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Decomposition and nitrogen mineralization in natural and agro-ecosystems: the contribution of soil animals

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Abstract. The present article centres on the contribution of soil animals to organic matter decomposition and nitrogen mineralization in natural and agro-ecosystems. Criteria are presented for the categorisation of the soil fauna in functional groups in order to be able to quantify the contribution of the soil fauna. Three types of classifications: size, habitat and food, are discussed. For various natural ecosystems, such as prairies and forests, and for agro-ecosystems a rather similar outcome of the faunal contribution to nitrogen mobilization of approximately 30% appears to exist. This value is dependent on various types of interactions among functional groups, changes in population density of microorganisms and soil fauna, seasonally changing abiotic factors and management, such as fertilization, harvesting and addition of harvest residues to the soil. Finally, to improve management of ecosystems as related to soil faunal activity in decomposition, lines are set out for further research such as the development of dynamic models, studies concerning the effects of perturbation in relation to microbial dominance and the integration of the study of below-ground food webs with ecological theories.

1. Introduction

In functional soil zoology studies there appears to be a dichotomy in approach. In one approach emphasis is laid on the processes of decomposition and nutrient mobilization and the animals are considered as one variable. In the second approach a complete description of the diversity of the decomposer species, their distribution, abundance and activity is aimed at, while the processes of decomposition and mobilization fade into the background (cf. Usher et al. 1982). In the first approach soil animals are considered mainly as favouring the microbial processes indirectly by changing the structural, physical and chemical properties of the soil. Models for nitrogen mineralization from leaf litter have been developed in which the effects of the soil animals were expressed proportionally to their total biomass (Anderson et al. 1985; Seastedt 1984). These models are useful for describing decomposition as a process, yet give little

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insight in how the process is regulated. Such insight is needed for the manipulation of decomposition towards higher use efficiency of nutrients in man-managed ecosystems, such as managed forests and agricultural land. Although the second approach in principle can contribute to obtain the necessary insight, it is too laborious to be practical, unless the diversity of species to be studied is reduced by lumping them in functional groups.

In the present article we will give criteria for the categorisation of the soil fauna in groups with more or less similar functions in decomposition, in order to be able to quantify the contribution of the soil fauna to organic matter degradation. We will focus on the contribution of the micro- and mesofauna to nitrogen mineralization.

After presenting the different ways of functional classification (section 2) we will give results from different natural ecosystems, such as prairies and forests and from agro-ecosystems (section 3). Following a discussion of intrinsic interactions among functional groups (section 4) and the effects of abiotic factors on animal-mediated decomposition and mineralization (section 5), the effects of various perturbations on the contribution of soil fauna to element turnover will be discussed (section 6). Finally, we set out some lines for further research, inspired by the obvious need for integration of the studies of below-ground food webs with ecological theories to improve management of ecosystems as related to soil faunal activity in decomposition (section 7).

2. Functional classification

The clear differences, both qualitative and quantitative, between different soil animals in their effects on nutrient mineralization, have led to their classification into functional groups. These are groups of organisms, which have, irrespective of their taxonomical origin, a similar function in the process of mineralization (Moore et al. 1988). For a critical review of the functional group concept see Hawkins & MacMahon (1989).

Size classification

An often used classification is that based on body width of the animals, since this should broadly reflect the scales at which they affect or effect soil processes: micro-, meso- and macrofauna (Fig. 1).

Microfauna (body width 2 μm–100 μm) comprises nematodes and protozoa and other less common groups. They live in water-filled pores and water films in the soil matrix, and represent a diverse assemblage of trophic groups, with fungal-, bacterial- and plant-feeding species as most abundant.

Mesofauna (100 μm–2 mm) comprises, among other groups, collembola, mites and enchytraeids. These animals are largely found in air-filled pores. This group, too, is a mixture of species with various trophic relationships.

Macrofauna (2 mm–20 mm) comprises, among others, millipedes, woodlice,

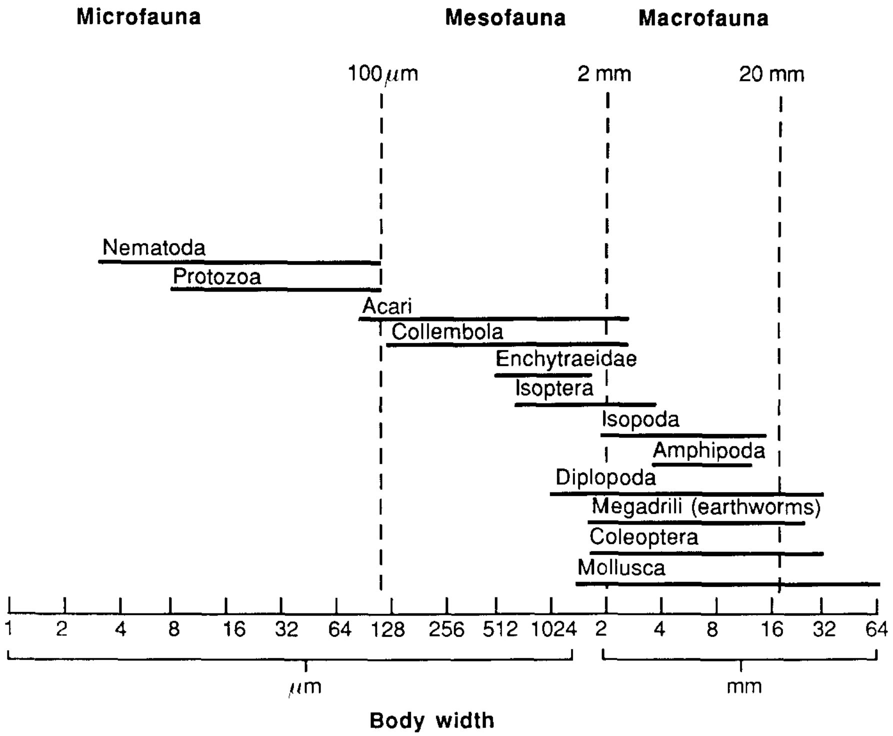

Fig. 1. Size-type classification of soil animals. (After Swift et al. 1979)

fly larvae, beetles, snails and earthworms. They have body sizes large enough to disrupt the physical structure of the soil through their feeding and/or burrowing activities, as e.g. has been shown for lumbricid earthworms, introduced into pastures (Hoogerkamp et al. 1983) and also for dung beetles (Brussaard & Hijdra 1986, Fig. 2).

This group, too, shows an assemblage of trophic relationships.

Habitat classification

A second functional classification is based on the depth in the soil profile, at which the animals live. Earthworms can be classified into epigeal (surface-active) species, which are largely involved in litter comminution; endogeic species, which are geophagous and live in the mineral soil; and anecic species which transport materials between mineral soil and the organic litter layer (Bouché 1977; Springett 1983). Such a stratified distribution has also been found for several linyphiid spiders (Kessler & van der Ham 1988).

In soils with pore sizes diminishing downwards, there is an overlap between size and habitat classification.

A similar classification has been proposed for collembola (Verhoef 1986). In

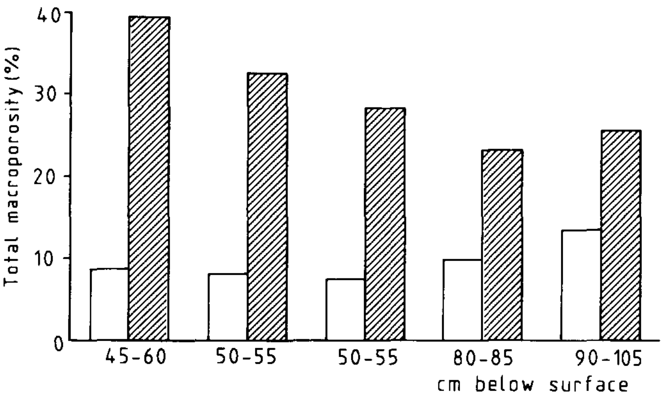

Fig. 2. Effect of back-filling burrows by dung beetles on soil macroporosity. Blank bars: undisturbed soil matrix; hatched bars: dung beetle burrows, back-filled to a lower bulk density than the original soil matrix. (From Brussaard & Hijdra 1986)

this group a distinction can be made between epigeic, hemiedaphic and euedaphic representatives (Fig. 3), originally based on morphological differences (Gisin 1943). Great differences between, and similarities within the three categories have been found concerning their ecophysiology (Verhoef 1978; Testerink 1981; Witteveen 1986; van der Woude 1988; Joosse & Verhoef 1987) and their population biology (van Straalen 1983; Vegter 1985). These properties have been summarized for the epigeic and the euedaphic category in Table 1. The hemiedaphic group is intermediate.

In addition, there is evidence that epigeic animals play a role in the initiation

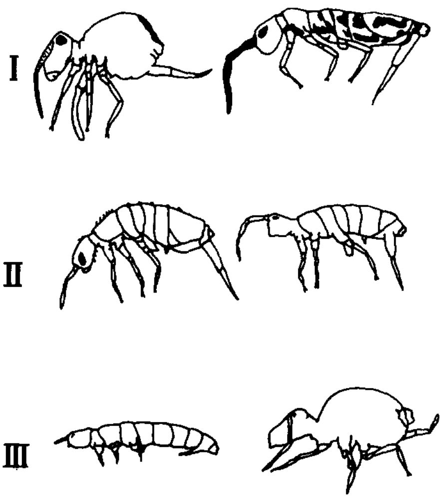

Fig. 3. Distinction in epigeic (I), hemiedaphic (II) and euedaphic (III) collembola, based on morphological differences. (From van Straalen et al. 1985)

Table 1. Ecophysiological and population biological characteristics of epigeic and euedaphic collembola.

Epigeic	**Euedaphic category**
Drought tolerance	Drought susceptibility
High metabolic rate	Low metabolic rate
High locomotory activity	Low locomotory activity
Temperature dependent development	Temperature independent development
Seasonally induced life cycle	Seasonally independent reproduction
Sexual reproduction, sexual dimorphism	Parthenogenesis
Courtship behaviour	Random spermatophore-deposition
High fertility, high mortality	Low fertility, low mortality

From van Straalen et al. 1985

of decomposition, whereas euedaphic animals would affect later stages of decomposition and have a direct effect on mineralization processes (Verhoef et al. 1988). This has been shown for three collembolan species coexisting in high abundances in coniferous forest soils, i.e. *Orchesella cincta* (L.), *Tomocerus minor* (Lubbock) and *Isotoma notabilis* (Schäffer). These three species are epigeic, hemiedaphic and euedaphic, respectively. Field experiments, in which presence and density per species were manipulated, showed for the three species different effects on decomposition rate, changes in total nitrogen and leaching of mineral nitrogen (Faber & Verhoef 1990).

