Ecology of microarthropods in arable soil

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ECOLOGY OF MICROARTHROPODS IN ARABLE SOIL

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Je zult moeten toegeven,' vervolgt Oehoeboeroe met een rood hoofd, 'dat het -hm- helendal wat anders is om in het Nederlands niks te schrijven, dan dat je het in het Frans doet. Is dat duidelijk?'

'Tja,' zegt Paulus, 'ik geloof wel dat ik het begrijp. Ik zou in ieder geval in het Frans niks kunnen schrijven. 'Precies, en ik nou wel, hè. Ik kan wel niks schrijven in het Frans.'

Jean Dulieu (1990) Het grote boek van Paulus de Boskabouter.

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Stellingen

1. De onderverdeling van het bodemvoedselweb in een web gebaseerd op verse organische stof, een web gebaseerd op "oude" organische stof en een rhizosfeer-web, is de "missing link", die de integratie van dynamische organische stofmodellen met voedselwebmodellen voor het voorspellen van stikstofmineralisatie mogelijk zal maken *(dit proefschrift)*.

2. De bodem valt te beschouwen als de "*poor man's rain forest*": alle mogelijke oecologische processen zijn goedkoop en dicht bij huis te onderzoeken.

3. In een ongestoorde, natuurlijke situatie zullen de door sommige auteurs aangetoonde positieve effecten van microarthropoden op de strooiselafbraak worden opgeheven door de door andere auteurs aangetoonde negatieve effecten *(dit proefschrift)*.

4. Uitsluitingsexperimenten hebben alleen waarde indien de uitsluiting ook gecontroleerd wordt *(dit proefschrift)*.

5. De waarde van wetenschappelijke publicaties voor toekomstig onderzoek zou enorm stijgen, als er ook in opgenomen kon worden wat er fout ging.

6. "Mislukte" proeven leveren de interessantste resultaten.

7. Invoering van grote grazers in het duingebied, zoals in de Wassenaarse waterleidingduinen, leidt wel tot verandering in de samenstelling van flora en fauna, maar niet noodzakelijkerwijs tot vergroting van de soortenrijkdom. Dit in analogie met modeverschijnselen, die ook gekenmerkt worden door verandering zonder verbetering.

8. De invoering van de tweede fase in het middelbaar onderwijs, die een grote mate van zelfwerkzaamheid van de leerlingen eist, staat haaks op de ontwikkeling bij de Nederlandse universiteiten, die in de loop der jaren steeds "schoolser" zijn geworden.

9. Er bestaat een sterke samenhang tussen de renovatie van een overheidsgebouw en een spoedige sluiting van de daarin gevestigde instelling.

10. Het beste bewijs voor de tweede hoofdwet van de thermodynamica is een huishouden met kleine kinderen.

11. In deeltijd werken betekent voor vrouwen met een gezin: twee verantwoordelijkheden hebben, maar voor maar één betaald worden.

12. Geen enkele fantasie is zo ongelofelijk als de werkelijkheid.

Stellingen behorende bij het proefschrift van Madelein Vreeken-Buijs: "Ecology of microarthropods in arable soil", Den Haag, 26 mei 1998.

Voor Arie

CONTENTS

ABSTRACT

Vreeken-Buijs, M. J. 1998. Ecology of microarthropods in arable soil. Ph.D. Thesis, Wageningen Agricultural University, Wageningen, The Netherlands. 113 pp.

The role of microarthropods was studied in relation to the functioning of the soil food web of agro-ecosystems. Soil inhabiting mites and collembolans were divided into seven functional groups. In order to assess their effects on the decomposition of organic matter in the soil and the mineralization of nitrogen, their mutual relationships and their relationships with other faunal groups within the soil food web were studied at three different abstraction levels. In a gnotobiotic microcosm experiment with bacteria, bacterivorous mites and amoebae, the direct contribution of the two microbial grazers to the N-mineralization was separated from possible combined effects. In a litterbag experiment, the effect of microarthropods on the decomposition of wheat straw was studied. Accidental colonization of the fine mesh litterbags by large numbers of fungal browsing mites and collembolans showed that overgrazing of the fungal population due to the absence of predators leads to a decreased decomposition rate. Field sampling of microarthropods as part of a two year soil food web sampling program in two wheat fields under conventional and integrated management revealed no striking differences in the annual mean biomass, but large variation in the within year dynamics. In a comparative field study in ten sites, differing in soil type and land use, relationships between functional groups were studied, as well as relationships between functional group biomass and land use, soil type, soil pore distribution and organic matter quality and dynamics. In general these experiments have lead to the conclusion, that in undisturbed situations, there is no net effect of microarthropods on organic matter decomposition or on N-mineralization. Top-down control of predatory mites on fungal browsing microarthropods, prohibits overgrazing of the fungal population. In agroecosystems, the soil food web can be divided into three spatially and temporally separated webs, based on three different carbon sources: fresh organic matter, "old" organic matter and root derived carbon. Microarthropods of the first and second food web differ in life history tactics. As a consequence of the subdivision, field sampling is the more useful tool for studying the "old" organic matter food web, while litterbags are more suitable as a tool for studying the fresh organic matter food web.

CHAPTER 1

GENERAL INTRODUCTION

Introduction to soil microarthropods

This thesis is about soil microarthropods and their relations with other organisms in the below-ground community. Microarthropods are those arthropods that are invisible to the naked eye. Soil microarthropods complete their whole life-cycle in the soil. The bulk of the soil microarthropods belongs to two major groups: free-living mites (Acari) and springtails (Collembola). I have studied their role in the soil food web: their mutual relations, their food preferences and their adaptation to environmental conditions and environmental stress. The charm of studying microarthropods in the context of the soil food web is, that in the soil all processes and interactions that take place also can be witnessed, at a much larger scale, in more visible ecosystems. We can compare it, for instance, with the African savanna: earthworms, with their burrowing activity, can shape and alter the physical conditions of the environment in a way similar to what elephants do. The same can be said for the large diversity of grazers, albeit that in the soil these are mainly fungal and bacterial grazers, while on the savanna we find mostly herbivorous mammals. Some organisms appear in large numbers and have a high fecundity, but are also prone to much predation, like for instance most rodents, while some cryptostigmaticmites carry heavy armor, comparable to the rhinoceros, and have less to fear from predators. Predators, even the tiny Gamasina, are just as fascinating to watch as all the well known large felines. And all this variety of organisms is represented in only a few cubic centimeters of soil, any soil.

Taxonomy

Soil organisms are classified by size into microflora, and micro-, meso-, and macrofauna, which broadly reflects the spatial and temporal scales at which they affect soil processes (Anderson, 1988). All organisms with body widths less then 120 µm are called microfauna. They include nematodes and protozoa. What we call the microflora, are usually the fungi and the bacteria. Organisms with body widths ranging from 120 µm to 2 mm are called the mesofauna and these include mites, springtails and also Enchytraeidae. The macrofauna have body widths of 2 mm and up and consist, among others, of earthworms, Isopoda, Diplopoda and Mollusca.

The mites belong to the class of the Arachnida of the phylum Arthropoda, and are subdivided into nine orders. The most important ones are: Scorpionidae (scorpions), Araneae (spiders), Pseudoscorpionidae (pseudoscorpions), Phalangida (harvestmen) and Acarina (mites and ticks). The Acarina are subdivided into five suborders. Only one suborder has no representatives in the soil fauna: the Ixodides (Metastigmata) or ticks, which are obligatory parasitic.

The five suborders, relevant to the soil biology are: Cryptostigmata or Oribatida (moss mites), Acaridida, Mesostigmata (predatory mites), Actinedida (spider mites, harvest mites, water mites, etc.) and Tarsonemida. Actinedida and Tarsonemida together are also called Prostigmata. Although adults always have eight legs, mites and ticks pass through a six-legged stage, the larva, during post-embryonic development. The body is sack-like in form and is never divided into a cephalothorax and abdomen, as is the case in, for example, the spiders and scorpions (Evans, 1955). Free-living mites inhabit all layers of the vegetation, the litter and the soil to depths of below 40 cm (Figure 1).

The order of the Collembola or springtails belongs to the subclass of the Apterygota or wingless insects, a subdivision of the arthropod class of Insecta. This subclass of 'primitive' insects shows no metamorphosis. Collembola possess no tracheae and most representatives have a springing organ or furca on the 4th abdominal somite. Collembola live in damp places under leaves, moss, bark, stones or on water or snow. In soil some species are commonly found at soil depths of 40 cm or more. Important families of soil inhabiting Collembola are: Onychiuridae, Poduridae, Isotomidae, Entomobryidae and Sminthuridae. In addition to the taxonomic classification of the springtails, Gisin (1943) proposed an ecological classification based on the vertical distribution. Species are divided into three stratified communities: the euedaphic collembolans live in the deeper soil layers and are characterized by the absence of eyes, pigment and a developed furca; the hemiedaphic collembolans inhabit the litter layers and are characterized by reduced eyes and furca and a rather homogeneous pigmentation; the epigeic collembolans, finally, are found on the soil surface and in the vegetation and have well developed eyes and furca and usually a spotted pigmentation. Also the amount of hair increases from the euedaphic to the epigeic life forms (Verhoef, 1996).

Ecosystem research in agricultural soils: objectives and history

Although ignored, or even denied by many people, agricultural soil is a habitat for a complete and diverse community, of which only its largest representatives, earthworms, centipedes and millipedes, generally come within eyesight of people working in their gardens. The primary source of energy for this community is organic matter: carbon stored in crop residues, litter, dead roots and organic manure. It is the functioning of this community, that is responsible for the release of nutrients from soil organic matter of various origin, enabling nutrient absorption by the root system of the crop. Therefore, in "ecological" farming much

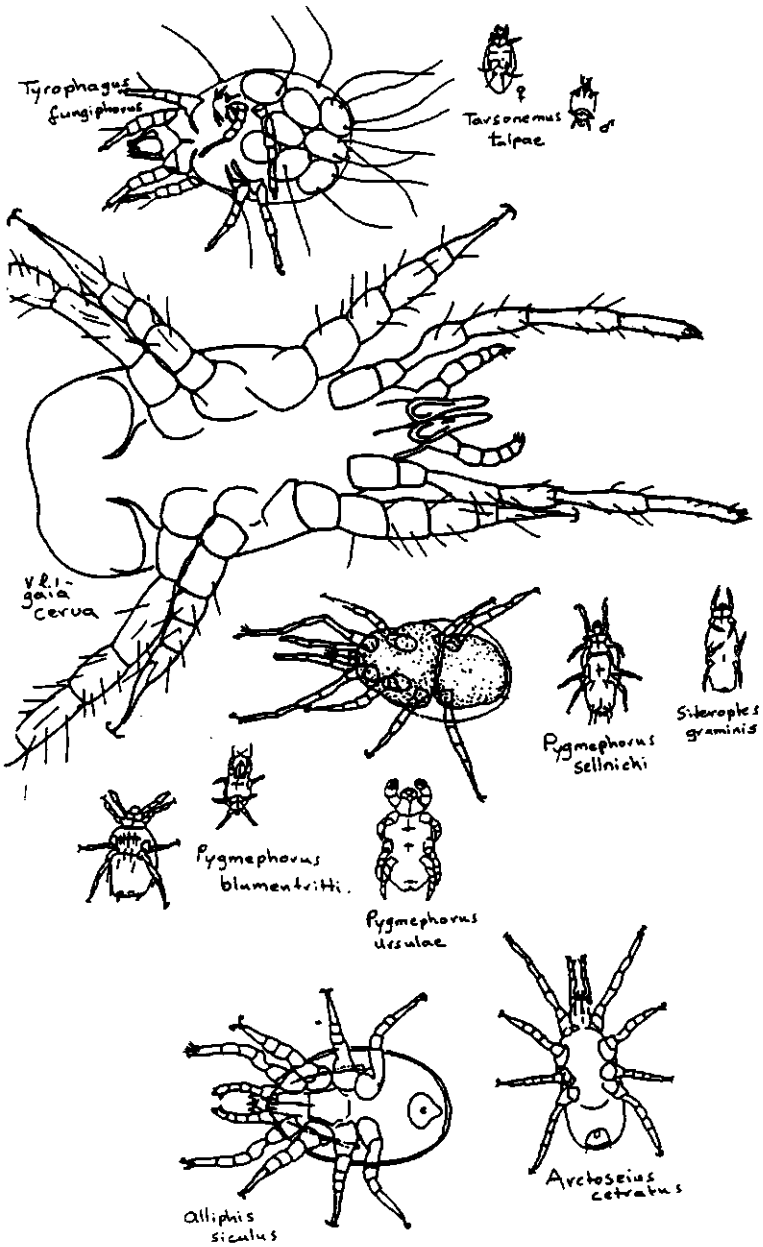
emphasis is put on the "natural" cycle of nutrients. My study too has been part of a much broader research program to support the development of a sustainable farming system. One of the objectives of sustainable agriculture is to minimize adverse effects to the environment, as there are: erosion, nutrient losses to soil and ground water and pollution of the soil and of surface- and ground water with biocides or derivatives of biocides.

The main problem with organic fertilizers is that part of the minerals are released during periods they are not needed for crop growth, which may lead to losses to the environment (overdoses of minerals threaten the ground water quality and raise the risk of gaseous N losses, which cause eutrophication and greenhouse gas effects). In a sustainable management system, the aim is to optimize the tuning of the input of minerals to the soil to the output in the crop yield (the "mineral balance"). Organic fertilizers are by nature "slow-release fertilizers" and therefore fit a sustainable management system. This "slow release" is in fact the work of the soil ecosystem. Organic matter is decomposed as the stored energy finds its way through the food web, from the primary decomposers (bacteria and fungi), through the secondary decomposers (protozoa, fungivorous and bacterivorous nematodes, fungivorous and bacterivorous mites and Collembola) to the higher trophic levels of predatory nematodes, Collembola and mites. With every step through the food web, part of the energy is released in the form of respiratory warmth and of CO_2, but also some mineral nitrogen is lost by excretion. In addition, bodies of organisms, that have fallen prey, will be partly left to be decomposed by micro-organisms, just as organisms that died of natural causes. This too will increase the pool of mineral nitrogen, that is crucial to crop growth. Therefore, central to our understanding of the complex nature of the process of nitrogen mineralization is the soil food web, its structure and its functioning.

