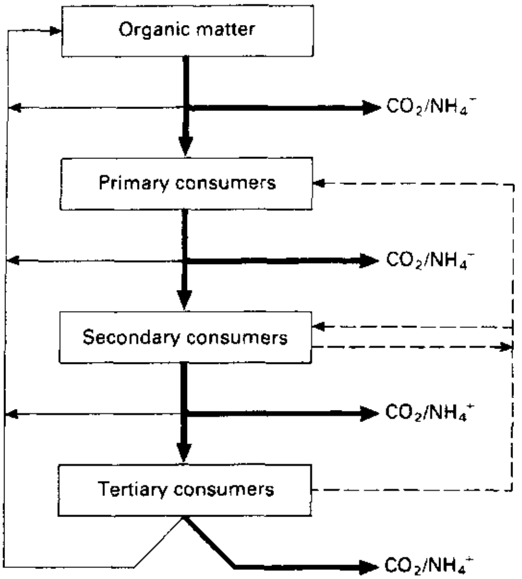


Fig. 8.4. The role of different trophic levels in a food web on mineralization of organic matter. Bold arrows indicate direct mineralization, fine arrows indicate recirculation of organic matter and dashed lines indicate possible effects on the activity of lower trophic levels.

50 years ago. Earthworms are still colonizing parts of the site. Both intensive tillage and the exclusive use of artificial fertilizers have probably prevented colonization of the conventionally managed trial fields (Marinissen 1990). The quantitative variations in some of these groups during the growing season are shown in Fig. 8.5 (Moore & De Ruiter 1990). Table 8.4 summarizes the biomass of several groups of organisms found in studies in Europe and North America. To allow comparison, the data are given as percentages of the total biomass. In all situations the microflora form the largest pool, followed by protozoa (if determined) and earthworms (if present). The role of each of these respective groups in mineralization are discussed successively in more detail.

Microflora

Although this paper is primarily concerned with soil fauna, their activities should not be isolated from the microflora. Bacteria and fungi are the major primary consumers and not only constitute by far the largest biomass pool, but also serve as food for many organisms in the below-ground food web.

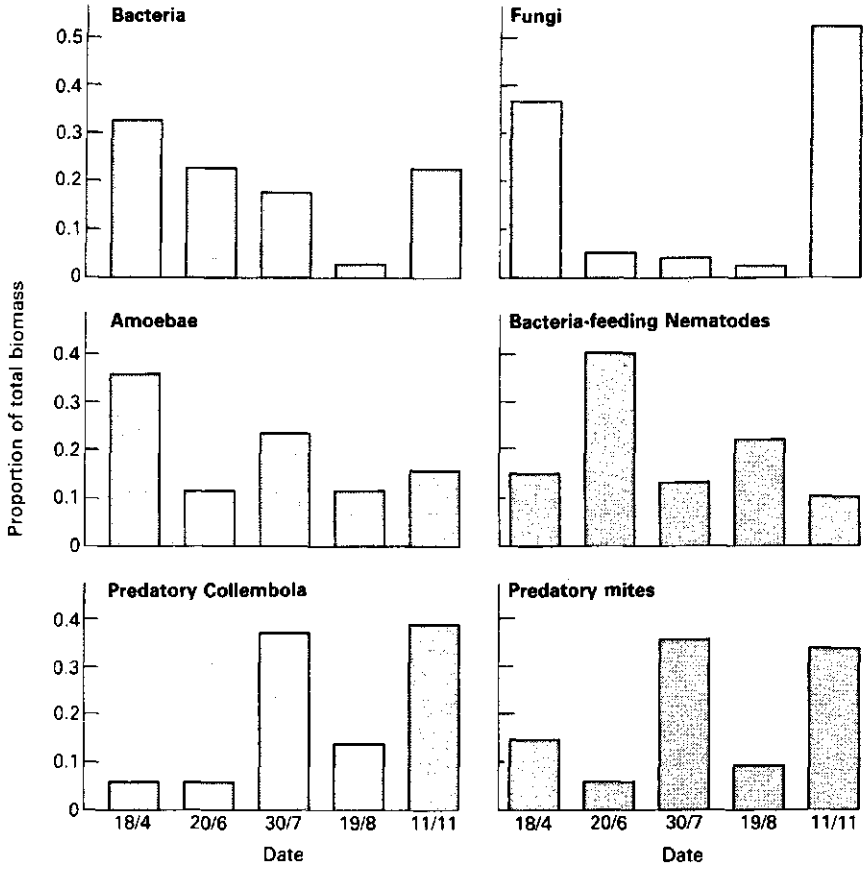


FIG. 8.5. Fluctuation in biomass of some functional groups at the Lovinkhoeve site under integrated farming. The columns represent the proportions of the total biomass of each group over the sampling period from April until November. From Moore & De Ruiter (1990).