The species are not strictly segregated vertically. They may migrate up and down due to microclimatical changes (van der Woude & Verhoef 1986). Laboratory studies using microcosms show only in the F layer a clear effect for the hemiedaphic *Tomocerus minor* (Verhoef & Dorel 1988, Fig. 4). So, it can be

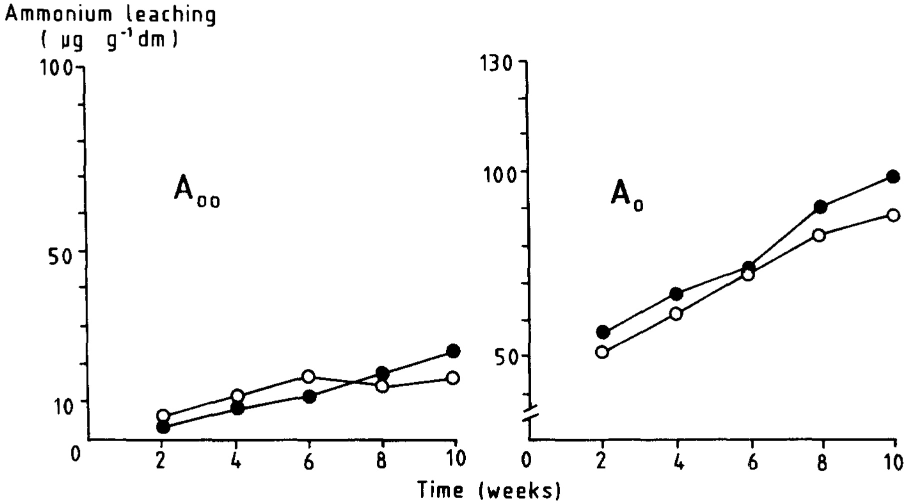

Fig. 4. Ammonium leaching from microcosms filled with L (A_{00}) and F layer material (A_0) from *Pinus nigra*, calculated per unit mass of substrate, per two weeks. ●—● = with *Tomocerus minor*, ○—○ = microorganisms only. (From Verhoef & Dorel 1988)

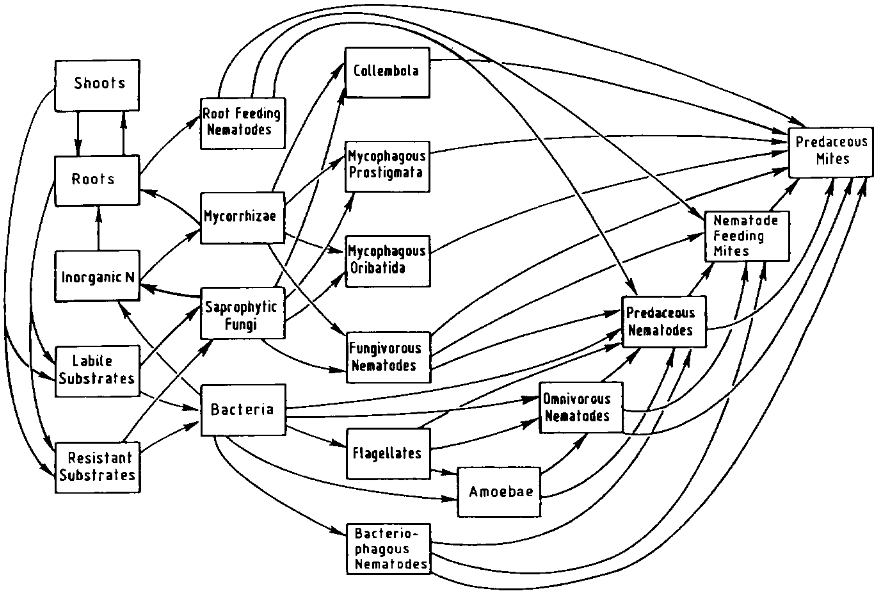

Fig. 5. Representation of the detrital food web in a shortgrass prairie. Fungal feeding mites are separated into two groups to distinguish the slow-growing cryptostigmatids from faster-growing taxa. Flows ommited from the figure for the sake of clarity include transfers from every organism to the substrate pools (death) and transfers from every animal to the substrate pools (defaecation) and to inorganic N (ammonification). (From Hunt et al. 1987)

concluded that in a well-stratified soil a functional classification of soil animals based on depth of occurrence is a valid one.

Food classification

The third type of classification can also be used for non-stratified soils, and is largely based on the trophic relationships of the different groups of animals (feeding mode, principal food source). This classification has been applied in a study in a shortgrass steppe (Hunt et al. 1987, Fig. 5).

Although functional groups in principle may consist of animals from different taxa, ecophysiological and population biological characteristics are usually so different among higher taxa that in practice no animals from different orders will be categorized in one functional group. Even families or species with similar trophic relationships may have to be placed in different groups. As our knowledge on feeding behaviour increases, further subdivision may be necessary. Predaceous mites (two functional groups in Hunt et al. 1987) were separated into four groups with different hunting behaviours and prey by Walter et al. (1988).

We will henceforth use food type classifications to quantify the contribution of soil animals to decomposition and nutrient cycling, with special emphasis on nitrogen.

3. Quantification of the contribution of soil animals to nitrogen mineralization in natural and agro-ecosystems

For use in decomposition studies, the ideal classification should, above all, reflect the trophic relationships between groups. In this section we give quantitative examples from a coniferous forest, a shortgrass steppe and arable land.

Persson (1983) gave a food type classification for the soil animals living in a *Pinus sylvestris* forest in Central Sweden. In a nitrogen mineralization model estimates were made with ratios C/N (faeces): C/N (food) increasing from 1 to 2. Recent budget analyses have shown a ratio of 1.3 for collembola (Verhoef et al. 1988; unpublished data). Depending on the choice of assimilation efficiency for nitrogen, the contribution of soil fauna to total net nitrogen mineralization was estimated to be between 10 and 49%.

In a *Pinus nigra* forest in The Netherlands the contribution of soil fauna to total nitrogen mobilization was approximately 30%. This was calculated with data from lysimeter studies in the presence or absence of soil animals and/or roots (Verhoef et al. in prep.).The *Pinus* stand was on a fungus dominated, stratified soil, where the fungivorous collembolan *Tomocerus minor* is abundant (mean annual density: 2,000 individuals m^{-2}). Using population biological parameters, such as population biomass, population turnover rate (van Straalen 1985), the nitrogen concentration of the animal and its food and data on the individual nitrogen budget (Verhoef et al. 1988), total excreted nitrogen (both faeces and urine) amounted to 620 mg $N m^{-2} y^{-1}$, which is 170 times their biomass nitrogen per year. This relatively high nitrogen output is caused by their high biomass turnover rate and high assimilation efficiency (see Table 2), causing high nitrogen excretion via urine (Verhoef et al. 1988). In such stratified coniferous forest soils the fungal route (Fig. 6) seems to be dominant.

Figure 5 concerned the below-ground food web of the shortgrass steppe of northeastern Colorado (USA) (Hunt et al. 1987; Moore et al. 1988). The sizes of the vectors and compartments of Fig. 5, representing the nitrogen pools and flows in this ecosystem, are given in Fig. 7. The vector F represents the flow of nitrogen, mineralized by the fauna. This is 37% of total nitrogen mineralization, even though total faunal biomass is only 2.5% of that of saprophytic fungi and bacteria. Bacterial feeding amoebae and nematodes together accounted for over 83% of nitrogen mineralization by fauna. This high contribution is due to the

Table 2. Efficiencies of nitrogen conversion in *Tomocerus minor* on an algal*, a fungal** and a mixed diet***: assimilation efficiency (A/C × 100%) and tissue growth efficiency (P/A × 100%). Values are means ± SE.

Diet	A/C × 100%	P/A × 100%
* *Desmococcus*	70 ± 1.5	32 ± 2.7
** *Cladosporium*	86 ± 2.2	37 ± 7.8
****Desmococcus* *Cladosporium*	78 ± 2.1	29 ± 3.5

From Verhoef et al. 1988

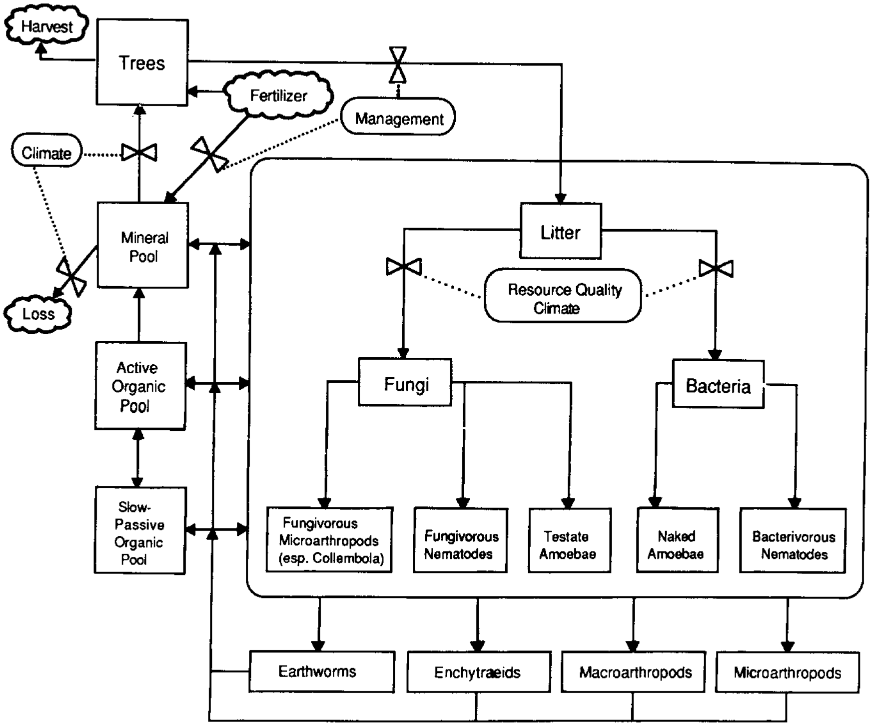

Fig. 6. Conceptual detrital food web in stratified coniferous forest soils. Boxes = nutrient storages, clouds = nutrient sources or sinks, and arrows = nutrient transfer pathways. Valve symbols on arrows indicate that nutrient transfers are influenced by factors connected with dotted lines. (Modified after Hendrix et al. 1986)

fact that like the collembolan *T. minor* these groups combine high turnover rates with a relatively high assimilation efficiency and a diet which is rich in nitrogen. In this model population numbers are presented as average values over the growing season. Nitrogen mineralization during the growing season was modelled to occur during 40 ideal days when the system was considered in steady state.

Andrén et al. (1990) published a nitrogen budget model for barley fertilized with 120 kg N ha^{-1}, largely based on taxonomic groups (Fig. 8). Pool sizes of organisms are mean annual estimates, considered to be in steady state and fluxes are expressed on a per year basis. They concluded that in this system 25% of the nitrogen mineralization was accounted for by the fauna. Here again, protozoa and nematodes contributed by far most to the nitrogen mineralization.