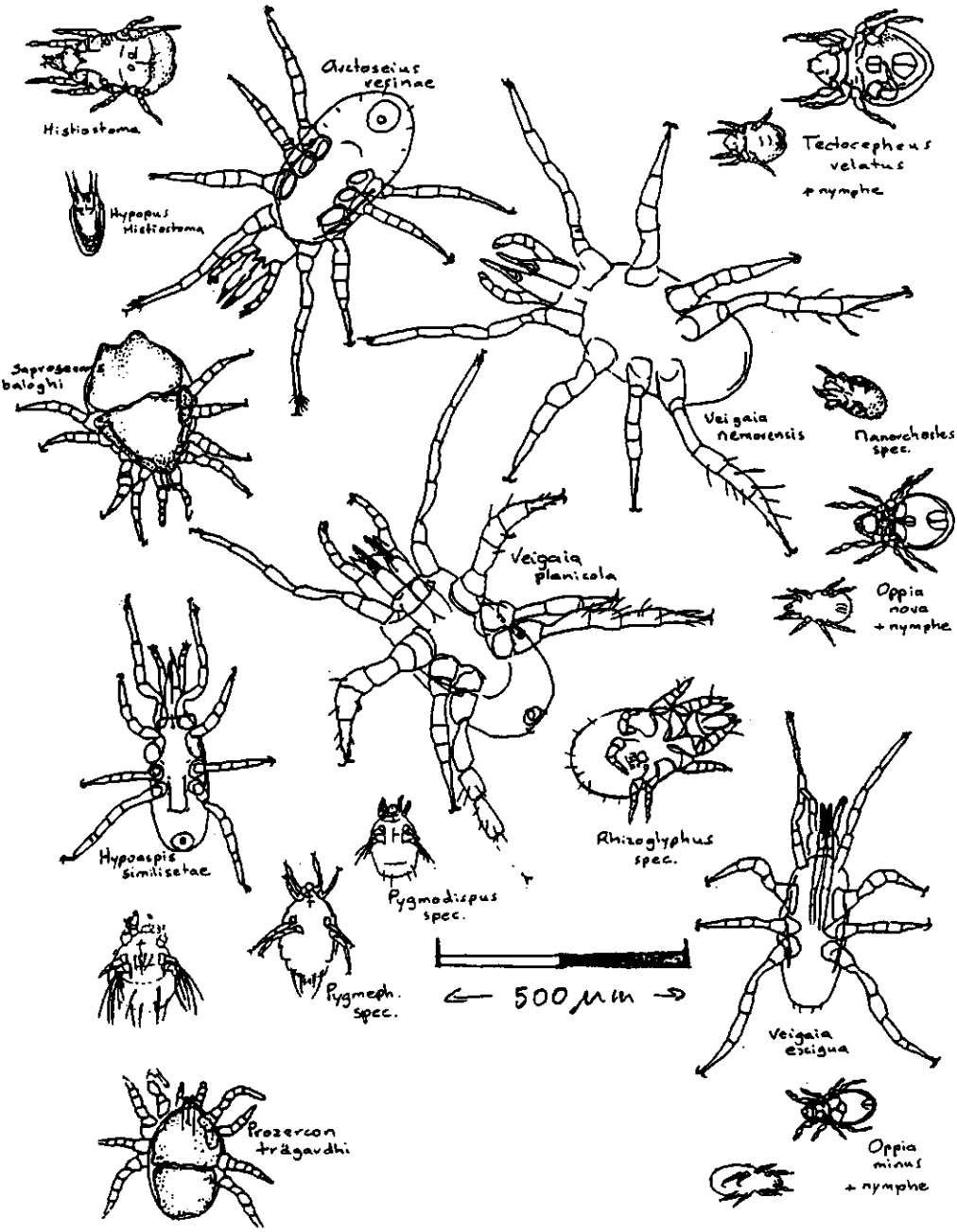
Apart from local small-scale studies by individual scientists all over the world, several major soil ecosystem research programs have been documented. In the United States at the Central Plains Experimental Ranch in Colorado, a large group of scientists unraveled and constructed a connectedness soil food web of the short grass prairie (Hunt et al., 1987). All soil flora and fauna found in a sampling scheme, from fungi and bacteria to earthworms, were grouped into functional groups; functional groups were then arranged into trophic levels. Numbers of individuals per volume of soil were used to calculate an estimate of the biomass-C content of the soil for each functional group. These data were used to run a simulation model, that was built to predict the total nitrogen mineralization in the soil. The model further uses consumption rates, assimilation and production efficiencies and an annual mean of the biomass-C, and is based on the assumption that the ecosystem is at equilibrium (annual production of each group equals annual mortality).

At Georgia's Horseshoe Bend experimental site a research program focused on the effects of different tillage practices on the soil food web and its implication on nitrogen mineralization and litter decomposition (Beare et al., 1992). At the Kjettslinge experimental site in Sweden in the 80's an extensive research program,

Figure 1: A collection of mites sampled from agricultural soil at "De Schreef"



experimental site (courtesy of dr. G. A. J. M. Jagers op Akkerhuis).



"Ecology of Arable Land", compared the food web structure and dynamics in four different cropping systems: barley without any nitrogen fertilizer, barley with 120 kg N $ha^{-1}y^{-1}$, a grass ley with 200 kg N $ha^{-1}y^{-1}$ and a lucerne ley without N application (Andrén et al., 1990).

Finally, the Dutch Programme on Soil Ecology of Arable Farming Systems, of which the major part of this thesis forms part, started in 1985 at the Lovinkhoeve experimental farm at Marknesse, Noordoostpolder. Its aim was to compare conventional agricultural management with so-called "integrated" management. "Integrated" management is a tool for sustainable agriculture, and aims at using biological processes to get a better nutrient use efficiency, a sustained improvement of the soil structure and an effective pest and weed control (Brussaard et al., 1988). Ahead of this program, the microarthropods of Dutch agricultural and grassland soils have been studied (among others) by Van de Bund (1970,1980), Siepel and Van de Bund (1988) and Jagers op Akkerhuis et al. (1988).

The Dutch Programme on Soil Ecology of Arable Farming Systems

The Dutch Programme on Soil Ecology of Arable Farming Systems was an integrated multidisciplinary research program, focused on the functioning of two differently managed agro-ecosystems. The field work was carried out at the Dr. H. J. Lovinkhoeve experimental farm at Marknesse in the Noordoostpolder, a polder reclaimed from the sea in 1942 (Kooistra et al., 1989). The program compared "conventional" agricultural management to "integrated" management. The alternative system, aimed at "integrating" biological processes in the farm management. The "integrated" management was characterized by :

- *reduced nutrient inputs*
- *a larger part of the nutrient inputs through organic amendments*
- *reduced (shallower) tillage*
- *reduced use of biocides*

In fact the "integrated" management was a compromise between the conventional practice and the so-called ecological or biological agriculture, that abolishes all use of biocides and artificial fertilizers. The hypothesis behind this "integrated" management system was, that application of biocides could be reduced, because fewer pests were expected at lower nutrient levels. Preventive soil fumigation, known to be devastating to the whole soil fauna was omitted, because resistant potato varieties were used in the 4 year crop rotation (winter wheat, sugar beet, spring barley, ware potato). Biological control agents were used when possible, as for instance the inoculation of potato tubers with a fungus, suppressing *Rhizoctonia solani.* Weeds were largely controlled mechanically. Apart from a reduced sensitivity to pests, the nutrient use efficiency was expected to increase at reduced

nutrient input levels. Lower costs should balance the lower returns from reduced yields, which were aimed at 80-90% of that under conventional management. Tillage depth was reduced for lesser disturbance of the soil food web in the top soil layer (Brussaard et al., 1988; Lebbink et al., 1994). Furthermore, an increased soil organic matter content may suppress pests and diseases and may also improve the soil structure.

The Lovinkhoeve soil food web and functional groups

In 1986, on five occasions during the growing season, data were collected from the soil of a winter wheat field under conventional and under integrated management. Samplings from the top 25 cm of the soil were taken for counts of bacteria and fungi, protozoa, nematodes, microarthropods, enchytraeids and earthworms (Brussaard et al., 1990). Based on these data, a food web was constructed by De Ruiter et al. (1993a)(Figure 2).
As shown in Figure 2, the different taxonomic groups are organized into so-called functional groups: organisms that share a principal food source, mode of feeding, reproductive rate, defenses against predation and distribution in the soil profile in a specific habitat (Moore et al., 1988), or more simply: *organisms that have a similar role in the soil ecosystem.*

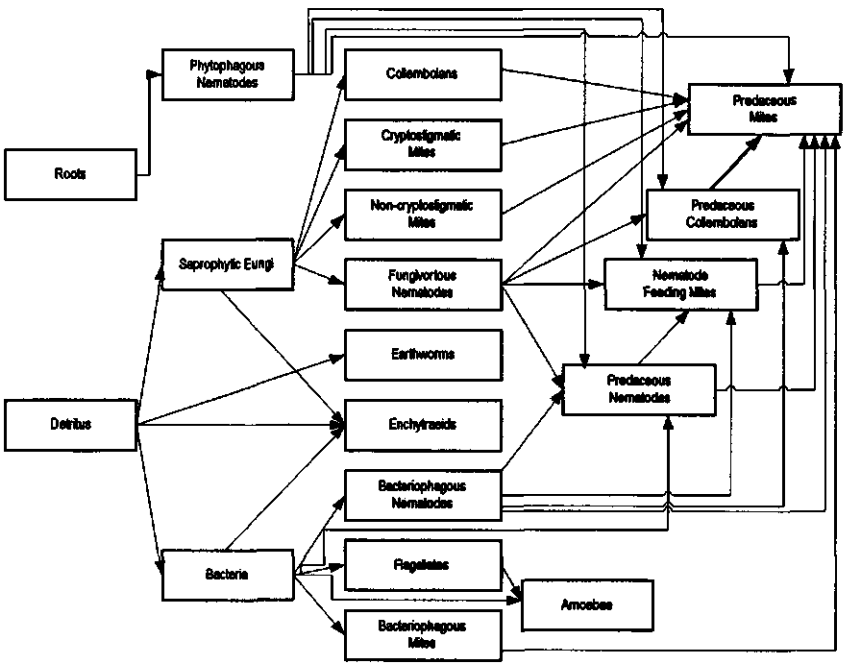


Figure 2: Below-ground detrital food web at the Dr. H. J. Lovinkhoeve experimental site (De Ruiter et al., 1993a).

Functional groups are arranged in trophic levels. At the first trophic level organisms (bacteria, saprophytic fungi and phytophagous nematodes) feed directly on the organic matter (detritus and roots) itself. The biomass of functional groups of a single level can differ tremendously: bacterial biomass for instance, is 10,000 times bigger than the herbivorous nematode biomass (Table 1). The second trophic level contains a great variety of life forms, ranging from protozoa to earthworms. These groups are bacterivorous, fungivorous or both. The third level is formed by predators on second trophic level groups.

This is of course a very rough partitioning, since most groups are no specialist feeders at all. Amoebae belong to the second as well as the third level, because the prey on bacteria as well as on flagellates. The group of the predaceous nematodes should be more correctly called omnivorous, since they can also graze on bacteria. In the case of the microarthropods the relationships are even more complicated than represented in the diagram. Collembola as a group are practically omnivorous: their food sources vary from fungi to bacteria, algae, young roots (in which case they can become a pest) and detritus to nematodes and nematode cysts, all depending on species, feeding preference and abundance of the food source (Walter, 1987; Lee and Widden, 1996). Only species known to be specialist predators (at the Lovinkhoeve site just one), are grouped separately.

In the case of mites the array of possible menus is even larger. Cryptostigmatic or oribatid mites are not very abundant in the Lovinkhoeve agricultural soil, but in natural soils they are the dominant group. They can be fungivorous or detritivorous, but also feeding on algae or nematodes, as was observed in cultured specimens (Walter, 1987). Analysis of cryptostigmatic mite species gut enzyme activity revealed that the diet was even more restricted (Siepel and De Ruiter-Dijkman, 1993). The non-cryptostigmatic mites are a very diverse group, consisting mainly of Prostigmata and Astigmata, that are predominantly fungivorous, but, especially the Astigmata, can be nematophagous as well. The predatory groups are more or less specialized feeders, that can vary their food source, depending on the abundance of the prey (Sardar and Murphy, 1987).

Non-cryptostigmatic mites are grouped separate from the Cryptostigmata due to their feeding mode: the first are considered to be mainly fungivorous browsers, because they possess small mouth parts or chelicerae, adapted to pierce the cell wall of the fungal hyphae. They only feed on the cell contents of the hyphae. Cryptostigmata found at the Lovinkhoeve have broader mouth parts, adapted to rip apart the fungal hyphae, and therefore they are classified as fungal grazing or chewing mites. Predatory mites, in general, have much longer, scissors-like chelicerae, adapted to catch a prey.

This classification method for the Acari is a useful tool for food web analysis, when large numbers of soil samples have to be analyzed and there is little opportunity for species identification, but it should be kept in mind that it is only a very crude method. A far more reliable method should be species identification, followed by a classification on the basis of enzyme activity, but this is a very

laborious process, in which only a limited number of species has been analyzed as yet (Siepel and De Ruiter-Dijkman, 1993).

Table 1: Annual mean population size of the functional groups in a wheat field soil under conventional and integrated management in kg biomass-C ha^{-1} in two depth layers. Data from the 1986 field sampling (after De Ruiter et al., 1993a).

	0 - 10 cm		10 - 25 cm	
	Conventional	Integrated	Conventional	Integrated
Microbes				
Bacteria	240.3	373.1	405.5	456.5
Fungi	11.7	21.0	19.1	25.9
Protozoa				
Amoebae	4.52	6.09	5.50	6.19
Flagellates	0.25	0.35	0.22	0.36
Nematodes				
Herbivores	0.023	0.122	0.019	0.087
Bacterivores	0.166	0.406	0.447	0.172
Fungivores	0.011	0.017	0.024	0.016
Predators	0.103	0.249	0.098	0.134
Microarthropods				
Cryptostigmata	0.012	0.003	0.010	0.002
Non-cryptostigmatic mites	0.018	0.010	0.019	0.010
Bacterivorous mites	0.004	0.001	0.051	0.001
Predatory mites	0.029	0.017	0.047	0.019
Nematophagous mites	0.015	0.013	0.058	0.004
Predatory Collembola	-	0.016	-	0.023
Fungivorous Collembola	0.204	0.245	0.327	0.275
Annelids				
Enchytraeids	0.077	0.190	0.465	0.233
Earthworms	-	8.860	-	4.740

It should further be noted, that functional groups differ not only in biomass, but also very much in number of species. Non-cryptostigmatic mites, omnivorous Collembola and predatory mites and to a lesser extent the Cryptostigmata are groups that consist of many different species, while bacterivorous mites, nematophagous mites and predaceous Collembola are represented by only one species in this particular food web. In soil food webs of other habitats, this situation can be much different.