In 1986 there was no significant difference in microbial biomass between CF and IF at the Lovinkhoeve site (Table 8.3). During the growing season of wheat, some variation in biomass was found (Fig. 8.5). This variation has also been found by others under cereals (Campbell & Biederbeck 1976; Carter & Rennie 1982; Elliott *et al.* 1984; Schnürer, Clarholm & Rosswall 1986; Granatstein *et al.* 1987) and other crops (Ross *et al.* 1981; Nannipieri 1984). It is explained by variation in temperature and moisture (Elliott *et al.* 1984; Schnürer *et al.* 1986; Granatstein *et al.* 1987), by addition of crop residues after harvesting (Granatstein *et al.* 1987) and by predation (Schnürer *et al.* 1986).

TABLE 8.4. Biomass of micro-organisms and fauna groups as a percentage of total carbon in arable soils under cereals of different locations in the world

	Lovinkhoeve[1]				Horse Shoe Bend[4]		Kjettslinge[5]		Akron[6]	
Organisms	CF	IF	Ellerslie[2]	Breton[3]	CT	NT	B0	B120	SM	NT
Total biomass (kg C/ha)	368	492	609	554	910	740	2360	3050	235	273
Bacteria	92·20	88·80	75·3*	47·6*	76	59·5	29·7	29·5	99*	99*
Fungi	4·40	5·00			16·5	21·5	63·6	68·9		
Protozoa	2·85	2·60	24·6	52·3	5·5	5·4	5·9	1·0	0·6	0·6
Nematodes	0·24	0·24	0·01	0·01	0·22	0·14	0·05	0·03	0·3	0·3
Micro-arthropods	0·19	0·13	0·06	0·03	0·08	0·27	0·02	0·01	0·06	0·09
Macro-arthropods	0·10	0·00	NA	NA	0·01	0·03	0·05	0·01	NA	NA
Enchytraeids	0·21	0·11	NA	NA	0·03	0·07	0·18	0·12	NA	NA
Earthworms	0·00	3·04	NA	NA	2·2	13·5	0·47	0·45	NA	NA

[1] Lovinkhoeve site, The Netherlands, Typic Fluvaquent, silt loam, 0–25 cm, spring/summer, winter wheat.

[2] Ellerslie, Alberta, Canada, Black Chernozem, silt clay loam, 0–10 cm, barley, summer/autumn (Rutherford & Juma 1989).

[3] Breton, Alberta, Canada, Gray Luvisol, silt loam, 0–10 cm, barley, summer/autumn (Rutherford & Juma 1989).

[4] Horse Shoe Bend site, Athens, Georgia, USA, Hiwassi loam, Typic Rhodudult, sandy clay loam, 0–15 cm, winter/spring, grain/rye (Hendrix *et al.* 1986, 1987).

[5] Kjettslinge site, Sweden, mixed, frigid Haplaquoll, loam, 0–27 cm, barley, 1982–83 (Andrén, Paustian & Rosswall 1988; Andrén *et al.* 1989a).

[6] Akron, Colorado, USA Mollisol, 0–10 cm, fallow/wheat, summer (Elliott *et al.* 1984).

* Including fungi.

CF, conventional farming. IF, integrated farming. CT, conventional tillage. NT, no tillage. Bo, no N fertilizer. B120, 120 kg N fertilizer/ha. SM, stubble mulch. NA, data not available.

Fungal populations, as estimated by direct counts, are quantitatively unimportant in the Lovinkhoeve soil. This observation is in agreement with several other investigations; in Sweden, however, the fungi seem to be more important than bacteria (Table 8.4). The relatively low contribution of fungi to organic matter degradation at the Lovinkhoeve site was confirmed by the presence of low numbers of fungivorous animals. Moore & De Ruiter (1990) performed cluster analysis of functional groups at the Lovinkhoeve site using the functional link approach, as suggested by Moore *et al.* (1988). The functional link approach attempts to project species into niche space and to study the collective behaviour of species (assembled in functional groups) and their impact on ecosystem-level processes, such as cycling of elements. Moore & De Ruiter (1990) distinguished three clusters of functional groups under CF and four under IF. Fungi formed a distinct cluster under IF, whereas under CF they were grouped together with bacteria. This might suggest that fungi were relatively more important under IF. Hendrix *et al.* (1986, 1987; Fig. 8.3) suggested that changing from conventional tillage to no tillage would result in a relative increase in the function of fungi and fungal-feeding organisms in organic matter degradation. Numerical data from both the Lovinkhoeve site and the Horse Shoe Bend site, however, indicate that bacteria rather than fungi are the most important primary consuming micro-organisms under all types of management (Table 8.4).