Brussaard et al. (in prep.) quantified soil, plant and biota nitrogen in winter wheat in The Netherlands. The data on nitrogen pools in various taxonomic groups are given in Fig. 9. As compared with the data from Sweden (460 kg N ha^{-1}, Andrén et al. 1990) for barley, fertilized with 120 kg N ha^{-1}, the fungal

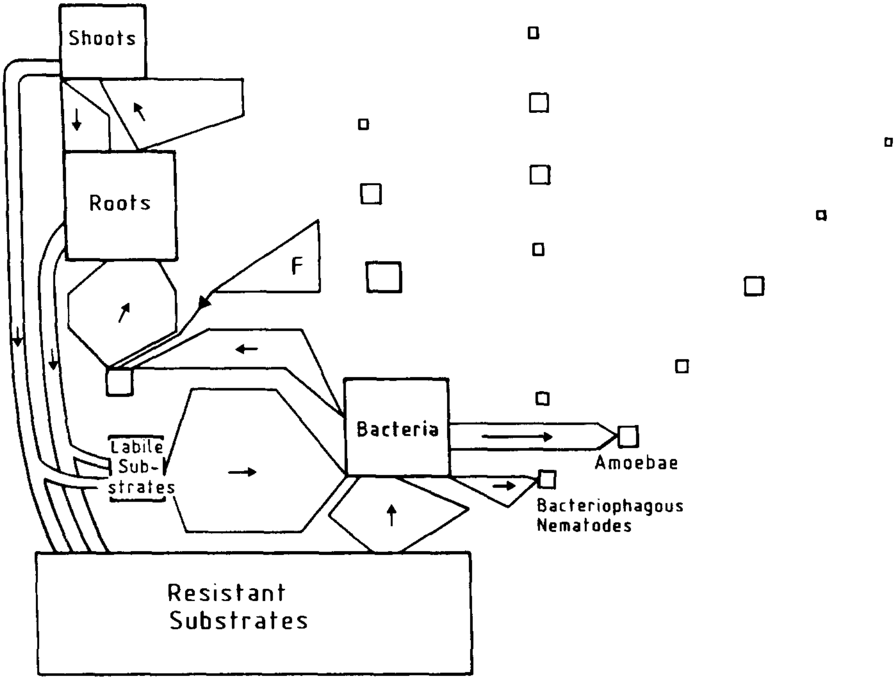

Fig. 7. Nitrogen flux description of the detrital food web. The sizes of vectors and compartments represent the relative sizes of nitrogen flows ($g\,N\,m^{-2}\,yr^{-1}$) and compartment biomass ($g\,N\,m^{-2}$). Vectors and compartments are laid out as in Fig. 5. F represents nitrogen mineralization by fauna. (From Moore et al. 1988; data from Hunt et al. 1987)

nitrogen pool was considerably lower in The Netherlands (3.1–4.7 kg N ha^{-1}, Fig. 9). Pools of protozoa, nematodes and enchytraeids were approximately half the sizes of the pools in the Swedish soil, while arthropod pools were similar in size. No apparent differences in faunal biomass were assessed between the two farming systems in The Netherlands, to which the data refer, during the first year of their existence. Presumably, modelling the contribution of the soil fauna to nitrogen mineralization in the two systems, will yield a result in the same order of magnitude as in the above-mentioned studies.

Perhaps the most striking feature of the studies described above is the rather uniform outcome of the faunal contribution to nitrogen mineralization of approximately 30%. The calculations of the studies are based, however, on assumed steady state populations. It is necessary to introduce into such models dynamic factors such as various types of interactions, changes in population density, seasonally changing abiotic factors, resource quality and management, e.g. to better describe and predict the match between supply of nitrogen by the soil and demand from the crop.

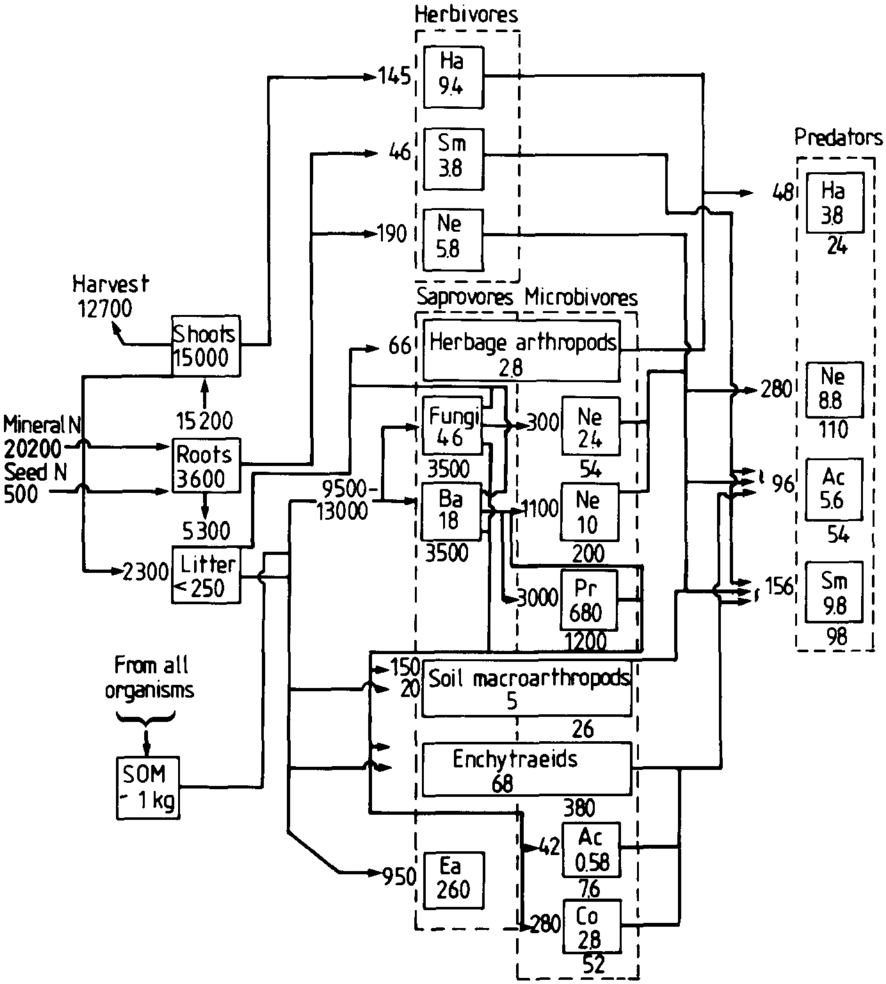

Fig. 8. Nitrogen food web of the Kjettslinge field, exemplified with data from fertilized barley (B120). Values in the boxes indicate biomass nitrogen (mg N m^{-2}) at harvest for the plant; for other organisms mean values for September 1982–1983 are given. On the left side of each box consumption (mg N m^{-2}yr^{-1}) is indicated, calculated using energetic quotients. All biomass values are given for the top soil, 0–27 cm depth. Nitrogen mineralization is indicated by values under each box. (Bacteria = Ba, Protozoa = Pr, Nematodes = Ne, Herbage arthropods = Ha, Soil macroarthropods = Sm, Acari = Ac, Collembola = Co, Earthworms = Ea). Nitrogen mineralization was divided between bacteria and fungi for practical reasons; only the sum (7000) is relevant. (From Andrén et al. 1990)

4. Dynamic interactions among functional groups

In quantitative studies of energy and nutrient transfer, mutualistic effects are implicit in the pool sizes and flow rates concerning the prey groups, whereby the importance of grazing or predator groups for energy and nutrient transfer may

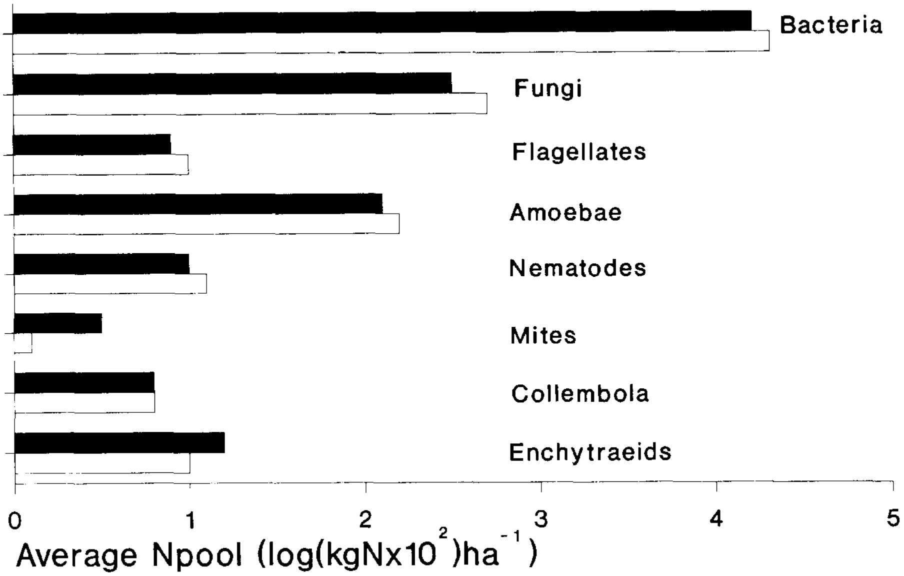

Fig. 9. Average nitrogen pools in various taxonomic groups of the soil biota in a winter wheat growing season in 1986 in a conventional and a first year's integrated cropping system on a silt loam soil (pH 7.5) in The Netherlands. Conventional (black bars): total soil C 2.2%; total N 0.09%; inorganic N (spring) + $Ca(NO_3)_2$-N 193 kg ha^{-1}. Integrated (open bars): total C 2.8%; total N 0.14%; inorganic N (spring) + $Ca(NO_3)_2$-N 156 kg ha^{-1}. (From Brussaard et al. in prep.)

be underestimated (cf. Hunt et al. 1987; Moore 1988; Moore et al. 1988). Evidence therefore can be derived from microcosm-studies and field studies at increasingly complex interactive levels:

Two-component interactions

Quantification of the effects of grazing on microbial metabolism gave different results depending on the interaction studied (Morley et al., cited by Elliott et al. 1986). In a microcosm-study with grassland soil organisms on the decomposition of purified cellulose in the presence of chitin the addition of the fungus *Fusarium oxysporum* caused a higher CO_2 evolution than the addition of the bacterium *Flavobacterium* sp. (Trofymow et al. 1983). Grazing by the fungivorous nematode *Aphelenchus avenae* did not increase total CO_2 evolution, whereas grazing by the bacterial-feeding nematode *Pelodera* sp. significantly increased CO_2 evolution. In both cases grazing enhanced ammonium mineralization.

In collembola-fungi interactions the density of the grazers is important. These effects of increasing density of collembola on fungal biomass and on nitrogen mobilization are shown in Fig. 10 (Anderson & Ineson 1984). At the start of this microcosm-experiment low numbers of the fungivorous *Folsomia candida* stimulated fungal biomass, whereas after 8 weeks high numbers of these animals

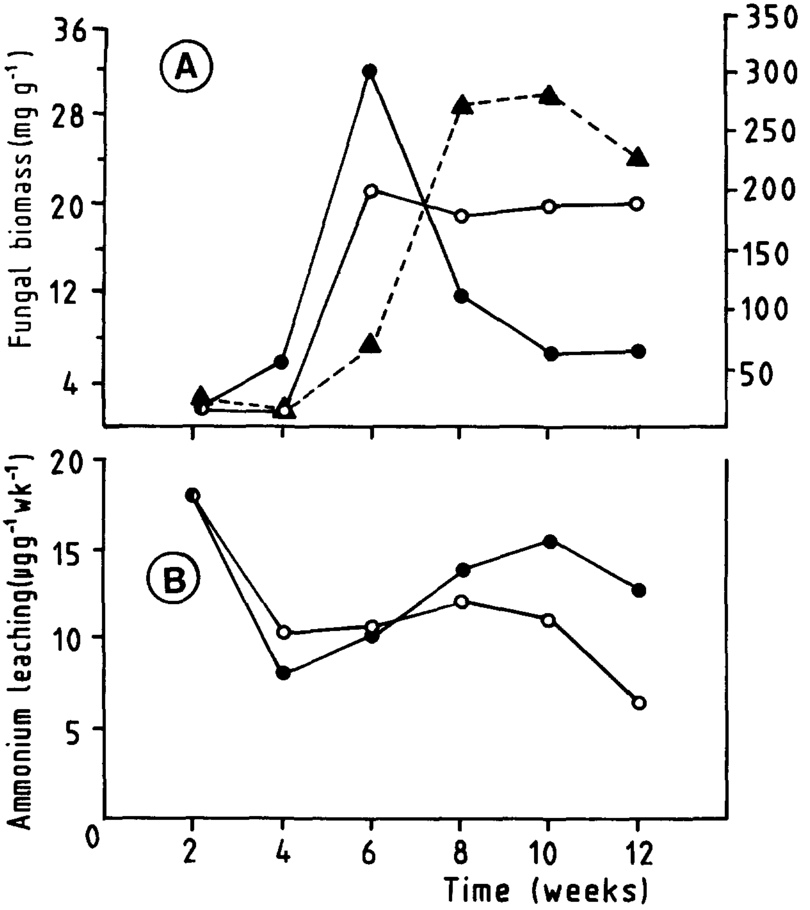

Fig. 10. A. Effect of increasing density of *Folsomia candida* (collembola) (▲----▲) on fungal biomass (mg g^{-1} litter) in microcosms filled with oak litter. B. NH_4^+-N leaching from oak litter (µg g^{-1} litter wk^{-1}). ●—● = with animals, ○—○ = without animals. (After Anderson & Ineson 1984)

decreased fungal biomass, associated with an increased ammonium mobilization.