Based on the 1986 results a more extensive sampling program started at the Lovinkhoeve site in the autumn of 1989. In the 1986 sampling program, no samples were taken during late autumn, winter or early spring, while during these seasons many problems related to leaching of nitrogen and the efficiency of nutrient use may occur. Therefore, in the new program, all functional groups were sampled every six weeks for two years (1989-1991). Biomass and activity of

bacteria, fungi and protozoa and N mineralization were monitored at intervals ranging from 1 to 6 weeks (Bloem et al., 1994). All these data were used to simulate the dynamics in nitrogen mineralization in the two arable farming systems (De Ruiter et al., 1994).

It should be noted, that apart from the biological sampling program, many parallel studies were conducted that contributed to the Programme. The development of the soil structure under the different management practices was followed (Boersma and Kooistra, 1994) and its effect on soil physical properties and simulated land qualities (Vos and Kooistra, 1994). Macroscopic soil physical processes were monitored (De Vos and Raats, 1994) and soil macroporosity and its effect on root- soil contact was studied (Schoonderbeek and Schoute, 1994). Other researchers investigated the effect of the earthworm population on soil structure stability (Marinissen, 1994), the production and decay of structural root material (Van Noordwijk et al., 1994) and the dynamics of root-derived organic matter (Swinnen, 1994). The farm management results have been described by Lebbink et al. (1994) and the actual dynamics of nitrogen and organic matter by Van Faassen and Lebbink (1994).

The role of microarthropods in the soil food web

Within the soil food web, microarthropods play a part in several trophic levels. Their mutual relations, their food preferences and their adaptation to environmental conditions and environmental stress and their role in the functioning of the soil ecosystem are the main subject of this thesis. Reviews on this subject have been published by Seastedt (1984), Visser (1985), Coleman (1986), Anderson (1988), Moore et al. (1988), Elliott et al. (1988), Persson (1989), Verhoef and Brussaard (1990), Zwart and Brussaard (1991), Crossley Jr. et al. (1992), Brussaard and Juma (1996) and Larink (1997).

As we can observe in Table 1, the total biomass of all microarthropod functional groups together is very small, compared to the total soil biomass. Bacteria form by far the largest part of the soil biomass, followed at distance by the fungi, the amoebae and, if present, the earthworms. However, the ability of an organism to influence a system is not necessarily related to its abundance, biomass or rate of energy use, but rather is a function of the ability of that organism to affect the organisms with which it interacts (Moore et al., 1988). In the case of the microarthropods, the ability of collembolans and of cryptostigmatic mites to affect fungi has been well studied. Three different mechanisms can be distinguished (Visser, 1985):

- *comminution, channeling and mixing*
- *grazing*
- *distribution*

Comminution of the organic matter and *channeling* and *mixing* of soil components stimulate bacterial activity, due especially to the formation of faecal pellets. At the same time damage to the fungi, caused by the disruption of the organic debris, may result in a reduction of fungal species numbers, due to variation in sensitivity of various fungi. This gives competitive advantage to fast-growing, short life-cycle micro-organisms such as bacteria and fungi like *Mortierella* spp. (Phycomycetes). *Grazing* by the fauna on selected fungi may considerably alter fungal distribution and succession on decomposing litter. The impact of faunal grazing on the microbial community appears to depend on the grazing pressure and on the growth rate of the organisms being grazed. Grazing may also deleteriously affect plant growth by reducing the effectiveness of the mycorrhizal symbiosis. Many soil micro-organisms rely on the soil fauna for *dispersal* of their propagules. The spread of inoculum may happen by means of propagules carried on external parts of the body and by inoculum passed through the gut and excreted as faeces. However, in this process the role of microarthropods may be limited, compared to earthworms. It may be apparent from the above, that the effects of the different mechanisms can be antagonistic, and therefore the result of their interaction is not straightforward.

The above mentioned mechanisms apply to the effect of second trophic level organisms on first trophic level organisms, but a tri-trophic effect of a predatory group on the micro-organisms through the microbivores and thereby on soil processes such as mineralization and decomposition, has been elegantly shown by Santos et al. (1981) in litterbags with and without nematophagous mites. This tri-trophic effect is an example of how a functional group with a relatively small biomass may have a major effect on a measurable soil process, in this case litter decomposition.

Other measurable soil processes are the soil respiration and the mineralization of nitrogen. Measurement of the effects of microarthropods on C-mineralization have often been attempted, but the results have been inconclusive in most cases. Persson (1989), for instance, found no measurable difference in CO_2 evolution rate after addition of a mixed microarthropod fauna to F/H layer material from a spruce stand. This is understandable, if we know that the contribution of the whole soil fauna to the total soil respiration is only 1 to 25%, depending on the soil characteristics. Clear increases in soil respiration have been measured as an effect of macrofauna, such as earthworms and as an effect of bacterial feeding nematodes and amoebae.

An increased nitrogen mineralization as a direct effect of grazing and excretory activities has been assessed for protozoans, for nematodes, and, sometimes, for microarthropods (Persson, 1983). Removal of excretory products from the immediate environment depends on leaching or volatilization, but in most instances, this nitrogen is probably rapidly reimmobilized by the microbes, inhabiting the litter, or by roots. The fauna themselves can immobilize nitrogen into animal tissues, but this amount in the microarthropods is very small compared with that in the litter and the microbial community. Thus, microarthropod feeding

activities on microflora probably result in rapid recycling of most nitrogen within the system (Seastedt, 1984). In this respect the effect of fungal browsers and fungal grazers can be opposite: grazers feed on the total fungal hyphae, thereby utilizing and mobilizing all the nitrogen stored in the fungal biomass. Especially in N-limited environments with large amounts of senescent hyphae, this can have a stimulating effect on the growth of the remaining active hyphae, thereby enhancing the decomposition rate. In contrast, the fungal browsers or piercers, that only ingest the cell content of the hyphae, leave a considerable amount of nitrogen immobilized in the dead hyphal cell walls. This may result in a retardation of the fungal growth and eventually a decrease in nitrogen mineralization (Siepel and Maaskamp, 1994).

In total, a 30 % contribution of the soil fauna to the soil nitrogen mineralization may exist, as calculated for various natural ecosystems as well as agroecosystems by Verhoef and Brussaard (1990).

Levels of resolution in soil ecosystem research

My research target was to study and, if possible, to quantify the effect of microarthropods on the decomposition of organic matter and the mineralization of nitrogen in agricultural soils, as part of the Dutch Programme on Soil Ecology of Arable Farming Systems. The sampling program had already started and the set-up of the sampling scheme had been assessed, when I joined the research group. I realized, that by field sampling only the effects of environmental factors on the soil fauna could be estimated. To understand the effects of microarthropods on soil processes, or rather their role in the food web, the microarthropod effects on the environment should be studied as well. But here we meet the largest problem in all soil studies, much less prominent in above-ground ecosystems: the impossibility of direct observations. Microarthropods are indeed much easier to handle then large mammals, but they live in the darkness of small soil pores. The soil was, is and will always remain a big black box, that can only be analyzed in a reliable way by destruction, no matter if it considers a chemical, a physical or a biological analysis. We can only manipulate the input and subsequently analyze the output of the soil.

One way to overcome this difficulty is to increase the resolution level in laboratory experiments by using small amounts of sterilized soil, inoculated with known numbers of specific species of the functional groups we want to study and incubated under controlled conditions in so-called microcosms. This way nitrogen mineralization and soil metabolism can be monitored over time. These experiments give detailed information on very specific elements of the food web (the interaction between two species) under very unnatural conditions. Relationships of the studied species with organisms that are not included in the experiment, and that might affect the dynamics of the target species, not by a trophic relationship, but in an alternative way, for instance by competition, symbiosis, commensalism or by affecting the environment, will then be missed.

The soil ecosystem can be conceptualized as a hierarchical structure with dimensions of time and space. Examples of processes affected by spatial and temporal heterogeneity are denitrification and the sequential development of organisms on fresh substrate. Also pulsed events like freeze/thaw and wet/dry cycles have considerable effect on microbial activity (Hunt et al., 1989; Bloem et al., 1992). Therefore, a useful tool for the integration of knowledge gained at the microcosm and the field level should be experiments with a less deterministic approach, a compromise between the microcosm and the field scale. On this scale, local manipulation of the soil fauna is possible in so-called mesocosms, larger units of soil in which a normally functioning soil ecosystem can be constructed, while climate conditions and nutrient levels can be manipulated. By starting off with sterilized soil, specific functional or taxonomic groups can be added by reinoculation or excluded. Much less disturbance of the soil physical properties and of the soil ecosystem can be achieved in experiments using litterbags or litterboxes. Litterbags are bags of various sizes, made of gauze with varying mesh sizes, containing a known amount of some kind of litter. When these bags are buried in or placed on the soil surface, the mesh size determines which organisms are admitted. In this case the climate conditions can not be manipulated, at least not at the litterbag level. Both types of exclusion experiments (by selective re-inoculation or by selective admission) can serve to study the effects of specific faunal groups on the functioning of the otherwise undisturbed soil food web. It should be kept in mind, that selection of groups through differences in mesh size, or hence body width, does not correspond with the aggregation of species into functional groups.

Outline of the thesis

When I started this thesis study, like most starting researchers, I had very ambitious plans. To assess the effect of microarthropods on soil processes as well as the effect of the soil environment on the functioning of the microarthropods, I had devised a program of experiments including three resolution levels (Table 2).

Table 2: Setup of experiments.

Resolution level	Experimental setup	Studied variables
Micro	Gnotobiotic microcosm experiment	Mineralization rates, population dynamical effects, species interactions: food preference, competition, predation, grazing effects
Meso	Litterbag experiment	Decomposition rate, grazing effects, predation effects, litter quality, management
Macro (field)	Field sampling	Management effects, soil properties, litter quality

The second chapter of this thesis describes the microcosm part. It is a study on possible relations (competition, predation) between two functional groups of

the same trophic level: the bacterivorous anoetid mite *Histiostoma litorale* and the amoeba *Acanthamoeba* spec.. It also describes their effect on the mineralization of C and N in Lovinkhoeve soil amended with lucerne meal. Chapter 3 describes the meso-scale litterbag work; it is about soil mesofauna dynamics in relation to wheat residue decomposition and nitrogen mineralization in buried litterbags. This litterbag experiment was carried out in 2 x 5 meter plots, filled with Lovinkhoeve soil and describes the effects of the exclusion of microarthropods on the decomposition and the mineralization of crop residues, in this case wheat straw. Chapter 4 presents the microarthropod results of the two year field sampling program of the two arable farming systems. The management effects on the population dynamics of the seven functional groups of microarthropods are discussed, and a comparison is made with other food web samplings of agricultural soils. In Chapter 5 a field program including a variety of soil ecosystems is described, presenting the biomass differences of microarthropod functional groups in soils under different land use (grassland, forest, and wheat field) in relation to the quality, the amount and the dynamics of the input of organic matter to the soil. Also the relation to the pore size distribution in a sandy a loam and a clay soil under grassland is investigated.

In the last chapter, the General Discussion, I will present a synthesis of all results and discuss them in view of current literature, ending with some general conclusions.

CHAPTER 2

THE EFFECTS OF BACTERIVOROUS MITES AND AMOEBAE ON MINERALIZATION IN A DETRITAL BASED BELOW-GROUND FOOD WEB; MICROCOSM EXPERIMENT AND SIMULATION OF INTERACTIONS

SUMMARY

The effects of two different bacterial grazers, an amoeba (*Acanthamoeba* spec.) and an anoetid mite (*Histiostoma litorale*), separate and in combination, on C- and N mineralization were compared in a microcosm experiment with sterilized silt loam soil, reinoculated with a bacteria. Lucerne meal was added as substrate. The aim of the experiment was to separate the direct contribution of the mites to the mineralization from possible indirect effects, such as enhancement of microbial grazing by protozoa. The results showed a higher nitrogen mineralization in the amoebae only treatment, compared to the mite treatment. From the comparison between the mite (BM) and the mite plus amoeba treatment (BMP), it could be concluded that the mite population had no measurable direct or indirect effect on the nitrogen mineralization, even though the N use efficiency of the mites was lower. No significant differences were found in the overall oxygen consumption, so no grazing effect on the microbial activity could be assessed. Model calculations showed that the low contribution of the mites to the nitrogen mineralization was due to a lower production rate, compared to that of the amoebae. Bacterial production in the protozoa treatments was 30 times the production in the mite only treatment.

INTRODUCTION

The effects of microbial grazers on mineralization of organic matter in soils have been widely investigated. Stout (1980), Coleman (1986) and Kuikman et al. (1990), assessed a marked increase in respiration and nutrient turnover of bacterial populations, when grazed by protozoa. Bacterial grazing by nematodes has been reported to lead to variable results. Anderson et al. (1981) reported an acceleration, but not an increase of total N mineralization in the presence of nematodes.

Comparable results were obtained by Bouwman and Zwart (1994) in silt loam soil. Woods et al. (1982) however, found a decreased nitrogen mineralization when nematodes were present. Brussaard et al. (1995) found the effect to depend on the presence of predators of the nematodes. A comparable conclusion had been drawn by Bouwman et al. (1994) from their study on the effects of nematophagous fungi as "predators".

Several different effects of microarthropods on the decomposition of organic matter have been reported thus far. Apart from the grazing effect on the bacterial and fungal population, comminution and mixing of the organic matter may be important, as well as an enhanced dispersal of microorganisms by the microarthropods (Visser, 1985; Seastedt, 1984). Santos et al. (1981) found an increased decomposition rate of buried litter with microarthropods, compared to insecticide treated buried litter. Brussaard et al. (1991) studied microbial grazing by *Histiostoma litorale*, a bacterivorous mite and *Acrobeloides buetschlii*, a bacterivorous nematode, in microcosms containing sterilized soil, amended with lucerne meal and inoculated with a soil suspension, containing a mix of bacteria and protozoa. Nematodes, mites and a combination of these two bacterivores were introduced to the microcosms in three different treatments, and a control treatment was included without mites or nematodes. N mineralization increased significantly in the presence of nematodes and of mites. Whether this increase was a result of bacterial grazing by the mesofauna only could not be concluded, since the sterile soil was inoculated with bacteria at the start of the experiment, implicating a simultaneous bacterial colonization process of the soil. This could mean that the positive effect of mites and nematodes found on the N mineralization was possibly a consequence of enhanced dispersal of bacteria and protozoa by the mesofauna. However, flagellates and amoebae showed much different population dynamics than the bacteria, possibly caused by nematodes, carrying and dispersing protozoa. This variation of the protozoan populations among the treatments, as well as the microbial colonization process, were major drawbacks of this experiment. The conclusion that the bacterivorous mite *Histiostoma litorale* enhanced N mineralization therefore needed further research.