Although microbial biomass is an important ecological parameter in relation to mineralization, microbial growth rate is even more important. Unfortunately, growth rate measurements in soil are very difficult to perform. Bloem & Brussaard (1989) used the frequency of dividing and divided cells (FDDC) as an indication of growth rates of bacteria in a field plot experiment during drying and rewetting of Lovinkhoeve soil under sugar beet. They found a non-significant increase in bacterial biomass (based on direct microscopic counts) shortly after rewetting, notwithstanding a FDDC indicating a generation time of approximately 10 h. This discrepancy was explained by assuming a high activity of predators. Based on total carbon input during 1985 and 1986 (Table 8.2), assuming a C : N ratio of 20 for this organic input and a bacterial C : N ratio of 5, one might expect a turnover rate for the bacterial biomass of 0·7 times per year on CF and 1·2 times on IF. In that case there was no net N mineralization by micro-organisms. In case of a very efficient remineralization of nutrients by the soil fauna, a turnover rate of 1·2 and 2·5 times per year was estimated for CF and IF, respectively. The turnover rate estimated for the Lovinkhoeve site is fairly close to the rate of 0·4–0·8 times per year found by Jenkinson, Ladd & Rayner (1980) for soil bacteria. Schnürer, Clarholm

& Rosswall (1985) reported an annual turnover rate of 0·5 for microbial biomass under fertilized barley. There is, however, an enormous discrepancy between growth rates resulting in a turnover rate of 0·7–1·2 per year and generation times of approximately 10 h. This may indicate that bacterial growth rates show wide variations with bursts of rapid growth followed by periods of very slow growth or dormancy. Therefore, a reliable and accurate method to establish bacterial production and consumption by predators in soil is badly needed.

Protozoa

Protozoa are the most predominant faunal group in arable land under cereals (Table 8.4). They constitute 1–6% of the total biomass, and Rutherford & Juma (1989) found even higher densities. However, the counting method used by Rutherford & Juma (1989) was different from the one of Darbyshire *et al.* (1974), which is employed most frequently in soil protozoan studies. This may explain, at least partly, the extremely high protozoan density in Canadian soils. At the Lovinkhoeve site, the protozoan pool in 1986 represented approximately 10 kg C; the amounts in CF and IF did not differ significantly (Table 8.3).

Protozoa probably are the most important bacterial consumers in soil, followed by bacterivorous nematodes. The major representatives at the Lovinkhoeve site are small naked amoebae and flagellates, which are well adapted to the thin waterfilms around soil particles. Ciliates are often used in model studies to test the effect of protozoa on soil processes (Darbyshire 1976; Griffiths 1986). The number of ciliates at the Lovinkhoeve site, however, was below the detection limit of the most probable number technique for enumeration of soil protozoa (Darbyshire *et al.* 1974). Clarholm (1983, 1989) considers naked amoebae as the most important protozoa in arable land under barley.

Initially, protozoa were assumed to have an adverse effect on soil fertility (Russell & Hutchinson 1909). Waksman (1916), however, considered them to have a beneficial effect or to be harmless. Since that time, evidence has been obtained for the positive effects of protozoa on soil processes. Nitrogen fixation by *Azotobacter* was stimulated by the presence of protozoa (Cutler & Bal 1926; Telegdy-Kovats 1932; Hervey & Greaves 1941; Nikoljuk 1969; Darbyshire 1972a,b) and protozoa also stimulate the mineralization of N and P in soil (Cole, Elliott & Coleman 1978; Elliott, Coleman & Cole 1979; Woods *et al.* 1982; Clarholm 1983; Griffiths 1986; Kuikman & Van Veen 1989). Elliott, Coleman & Cole (1979), Clarholm (1983) and Kuikman (1990) demonstrated that plant N uptake from an organic source is stimulated by protozoan activity.

Several explanations for the stimulatory effect of protozoa have been presented. One obvious explanation is that protozoa excrete excess N and/or P (phosphorus) from bacteria which they use as a source of energy. Furthermore, protozoa may excrete residues of their food (e.g. bacterial cell walls). Further digestion of these organic excretion products by bacteria may be facilitated, which will then lead to an increase in mineralization. Finally, several authors have suggested that grazing of protozoa on bacteria stimulates bacterial activity by preventing or releasing nutrient limitation (Barsdate, Prentki & Fenchel 1974; Cutler & Crump 1929; Fenchel & Harrison 1976; Meiklejohn 1930, 1932; Pussard & Rouelle 1986). These authors contend that, although grazing leads to a decrease in the bacterial population, the specific activity of bacteria will increase to such an extent that the total activity of a grazed population is higher than that of an ungrazed population.

Mathematical simulation models are used to estimate the fluxes of C and N through different functional groups (O'Neill 1969; Hunt *et al.* 1984; 1987). De Ruiter (personal communication) estimated the flux of nitrogen via animal consumption of bacteria at CF and IF under winter wheat in the top 25 cm of soil. The protozoan contribution was 40 and 65 kg N/ha per year in CF and IF respectively, which was over 70% of the total faunal flux. In Sweden protozoan contribution to the flux of N under fertilized barley was approximately 30 kg/ha per year, i.e. 16% of the total N flux, which was over 50% of the flux via the soil fauna (Andrén *et al.* 1989a). According to Hendrix *et al.* (1987) the protozoan contribution to soil respiration was 7.6 and 6.6% under CT and NT, respectively (Table 8.5), which was 56 and 18%, respectively, of the faunal respiration. From these figures it may be concluded that protozoa play a major role in mineralization of microbial biomass under cereals. The accuracy of simulation models with respect to protozoan activity may be further improved. For example, one should distinguish between active and encysted cells. Furthermore, the effects of abiotic factors on growth of protozoa need to be included to allow for the temporal dynamics of protozoa (Kuikman 1990). Little is known about the effect of moisture on small amoebae and flagellates. There is some information that protozoan growth ceases when pores with a diameter larger than 6 μm become dry (Darbyshire 1976; Alabouvette *et al.* 1981). Postma (1989) and Kuikman (1990) assumed that pores with neck diameters smaller than 3 μm are not accessible to protozoa. However, common soil flagellates of the genus *Cercomonas* showed almost maximum growth rates in sterilized Lovinkhoeve soil with a moisture content of 18·6%, which is equivalent in this soil with a water potential of −100 KPa, where only pores smaller than 3 μm in diameter are filled with water (Fig. 8.6). Moreover, also at lower moisture conditions, where only pores smaller