This association has also been found for the interaction collembola-microorganisms at constant grazing intensities: in microcosm-studies with 15 *Tomocerus minor,* the microbial activity (as CO_2-production and urease activity) decreased, whereas the ammonium mobilization increased (Verhoef & Meintser 1990, Fig. 11).

In this study animal addition negatively influenced both respiration and urease activity. In similar microcosm-studies addition of collembola or isopods showed positive effects on respiration but negative ones on dehydrogenase and cellulase activity (Teuben & Roelofsma 1990). Small differences in degradation stage of the pine needle litter substrate may be the reason for these differences (Teuben & Roelofsma 1990).

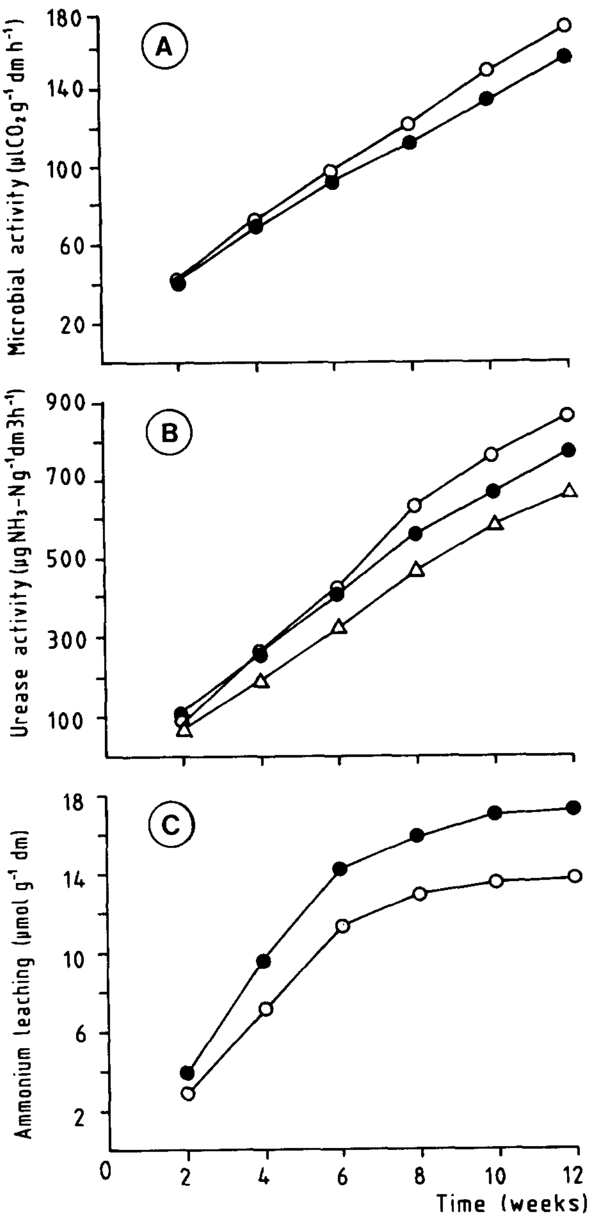

Fig. 11. Effects of constant grazing intensity of *Tomocerus minor* (collembola) in microcosms filled with coniferous litter. A: on microbial activity, measured as cumulative CO_2 production (μl. g^{-1} d.m. h^{-1}). B: on microbial activity measured as cumulative urease activity, according to Hoffman and Teicher (1961) (μg NH_3-N g^{-1} d.m. 3 h^{-1}). C: on cumulative NH_4^+ - N leaching (μmol . g^{-1} d.m.) ○—○ = without animals, ●—● = with 15 animals, △—△ = with 50 animals. (From Verhoef & Meintser 1990)

Three-component interactions

Studies with more than two interactive components are more natural but also more difficult to interpret, whereas the effects of animal addition on decomposition are often insignificant or inconclusive (see e.g. Bååth et al. 1981). In microcosm-experiments with barley straw as substrate and with microflora, protozoa and collembola (*Folsomia fimetaria* (L.)), no significant effects were found in respiration, mass loss or microbial biomass by addition of collembola (Andrén & Schnürer 1985). In microcosm-studies with both protozoa and nematodes present, metabolic activity (as CO_2-production) was enhanced in comparison with systems with one of the grazers only (Coleman et al. 1978; Elliott et al. 1980).

Similar studies have been performed with various combinations of bacteria (B), protozoa (P), bacterivorous nematodes (N) and bacterivorous mites (*Histiostoma litorale,* M) in relation to nitrogen mineralization (Brussaard et al. 1990). A combination of protozoa and nematodes (BPN) increased nitrogen mineralization as compared with protozoa-only (BP). Replacing nematodes by mites (BPM) did not yield a significant increase in nitrogen mineralization as compared with the protozoa-only treatment (BP). In comparison with the protozoa-only treatment (BP) the nitrogen mineralization was significantly enhanced with both nematodes and mites present (BPNM, $P < 0.05$), but not to the same extent as in the treatment with nematodes as the only grazers besides protozoa (BPN, $P < 0.001$). So the mites counteracted to some extent the effect of nematodes. In agreement with this result, numbers of nematodes were significantly lower in the presence of the mites (BPNM; $P < 0.01$), whereas those of amoebae were significantly higher (BPM and BPNM) than in the absence of the mites (BP and BPN; $P < 0.001$). It was calculated that 1 μg of mite $C.g^{-1}$ soil caused a 25 μg increase in amoebal $C.g^{-1}$ soil. Perhaps the filter feeding activity of the mites increases the encounter rate between amoebae and bacteria, leading to an increased amoebal growth rate.

In general, the results of microcosm-studies carried out under conditions of nitrogen limitation and in the absence of overgrazing agree with the conceptual model given in Fig. 12 (Anderson et al. 1981).

Multi-component interactions

An important question is whether the observed effects of faunal activity in microcosm and pot experiments also occur under multi-component field conditions. Field research during the fallow part of a wheat-fallow cropping system allowed the study of mineralization by the fauna because of the absence of plants taking up the nutrients. Temporal displacement of peak biomass of primary decomposers, their grazers and the latter's predators was reported following an imposed pulse of rainfall in a near-natural greenhouse experiment with large cylinders of undisturbed soil from the fallow part of the rotation (Elliott et al. 1986). These results confirmed those obtained under real field

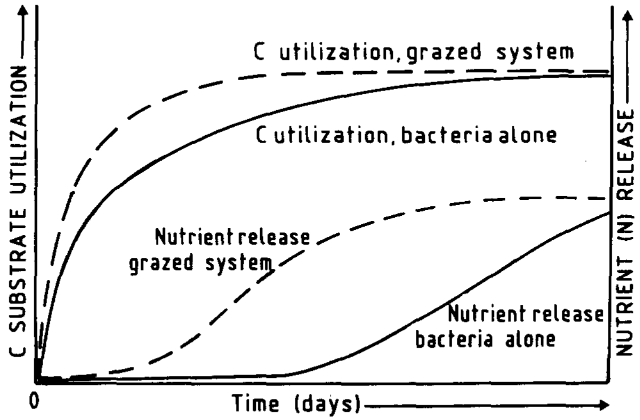

Fig. 12. Conceptual model of substrate utilization and nutrient mineralization with and without grazers. (From Anderson et al. 1981).

conditions where mineralization rates and nitrogen concentrations in the soil coincided with a rapid increase in protozoan biomass, while a clear temporal displacement of faunal groups was apparent even at sampling intervals of 3 to 4 weeks. This suggested decomposition of lower trophic levels' biomass, resulting in net mineralization (Elliott et al. 1984). Clear temporal displacements of primary decomposers, their consumers and the latter's predators have also been assessed following rainfall events in semi-deserts, especially for the bacteria-nematodes-mites food chain which led to enhanced decomposition and mineralization as compared to conditions without predators (Santos & Whitford 1981; Santos et al. 1981; Elkins & Whitford 1982; Whitford et al. 1982).

Similar results were found in natural (blue grama) grasslands: in spring, protozoa and nematodes increased concomitantly with bacteria and fungi; the fauna subsequently reduced their food sources which coincided with an increase of soil inorganic nitrogen (Ingham et al. 1986a). This was not observed following an increase of bacteria during autumn, suggesting that during that period of the year the nitrogen was immobilized in the microflora and/or the plants took benefit from the mineralized nitrogen.

There is evidence that plants indeed benefit from the increased nitrogen mineralization by the fauna. Higher shoot biomass and N contents of shoots of plants growing in the presence of protozoa and nematodes as compared with plants growing without fauna were often found (Woods et al. 1982; Clarholm 1985; Ingham et al. 1985; Kuikman & van Veen 1989). Both rhizosphere and non-rhizosphere nematodes may contribute to the observed effect when plants are grown in soil. However, pot experiments with nitrogen limited spring wheat grown in perlite showed that between 4 and 8 weeks after the start of the experiment nematode numbers averaged about 260 g^{-1} fresh roots and only 4.7 g^{-1} perlite. The shoots of the wheat plants contained slightly but significantly ($P < 0.05$) more nitrogen in the pots with nematodes as compared to those without (Bouwman et al. pers. comm. 1989).

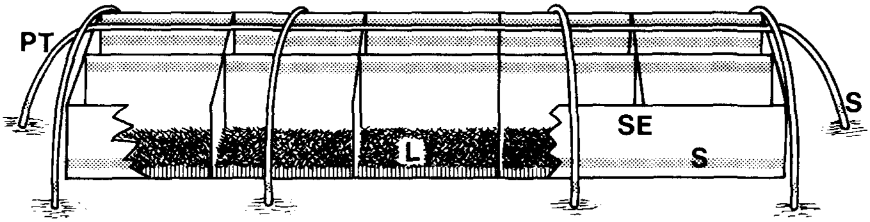

Fig. 13. Set-up of an enclosure experiment in the field. L, litter; PT, plastic tubes; S, strip with glue; SE, stainless steel enclosures. A gauze net was spread over the plastic tube-frame (: not on drawing).

Further evidence for animal mediated nitrogen availability for plants comes from field studies with lysimeters with and without plants in the absence or presence of soil animals (Anderson et al. 1985; Verhoef et al. in prep.). They show that the surplus inorganic nitrogen mobilized in the presence of soil animals without plants disappears in lysimeters with plants.