The aim of the present experiment was to distinguish between the (primary) direct effect of bacterial grazing by mites on the N mineralization and a possible stimulating effect of mites on the protozoa. This secondary mite-effect could result from an enhancement of the amoebal colonization rate of the organic matter. This effect is conceivable, since amoebae, although very numerous, are the least mobile protozoa in soil (Kuikman et al., 1990). An other possible effect, hypothesized by Brussaard et al. (1991), could be that amoebal feeding rates are increased in the water currents that are caused by the movements of the filter-feeding chelicerae of the anoetid mites. A third hypothesis was raised by finding in a pilot experiment of a particular amoebal species that was always found in great numbers in the presence of mites from (non-sterilized) culture plates, indicating that there might be a certain, perhaps symbiotic relationship between this amoeba and these mites.

In the present experiment, four treatments were compared: microcosms with bacteria and protozoa (BP), bacteria and mites (BM), bacteria, mites and protozoa (BMP) and control microcosms, i.e. without any organisms, but with substrate added (C). In order to control the protozoan population the experiment had to be performed under gnotobiotic conditions. Because the aim of this experiment was to assess the mutual effects of representatives of two different functional groups of the same trophic level, flagellates had to be excluded, as flagellates graze bacteria too, but are themselves prey to amoebae. The genus *Acanthamoeba*, previously used by Anderson et al. (1978), was chosen for our experiments, because these amoebae are common soil protozoa, relatively large in size and easily recognizable. The BP treatment in this experiment can be compared with control treatments in the experiments previously mentioned, in which a soil microbial inoculum was added, containing both bacteria and protozoa. The BM treatment was included to assess the importance of the primary effect of bacterial grazing by mites alone on C- and N mineralization. A prerequisite of the experiment was that the mites used had to be free of protozoa. The control treatment (C) was included to check if the sterilization of the soil was complete and if any contamination of the microcosms would occur during the experiment due to aeration of the containers or the sampling methods used.

The following hypotheses were postulated:

1. In case a stimulating effect of mites on N mineralization exists through the increased activity of the amoebae, more nitrogen is expected to be mineralized in the BMP treatment then in the BP treatment.
2. A quantitative difference between effects on nitrogen mineralization of grazing by a growing population of bacterivorous mites only and of a population of amoebae only, will show from the increase in nitrogen content of the soil in the BM treatment compared to the BP treatment.
3. If different microbivores have different effects on the bacterial activity, and thereby on C-metabolism, this should be reflected in the O_2 consumption.
4. An increase in the population of *Acanthamoeba* spec. in the BMP treatment, compared to the BP treatment, will proof the existence of a certain stimulating effect of these mites on these amoebae.

Finally, the pools and flows of C and N among organisms were estimated, using the model of Hunt et al. (1987), in an attempt to interpret the present results in terms of microbial activity. Using the measured increase in biomass C and N of protozoa and mites, as well as the measured increase of soil mineral N and the total C respiration over the experimental period as inputs, an estimation of the microbial production could be calculated, that is hard to obtain otherwise.

MATERIALS AND METHODS

The microcosms

The experiment was carried out in 0.5 l plastic containers with air-tight lids, with a septum to allow gas sampling. The soil used was a calcareous silt loam (pH-KCl: 7.3) from a fallow field at the Lovinkhoeve experimental farm, Marknesse. Organic matter content was 2.6%. This soil was air-dried, sieved twice (4.5 mm) and dried further to 5% (w/w) water content. The vials contained 236.5 g(± 0.05) soil (225 g dry soil, 5% water) each. For each vial 0.445 g (2 g kg^{-1}) lucerne meal was weighed. The C/N ratio of the lucerne meal was 13. Both soil and lucerne meal were sterilized with 4 dosages of 1.5 Mrad gamma-irradiation and stored at 0°C.

The organisms

To prepare a soil bacterial suspension 350 g of fresh Lovinkhoeve soil was mixed with 350 ml tap water for 1 minute in a blender. This suspension was filtered through paper first and subsequently through a sterile 1.2 µm filter to remove protozoa, fungal spores and nematode eggs. The filtrate was added to 0.4% proteose peptone and 0.4% glucose amended "Prescott & James" solution (Prescott and James, 1955), amended with 0.1 % vishniac (abbreviated as P.J.V.) and cultured 24 hours at 20°C, rotating at 125 r.p.m.. The suspension was centrifuged (3660 rpm, 30 minutes), washed with sterile water and the bacterial density was estimated with a Bürker Türk counting chamber. The inoculation density was aimed at 10^5 bacteria g^{-1}soil. To increase the water content of the soil from 5% to 15% (w.w.), 22.5 ml of a bacterial suspension of 10^6 bacteria per ml had to be added. Bacterial inoculation of the sterilized containers took place 14 days in advance of the experiment (day -14). By means of a calibrated sterile pump the suspension was added to the surface of the soil in the containers. These were incubated at a temperature regime of 10 hours at 10°C and 14 hours 14°C, in the dark. This temperature regime was chosen to imitate Dutch spring conditions and was maintained during the rest of the experiment. After one day (at day -13) all the vials were mixed to improve the distribution of the bacterial suspension through the soil. By inoculating the containers with bacteria 14 days in advance of the experiment the moisture content as well as the bacterial population was stabilized and colonization effects avoided (Huhta et al., 1989). Equally important was the microbial mineralization of the biomass, killed by the gamma-radiation. This caused a mineral N flush that would otherwise have interfered with the mineralization of the substrate, added at the start of the experiment. To the control pots 22.5 ml of sterilized water was added at day -14. Otherwise these vials were treated equally. During the first two weeks (day -14 to 0) gas samples were taken twice to monitor

the mineralization of the dead biomass. After gas-sampling all vials were aerated in a laminar-flow cabinet for 1 hour to prevent anoxic conditions.

Acanthamoeba spec. was cultured from a stock culture. First *Pseudomonas fluorescens*, used as food source, was cultured on agar-plates, which were soaked in P.J.V. for half a day and the suspension divided over 10 Petri-dishes. The *Acanthamoeba* stock fluid was gently stirred and a few drops were added to each Petri-dish. These were incubated at 20 °C. Four times 250 ml 0.4% proteose peptone and 0.4% glucose amended P.J.V. were inoculated with *Pseudomonas fluorescens* and cultured overnight at 20°C. These cultures were centrifuged (1 h., 3660 r.p.m., 10°C) and the pellets resuspended in P.J.V. to 1800 ml total volume. This was then divided over 9 siliconized 1 l Fernbach flasks which were each inoculated with the contents of one *Acanthamoeba* Petri-dish and cultured for 6 days at 20°C. Protozoan inoculation density was aimed at 10^3 cells/g dry soil. At day 0 the amoebal density of the suspension was assessed in a Bürker Türk counting chamber and subsequently diluted to ca. 2.25×10^4 cells per ml with sterile water. Ten ml of this suspension was pipetted to the surface of the soil of the BP and BMP treatment containers.

Histiostoma litorale was cultured on 2% water-agar plates. Adult females were collected and placed in small (3 cm diameter) Petri-dishes containing 100 mg l^{-1} Fungizone- Jager's solution (Jager's solution (6150 mg l^{-1}): 400 mg neomycin + 200 mg streptomycin + 15 mg vendarcin in 100 ml de-mineralized water) each for one night at 4°C. The next day the females were rinsed with sterile water and placed on sterile Actidion-agar plates (50 mg l^{-1}) and stored 72 hours at 14°C. These females were transferred with a sterile preparation needle to clean 2% water-agar plates and left one night at room temperature. Afterwards the plates were checked for egg deposition and the females removed. Mites hatched from these eggs were reared at room temperature till adulthood (7-10 days) and subsequently divided over more sterile agar plates. Before the experiment started the mites were sampled to check for the presence of protozoa in small Petri-dishes, filled with *Pseudomonas fluorescens* suspension. These were kept at room temperature for 3 days and microscopically checked for protozoa. At day -4 before the start of the experiment 20 adult mites at a time were placed on small Actidion-agar plates. At day 0 the 20 mites were washed from these plates with 4 ml sterile water and carefully pipetted on to the surface of the soil in each BM and BMP pot.

Experimental setup

At day 0 all vials were emptied one by one in a sterile tray in a laminar flow cabinet. Lucerne meal and a volume of sterile water were added to obtain the intended 80% dry weight content of the soil. After careful mixing of the soil with a sterile spoon, the containers were refilled. Subsequently 10 ml of amoeba suspension was pipetted to the surface of the soil in the BP and BMP pots and 20 mites in 4 ml water were pipetted to each BM and BMP pot. All containers were incubated in darkness at 10 hours 10°C and 14 hours 14°C.

Destructive sampling of 3 replicates per treatment took place at day 0, 1, 3, 5, 7, 10, 14, 17, 21, 24, 28, 35, 42 and 57. For the protozoan counts, 40 g of soil per container was added up to 200 ml with P.J.V. in a graduated cylinder, sealed with Parafilm and mixed by turning it upside down several times. Further mixing took place in an electric blender for 30 seconds. Two ml of the suspension was pipetted to a test tube and 4 ml of P.J.V. was added. Amoebal numbers were established using a modified MPN method of Darbyshire et al. (1974) using 96-wells microtiter plates, a 4-fold dilution series in P.J.V. and washed *Pseudomonas fluorescence* as a food source. After one week of incubation at 20°C in dark all trays were screened for flagellates and amoebae at 250x magnification using an inverted light microscope and screened again one week later. Mites were extracted using a modified high-gradient extractor (Andrén, 1985). Two 6 cm diameter sieves were filled with soil from the containers, weighed and extracted in 10 days. Mites were collected in cups containing saturated picric acid solution. Mites were counted under a preparation microscope.

To determine the mineral nitrogen content of the soil 80 g of soil per vial was mixed with 200 ml 1 N KCl and shaken for 1 hour. This suspension was paper-filtered and the NH_4^+ and the NO_3^- content of the extract was determined colorimetrically (Vierveijzer et al., 1979). Dry matter content of the soil was determined by oven-drying of a soil sub-sample (18 hr., 105°C).

For the (non-destructive) oxygen consumption measurements 5 vials of each treatment were chosen randomly at each sampling date. Oxygen content of the 5 ml air samples was measured by gas-chromatography. The C respiration was calculated by multiplying the oxygen consumption by 0.375.

The N- and C mineralization and the log-transformed numbers of protozoa and mites were analyzed by analysis of variance (ANOVA).

Food web model calculations of pools and flows of C and N

C- and N pools and flows were calculated using the food web model of Hunt et al. (1987):

Fout!

N_m = nitrogen mineralization rate (mg N/ kg/ day)
E_{ass} = assimilation efficiency
E_{pro} = production efficiency
R_{prey} = C/N ratio of the "prey"
R_{pred} = C/N ratio of the "predator"
F = consumption rate (mg C/ kg/ day)

ERRATA

At page 30 the following equation is missing:

1) $$N_m = E_{ass} * \left(\frac{1}{R_{prey}} - \frac{E_{pro}}{R_{pred}} \right) * F$$

At page 31 the following equations are missing:

The Hunt et al. (1987) model .....

2) $$F = \frac{D_{nat} B + P}{E_{ass} E_{prod}}$$

....., De Ruiter et al. (1993a) extended the model of Hunt et al.....

3) $$F = \frac{D_{nat} B + P + dB/dt}{E_{ass} E_{prod}}$$

..... Therefore the equation for those groups could be simplified as:

4) $$F = \frac{dB/dt}{E_{ass} E_{prod}}$$

The Hunt et al. (1987) model uses a mean annual consumption, assuming that in a steady-state situation the consumption and subsequent biomass production compensates for losses by natural mortality and predation:

Fout!

Following O'Neill (1969), De Ruiter et al. (1993a) extended the model of Hunt et al. (1987) by including population dynamics:

Fout!

D_{nat} = natural mortality (/ day)
B = biomass-C (mg C/ kg)
P = mortality due to predation (mg C/ kg/ day)
dB/dt = mean daily biomass increase (mg C/ kg/ day)

Since, in the present experiment, only the experimental growth phase was considered , we assumed D_{nat} to be 0; dB/dt is the observed mean daily biomass increase. Assuming no predation on amoebae, P was also 0, for both mites and amoebae. Therefore the equation for those groups could be simplified as:

Fout!

A steady-state could be assumed for the bacterial numbers, because bacterial counts at day 28 were not significantly different from day 0 in any of the treatments (unpublished epifluorescence microscopy results, after Bloem & Bolhuis 1990), so we may assume bacterial grazing to be compensated for by bacterial production. Respiration was calculated as follows:

$$Respiration = E_{ass}\ E_{prod}\ F$$

Parameters used for the calculations were adopted mainly from Didden et al. (1994) (Table 3). Net bacterial N mineralization and C respiration was estimated by subtracting the calculated mite and amoebal C respiration and N mineralization from the measured values. Bacterial production was calculated by adding the mite and the amoebal consumption.

Table 3: Parameters used for model calculations after [1] Didden et al. (1994), [2]Zwart (pers. comm.), [3] Hassink (1994) and [4]De Ruiter et al. (1993a).

	C/N	E_{ass}	E_{prod}
Amoebae	5[2]	0.95[1]	0.38[1]
Bacteria	5[3]	1[1]	0.3[1]
Mites	8[1]	0.5[1]	0.18[1] - 0.35[4]

RESULTS

Protozoa

The *Acanthamoeba* population increased until day 35 (Fig 3). ANOVA (time * treatment) showed no significant difference between the BP and BMP treatment over the whole experimental period (Table 4). From day 14 onward a contamination by *Vahlkampfia* spec., a small (18-37 µm), mobile amoeba (Page, 1988), was spotted in all treatments except the controls. Since all amoebae are assumed to be of the same trophic level, *Acanthamoeba* spec. and *Vahlkampfia* spec. numbers were totaled. The total amoeba numbers showed no significant differences (ANOVA) among the BP- and the BMP treatment either (Table 4).