TABLE 8.5. Flows of carbon or nitrogen through micro-organisms and fauna of arable fields under cereals as a percentage of total annual flows/ha at the Horse Shoe Bend site (Hendrix *et al.* 1986) and the Kjettslinge site (Andrén *et al.* 1989)

Organisms	Horse Shoe Bend rye CT	Horse Shoe Bend rye NT	Kjettslinge barley, 120 kg N fertilizer/ha
Bacteria	81.0	56.8	69.1*
Fungi	5.7	6.6	—
Protozoa	7.6	6.6	16.0
Nematodes	0.4	0.2	9.4
Micro-arthropods	0.08	0.25	2.2
Macro-arthropods	0.008	0.03	0.2
Enchytraeids	0.04	0.02	1.6
Earthworms	5.3	29.0	0.5
Total annual flow/ha	2630 kg C	2410 kg C	198 kg N

* Including fungi.
CT, conventional tillage. NT, no tillage.

than 1 μm were filled with water, the flagellates still showed maximum growth (Fig. 8.6). This may indicate that small flagellates, like *Cercomonas*, are able to consume bacteria even under dry conditions, when other bacterivorous organisms are no longer active. Their growth rates under

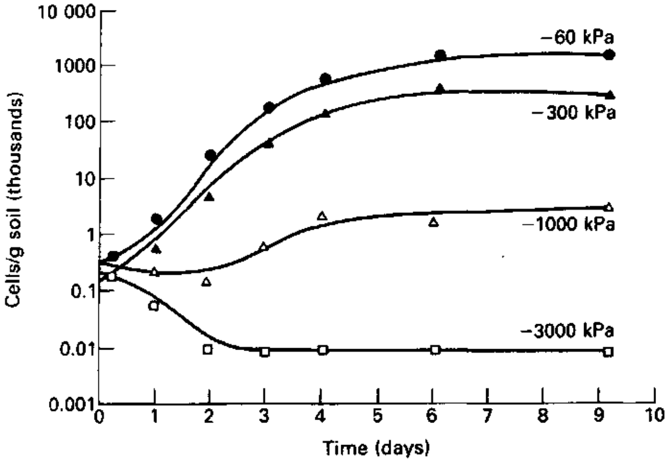


FIG. 8.6. Growth of the common soil flagellate *Cercomonas* sp. in microcosms of sterilized soil from the Lovinkhoeve site, in the presence of bacteria, *Pseudomonas fluorescens*, as food, under different moisture conditions at 20°C.

these conditions may indicate that these organisms have turnover rates which are higher than assumed thus far in simulation model studies.

Nematodes

Total nematode biomass at the Lovinkhoeve site was less than 0·15% of the total biomass (Table 8.4), representing approximately 1 kg C/ha. This fraction of 0·15% is in between the ones observed at other locations (Table 8.4). Under conventional tillage (CT) at Horse Shoe Bend and in Akron nematodes constitute between 0·25 and 0·3% of the total biomass and in Sweden and Canada the nematode fraction is 0·05% or less (Table 8.4). Biomass under CF was almost similar to that under IF at the Lovinkhoeve site. Stinner & Crossley (1982) found no differences in biomass under CT or no tillage (NT). Hendrix *et al.* (1986, 1987), however, reported somewhat higher numbers under CT than under NT. According to Boström & Sohlenius (1986), there was no difference in taxonomic diversity of nematodes under single or continuous crops of barley. Plant-parasitic nematodes were more abundant under IF than under CF due to diminished nematocides on CF (Bouwman, unpublished result).