In field studies in a *Pinus nigra* forest, the density of the dominant collembolan *Tomocerus minor* was manipulated in enclosure experiments (Fig. 13). It was shown that at high densities (approximately 4,000 individuals m^{-2}) the nitrogen concentration of the F layer became 2.3 times as high as that of the same layer in defaunated plots (Verhoef & de Goede 1985). Similar findings of microbial nitrogen immobilization in the presence of high numbers of microbivorous animals have been shown in microcosms containing Scots pine seedlings (Bååth et al. 1978). According to these authors this is due to the high effectiveness of the internal circulation of nitrogen between the soil organisms, being superior to root uptake.

These studies indicate that the contribution of functional groups of soil animals to decomposition and mineralization depends on their population density, which can fluctuate considerably even over short time periods.

Paradoxically, the decomposition rate of organic matter can often be described by simple first-order kinetics (Janssen 1984; Andrén et al. 1988) without considering organism dynamics. In fact, total organism **biomass,** including bacterial and fungal biomass, may be a poor indicator of biological **activity.** Rather than pointing to the low importance of the fauna at the observed level of microbial biomass, this may instead indicate that the microbial biomass is kept at a low level by microbial grazers (Andrén et al. 1988). In their turn, the grazers may not build up a large biomass, but instead be consumed by predators (Elliott et al. 1988). Hence, it appears that in a variety of ecosystems, microbial grazers and their predators significantly contribute to the mineralization of nitrogen, despite their often low biomass. This may well be due to the rapid replacement among the various functional groups of decomposers, their grazers and the latter's predators, whereby patterns in nitrogen dynamics remain the same (Ingham et al. 1986b).

A common feature of these studies is that most of the effects of biological interactions on decomposition and mineralization becomes apparent after imposed changes of the densities of functional groups, e.g. by drying-rewetting or eliminating/adding animals.

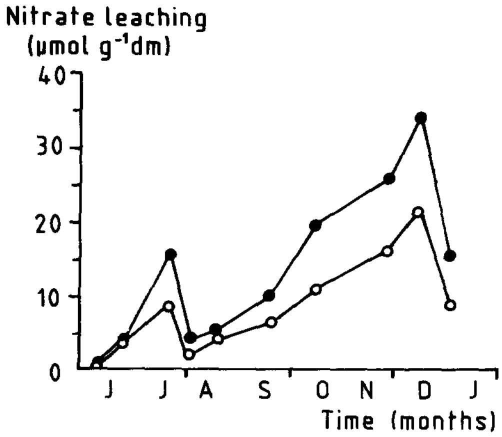

Fig. 14. Nitrate leaching from lysimeters in a *Pinus nigra* stand with (●—●) and without (○—○) meso- and macrofauna.

In field studies under natural conditions in coniferous forest soils meso- and macrofauna significantly increased nitrate mobilization in autumn ($F_{1,48} = 6.02$; $P < 0.05$). In summer there was no significant effect (Verhoef et al. in prep.; Fig. 14). In the same habitat, collembola have an immobilizing effect on nitrogen mobilization in winter (Verhoef & de Goede 1985).

Hence, it would appear that under natural conditions in a pine forest the nitrogen mobilization by the fauna to some extent was synchronized with plant demand, whereas during winter soil animals such as collembola, reduce nitrogen losses from the system. In microcosm studies with litter similar buffering effects by collembola and isopods have been found concerning the concentrations of exchangeable nutrients such as calcium, magnesium and nitrate (Teuben & Roelofsma 1990).

If additional studies confirm the generality of these observations, a thorough understanding of biological functions, interactions and processes within the soil community is required for predicting the impact of perturbations of natural ecosystems. Soil ecological knowledge would also be necessary for improving the organic matter status and nutrient economy of perturbed systems such as those in forestry and agriculture. Therefore we will henceforth discuss the impact of some abiotic soil factors (temperature, moisture), and management (fertilization, harvesting, litter/crop residue addition and placement) on seasonal patterns of soil animal activity and the associated dynamics of organic matter and nitrogen.

5. Effects of abiotic conditions on animal-mediated decomposition and mineralization processes

Soil temperature and moisture and to a lesser extent resource quality have been found to influence the seasonal nitrogen mineralization in forest soils (Vitousek

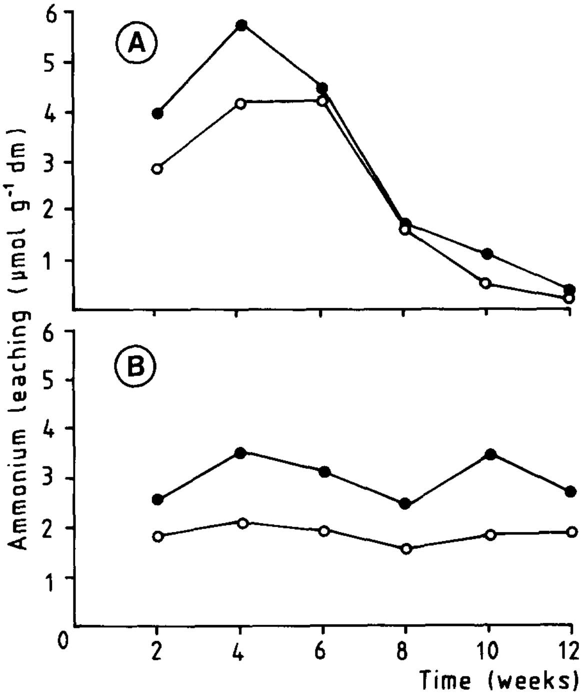

Fig. 15. Ammonium leaching from microcosms filled with F layer material from *Pinus nigra*, calculated per unit mass of substrate, per two weeks. ●—● = with *Tomocerus minor*, ○—○ = microorganisms only. (A) at constant 19° C (B) at dielly fluctuating 10/19° C.

& Matson 1985). During periods with increasing temperatures and relatively high moisture, mineralization increases, whereas in spite of high temperatures mineralization decreases when the soil is dry.

Optimal temperatures for nitrogen mineralization have been assessed in field and laboratory studies with organic soil layers (Anderson et al. 1983; Verhoef & de Goede 1985), the optima being different for the different soil horizons. At dielly fluctuating temperatures (10–19° C) the ammonium mobilization from pine litter showed a constant pattern over a period of several weeks, whereas at a constantly high temperature (19° C) mineralization was rapid but short (Verhoef & Meintser 1990; Fig. 15).

Relatively high decomposition rates of organic material during colder seasons (late autumn to early spring) (cf. Bleak 1970; Hågvar & Kjöndal 1981; Vogt et al. 1983; Verhoef & de Goede 1985) could be attributed to temperatures fluctuating around 0° C. The repeated freezing and thawing of leaves could cause fragmentation, increased leaching and/or enhanced accessibility to microbial attack (McBrayer & Cromack 1980; Berg et al. 1982; Staaf & Berg 1982). However, recent studies on the effects of repeated freezing and thawing on rates of decomposition in aspen and pine litter have shown that simple freezing and

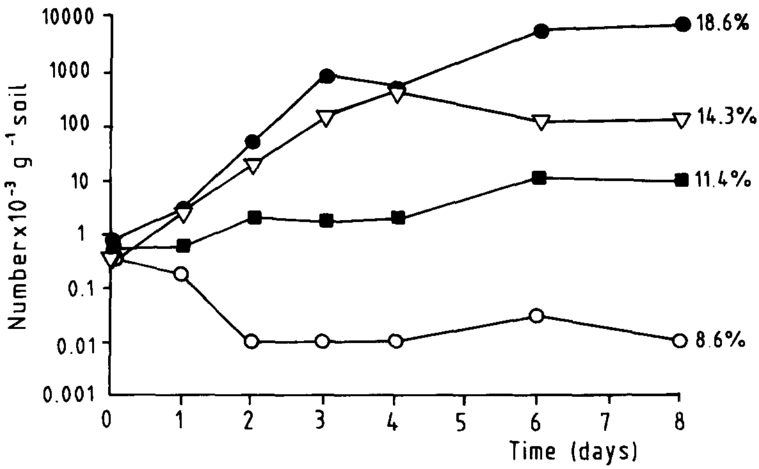

Fig. 16. Effect of soil moisture (% w/w) on the population growth of the flagellate protozoan *Cercomonas* sp. growing on *Pseudomonas fluorescens* at 20° C in a microcosm experiment with silt loam soil. (From Zwart et al. in prep.)

decomposer activities beneath the snow are more important factors in hibernal litter decomposition than freeze-thaw cycles (Taylor & Parkinson 1988).

While the pattern of change in soil temperature in the course of the day or the season is rather predictable, this is far less so with changes in soil moisture. Various studies have been aimed at quantifying the effects of soil moisture on the activity of soil animals and nutrient dynamics. It is obvious that animals living in water-filled pores and water films around soil particles (such as protozoa and nematodes) are sensitive to desiccation. Studies on the growth of flagellates in microcosms with silt loam soil showed a sharp boundary between the soil moisture contents where the protozoa hardly showed any growth (11.4% w/w) and most rapid growth (18.6% w/w) (Zwart et al. in prep.; Fig. 16). In another microcosm-experiment a silt loam was incubated under moisture conditions ranging from 14.4 to 19.5% (w/w) after amendment with lucerne meal and numbers of nematodes belonging to various functional groups were counted after six months (Bouwman in prep.; Table 3). Here again, clear boundaries of activity were assessed for some quantitatively important bacterivores (Rhabditidae) and fungivores (Aphelenchida), but others (bacterivorous Cephalobidae) appeared unaffected. Although increases in numbers of protozoa and bacterivorous nematodes have been observed in the field or in field experiments following rewetting of dried soil (Elliott & Coleman 1977; Clarholm 1985; Schnürer et al. 1986) these results are difficult to interpret quantitatively in terms of decomposition and mineralization without estimates of physiological activity and population turnover.

In various studies, however, soil faunal activity under moisture stress has been reported as important for continued decomposition and mineralization. In a soil microcosm-experiment with plants the interaction between ^{15}N-labelled bacteria

Table 3. Effect of soil moisture (% w/w) on numbers. 100 g^{-1} soil of various groups of nematodes, after six months of incubation at 15° C in soil microcosms with silt loam soil amended with lucerne meal.

Moisture	Bacterivores		Fungivores		Omnivores
(% w/w)	Rhabditis	Cephalobidae	Aphelenchida	Tylenchus	Dorylaimida
14.4–15.6	175^a	932^a	311^a	99^a	317^a
15.6–16.7	$255^{a,b}$	907^a	$150^{a,b}$	70^a	$168^{a,b}$
16.7–17.6	672^b	1008^a	$42^{b,c}$	61^a	128^b
17.6–19.5	1236^c	954^a	80^c	24^a	222^b

Figures followed by different symbols are significantly different (P < 0.05). Statistical analysis carried out on log-transformed data. (From Bouwman in prep.)

and protozoa was studied, as affected by moistening the soil every first, second or third day.

In soils with bacteria only significantly less ($P < 0.05$) nitrogen was taken up by the plants if the soil was moistened every second or third day as compared with daily water additions. In the presence of protozoa nitrogen uptake increased ($P < 0.01$) by 5, 10 and 18% at moistening the soil every day, every second and every third day, respectively. This was accounted for by increased uptake of bacterial ^{15}N, apparently made available by protozoan grazing (Kuikman et al. 1989; Fig. 17).