The amoebal C/N ratio is estimated to be 5 (K. B. Zwart, pers. comm.) and the biomass-C of one *Acanthamoeba polyfaga* cell is assumed to be $6*10^{-4}$ µg (Hunt et al., 1984). This means that at day 57 in the BMP treatment the C pool in the *Acanthamoeba* population was calculated to be to 27.0 mg C/kg dry soil and 13.6 mg C/kg dry soil in the BP treatment. The *Acanthamoeba* N pool amounted to 5.4 mg N/kg soil in the BMP treatment and 2.7 mg N/kg soil in the BP treatment. If we assume the biomass of *Acanthamoeba* spec. and *Vahlkampfia* spec. to be comparable (Page, 1988), than total amoebal biomass-C in BM was 9.44 mg C/kg, in BMP 36.68 mg C/kg and in BP 30.53 mg C/kg. Total amoebal biomass-N was in BM 1.88 mg N/kg, in BMP 7.34 mg N/kg and in BP 6.11 mg N/kg.

Flagellate contamination was found in all three treatments from day 10 onwards. Their numbers did not differ significantly between the three treatments (Table 4). Flagellate biomass was very low, compared to amoebal biomass (BM: 0.032 mg C/kg, BMP: 0.014 mg C/kg, BP: 0.07 mg C/kg at day 57) and therefore was ignored in further calculations. Comparative numbers of microcosms were contaminated with either flagellates or *Vahlkampfia* in all three treatments, with exception of the control, which remained sterile throughout the experiment.

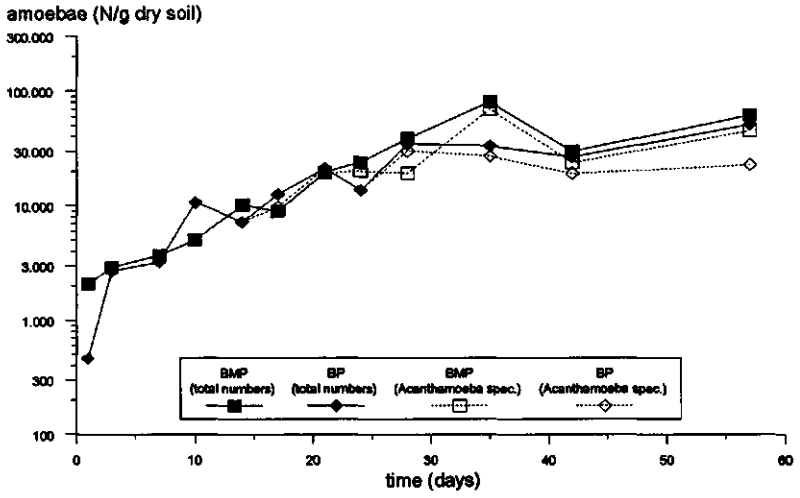


Fig. 3: Mean estimated densities (MPN-method, n=3) of Acanthamoeba spec. and total density of amoebae (Acanthamoeba spec. plus Vahlkampfia spec.) in the treatment with bacteria, mites and protozoa (BMP) and the treatment with only bacteria and protozoa (BP).

Table 4: ANOVA on log transformed numbers of organisms: F probability

	Time	Treatment		Time * Treatment
		Protozoa	*Mites*	
Acanthamoeba spec.	< 0.001	-	0.166	0.653
Vahlkampfia spec.	< 0.001	-	0.723	0.002
Total amoebae	< 0.001	-	0.144	0.600
Flagellates	< 0.001	-	0.698	0.203
Histiostoma litorale	< 0.001	0.222	-	0.121

Mites

The mite *Histiostoma litorale* exponentially increased in number from 1 mite per 100 g dry weight of soil at day 1 to over 400 per 100 g dry weight at day 28 (Figure 4). After this day the population growth rate decreased. At day 57 they numbered 1215 per 100 g dry soil in BM and 1771 per 100 g dry soil in BMP. Analysis of variance on the log-transformed data revealed no significant difference

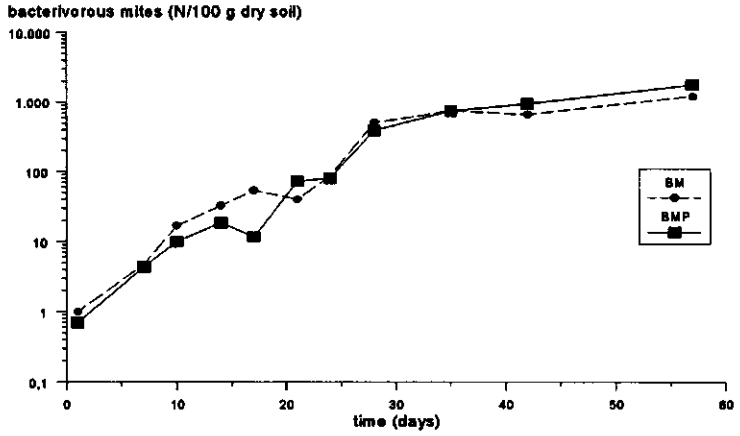


Fig. 4: Mean densities of Histiostoma litorale (n=3) in the treatment with only bacteria and mites (BM) and in the treatment with bacteria, mites and protozoa (BMP).

(Table 4). No contamination with other mite species was found nor were ever any mites found in the BP treatment. No hypopi or deutonymphs, indicative of unfavorable environmental conditions, were found.
The biomass-C of an average adult female *Histiostoma litorale* amounts to 0.0425 µg. Her C/N ratio is ca. 8 (Edwards, 1967; Brussaard et al., 1990). This means that at day 57 mite biomass-C amounted to 0.516 mg C/kg dry soil in the BM treatment and 0.753 mg C/kg in the BMP treatment. The amount of mite biomass-N in the BM treatment was 0.065 mg N/kg and 0.094 mg N/kg in the BMP treatment.

Nitrogen mineralization

Total mineral nitrogen content at day 0 was 24.7 mg N/kg dry soil. Mineralization of the soil biomass killed by gamma-ray sterilization was 9.4 mg N/kg, calculated from the difference between the N content of the control vials and the bacteria-inoculated vials before adding the lucerne meal at day 0.

A major increase in soil nitrogen started at day 3 (Figure 5). From that moment on, total nitrogen content of the soil was significantly lower in the BM treatment, then in the BP and BMP treatment (Table 5). There was no significant difference between the BP and the BMP treatment. At the end of the experiment, at day 57, mineral N content of the soil had increased by 34.3 mg/ kg dry soil in the BM pots, 45.0 mg/ kg dry soil in the BMP pots and 46.3 mg/ kg dry soil in the BP pots.

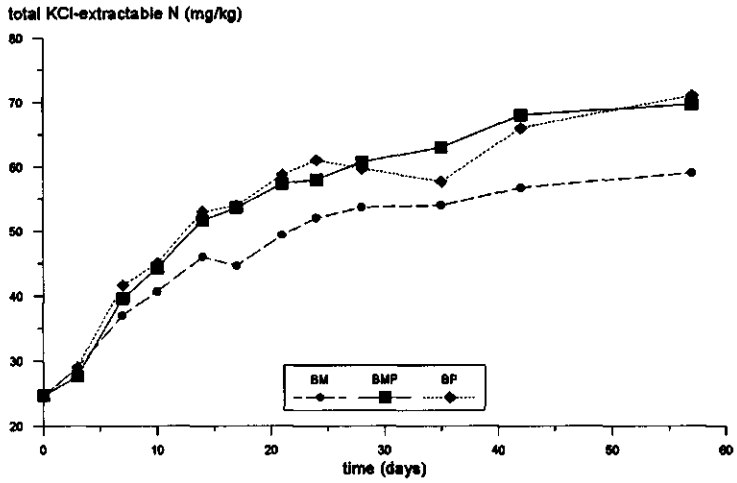


Fig. 5: Mean nitrogen mineralization (n=3) in the treatment with only bacteria and mites (BM), the treatment with bacteria, mites and protozoa (BMP) and the treatment with only bacteria and protozoa (BP).The BMP treatment does not differ significantly from the BP treatment; the BM treatment differs significantly from the other two treatments from day 15 onwards ($P < 0.05$).

Table 5: ANOVA on nitrogen mineralization and oxygen consumption: F probability.

	Time	Treatment	Time * Treatment
Soil mineral N	< 0.001	< 0.001	0.002
Cumulative O_2 consumption	< 0.001	0.160	0.043

Oxygen consumption

Cumulative oxygen consumption in the vials did not show any significant difference among the three treatments (Figure 6, Table 5). The oxygen consumption showed a flush immediately after the substrate was added. Total respired CO_2-C at day 57 amounted in the BM treatment to 319 mg C/kg dry soil, in the BMP treatment to 337 mg C/kg dry soil and in the BP treatment to 314 mg C/kg dry soil.

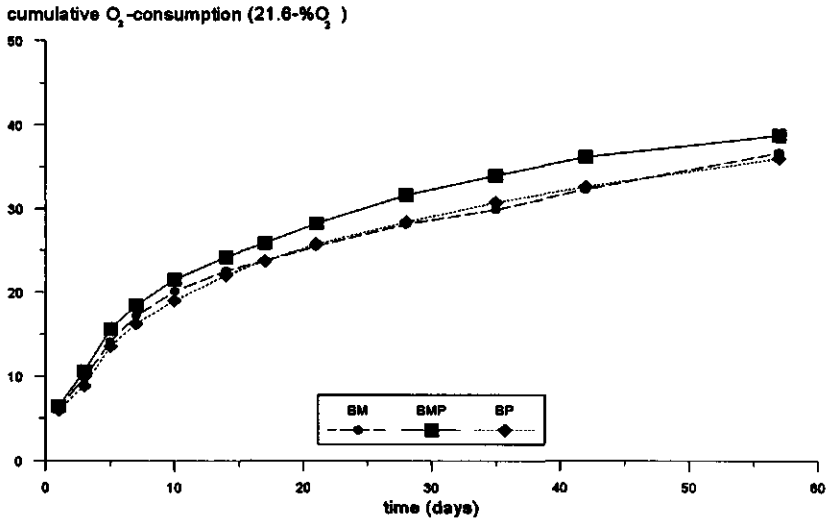


Fig. 6: Average cumulative oxygen consumption per microcosm (n=5) in the treatment with only bacteria and mites (BM), the treatment with bacteria, mites and protozoa (BMP) and the treatment with only bacteria and protozoa (BP).

Table 6: Model calculations after Hunt et al. (1987) on the experimental data (days 0 - 24).

Treatment	Functional group	Biomass production (N and C)		Respiration (C)	Mineralization (N)
		(mg N/kg dry soil/ day)	(mg C/kg dry soil/ day)	(mg C/kg dry soil/ day)	(mg N/kg dry soil/ day)
BM					
	Bacteria	0.013	0.065	8.74	1.035
	Bacterivorous mites	0.001	0.008	0.023	0.0054
BP					
	Bacteria	0.30	1.51	8.38	1.08
	Amoebae	0.12	0.58	0.94	0.18
BMP					
	Bacteria	0.38	1.90	9.06	1.07
	Amoebae	0.14	0.70	1.15	0.22
	Bacterivorous mites	0.001	0.006	0.017	0.0041

C and N pools and flows

The pools and flows of C and N within the microcosms were calculated only for the first 4 weeks of the experiment, because the exponential growth of the mites had halted by that time, indicating mite mortality or a decreased growth rate due to shortage of food or self limitation. Except for bacteria, the biomass of the different organisms at day 0 was assumed to be 0 mg/kg dry soil, since inoculation densities were below detection limits.

Table 6 shows the C- and N pools and flows in the three different treatments as calculated by the food web model of Hunt et al. (1987). As no evidence of predation on amoebae was detected, 0 as value for both mites and amoebae was a justified assumption.

Calculated bacterial production in the BM treatment was only 3 to 4% of the bacterial production in both amoebae treatments (BP and BMP). Only amoebae significantly enhanced nitrogen mineralization (14- 17% of total N mineralization). This was not due to enhanced bacterial N mineralization, but to amoebal activity only. The calculated bacterial N mineralization was remarkably constant. C mineralization or respiration however, showed slight differences: bacterial respiration was lowest in the BP treatment and highest in the BMP treatment.

DISCUSSION

Population dynamics

No increasing effect of mites on amoebal numbers, either as a result of the enhanced dispersal of *Acanthamoeba* spec. or by enhancement of the amoebal feeding rate, as suggested by Brussaard et al. (1991), was found. The increased amoebal densities in the mite treatments in the experiment of Brussaard et al. (1991) probably were a slime mold contamination (Mycetozoa), that may have caused the emergence of hypopi, the non-feeding larval instar of *H. litorale*, due to food limitation resulting from competition by the molds. In the present experiment no Mycetozoa were detected.

No effect of the presence of amoebae on the population dynamics of the mites was found. The amoebae in our experiment were free living protozoans, probably feeding in soil pores inaccessible to bacterivorous mites or even nematodes, so a negative effect due to competition was not likely to be found (Foster and Dormaar, 1991; Alphei et al., 1996).

Nitrogen mineralization

In all three treatments net N mineralization lagged a few days behind oxygen consumption, probably due to immobilization of N by actively growing bacteria.

Net immobilization of nitrogen by bacteria could not be assessed, probably due to the low C/N ratio of the substrate (± 13). The significant difference between the N mineralization in the BM treatment and the BP and BMP treatments explicitly showed the stimulating effect of the amoebae.

Alphei et al. (1996) found protozoa (a mixed population of amoebae, flagellates and ciliates) to increase total N in leachates from planted microcosms and this effect was attributed to a decreased microbial competition due to predation by protozoa on the microbes in general, benefiting especially the nitrifying bacteria. In the non-rhizosphere soil both protozoa and nematodes caused a decrease in the extractable mineral N content after 16 weeks, compared to the control (with only bacteria). This, however, could have been an effect of leaching: as more N was mineralized, and therefore mobilized, this N was leached. Persson (1979) studied the effect of grazing by a mixed population of microarthropods in pine needle-microcosms. Like in the present experiment, he neither found a difference in CO_2 evolution rate, but N mineralization was significantly enhanced in the presence of microarthropods. In the artificial soil system we studied, only the amoebae had such an impact, for no measurable effect of the mite *Histiostoma litorale* on N mineralization was found. This only proofs, however, that this functional group of bacterivorous mites, does not show a measurable effects on N mineralization, but a complete microarthropod population, including much more trophic levels can affect nitrogen mineralization through other mechanisms, as for instance by controlling other grazers, like nematodes (Santos and Whitford, 1981).