Free-living nematodes under barley responded positively to manure and fertilizer (Andrén & Lagerlof 1983). The very low nematode biomass may indicate that the role of these organisms in mineralization will probably be small. Sohlenius, Boström & Sandor (1988) estimated that only 1·3–2% of the total C input on arable land was respired by nematodes. They also calculated the annual turnover rate of the nematode population under barley. In rotational cropping systems, the turnover rate was 9·5 times per year v. 9·1 times per year with continuous barley. Based on standing stock population and turnover rates the impact of free-living nematodes on mineralization appears to be small. This is confirmed by estimations of respiration. Carbon respiration of nematodes under CT and NT was only 0·4 and 0·2% of total respiration, respectively (Hendrix *et al.* 1986, 1987; Table 8.5). Andrén *et al.* (1989a), on the other hand, estimated that 9·4% of the total N flow through the biomass was via nematodes (Table 8.5). Microcosm studies with sterilized soil and an organic N or P source, have sometimes indicated higher mineralization rates in the presence of nematodes than in their absence (Griffiths 1986). Nevertheless, Woods *et al.* (1982) observed a stimulation of nitrogen mineralization only during the decline of the nematode population, while Cole, Elliott & Coleman (1978), on the other hand, found little effect of nematodes on phosphorus mineralization in microcosm studies. Although these results are rather conflicting, it could mean that the impact of nematodes on mineralization is larger than expected solely from standing stock and population turnover rates. Possibly, nematodes have considerable indirect effects on the activity of other groups of organisms. Cole, Elliott & Coleman (1978) observed a positive effect of nematodes on amoebal activity and Brussaard *et al.* (1991) explained part of the positive effect of bacterivorous nematodes on N mineralization by suggesting that nematodes carry commensal or epizoic flagellates. Finally, there are indications that nematode turnover rates are higher than the values given by Sohlenius, Boström & Sandor (1988). Nematophagous fungi, organisms not considered in most food web studies, may effectively keep the nematode population at a low level in the Lovinkhoeve soil (Bouwman, unpublished). So, possibly the role of nematodes is more likely to be underestimated than overestimated.

Micro-arthropods

Micro-arthropods (acari and collembola) represent only a minor fraction of the total biomass at the Lovinkhoeve site (Tables 8.3 and 8.4) and other sites (Table 8.4). Their overall densities at IF were similar to those at CF, but there was a large difference in abundance of species under both types of management (Brussaard *et al.* 1988). Andrén & Lagerlöf (1983) found a negative response of collembola and most of the acari to N fertilizer in various cropping systems. However, no effect of N fertilizer on micro-arthropods under barley was found (Lagerlöf 1987; Lagerlöf & Andrén 1988). Acari and collembola consumed less than 1% of the estimated microbial production (Lagerlöf 1987; Lagerlöf & Andrén 1988). Andrén & Schnürer (1985) found little effect on C mineralization of barley straw by the collembolan *Folsomia fimetaria* in pot experiments. Different numbers of grazing collembola did not result in differences in respiration, mass loss or microbial biomass. Based on these data, it would seem unlikely that micro-arthropods would have a great impact on mineralization. Indeed, less than 3% of the N flow under fertilized barley was via arthropods, macro-arthropods including (Andrén *et al.* 1989a; Table 8.5). Carbon respiration of micro-arthropods under CT and NT was 0·08 and 0·25%, respectively, of total respiration (Hendrix *et al.* 1986, 1987; Table 8.5). However, in other cases fungal-grazing collembola or mites played an important role as regulators of decomposition in microcosms (Morley *et al.* quoted by Elliott *et al.* 1986) and in the field, both under natural (Whitford *et al.* 1982) and agricultural (Parmelee, Beare & Blair 1989) conditions. In microcosm studies by Morley *et al.* (quoted by Elliott *et al.* 1986) the presence of mites resulted in a four-fold increase of the specific respiration rate of the microflora.

Besides microbivorous micro-arthropods, nematophagous mites have been reported to affect decomposition and mineralization rates. Lagerlöf & Andrén (1988) found that the consumption by predatory mites corresponded to 20–60% of the total nematode production. In terms of biomass this may be small, but it may affect bacterial production considerably. Despite their low direct contribution to carbon and nitrogen dynamics, micro-arthropods therefore may exert a stabilizing effect on microflora, nematode abundance, decomposition and mineralization rates (Moore, Walter & Hunt 1988). The available evidence (Coleman *et al.* 1984; Seastedt 1984; Verhoef & Brussaard 1990), however, suggests that the importance of such activities is greater in the case of more recalcitrant substrates, i.e. more important in natural systems than in agro-ecosystems (Crossley, Coleman & Hendrix 1989).

Enchytraeids

At the Lovinkhoeve site, the enchytraeids constituted approximately 0·2% of the total biomass under wheat in 1986 both under CF and IF (Tables 8.3, 8.5 and 8.6). In IF however, the organisms were concentrated in the upper 10 cm of the soil ($P < 0{\cdot}01$, Friedman test), whereas in CF more animals occurred in the 10–40 cm layer ($P < 0{\cdot}05$, Friedman test) (Didden 1991). Lagerlöf, Andrén & Paustian (1989) found that different cropping systems had no effect on enchytraeid densities. Using the values of Persson &

TABLE 8.6. Presence of enchytraeidae: abundance (10^6/ha), biomass (kg C/ha) and carbon flows (kg C/ha per year)

	Lovinkhoeve[1] (0–25 cm)		Kjettslinge[2] (0–20 cm)	
	CF	IF	B0	B120
Abundance	90	83	100	81
Biomass[3]	0·78	0·55	3·2	2·7
Respiration	8·75	7·75	25·9	20·7
Respiration, percentage of organic C input	0·46	0·19	1·73	1·15
Consumption	58·33	51·67	172·8	138·2
Consumption, percentage of organic C input	3·06	1·27	11·52	7·62

[1] Samples from wheat (January–December), Lovinkhoeve site (Didden 1991).
[2] Samples September 1980–1984, barley, Kjettslinge site (Lagerlöf, Andrén & Paustian 1989).
[3] Biomass and C-flow calculations according to Persson & Lohm (1977) (B0 and B120).
CF, conventional farming. IF, integrated farming. B0, no N fertilizer. B120, 120 kg N/ha.