Microarthropods also, have been reported to release the decomposition of organic matter from environmental stress under certain field conditions. After exclusion of mites, seven abiotic factors explained 80–90% of the variation in organic matter decomposition, whereas only 50% was explained by these factors in the presence of mites, particularly nematode-feeding Tydeidae (Santos &

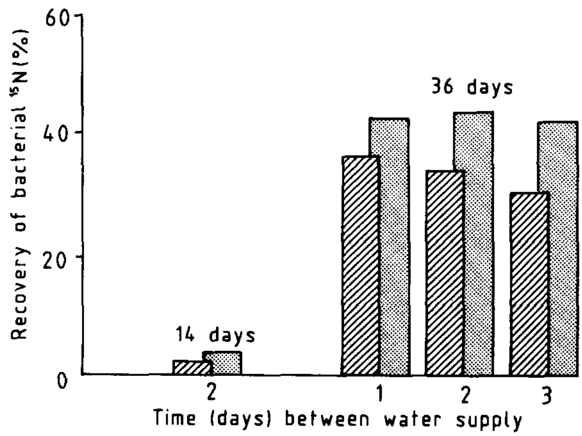

Fig. 17. Recovery of bacterial ^{15}N-nitrogen in plant nitrogen as a percentage of the inoculated amount at three soil moisture regimes and two sampling dates in a microcosm (day: 14 h light, 20° C; night: 16° C) experiment. bacteria: ■, bacteria and protozoa: ▨ (From Kuikman et al. 1989).

Whitford 1981; Santos et al. 1981). Similar results were reported for mesostigmatid mites (Elkins & Whitford 1982). These studies were carried out in semi-deserts where soil moisture is the most important limiting factor for decomposers as long as sufficient organic matter is available. No such effects were reported in these studies for fungivorous nematodes or mites during later stages of decomposition, possibly due to the low productivity of the system as compared to the early bacterial-dominated stage of decomposition. In another study by Persson (1989), organic matter decomposition, measured as CO_2-evolution and net nitrogen mineralization were measured in F/H layer materials from a Swedish spruce stand under various combinations of temperature (5 and 15° C) and moisture (15, 30 and 60% WHC). Addition of a mixed, mainly microarthropod, soil fauna did not change the CO_2-evolution as compared to a defaunated variant (cf. Andrén & Schnürer 1985). However, it significantly increased net nitrogen mineralization for each of the combinations of temperature and moisture conditions. The increase was dependent on soil temperature, but not on soil moisture. Because the net nitrogen mineralization in the absence of the arthropods was dependent on both temperature and moisture, it was concluded that the arthropods were important for switching from immobilization to mobilization of nitrogen in maintaining net nitrogen mineralization under dry conditions.

Hence, it would appear that while under the development of moisture stress bacterial and subsequently fungal decomposition and nitrogen mineralization are slowed down and finally inhibited, these processes are to some extent continued under moisture stress in the presence of the soil micro-and mesofauna.

6. Effects of management on animal-mediated decomposition and mineralization processes

Fertilization

In textbooks it is generally stated that input of nutrients into a nutrient deficient system leads to increasing decomposition rates. The addition of nitrogen, e.g., to a shortgrass prairie, a mountain meadow and a lodgepole pine forest increased decomposition rates with 5, 21 and 13%, respectively, relative to the controls (Hunt et al. 1988; Table 4). Primary production showed a greater response to nitrogen fertilization than did decomposition, suggesting that primary production is the more nitrogen limited process.

However, many examples exist in which addition of nitrogen to nitrogen deficient systems (with high C/N ratio) slows down decomposition, especially if it concerns recalcitrant organic material (Fog 1988). For pine needle litter, e.g., decomposition rate is mainly governed by the rate of lignin decomposition (Berg 1986) and this rate is decreased by nitrogen addition. The ligninolysis, a process in which various basidiomycetes are involved, appears to be inhibited by the addition of nitrogen (e.g. Arnolds 1988).

Table 4. Effects of addition of nitrogen to three ecosystems.

Variable	Ecosystem Prairie	 Meadow	 Forest
	Percent increase over control		
Plant production*	81	102	52
Plant N content**	56	39	24
Decomposition rate***	5	21	13
Litter N content***	20	11	29

*Aboveground standing crop after the growing season in grasslands and radial increment in forest.
**Live shoots in grasslands and live needles in forest.
***Of litter placed in its system of origin. (From Hunt et al. 1988)

Similar effects were found in microcosm-studies with *Pinus nigra* litter, to which nitrogen was added as NH_3 (Verhoef & Meintser 1990). The organic material was from the F layer with a low C/N ratio. Continuous supply of nitrogen decreased decomposition rate and the stimulatory effect of the collembolan *Tomocerus minor* on nitrogen mobilization (Table 5).

It is noteworthy that in microcosms, filled with F layer material from areas with a high nitrogen input from atmospheric deposition (up to $50\,kg\,ha^{-1}\,yr^{-1}$) after two months at 19° C without further nitrogen input, the excess nitrogen has been mobilized and leached out, whereas the decomposition rate had increased to control values (Verhoef & Dorel 1988; Verhoef & Meintser 1990).

Thus it can be concluded that addition of nutrients to nutrient deficient systems can have negative effects on certain microorganisms causing shifts in microbial composition, which negatively affects soil fauna (Fog 1988). As a result decomposition and mineralization rate may decrease.

In agriculture, with the current emphasis on reduced input farming, fertilization is reduced or left behind as an experimental treatment in research projects. In Swedish arable land no significant differences were assessed for biomass of protozoa and numbers and biomass of nematodes, mites, collembola, enchytraeids (with the exception of two years) and earthworms between unfertilized spring barley and barley receiving $120\,kg\,N\,ha^{-1}$, but significant differences were found at lower taxonomic levels of these groups and on specific sampling occasions (Andrén et al. 1988; Hansson et al. 1990).

Table 5. Effects of addition of nitrogen to pine needle litter

Variable	Control	$+NH_3$ (150 ppb)
Decomposition rate*	12.0%	8.3%
Animal-stimulated N mobilization**	54.0%	32.0%

*Dry mass loss over 12 weeks at 10/19° C
**Percent increase in presence of 15 *Tomocerus minor* over total inorganic N mobilization with microorganisms only. (From Verhoef & Meintser 1990)

Effects of the **kind** of nutrients added on soil fauna can be derived from a study on arable land in a Dutch polder soil. In one of two arable farming systems average amounts of 5650 kg organic matter $ha^{-1} yr^{-1}$ were added as farmyard manure, crop residues and green manure during thirty years. In the other system on average 3200 kg $ha^{-1} yr^{-1}$ was added as crop residues only and extra nutrients given with the organic matter in the first system, were compensated for by artificial fertilizer additions in the second system (for details see Kooistra et al. 1989). After the treatment period of 30 years soil animals were sampled during the growing season when amounts of mineral nitrogen available to the winter wheat crop were similar. Here again, no differences in protozoa, nematodes, mites, collembola and enchytraeid biomass were assessed between the treatments (Fig. 9). Differences for earthworms were mainly due to the unique colonization history of the site for this group. There were, however, important differences at lower taxonomic levels of microarthropods between the two systems (Brussaard et al. 1988; Table 6). It seems to be still open for research whether the clear differences in species diversity and abundance within the various taxonomic families and orders of soil animals which have come about under the influence of fertilization and manuring affect decomposition and nutrient mineralization to a measurable extent.

Harvesting and addition of harvest residues

Many studies of the direct effects of forest cutting have shown changes in chemical and physical factors, nutrient supply, root dynamics, decomposition rate and soil biota (Bååth 1980; Vitousek & Matson 1985; Huhta 1971; Seastedt & Crossley 1981). The impact of these changes strongly depends on the utilization intensity. In conventional stem harvesting only large logs are utilized, leaving much or even most of the forest biomass on the site. This results in only small withdrawals of nutrients and relatively small changes in chemical and physical factors, decomposition rate and soil biota. However, "complete-tree harvesting", in which tree stumps, root systems and foliage are harvested has great effects (Young 1968; Kimmins 1987) and a shift from conventional to complete-tree harvesting shows strong increases in removal of plant nutrients (Kimmins 1987). Harvesting of stumps and root systems greatly changes the whole soil system, causing a thorough mix of the soil and a disappearance of the structure of the organic soil layer. Apart from that, stumps are considered refugia for all types of soil animals directly after tree harvesting, from which the soil layers can be recolonized (Ehnström 1984).

The input of harvest residues may be beneficial in terms of nutrient supply, but this depends strongly on the chemical composition of the material. Green foliage and fine twigs contain readily decomposable tissues, relatively rich in nutrients. If they remain on the forest floor as harvest residues, together with the soil organic layer, the fungi present in these layers may temporarily immobilize nutrients, preventing premature nutrient flush. These immobilizing effects can be augmented by fungivorous soil animals (cf. Verhoef & de Goede 1985).

Table 6. The 12 most abundant taxa of mites and collembola from the layers 0–5, 7.5–10, 15–17.5 and 22.5–25 cm below the surface of two fields differing in organic matter content of the topsoil (A: 2.8%; B: 2.2%) as a consequence of 32 years of differential manuring. Sums of six soil cores (diameter 6 cm) per date per field.

Taxon		18 Apr.	19 Jun.	30 Jul.	19 Aug.	18 Nov.	Total for 1986
Associated with a relatively high organic matter content (A: 2.8%)							
Friesea mirabilis	A	9	4	55	8	35	111
	B	0	0	0	0	0	0
Tullbergia quadrispina	A	24	2	16	19	45	106
	B	1	0	0	0	0	1
Tullbergia krausbaueri	A	16	15	115	99	151	396
	B	3	16	16	46	8	89
Onychiurus armatus	A	34	47	170	31	56	338
	B	6	21	61	4	0	92
Associated with a relatively low organic matter content (B: 2.2%)							
Eupodidae	A	5	11	52	13	21	102
	B	1	100	55	27	3	186
Pyemotidae	A	7	20	88	34	89	238
	B	10	144	80	196	23	453
Alliphis halleri	A	40	13	20	5	10	88
	B	8	150	34	39	2	233
Tarsonemidae	A	2	1	10	4	11	28
	B	4	8	23	60	17	112
Folsomia candida	A	18	9	16	4	18	65
	B	2	237	68	38	6	351
Histiostoma litorale	A	24	11	23	11	21	90
	B	4	501	59	9	0	573
Arctoseius cetratus	A	0	3	1	0	1	5
	B	0	71	63	20	0	154
Hypogastrura denticulata	A	0	6	2	1	0	9
	B	0	25	137	251	21	434

*crop: winter wheat
soil: sandy loam, pH-KCl 7.5 (After Brussaard et al. 1988)

Few studies have analyzed soil surface organic matter dynamics on a single site after harvesting, combined with changes in decomposition rate, nitrogen dynamics and soil fauna.

In a recent study in a native hardwood forest of *Quercus, Carya* and *Acer* spp. (Blair & Crossley 1988) data on decomposition rates, nitrogen dynamics and microarthropod densities in a watershed up to its eighth year of regrowth following clearcutting were compared with data from an adjacent uncut reference watershed.

In the first year following clearcutting the mean annual density of total litter microarthropods was reduced with over 50%, relative to the uncut reference

Table 7. Seasonal means of maximum and minimum soil temperatures (°C) in an unthinned reference site and a thinned site.