Oxygen consumption

Oxygen consumption and CO_2 production are assumed to relate directly to the soil metabolism. Oxygen consumption is usually regarded as a measure for soil microbial activity, since microorganisms form the main portion of the soil biomass. Since we did not find significant differences between the treatments, we conclude that the bacterial activity was not affected by mites, nor by amoebae. This is in agreement with the findings of Bouwman and Zwart (1994), who found no significant difference in C mineralization between a protozoan, a nematode and a combined treatment. Alphei et al. (1996) found no effects on basal respiration either, but a significant effect of protozoa on specific bacterial respiration was found, despite reduced bacterial biomass. Oxygen consumption therefore bears no necessary relation with bacterial numbers or biomass. An unchanged oxygen consumption might be related to a decreased bacterial population, exhibiting a higher activity.

C- and N fluxes and pools

The assumptions, on which the calculations of the C- and N fluxes and pools are based, such as averaging all population growth rates over time, or the unchanging microbial biomass, may not be fully justified, and this should be kept in mind when discussing the results presented in Table 6. In the present experiment direct counting exerted very large standard deviations, so that no statistical test could produce any significant difference, either in time or between treatments. Perhaps the assessment of the microbial biomass with more advanced techniques, like for instance confocal laser scan microscopy, could have shed more light on the actual development of the microbial population.

Nevertheless, some general conclusions can be drawn from the calculations: Table 6 shows that the contribution of the amoebae to the N mineralization is 5 times the mite contribution. The bacterial N mineralization was 5 to 6 times the amoebal contribution, however. This bacterial contribution was not notably affected by the presence of either one of the grazers. However, the N efficiency (percentage of N immobilized per unit of N mineralized) of the mites was lower than that of the amoebae (18.5% vs. 66.7%, calculated from the BM and the BP treatment, respectively). Since the mite production was too low ever to reach a total biomass equal to that of the amoebae, this difference could never noticeably affect the net N mineralization.

The most striking effects showed in the bacterial production. If the assumption, that bacterial grazing is completely compensated for by bacterial production is justified, we must conclude that the bacterial production needed to compensate grazing in the treatments with protozoa was 30 times the production in the BM treatment. However, this increased activity was not reflected in the bacterial N mineralization, nor in the respiration. We could not find a direct relation between bacterial consumption (equals production) and activity (respiration). An explanation of this may lie in the observation that the bacterial turnover, i.e. the ratio between bacterial-C production and total bacterial-C pool (= ca. 66 mg C/kg dry soil on average), was very low, resulting in a low susceptibility of the O_2 consumption to any soil fauna treatment. A more satisfactory explanation may be that bacterial activity, as estimated from the soil respiration flush, was highest in the first few days after the substrate amendment, when grazing pressure was lowest. The bacterial grazing can be expected to be low at the start, and to increase as grazer populations increase. This too renders total O_2 consumption an inadequate tool for measuring grazing effects. After four weeks, however, bacterial C mineralization as well as total soil respiration was highest in the BMP treatment. This may indicate a relatively larger secondary effect of mites on bacterial respiration than of amoebae, particularly in regard of their low total biomass.

It may be apparent from the above, that microcosms can be a helpful tool to study model ecosystems, but microcosm studies on possible direct and indirect effects of the soil fauna only have added value over a "black box" approach, if population dynamics of all organisms, also non-target organisms, are closely

monitored, since any deviation from the intended food web structure may have important implications at the process level. It may also help to explain why seemingly similar microcosm experiments sometimes show contradictory results.

CHAPTER 3

SOIL MESOFAUNA DYNAMICS, WHEAT RESIDUE DECOMPOSITION AND NITROGEN MINERALIZATION IN BURIED LITTERBAGS

SUMMARY

The effect of soil microarthropods and enchytraeids on the decomposition of wheat straw in buried litterbags was studied by selective admission and exclusion. Litterbags with 20 µm mesh size admitted nematodes, but excluded microarthropods, although temporarily. After 27 weeks of incubation, part of these litterbags were colonized, probably through egg-deposition of mainly fungivorous Collembola and mites. When litterbags with a complete microarthropod community (1.5 mm mesh size) were compared to litterbags with strongly reduced microarthropod numbers (20 µm mesh size), no differences between decomposition rates were found. However, in colonized 20 µm mesh bags, we found reduced decomposition rates compared to the coarse mesh litterbags, probably due to overgrazing of the fungal population by large numbers of fungivorous microarthropods. These large numbers might be caused by the absence of predators. Extraction of microarthropods as well as enchytraeids and nematodes from the coarse mesh litterbags showed a distinct succession during decomposition. The decomposition process was dominated in the first phase by bacterivorous nematodes, nematophagous and bacterivorous mites, and in the later phase by fungivorous nematodes, fungivorous and omnivorous mites and Collembola, and predatory mites. This succession is indicative of a sequence from bacterial to fungal dominated decomposition of the buried organic matter. The results indicate that the decomposition rate is predator-controlled.

INTRODUCTION

Crop residues in the field are an important source of N, necessary for crop production. Mechanistic understanding of the decomposition process will give clues to predict the dynamics of N mineralization from organic matter under field conditions. This is important to achieve optimal fertilization that will minimize the loss of nutrients to the environment.

Decomposition and mineralization are largely biological processes, mainly accounted for by the activity of the soil microflora. The direct contribution of the soil mesofauna to these processes, primarily derived from their share in the soil biomass, has been estimated as small (e.g. Andrén and Schnürer, 1985; De Ruiter et al., 1993b; Didden et al., 1994), but indirect contributions, through affecting the functioning of other groups of organisms or even the structure and functioning of the food web as a whole have been postulated (Moore et al., 1988). Better establishment of cause-effect relationships of such indirect effects can be obtained in exclusion experiments, rather than derived from field samplings. In this experiment we studied the effects of the soil mesofauna on the decomposition of crop residues by means of buried litterbags, filled with wheat straw. We chose this method, as on arable fields in temperate regions it is common practice to plough in late autumn, on which occasion surface crop residues are buried.

With this experiment we aimed to:

1. Establish the overall contribution, direct and indirect, of microarthropods to decomposition of crop residues and nitrogen mineralization in arable fields. The experiment does not distinguish direct from indirect effects, but in view of earlier research we may assume that we will measure predominantly indirect microarthropod effects. We used litterbags with different mesh sizes: coarse mesh that admit all mesofauna, and fine mesh to exclude all microarthropods;
2. Monitor the seasonal and successional dynamics of the main soil mesofaunal groups in relation to litterbags mesh size.

MATERIALS AND METHODS

One hundred and twenty fine mesh bags (polyester, 0.02 mm mesh size) and 120 coarse mesh bags (polyvinylchloride screen, ca. 1.5 mm mesh size), 15 x 15 cm, were filled with 5 g (dry weight) of stubble material of spring wheat. This material was collected after harvest in September 1991 from 4 experimental microplots (2 x 5 m^2) on the premises of the Research Institute for Agrobiology and Soil Fertility, Haren, the Netherlands. The soil in the microplots was a calcareous silt loam originating from the Lovinkhoeve Experimental Farm (Marknesse, Noordoostpolder) (Kooistra et al., 1989). The crop rotation in the microplots was winter wheat, sugar beet, spring barley and ware potatoes. After the wheat stubble had been collected from the plots, roots and root nods were removed. The remaining material was thoroughly rinsed with tap water, dried (80 ° C, 48 h), cut (1-3 cm) and sieved over a 3-mm sieve. After filling, the bags were closed by sewing with polyester yarn and marked with plastic tags. The bags were soaked in diluted filtered soil extract (Enderol paper filter) one night prior to introduction to the field to provide an equal initial inoculum of bacteria and fungal spores to all the bags and to rewet the litter. In November 1990, at the time of the

main tillage, all litterbags were buried in sets of four (two fine, two coarse mesh bags). Thirty sets of bags were buried at approximately 15 cm depth in two of the microplots, whereas the other 30 sets were buried at 25 cm depth in the other two microplots, according to different tillage practices. In the year of the experiment sugar beet were grown in the microplots where the litterbags had been buried. Sugar beet were sown in March.

Ten sets of bags (5 from each depth), i. e. 20 replicates per mesh size, were randomly sampled at each sampling occasion. Ten bags per mesh size were to be used for physical-chemical analyses and ten for the extraction of microarthropods, enchytraeids and nematodes. Bags were recollected at six time intervals, unevenly divided over 1 year. One day after the introduction the first recollection was made to assess the mass loss that was due to the handling of the bags and the rinsing of the material.

After exhuming, one coarse and one fine bag of each of the sets were used for physical and chemical analyses. These bags were emptied over a sieve (0.35 mm) and the litter was rinsed with tap water to remove soil. The litter content of each bag was spin-dried in blotting paper (2800 rpm, 30 s) and oven-dried (80°C, 48 h). After dry weight had been determined, the straw material was milled (< 0.2 mm) and 2 g was used to determine total nitrogen content (Vierveijzer et al., 1979). The remaining material was burned in a muffle furnace (700°C, 4 h) to obtain the ash-free oven-dry weight.

Within 24 h after collecting the litterbags, biological analyses of the other fine and coarse bag of each set commenced. The 20 bags were cut in half with a pair of scissors. One-half was used for the extraction (10 days) of microarthropods by high gradient extraction (Andrén, 1985), using picric acid as collection fluid. Microarthropods were divided into seven functional groups (Brussaard et al., 1990): predatory mites (mainly Mesostigmata), cryptostigmatic mites, non-cryptostigmatic mites (mainly Prostigmata), nematophagous mites (*Alliphis halleri* (G. and R. Canestrini 1881)), bacterivorous mites (predominantly *Histiostoma litorale* (Oudemans 1914)), predatory Collembola and omnivorous Collembola. The other half of the content of the bags was used to extract enchytraeids and nematodes by a modified wet Tullgren method: the litter samples were placed in sieves lined with a piece of cheesecloth, and placed in funnels filled with tap water. After one night at 23 °C to let the nematodes precipitate, enchytraeids were chased downwards into the collection tubes by heating the air above the samples in 3 h to 50 °C. It is known that this method does not suffice to collect all the nematodes from a sample, but it does allow relative comparison of numbers among treatments.

To monitor the population dynamics of the microarthropods in the bulk soil, six undisturbed soil cores (0-25 cm depth, 6 cm diameter) were taken at random from the plots at each litterbag sampling occasion and extracted in the high gradient extractor (Vreeken-Buijs et al., 1994). In three nearby microplots soil temperature was measured at 15 cm and at 25 cm depth.

Because microarthropod counts from the soil samples and from the litterbags have different dimensions (numbers per volume of soil v.s. numbers per

litterbag or g dry litter) the Spearman rank correlation test on the mean numbers per functional group per sampling was used to compare population dynamics in coarse mesh litterbags with bulk soil samples from equal depth. On all other data effects of litterbag mesh size and sampling date were tested by means of analysis of variance (ANOVA). All faunal data were log-transformed before statistical analysis. Means were separated by Student's *t*-test. Differences between microplots were not tested.

RESULTS

Effects of mesh size on litter decomposition and nitrogen mineralization

Litterbag mesh size had a significant effect ($P < 0.05$) on mass loss, measured as ash-free oven-dry weight, but this effect was almost completely due to the differences at the last sampling date (Figure 7). The decomposition can be well described by the negative exponential function (Olsen, 1963; Andrén, 1987):

$$M_{(t)} = M_{(t=0)} * e^{-k*t}$$

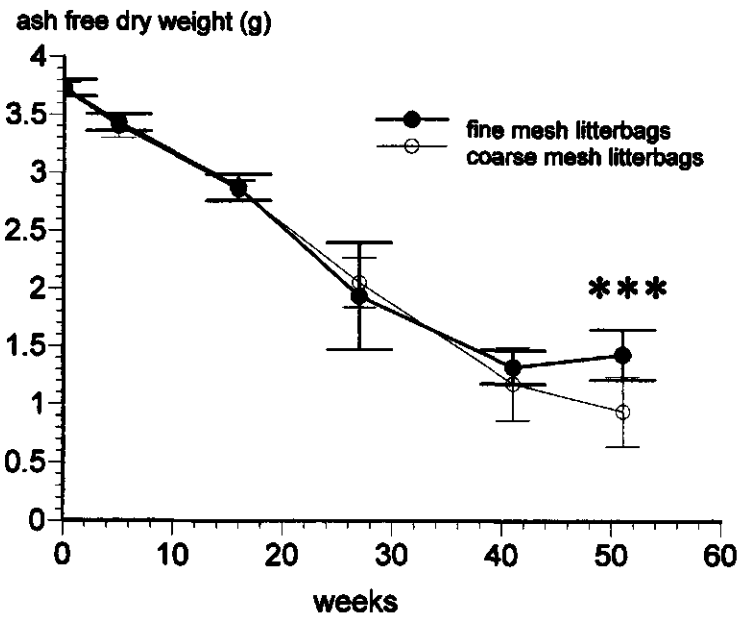


*Fig. 7: Ash free dry weight of wheat straw litter remaining in coarse and fine mesh litterbags. Bars indicate standard error of differences of means (ANOVA: ***: $P < 0.001$).*

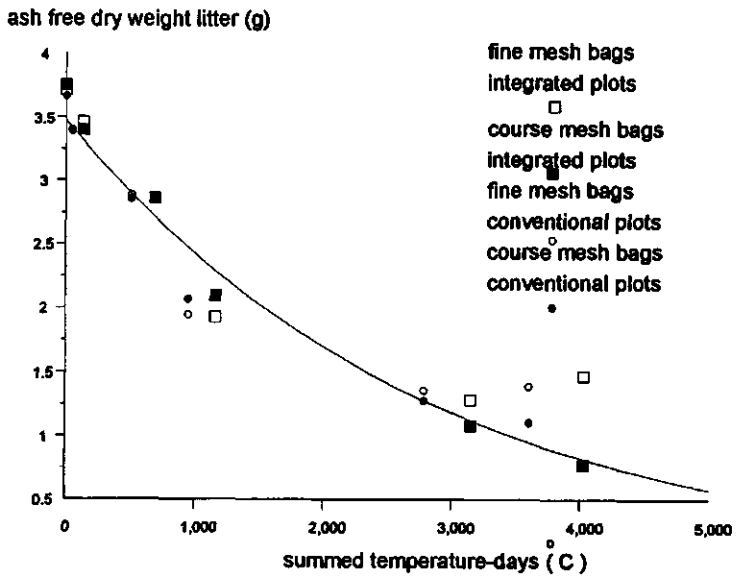


Fig. 8: Dry weight of wheat straw litter remaining in fine and coarse mesh litterbags placed at different depths. Line: negative exponential regression of all coarse mesh litterbags (solid symbols).