Lohm (1977), they assumed that enchytraeids are 50% microbivorous and 50% saprovorous. Based on this assumption and figures of Heal & MacLean (1975), they used values 0·12 and 0·18 for production: consumption and respiration : consumption efficiencies, respectively. The estimates on enchytraeid abundance, biomass and carbon flows under barley and winter wheat are listed in Table 8.6. The numbers of enchytraeids under barley and wheat were in the same range, despite different farming methods (Table 8.6). Tables 8.5 and 8.6 clearly show that the contribution of enchytraeids to soil respiration is small. Lagerlöf, Andrén & Paustian (1989) reported an enchytraeid respiration under barley of 12–26 kg C/ha per year. Enchytraeids however, have a low assimilation : consumption ratio (Heal & MacLean 1975), and therefore consume a significant amount of organic matter. When all enchytraeids found in the 0–40 cm layer are taken into account, the respiration as a percentage of organic C input was 1·0% and 0·52% for CF and IF, respectively, while the values for consumption were 6·78% and 3·44%. The calculated amount of microbial C consumed by enchytraeids was 69–86 kg/ha per year under barley (0–25 cm) (Lagerlöf, Andren & Paustian 1989) and 36–47 kg/ha per year under winter wheat (0–40 cm). This is up to 10% of the total microbial production under barley and almost 6% under wheat. Andren & Lagerlöf (1983) and Lagerlöf, Andren & Paustian (1989) found a positive response of enchytraeids to organic matter addition. This was explained by the increase in microbial biomass after the addition of a fresh nutrient and energy source. The higher OM content under NT compared with CT probably also explains why more enchytraeids were found under NT (Hendrix *et al.* 1986, 1987; Table 8.4). Therefore, it is somewhat puzzling that House & Parmelee (1985) found exactly the opposite: in contrast to all other functional groups enchytraeids were more abundant under CT than under NT, whereas the OM content under CT was lower. In many arable soils, the enchytraeid biomass is considerably lower than earthworm biomass. House & Parmelee (1985) state that enchytraeids may have a more pronounced effect on OM decomposition than earthworms, because of their much higher respiration rate, but Ryszkowski (1985) demonstrated that this does not always outweigh the effect of lower numbers.

Assuming values from the literature for N contents of 11–13%, depending on species, Didden (1991) calculated the N turnover rate of enchytraeid tissue, using daily estimates of standing stock and productivity. In 1986 the N flux in the 0–40 cm layer was 1·9 and 2·7 kg/ha under IF and CF, respectively. Since these organisms have a very low assimilation efficiency, the total N flux is almost ten times higher.

Earthworms

The number of earthworms may vary considerably in arable soils. It has been shown in many studies that management has a predominant effect on earthworm abundancy. For instance, under CT their number was much lower than under NT (Gerard & Hay 1979; Edwards & Lofty 1982; House & Parmelee 1985). Andrén, Paustian & Rosswall (1988) found no effect of N addition on the numbers of earthworms under barley. At the Lovinkhoeve site previous and present management has affected the colonization of earthworms, causing them to be present in IF, but not in CF.

Hendrix *et al.* (1986, 1987) estimated an earthworm respiration of 14 and 700 kg C/ha per year under CT and NT, respectively, equivalent with 5·3 and 29% of total soil respiration (Table 8.5). These results suggest that, at least under NT, earthworms play a major role in direct mineralization. Parmelee (1987) and Parmelee & Crossley (1988) calculated a population turnover of earthworms of 3·3 times per year. Based on this figure and a standing stock population under NT of approximately 143·5 kg dry matter/ha, they calculated an N flux from earthworm tissue of 40 kg/ha per year. At the Lovinkhoeve site, under winter wheat (IF only) and in Sweden under barley (Table 8.4), earthworm biomass was much lower, and consequently the N flux from tissue was lower as well. Figures for N flux for a number of ecosystems were in the wide range of 10–225 kg/ha per year as mentioned by Lee (1985). Besides nitrogen turnover from tissue, nitrogen excreted as urine and mucoproteins may quantitatively be important. Depending on earthworm abundance, mineral N flux from these sources was estimated to be 18–50 kg/ha per year (Lee 1985). In contrast to urine, the amounts of mineral N released via casts is relatively insignificant. It ranges from less than 35–50 g (Lee 1985) to 3·5 kg/ha per year in pasture (Syers, Sharpley & Keeney 1979). In addition to their contribution to direct mineralization, earthworms may through mucus production and casting have a strong effect on indirect mineralization by stimulating the microflora (Scheu 1987). Earthworms have high consumption rates and low assimilation efficiencies, resulting in comminution of large amounts of organic matter, followed by mixing with mineral soil and excretion in casts. Microbial activity in casts and soil around burrows is often several-fold increased compared with the surrounding soil (Shaw & Pawluk 1986; Scheu 1987). Boström (1988) reported the nitrogen flow to the soil resulting from earthworms and cocoons and from the excretion of urine and mucus to range between 3 and 12 kg N/ha per year in four arable cropping systems, the lower figure being typical for barley. If indirect effects on the microflora as a consequence of comminuting organic matter are included, these figures increase to 13–52 kg N/ha per year, corresponding to 16–25% of net annual mineralization. Altogether, the impact of earthworms on mineralization in arable soils is significant.