	Unthinned site				Thinned site			
	Spring	Summer	Autumn	Winter*	Spring	Summer	Autumn	Winter*
Temperature max.	10.5	15.1	14.3	10.3	12.3	17.4	15.2	10.2
Temperature min.	4.6	10.9	9.3	4.7	4.3	11.5	10.7	6.3

Means are based on 10 recording intervals per season, recorded in the litter layer.
*Winter data are based on recordings in December only. (From Verhoef et al in prep.)

site. The pattern of seasonal abundance was also changed from a unimodal curve (with maximal summer densities) in the uncut reference site to a bimodal curve (with a spring- and an autumn peak) in the cut site. This was presumably caused by high summer temperatures and reduced litter moisture. Eight years after cutting mean annual densities were still lower than those of the reference site. The bimodal curve, however, had been changed into a unimodal one. These effects were probably strongly linked with the changed microclimatological conditions after cutting. Decomposition rates were slowed down in the cut site, whereas slower increases in nitrogen concentration and lower levels of immobilization were observed in the cut site, relative to the uncut site. This may indicate that the reduced microarthropod densities were related to changes in decomposition and nutrient dynamics following clearcutting.

The data on decreasing decomposition and nutrient concentration are in contrast with results showing increasing decomposition at increased temperatures and AET following clearcutting (Meentemeyer 1978; Meentemeyer & Berg 1986). This contradiction can be explained by the conditions prior to felling in the forest. In forests with relatively low decomposition rates, low densities of soil biota and a cold climate (as in large parts of Swedish boreal forests) canopy removal increases insolation, leading to improved conditions for both soil biota and decomposition. In the above-mentioned hardwood forest, conditions under a closed canopy apparently were favourable for primary (bacteria and fungi) and secondary decomposers (microarthropods, nematodes, etc.) and decomposition. Canopy removal created sub-optimal conditions by increasing temperature extremes and moisture stress.

Similar results were found in a study on the effects of thinning in a temperate *Pinus nigra* forest. One site was thinned 20% in a regular way, and an adjacent unthinned site was used as a reference. During a ten months' period, four years after thinning, temperature extremes, water economy, faunal densities and diversities were established. In lysimeters decomposition rates of the organic layer and nitrogen mobilization were established (Verhoef et al. in prep.). Thinning caused an increase in temperature extremes (Table 7). In general, evaporation from the soil was higher in the thinned site, whereas evaporation from the canopy was higher in the unthinned site. The density of the total soil fauna was higher (up to 53%) in the reference site compared with the thinned site. The difference was caused by reproduction peaks of collembola and mites in the reference site. The diversity indices were similar for both sites. Decomposition of the litter layer in the thinned site was 17% lower compared to the reference site. Total mineral nitrogen in the thinned site was 39% lower compared to the reference site, whereas total nitrogen mobilization was 30% lower (Verhoef et al. in prep.).

This study, too, showed that harvesting can create sub-optimal conditions. However, the effects of this form of perturbation depend not only on the perturbation itself, but also on the conditions prior to the perturbation.

Agricultural systems are perturbed systems by their very nature, but harvesting, especially of annual crops, has a relatively strong impact on decomposition and mineralization because of the rapid dying-off of roots and because it is usually associated with the addition of crop residues to the soil. The pattern of decomposition and the speed at which it proceeds have been reported to relate to the placement of the litter. Various studies have shown that organic carbon and nitrogen accumulate in the top 10 cm under no-till or minimum tillage as compared with conventional tillage (Westmaas Research Group on New Tillage Systems 1984; House et al. 1984; Juma & McGill 1986).

Few studies, however, have analyzed these effects in terms of the associated changes in the microbial and faunal community, and the dynamics of organic matter and nitrogen. The depth distribution of fungal biomass on winter wheat straw residues placed on or incorporated in a clay loam soil indicated that fungi may be important decomposers of surface straw and less so of incorporated straw. Fungal biomass increased with increasing nitrogen fertilization at the time of residue placement. The fungi may have been able to use the surface straw carbon and translocate the soil nitrogen with their extensive hyphal network (Holland & Coleman 1987). Moreover, microbial biomass carbon and nitrogen and microbial activity, measured as ^{14}C taken up from labelled straw and as cumulative CO_2 respired, were higher in the incorporated-straw treatment than in the surface-straw treatment, which indicates a more rapid decomposition of organic carbon. Although soil nitrogen availability had no significant effect on the decomposition rate of either the surface litter or incorporated litter, microbial biomass carbon of incorporated straw and cumulative CO_2 respired were lowest in the low-nitrogen treatment. In the surface straw microbial biomass carbon increased as nitrogen availability increased, but cumulative CO_2 respired decreased. This suggests that the total microbial community of surface straw became increasingly efficient at carbon utilisation as nitrogen availability and the proportion of fungal biomass increased.

This agrees with the known high assimilation efficiency of fungi for carbon as compared to bacteria and was confirmed by the higher percentage of ^{14}C from labelled residue retained in the microbial biomass in the surface-straw treatment than that in the incorporated-straw treatment. Also the microbial biomass will have turned over more slowly with the increasing importance of fungi as a component of the microflora. At the same time maximum net nitrogen immobilization was higher in the surface straw than in the incorporated straw. It was concluded that the microbial community structure can control carbon retention in ecosystems and that no-till systems may conserve organic matter because of a higher proportion of fungi and hence a higher substrate use efficiency (Holland & Coleman 1987). An alternative, perhaps more realistic interpretation, is that differences in substrate quality were brought about by adding weed residues with different C/N ratios to the surface rather than adding artificial fertilizers as in the above-mentioned study. The weeds with the lower C/N ratios (16 or 17) decomposed more rapidly and supported greater populations of bacteria, fungi and nematodes, than the weed with the higher C/N ratio (29). One might expect that in no-till agriculture the fungivorous fauna is more numerous and more important for mass and nutrient transfer than in the conventional tillage systems. In spite of its importance for the dynamics of organic matter the fungal biomass in no-till, however, was not more than twice as high (up to 1.8 μg/g soil) in surface straw as in incorporated straw in a laboratory experiment and its biomass was less than 1% of that of bacteria in all cases (Holland & Coleman 1987). As mentioned earlier in the text, this may either mean that fungivores are not important or, in contrast, that they exert a heavy grazing pressure. Consistent with the latter hypothesis, significantly more biomass of the largely fungivorous collembola and mites was found in the top 10 cm of no-tillage fallow dryland wheat plots than in stubble mulched plots, whereas no significant differences in the biomass of the largely bacterivorous protozoa and holophagous nematodes were established (Elliott et al. 1984).

Likewise, Hendrix et al. (1986) found significantly higher numbers and biomass of fungivorous nematodes and largely fungivorous microarthropods in the topsoil of a sandy clay loam; in this case the bacterivorous nematodes were significantly lower in number and biomass. Lower abundances of fungi and higher numbers of fungivorous nematodes and prostigmatid mites were found in surface weed residues on an upland site, suggesting reduced fungal populations caused by grazing, but no such results were found in the same litter at a lowland site (Parmelee et al. 1989).

In conclusion, there is circumstantial evidence for the quantitative importance of the fungal energy channel including the fungivorous fauna for decomposition and mineralization in no-tillage or reduced tillage agriculture.

7. Research needs

Dynamic models

The use of simulation modelling is indispensable for the description, prediction and, ultimately, the application in management of the contribution of the soil biota to element turnover in soil. The approach we have chosen in this article relies heavily on the applicability of food web models such as the one by Hunt et al. (1987; Fig. 5). Although this model appears to be the best available for the description of faunal influence on decomposition and mineralization, several

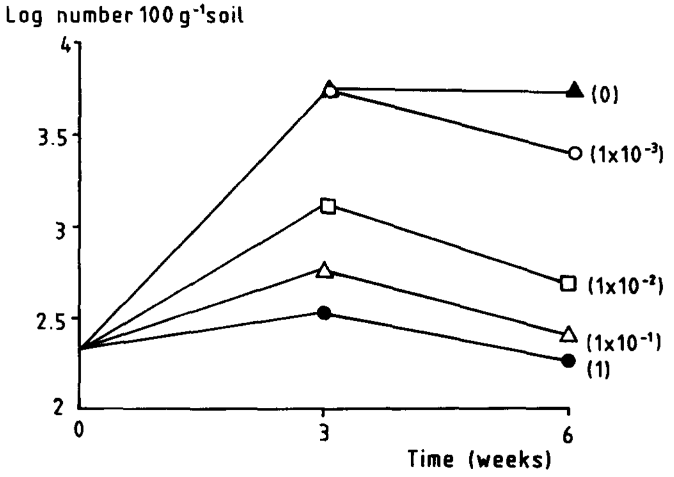

Fig. 18. Population growth of the bacterivorous nematode *Rhabditis* sp. at 10° C in the absence and at various inoculum densities of the nematophagous fungus *Arthrobotrys* sp. (:1, 1 × 10^{-1}, 1 × 10^{-2}, 1 × 10^{-3}, 0) in a microcosm experiment. (From Bouwman et al. in prep.).

limitations have to be kept in mind. The basic assumption is that the functional groups process energy and nutrients by digestion of food and through their own population turnover. However, top predators not only process matter, but can also impact the abundance and amount of energy and nutrients processed by prey, even though they have a relatively low biomass compared with the lower trophic groups. One may argue that these effects are accounted for by the model in the biomass and the turnover of the lower trophic level groups, but our point is that the higher animals are more important than is apparent from the amount of matter processed by them. Moore et al. (1988) estimated from the model of Hunt et al. (1987) what fraction of the secondary production of each functional group went to consumers. The fraction ranged from 1–4% in protozoa, 0–11% in microarthropods, 10–52% in nematodes and just over 30% in bacteria and fungi. Among the predators a strong regulation potential on bacteria was calculated for predatory nematodes and mites and on fungi for predatory mites.

The second limitation to be considered is that any effects of pathogens and parasites on abundance and activity of the functional groups are not accounted for in the trophic relationships. The effect of the presence of predatory fungi on the population growth of bacterivorous nematodes was measured in microcosms to which pulverized beet leaves were added in amounts equivalent to those normally applied to the field soil in autumn (Bouwman et al. in prep.). After a treatment of γ-irradiation (1 Mrad) which was followed by addition of a suspension of bacteria and nematodes, the nematode-trapping fungus *Arthrobotrys* sp. was able to reduce the numbers of the nematodes *Rhabditis* sp. (Fig. 18) and *Acrobeloides* sp. depending on the inoculum density of the fungus. The same held for the nematode-trapping fungus *Dactylaria* sp. versus *Rhabditis* sp. and to a lesser extent versus *Acrobeloides*.

The third limitation of the model is that the saprophagous fauna is not included.

Sensitivity analysis showed that reliable information about population sizes, population turnover rates, C/N ratio of fauna, digestibility of prey and P/A ratio is necessary to successfully apply this model (Hunt et al. 1987). There is an urgent need for more reliable estimates of ecophysiological and population biological parameters of the most important representatives of the functional groups, i.e. of the most numerous and metabolically most active species. Furthermore, nitrogen mineralization during the growing season was modelled by Hunt et al. (1987) to occur during 40 ideal days when the system was considered in steady state. Evidently, this is a justified first approximation. Yet, accounting for short-term changes is necessary for the model to be applicable under perturbation conditions.

Recently Hunt et al. (1989) developed a more dynamic model for estimating components of secondary production in the detrital food webs of a native shortgrass steppe, winter wheat and fallow plots after wetting. This model has been fitted to observed net changes in biomass and has been constrained to use transfer rates compatible with the physiology and population attributes of the organisms. The authors found high agreement between predicted and observed net changes in biomass and CO_2 evolution. However, the model failed to account for data with the same parameter values across data sets (as time and location). Therefore, a more mechanistic model including effects of the environment on organism activity is to be developed.