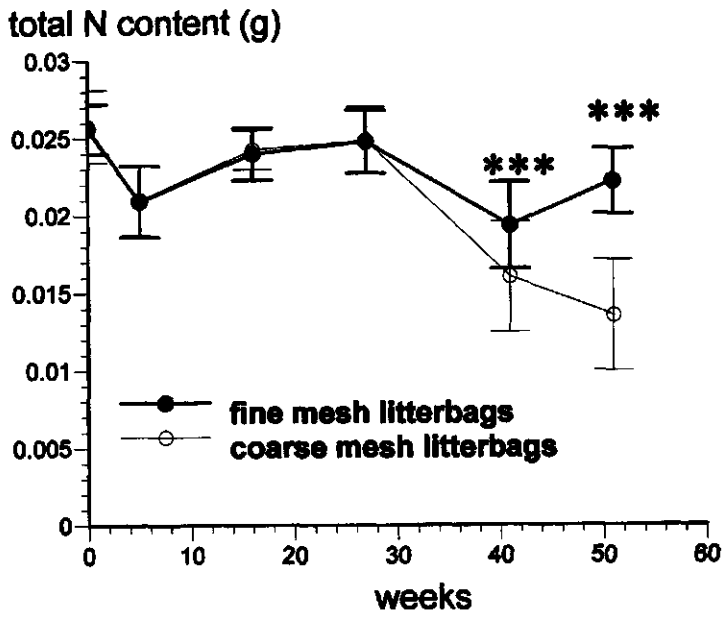


*Fig. 9: Total nitrogen content of wheat straw litter remaining in coarse and fine mesh litterbags. Bars indicate standard error of differences of means (ANOVA: ***: $P < 0.001$).*

Time t can either be expressed as cumulative mean daily temperature above freezing, in either days or years. Figure 8 shows the litter ash-free dry weight plotted against the summed mean daily temperature for fine and coarse mesh bags incubated at 15 and 25 cm depth. The decomposition of the litter in the coarse mesh bags is best described with k = 0.00036 °C^{-1} (R^2 = 0.98). The graph also shows that at the last sampling occasion the ash-free litter dry weight in the fine mesh bags deviated from the exponential curve. No significant coefficient of correlation was found for the fine mesh litterbags.

In both types of litterbags total nitrogen of the straw litter, i.e. N content of the litter together with the N content of the microbial biomass on the litter, decreased during the 1st month, but subsequently rose slightly, probably due to immobilization of inorganic soil N by the bacterial biomass (Figure 9). In spring, total litter nitrogen decreased due to net mineralization from the litter. However, at the 41-week sampling, net mineralization from the fine mesh bags was significantly less than from the coarse mesh bags, while at the 51-week sampling the litter in the fine bags had again immobilized nitrogen (ANOVA, P< 0.001). In the meantime, the coarse mesh litterbags continued to show net mineralization of nitrogen at a constant rate.

Table 7: Effects of litterbag mesh size on mesofauna numbers (ANOVA on log-transformed fauna data, F grand mean of the 20-µm-mesh litterbags, C grand mean of the 1.5-mm-mesh litterbags)

	Mesh size		Time	Mesh size * Time
	P		*P*	*P*
Total nematodes	0.005	*(F>C)*	<0.001	0.031
Total enchytraeids	0.234		<0.001	<0.001
Total microarthropods	0.004	*(F>C)*	<0.001	<0.001
Bacterivorous nematodes	<0.001	*(F>C)*	<0.001	0.438
Fungivorous nematodes	<0.001	*(C>F)*	<0.001	<0.001
Omnivorous nematodes	0.013	*(F>C)*	<0.001	<0.001
Herbivorous nematodes	0.239		<0.001	<0.001
Bacterivorous mites	<0.001	*(C>F)*	<0.001	<0.001
Cryptostigmata	0.021	*(C>F)*	<0.001	0.196
Non-cryptostigmatic mites	0.574		<0.001	0.050
Omnivorous Collembola	0.638		<0.001	<0.001
Nematophagous mites	<0.001	*(C>F)*	<0.001	<0.001
Predatory mites	<0.001	*(C>F)*	<0.001	<0.001
Predatory Collembola	0.931		0.125	0.111

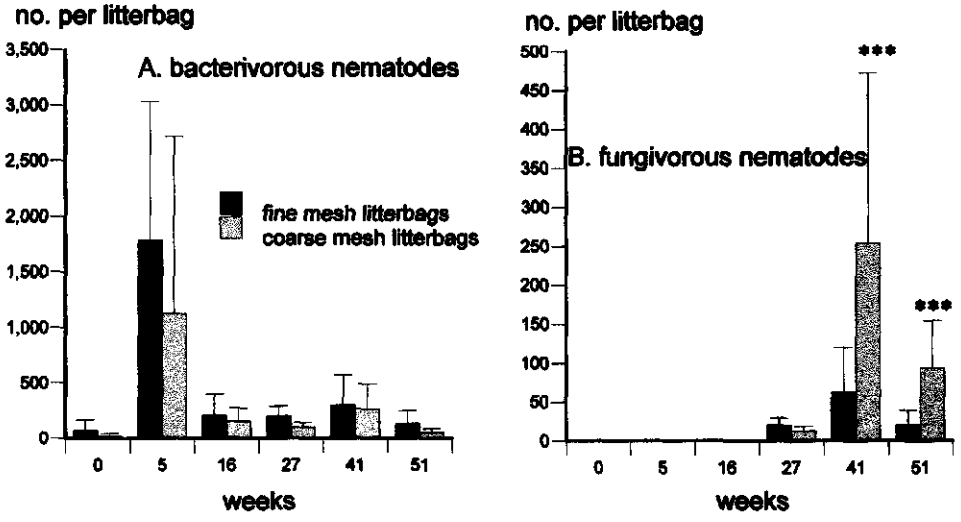


*Fig. 10: Nematode dynamics in fine and coarse mesh litterbags: A: bacterivorous nematodes; B: fungivorous nematodes (ANOVA; ***:P < 0.001).*

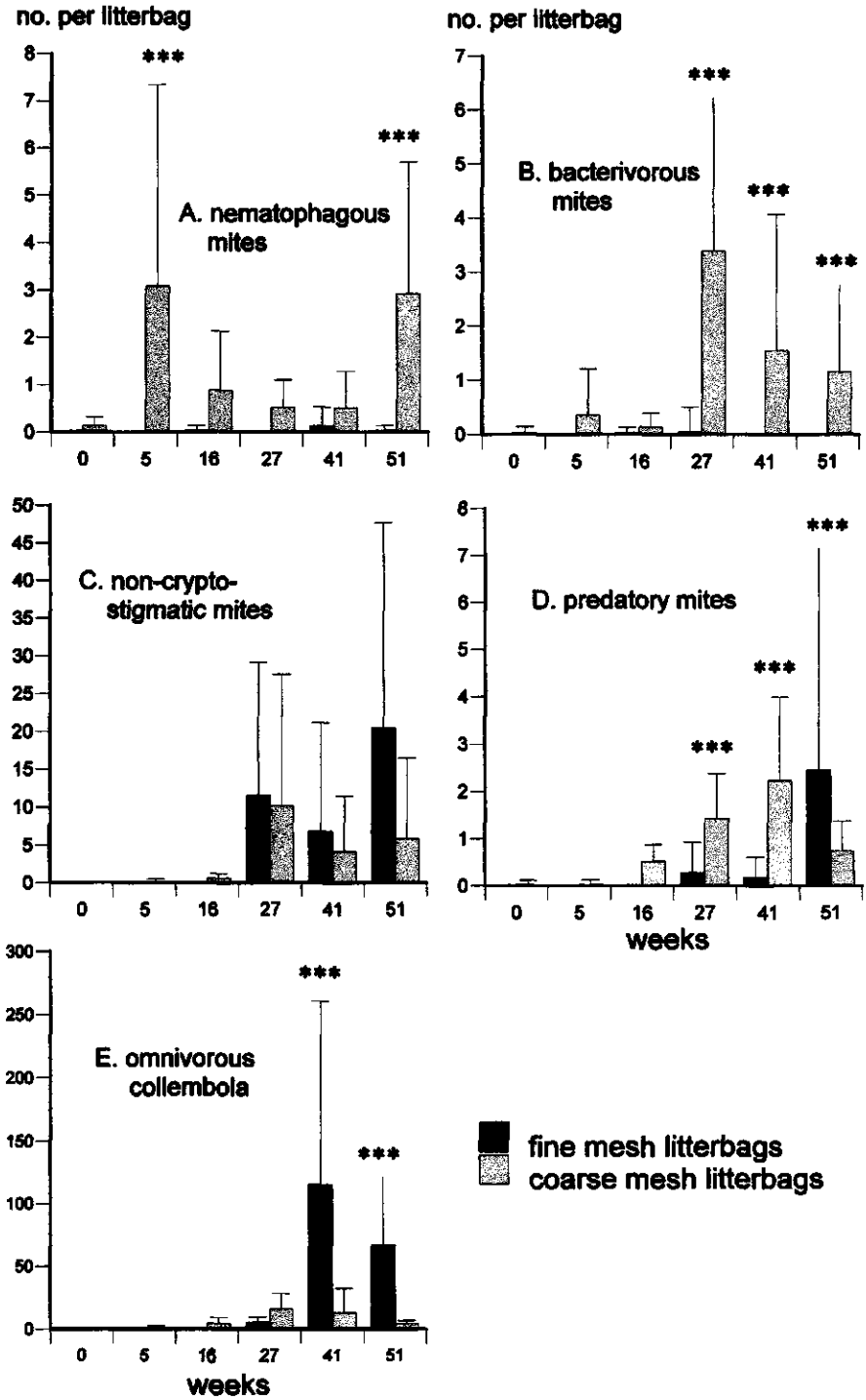
Effects of mesh size on the population dynamics of litter faunal groups

Table 7 shows that the total nematode numbers, extracted from the litterbags, were higher in the fine mesh litterbags ($P < 0.01$). Bacterivorous nematodes were found in both types of litterbags during the whole period of observation and reached highest numbers 5 weeks after the start of the experiment (Figure 10A).

Analysis of variance of the log-transformed nematode data showed that bacterivorous nematodes occurred in higher numbers in the fine mesh litterbags ($P < 0.001$; Table 7). Fungivorous nematodes were below the detection limit till week 27 and reached highest numbers in week 41 (Figure 10B). Numbers were significantly higher in the coarse mesh bags than in the fine mesh bags ($P < 0.001$, Table 7). Omnivorous nematodes were below the detection limit until week 27 and thereafter occurred only in very low numbers. Highest numbers were found at the last sampling date in the coarse mesh bags (approximately 10 nematodes per litterbag on average). Herbivorous nematodes were undetectable till week 41 and very rare in the last sampling (highest mean numbers: approximately 2.5 per litterbag).

Nematophagous mites, specifically *Alliphis halleri*, were found in the coarse mesh bags from the start of the experiment, but highest numbers were reached in the sampling in week 5. A second peak occurred at the last sampling. Nematophagous mites were only occasionally found in the fine mesh bags (Figure

*Figure 11: Microarthropod dynamics in fine and coarse mesh litterbags: A: nematophagous mites; B: bacterivorous mites; C: non - cryptostigmatic mites; D: predatory mites; E: omnivorous Collembola (ANOVA; ***:P < 0.001).*



11A). Low numbers of bacterivorous mites (i.e. *Histiostoma litorale*) were found in the coarse mesh bags with a maximum number of three mites per litterbag on average found after 27 weeks (Figure 11B). Afterwards, numbers gradually declined. Non-cryptostigmatic mites occurred in very low numbers until week 27 (Figure 11C). Highest numbers were reached in the fine mesh bags at the 51-week sampling. Their numbers were not influenced by mesh size. Predatory mite numbers in the coarse mesh bags started to increase from week 16 onwards and reached highest numbers in the 41-week sampling. In the fine mesh bags they were only occasionally found, apart from a few litterbags at the last sampling occasion, when significantly higher numbers were reached (Figure 11D). Cryptostigmata were only sporadically found, mainly in the coarse mesh bags. Their numbers were highest at the end of the experiment (51 weeks): 0.4 mites per litterbag on average.

Omnivorous Collembola were the most numerous group of microarthropods in both litterbag types. In the coarse mesh bags their numbers gradually increased towards week 27, while in the fine mesh bags their numbers continued to increase until week 41, when numbers were on average 10 times higher than in the coarse mesh bags (Figure 11E). At week 51 numbers had decreased in both litterbag types, but were still over 10 times higher in the fine mesh bags then in the coarse mesh bags. Predatory Collembola were only found in some of the fine mesh bags at the last sampling occasion (0.4 mites per litterbag on average).

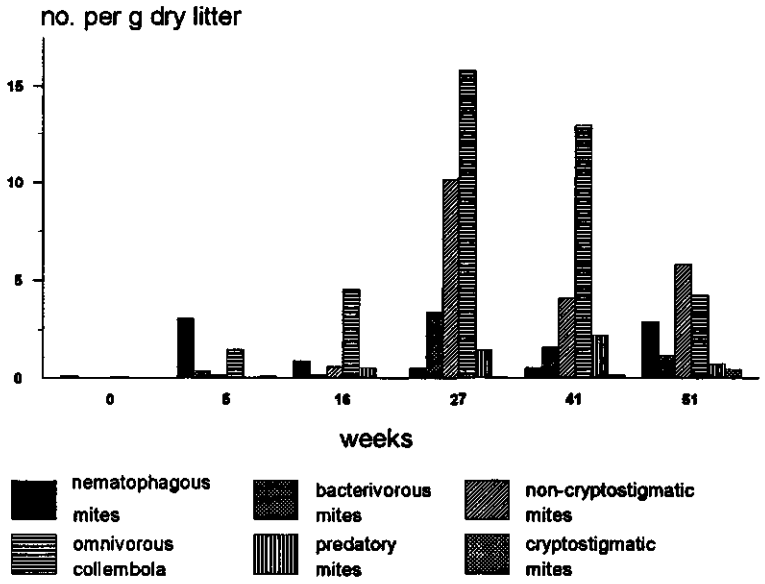


Fig. 12: Microarthropod colonization succession of coarse mesh wheat straw litterbags in box plots by six microarthropod functional groups (mean numbers per litterbag).