Macro-arthropods

Very little is known about the effect of macro-arthropod activity on mineralization dynamics under cereals. Where investigated, their biomass is generally low. If one assumes rather low turnover rates, their effect on direct mineralization will probably be small. Similar to earthworms, macro-arthropods will have an indirect effect through comminution of organic matter and stimulation of microbial activity in excrements. The significance of this indirect effect is unknown due to a lack of quantitative data.

SOIL FAUNA AND SOIL STRUCTURE

There is extensive literature on the interactions between soil fauna and soil structure (e.g. Spence 1985; Mitchell & Nakas 1986; Edwards *et al.* 1988; Elliott & Coleman 1988; Lavelle 1988). Oades (1984) defined soil structure as the size and arrangement of particles and pores in soil. Soil fauna may create new pores by burrowing, enlarge existing pores, or reduce these pores as a result of lateral pressure elsewhere in the soil, or deposition of material from elsewhere. Soil aggregates may be created and stabilized by excretory products from the fauna. Existing aggregates may be reduced in size, or destroyed completely by passage through soil animals. Complex polysaccharides and gums from micro-organisms and plant roots may also play an important role in the creation and stabilization of aggregates and pores (Tisdall & Oades 1982; Oades 1984).

In this contribution we restrict ourselves to recent findings at the Lovinkhoeve site, where the significance of the soil fauna in the maintenance or improvement of soil structure is likely to be accentuated more in IF than in CF. The effects of the soil biota on soil porosity after 20 years of farming was studied by Kooistra, Lebbink & Brussaard (1989) in CF, a CF-ley rotation with regular farmyard manure addition (CFL) and in CF with minimum tillage (CFMT). Earthworms had only colonized CFL. In CF less than 10% of the macropores larger than 30 μm in diameter, in the tilled layer had been influenced by the soil biota, including roots, whereas over 90% of the macropores had been affected by tillage, traffic and internal slaking (Fig. 8.7). In CFMT, however, the fraction of macro-