Perturbation in relation to microbial dominance

Several examples have been given of nutrient leaks following perturbation and coinciding with fewer soil animals, which also show a shift in their seasonal abundance as compared with natural conditions. Also, several studies were referred to, in which the soil fauna was shown to mitigate the effects of changes in abiotic conditions, notably soil moisture, so that mineralization of nitrogen continued for some time as stress developed. It is a provoking thought that under those conditions mineral nitrogen would accumulate, being immediately available for plant uptake upon rewetting of the soil. Other studies showed that immediately thereafter the fauna is also important in grazing the rapidly increased microbiota, thereby again making nitrogen available to the plant. Some evidence was referred to, that also on a seasonal scale the fauna under natural conditions is instrumental in supplying the plant with nitrogen when it needs it and in preventing nitrogen loss when there is no plant demand. This hypothesis warrants careful study because the answer may have important implications for the degree and the timing of man-imposed perturbations since we aim at improvement of the nutrient use efficiency in agriculture and forestry.

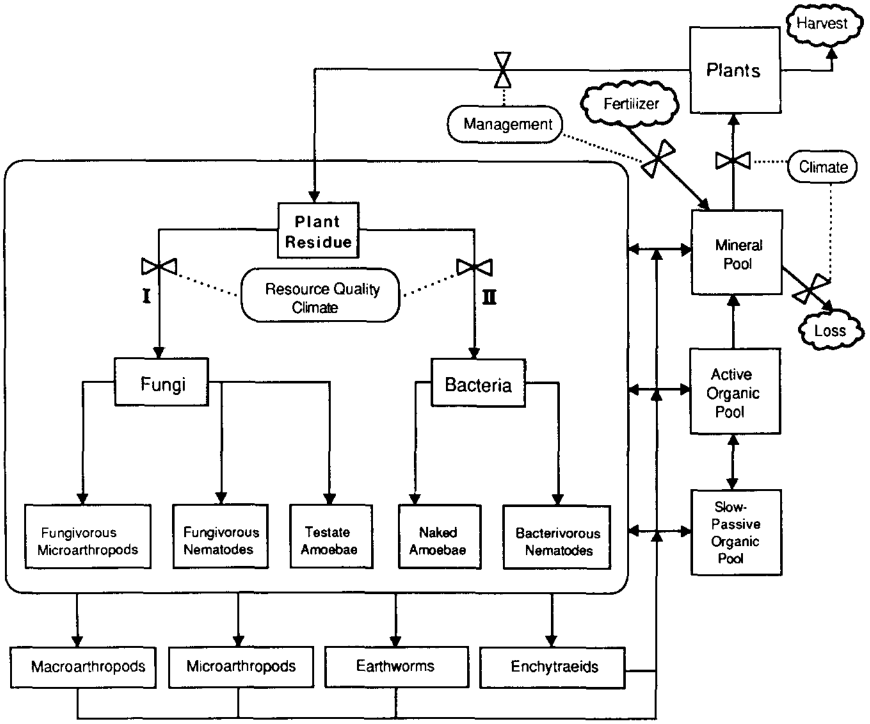

Fig. 19. Conceptual model of detritus food web in fungal dominated no-till systems (I) and bacterial dominated conventional tillage systems (II). For description of symbols see Fig. 6. (After Hendrix et al. 1986).

Conceptual models of detritus food webs, being relatively more fungal dominated in no-till systems and bacterial dominated in conventional tillage systems (Hendrix et al. 1986; Fig. 19) can be a useful framework for further research. These conceptual models are being tested also for nutrient poor coniferous forest floors and those subjected to increased nitrogen deposition, the hypothesis being that they show more fungal and bacterial dominated nutrient pathways, respectively (Verhoef et al. 1989).

In the absence of concurrently collected data on microbial and faunal biomass and activity the question whether the fungal biomass in no-tillage and reduced tillage agro-ecosystems can support a fungivorous fauna that is able to influence or even regulate the standing stock of fungi with quantitatively important effects on the decomposition of organic matter and the mineralization of nutrients, is still open for research. Experiments with litterbags with various mesh-sizes, extending the research of Holland & Coleman (1987) to include the soil fauna seem to be promising in this respect. Similar experiments with forest litter under conditions of low and high aerial deposition of nitrogen are performed in current research in the Netherlands (Verhoef et al. in prep.).

In studying nutrient pathways through the fauna in supposedly fungal dominated no-tillage and bacterial dominated conventional tillage systems, differences in soil structure between these systems should be taken into account. Small, lower trophic level animals living in water-filled pores or water films may make more food available to bigger, higher trophic level animals by entering soil pores inaccessible to the latter. Evidence therefore was found for amoebae emerging from small pores and subsequently eaten by nematodes that were unable to enter those pores (Elliott et al. 1980). Also, microarthropods living in the air-filled pores will be largely restricted in their grazing and predatory activities to interconnected pores exceeding certain diameters in neck size. On the other hand, although no-tillage soil may have a higher bulk density (Westmaas Research Group on New Tillage Systems 1984), a greater proportion of pores and channels can be formed by the soil biota, i.e. roots and fauna (Kooistra et al. 1989; Fig. 20), while the fauna also mixes crop residues with mineral soil. To what extent these processes interact to yield the contributions of various functional groups of soil fauna to organic matter dynamics (decomposition **and** humification) and nutrient mobilization seems to be a research area hardly touched upon hitherto.

Ecological applications and ecological theory

In this paper we stressed the need to further test the hypothesis that different assemblages of species with a common resource base, i.e. energy channels, are important during decomposition of organic matter and mineralization of nutrients. We also put forward the hypothesis that the nutrient supply from the soil and the uptake by the plants are better synchronized and synlocalized under natural conditions than under perturbation. If these hypotheses are true the implications for forestry and agriculture are clear: the energy channels and nutrient pathways should be manipulated towards retention of organic matter where needed and reduction of nutrient leakage where possible.

A recent revival in the discussions on ecological theories on food webs is apparent (Schoener 1989; Briand & Cohen 1987; Moore & Hunt 1988). Schoener (1989) states in his thorough review that there is few integration between the three levels at which trophic ecology can be conceptualized: the individual, population and community level. At the population level the stable dynamical theory (review in Pimm 1982) has proved its worth to explain specific food web phenomena, such as the destabilizing effects of feeding on more than one trophic level (Pimm & Lawton 1978). However, it fails to link individual-level concepts to food web patterns. The community level approach of Cohen et al. (1985) hardly draws on lower level concepts. According to Schoener (1989) a more reductionist approach would help to unify the different theoretical levels.

Partly based on his own studies on a simple terrestrial food web on Bahamian islands and partly on an analysis of 98 food webs compiled by Briand & Cohen (1987), Schoener (1989) proposes the 'productive space' hypothesis. It states that maximum food chain lengths are determined by the amount of productive

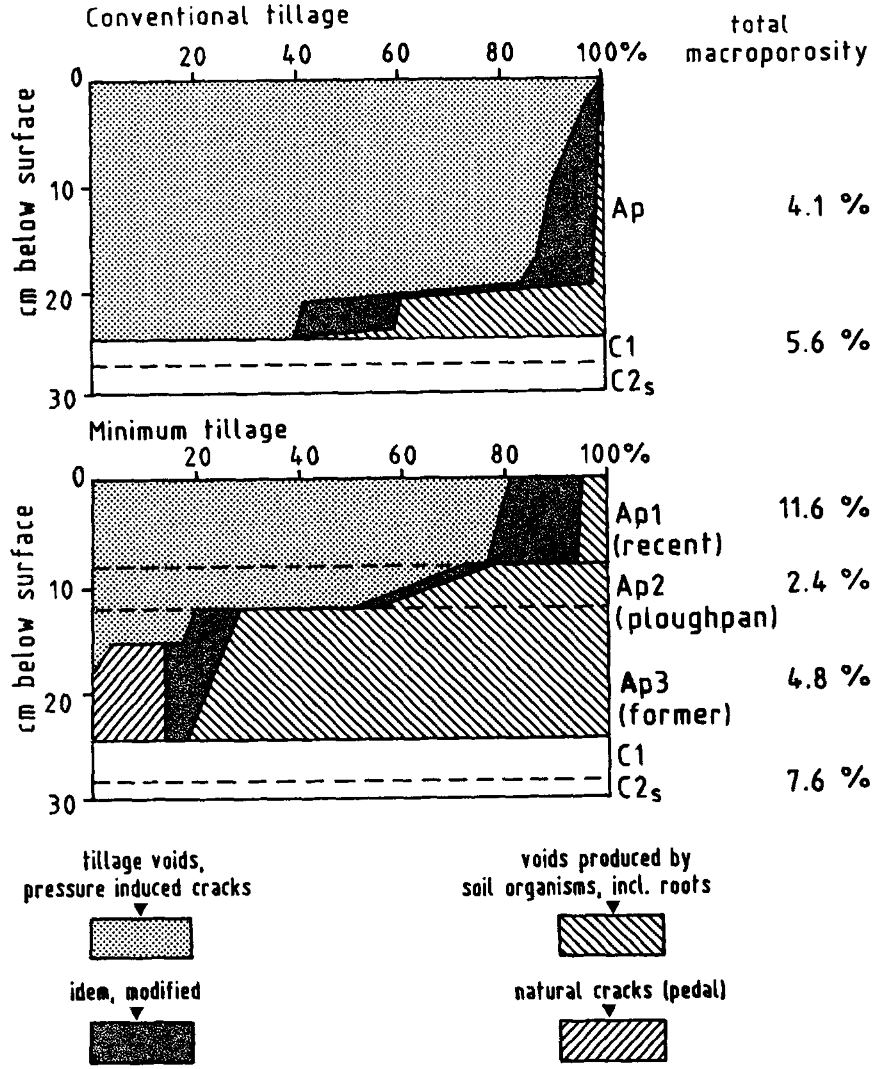

Fig. 20. Macroporosity and origin of pores in a conventional and a minimum tillage arable cropping system on a sandy loam soil. (From Kooistra et al. 1989).

space (= space times productivity) required to allow critical component species populations to persist with some high probability (Schoener 1989; p. 1568). The food webs concern above-ground terrestrial and aquatic system categories, and show striking similarities, such as in the number of trophic species, but also major differences in food chain lengths. This latter conclusion is critized by Moore et al. (1989) by stating that many of the food webs used show considerable incompleteness: they are missing predatory birds and insects and primary decomposers such as bacteria and saprophytic fungi. They suggest that the aquatic two-dimensional and the terrestrial three-dimensional webs are descriptions of habitat compartments of real food webs, which is consistent with the resource compartmentation hypothesis and niche theory. Yodzis (1984) found, based on 34 webs of the Briand & Cohen-collection (1987) that energy flow explains variation in food chain length better than do limitations resulting from dynamical stability or the body size of predators. According to Briand & Cohen (1989) the influence of energy versus that of other factors on food chain length must be further analyzed. Moore & Hunt (1988) have provided evidence of resource compartmentation based on structural characteristics of a below-ground connectedness web and on biomass estimates and nitrogen flux rates from its energy flux-web description. According to these authors analyses of the utilization of energy coupled with qualitative analyses of connectedness webs are appropriate to reveal aspects of food web structure and stability. This below-ground study concerns the earlier mentioned shortgrass steppe food web (see Fig. 5). Similar below-ground studies are performed in current research in the Netherlands, both in agro-ecosystems and pine forests. We feel that the hypotheses on energy channels, nutrient pathways and synchronization and synlocalization both should dwell on recent developments in ecological theory and contribute to it, because it is only on a sound theoretical basis that ecological knowledge of the soil fauna can be applied to the management of element transfer in forestry and agriculture.

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