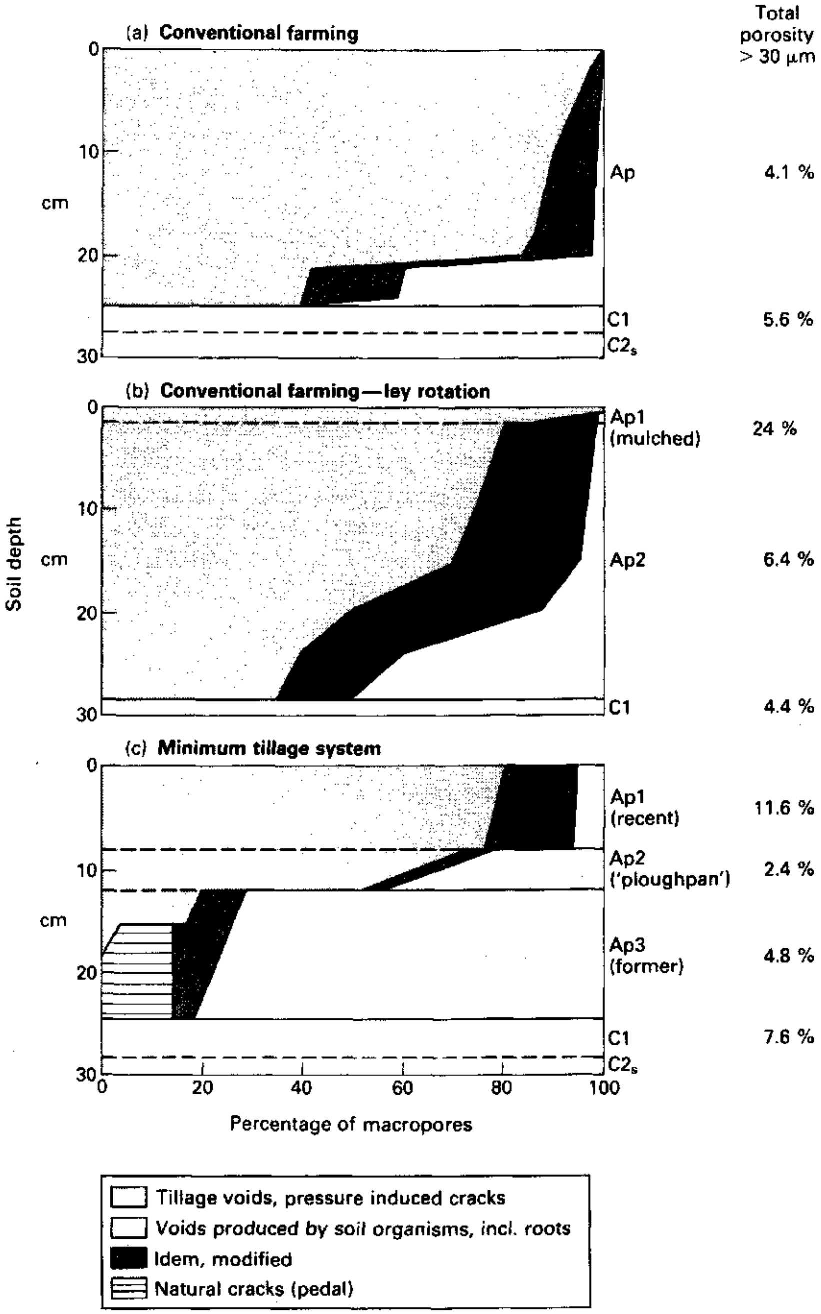


FIG. 8.7. Total soil porosity (>30 μm in diameter) at different soil depths and horizons at the Lovinkhoeve site under (a) conventional farming (CF), (b) conventional farming in a rotation with leys and regular farmyard manure addition (CFL) and (c) conventional farming with minimum tillage (CFMT). From Kooistra, Lebbink & Brussaard (1989).

pores affected by the soil biota rapidly increased below the shallow tilled Ap2 horizon to 80% at a depth of 25 cm. CFL was intermediate between CF and CFMT. Analysis of thin sections showed that the soil fauna, particulary enchytraeids and micro-arthropods, was the chief agent creating these voids or modifying existing voids by filling them with excrements.

Enchytraeids

The role of enchytraeids in soil structure evolution in agricultural fields under different management systems has been studied by Didden (1990). Enchytraeids transported only a very small part (0·001–0·01%) of bulk soil as mineral material. Their activity was somewhat higher in CF than in IF and their role in structure formation is probably small. However, in field-incubated soil cores they significantly ($P < 0{\cdot}005$) increased the volume of pores with diameters of 50–200 μm, corresponding with their own diameter, and enhanced pore continuity. As a result, they increased air permeability up to two-fold depending on the time of the year. In addition, they increased the proportion of soil aggregates corresponding with the size of their fecal pellets (Didden 1990).

Earthworms

Earthworm activities have a clear effect on soil physical properties. Soil porosity and hydraulic conductivity are affected by burrowing. It is well known that the type of cultivation and cropping may affect earthworm populations dramatically (Edwards 1983). As casting may either increase or decrease soil aggregate stability (Lee 1985; Marinissen & Dexter 1990), earthworms may affect aggregate stability in different ways in different soils. In loamy sand or sandy clay loam soils of Georgia, USA, earthworm activity increased the average diameter of water stable aggregates, especially in the >2000 μm class. The effect in the loamy sand was stronger than in the sandy clay loam (Brussaard *et al.* 1990). In fluvial soils of the Netherlands, however, with textures ranging from sandy clay loam to clay loam and loam, earthworms caused a shift in diameter of water stable aggregates from 2000–8000 to 300–2000 μm (Brussaard *et al.* 1990).

CONCLUDING REMARKS

In terms of C and N mineralization only a few animals, notably protozoa and earthworms, seem to increase the amounts processed by the soil microflora substantially. A more detailed study of the activity of these groups of organisms is needed before a better understanding of the dynamics of mineralization can be gained, especially if one aims to match the supply of nutrients from organic matter and the demand of nutrients by plants. Enchytraeids, nematodes, micro- and macro-arthropods are less important in this respect. These groups may, however, exert an indirect effect on mineralization by stimulating (nematodes) or stabilizing (arthropods) the soil organisms that they consume. Also, their role may be more important in natural systems than in agricultural ecosystems (Crossley, Coleman & Hendrix 1989), but this warrants further research.

Moore *et al.* (1988) proposed the functional link approach as a means of integrating several ecological studies of soil fauna and of establishing the impact of functional groups within a food web on cycling of nutrients. Functional food webs have the capability to assess the regulatory capacity of any functional group and to represent interactions between the functional groups. This approach was applied to the data from the Lovinkhoeve site by Moore & De Ruiter (1990) and is currently being used to estimate the proportional contribution of the soil fauna to nitrogen mineralization in CF and IF. A preliminary analysis has yielded figures of 40% in CF and 50% in IF (P.C. De Ruiter, personal communication).

In terms of soil structure formation and soil aggregate stability, the meso- and macrofauna, especially earthworms, appear to be important but the contribution of the soil microfauna needs to be studied in more detail. Long-term studies with the soil fauna using labelled organic matter should provide a better understanding of the formation and maintenance of soil structure. Field and laboratory studies with known assemblages of organisms are needed with micromorphological and submicroscopical analysis of soil-thin sections.

With the current emphasis on soil conservation and reduced input agriculture, there is an increasing scope for research into the interplay between soil biota, soil structure and nutrient cycling. With the results of such research we aim to reach the point where we can, rather than bypassing the biology of soils by chemical and mechanical means, let the soil work for us (Elliott & Coleman 1988).

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