Enchytraeids showed the same colonization pattern as the omnivorous Collembola. They first occurred in the coarse mesh bags, but reached highest numbers in the fine mesh bags in week 41 (approximately 16 enchytraeids per litterbag on average). No significant effect of mesh size on enchytraeid numbers was found. ($P = 0.234$).

Finally, we investigated whether the dynamics of microarthropods in the coarse mesh litterbags (Figure 12) was similar to that in the bulk soil. We performed the Spearman rank correlation test on the relative size of microarthropod functional groups found in the coarse litterbags compared to microarthropods found in the bulk soil samples, taken at the same time in the same plots. With the exception of the first two dates, the dynamics in the coarse mesh litterbags and the bulk soil showed the same pattern ($P < 0.05$ at weeks 16, 41 and 51; $P < 0.01$ at week 27).

DISCUSSION

Effects of mesh size on litter decomposition and nitrogen mineralization

In our experiment exclusion of microarthropods had no effect on the net mass loss of litter. This could be observed in the first period of the experiment (until week 27), when colonization of the fine mesh litterbags was still absent or very low compared to the coarse mesh litterbags. This result corresponds with the findings of House and Stinner (1987), House et al. (1987) and Anderson (1973). The only faunal effect Anderson (1973) found on the decomposition rate was caused by Lumbricus terrestris in coarse mesh bags and juvenile L. terrestris in medium mesh bags. We agree with Anderson in his criticism on the use of the negative exponential model to describe the decomposition of litter in natural systems over longer time periods, that deviations may occur if litter material is exposed to feeding activities of soil animals like earthworms. However, in the present experiment, litter mass loss results deviated from the exponential model in the fine mesh litterbags only (Figure 8). This was most probably a result of the disturbance of the soil fauna composition. Presumably due to the initial absence of predatory mites and Collembola, fungal feeding Collembola increased tenfold in numbers, resulting in overgrazing of the active fungal population and retardation of the litter decomposition. Moreover, in some studies, claiming effects of microarthropods on the decomposition of litter, litterbags were apparently not checked for the effectiveness of microarthropod exclusion (Singh and Shekhar, 1989; Scholle et al., 1992, 1993).

In other field studies biocides were used as a means of excluding microarthropods. In such experiments Santos et al. (1981), Santos and Whitford (1981), Elkins and Whitford (1982), Blair et al. (1992) and Beare et al. (1992) found a positive effect of microarthropods on the decomposition rate of litter of various

origins. All other experiments reporting either a positive or a negative effect of microarthropods on litter decomposition rates were conducted in meso- or microcosms and often regarded only one mite or Collembola species, hampering comparison with the present litterbag field experiment due to the effects a major reduction of the decomposition food web may have on the population dynamics of the species involved.

From week 27 onwards colonization of the fine mesh bags by microarthropods took place, but exclusively by some small and fast reproducing mite (predominantly *Pygmephorus* spp.) and Collembola species (*Folsomia candida* (Willem)), which reached high densities. The absence of predators, especially Mesostigmata, until the last sampling may have caused the high densities, compared to the coarse mesh bags. Although the statistical support is weak, we tentatively conclude from the data of the last period of the experiment (week 27-51), that a mesofauna community without predators has a negative effect on the decomposition rate of the litter, whereas in an undisturbed mesofauna community no net effect on the decomposition can be measured.

Furthermore, exclusion of microarthropods had no effect on the mineralization of N or the ash-free mass loss of the litter during the first 27 weeks. From week 27 onwards net mineralization of N occurred, at a higher rate in the coarse mesh litterbags than in the fine mesh bags. In the fine mesh bags we found large numbers of fungivorous Collembola, especially *Folsomia candida*. At the same moment in the coarse mesh bags, this population was approximately 10 times smaller, probably due to mesostigmatic predators. *F. candida* may have overgrazed the fungal population in the fine mesh bags, as it feeds preferably on active fungal hyphae (Moore et al., 1987), resulting in a decrease in fungal-based mineralization of nitrogen. Similar effects of overgrazing by Folsomia candida have been reported by Hanlon and Anderson (1979), Leonard and Anderson (1991) and Moore et al. (1987). This explanation is supported by the observation that fungivorous nematodes reached significantly lower numbers in the fine mesh bags then in the coarse mesh bags, possibly due to shortage of food.

Effects of mesh size on the population dynamics of litter faunal groups

Colonization by bacterivorous nematodes was immediate, since rhabditid nematodes are known to migrate towards organic matter amendments in the soil (Griffiths and Caul, 1993), and mesh size did not interfere with the rate of colonization. Bacterivorous nematodes in both litterbag types showed a peak in numbers in the 5-week sampling. The difference found is not statistically significant, but shows a trend in accordance with results described by and Santos et al. (1981), Elkins and Whitford (1982), Martikainen and Huhta (1990) and Brussaard et al. (1995), showing the effect of predation by nematophagous mites in coarse mesh litterbags. The fact that in our experiment in both litterbag types bacterivorous nematode numbers decreased considerably after the 5-week sampling

can be explained by an expected decrease in bacterial numbers in the litter (Wessén and Berg, 1986), though we have no data on this. Rhabditidae, which represented the largest proportion of the bacterivorous nematodes, need a very high bacterial production for their development (Sohlenius, 1973). After the decrease in bacterivorous nematodes, an increase in fungivorous nematodes was found. This same succession was described by Sohlenius and Boström (1984) to occur in buried barley litterbags. A shift in time from bacterial-based decomposition to fungal-based decomposition may be explained by the depletion of readily decomposable compounds, leaving only holocellulose and lignin for fungi to digest (Wessén and Berg, 1986). In the fine mesh litterbags we found significantly lower numbers of fungivorous nematodes than in the coarse mesh bags, which might have been due to overgrazing of the fungi by the microarthropod population. Predation by Collembola on nematodes may also have played a role (Walter and Hudgens, 1986; Walter, 1987; Moore et al., 1988).

If microarthropod colonization of substrate in the soil would be at random, we would expect the distribution of the community over the functional groups in the coarse mesh litterbags to correspond to that of the bulk soil. The results of the Spearman rank correlation test indicated a different distribution in the first months of the experiment. The observation that nematophagous and bacterivorous mites were found in higher numbers in the substrate in the litterbags then might be expected from their densities in the bulk soil, although their numbers were very small, could be due to phoresy (Siepel, 1994). Phoresy is the ability of mites to disperse from areas unsuitable for further development by attaching to passing carrier organisms. Both nematophagous (predominantly *Alliphis halleri*) and bacterivorous mites (predominantly *Histiostoma litorale*) are regularly found in bulk soil field samples, but always in low densities (Vreeken-Buijs et al., 1994). The early colonization of the litterbags by the nematophagous mites enabled them to profit from the bacterivorous nematode population peak. Bacterivorous mites were some months later in colonizing the litterbags than the nematophagous mites, but presumably were still in time to profit from the bacterial activity peak. Their decline might be an effect of the decline in bacteria or of predation by predatory mites, which increased in numbers in the same period. Predominantly fungal-feeding non-cryptostigmatic mites (mainly Prostigmata) and Collembola as well as predatory mites only reached their peak in summer, together with the fungivorous nematodes, indicating the importance of fungal activity to that specific decomposition stage. Cryptostigmata were the last to colonize the litterbags due to their low density in the bulk soil and, probably, absence of phoresy. We are aware of the fact that in this experiment successional stages cannot be separated from seasonal influences, but our observations fit in very well with earlier succession studies in different climates and in different seasons (Naglitsch, 1966; Eitminaviciuté et al., 1976; Santos and Whitford, 1981; Lagelöf and Andrén, 1985; Beare et al., 1992; Mueller et al., 1990; Siepel, 1990). Santos and Whitford (1981) showed that the successional pattern of functional groups is independent of the microclimate of a particular site.

Microclimate seems to affect just the rate of succession, since temperature affects the rate of decomposition, independent of the season.

Once the fine bags had become invaded, a tenfold population increase of predominantly fungivorous Collembola compared to the coarse mesh bags occurred, which was probably due to the absence of predation. As predatory mesostigmatic mites are on average much bigger than other mites only occasional penetration of fine mesh bags occurred before last sampling date. These and earlier findings by Hendrix and Parmelee (1985), together with experiences in microcosms (Vreeken-Buijs et al., 1997), indicate that microbivorous microarthropods are predator controlled instead of food controlled. Our results lead to the assumption that lack of predation results in overgrazing of the microbial population, as reported by Van der Drift and Jansen (1977) and Andrén and Schnürer (1985). Thus far the most convincing evidence of a positive effect of microarthropods on the decomposition of organic matter concerns the role of predators controlling either bacterivorous nematodes (Santos et al., 1981) or fungivorous microarthropods (Hendrix and Parmelee, 1985). Our results add to the evidence that the absence of predators causes a decrease in decomposition rate in the fungal based decomposition phase of wheat litter.

CHAPTER 4

MICROARTHROPOD BIOMASS-C DYNAMICS IN THE BELOW-GROUND FOOD WEBS OF TWO ARABLE FARMING SYSTEMS

SUMMARY

Microarthropod biomass-C dynamics in arable soil were observed in a 2 year sampling programme in a conventional and an integrated farming system. The most abundant functional groups were omnivorous Collembola, omnivorous non-cryptostigmatic mites and predatory mites. Management practice, especially soil fumigation, affected the short-term dynamics of most groups but no effects were observed on the mean annual biomass of these groups. In the food webs studied in the Netherlands (Lovinkhoeve) or in Sweden (Kjettslinge) and Georgia, USA (Horseshoe Bend), no relation between the biomass of the microarthropods and their main food source (primary decomposers) could not be identified from the biomass annual means. The sampling results of the present study indicated that the microarthropod functional groups were able to recover rapidly from harsh management practices.

INTRODUCTION

In 1985 the Dutch Programme on Soil Ecology of Arable Farming Systems started as a multidisciplinary research programme on the effects of management practice on biotic and abiotic properties of arable soil (Brussaard et al., 1988). Two management practices were compared: integrated and conventional. The integrated practice (INT) differed from the conventional practice (CONV) in the use of organic manure and fertilizer as opposed to inorganic fertilizer only, reduced tillage and reduced use of pesticides. The management systems were practiced at the Lovinkhoeve experimental farm (Marknesse, Netherlands). For details on the management practices see Kooistra et al. (1989) and Lebbink et al. (1994). One of the objectives of the programme was to trace the mechanisms behind C- and N cycling in the soil (Brussaard et al., 1988). A food web diagram was constructed to analyze the flows and pools of C and N through the soil biomass in the Lovinkhoeve (Figure 13). All species found were aggregated into functional groups, mainly according to their

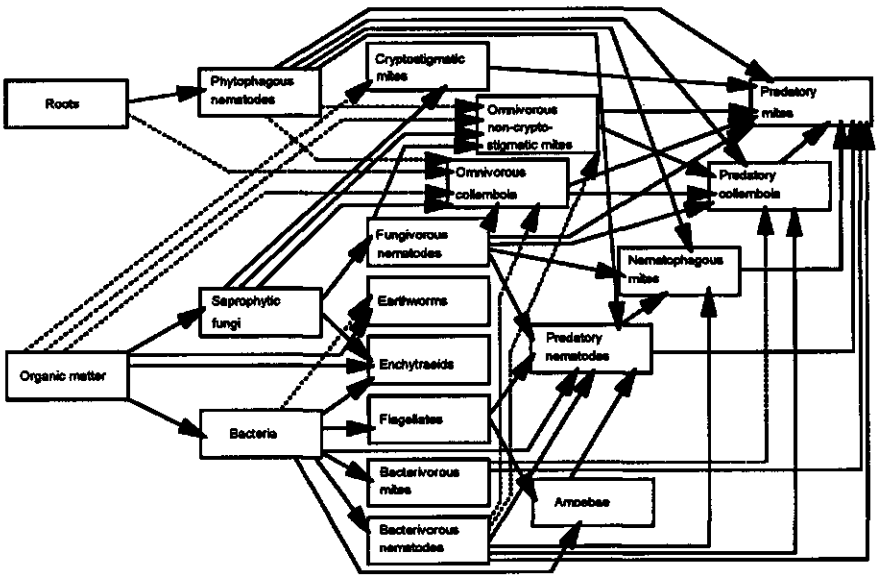


Fig. 13: Diagram of the food web of the Lovinkhoeve experimental farm. Dotted lines indicate assumed trophic relations that were not quantified in the food web model (after De Ruiter et al., 1993a).

feeding behavior (sensu De Ruiter et al., 1993a). A sampling programme started in 1989 in which the biomass of these groups was estimated every six (nematodes, microarthropods, fungi, enchytraeids, earthworms) or every three weeks (bacteria, protozoa). Zwart et al. (1994) described the observed population dynamics and the relations among the dynamics of the different functional groups in the food web.

Bloem et al. (1994) described the dynamics and growth rates of the microbial populations and how these related to nitrogen mineralization. De Ruiter et al. (1994) presented a model with which N-mineralization was calculated based on the observed population dynamics and compared these simulated rates with the observed N-mineralization in the fields. In the present paper, the biomass-C dynamics of the microarthropods are highlighted, especially how these dynamics were affected by management practice.

In accordance with Brussaard et al. (1990), seven different microarthropod functional groups were distinguished (Figure 13):

1. Omnivorous Collembola, that feed on fungi, algae and organic matter.
2. Cryptostigmata, that feed on fungi and organic matter.

3. Omnivorous non-cryptostigmatic mites, that feed on fungi, organic matter and possibly nematodes.
4. Bacterivorous mites, feeding on bacteria only.
5. Nematophagous mites, that are specialized predators of nematodes.
6. Predatory Collembola, that take various kinds of prey.
7. Predatory mites, that take various kinds of prey, including predatory Collembola.

Mean annual biomass-C per functional group per depth layer (0-10 cm, 10-25 cm) and per year (1990 and 1991) is presented for the two management systems as well as the within-year dynamics of the three most abundant microarthropod functional groups.

The hypothesis was that the integrated management system combined with the higher organic matter content of the soil would favor the microarthropods, which in turn might positively affect the nitrogen mineralization, now more important to the crop to compensate for the reduced fertilizer-N input.

Subsequently a comparison is made between the Lovinkhoeve food webs and the food webs studied in Sweden (Lagerlöf and Andrén, 1988; Andrén et al., 1990) and Georgia, USA (Hendrix et al., 1986), with special emphasis on the microarthropod functional groups.

MATERIALS AND METHODS

Site description and management practices

The Lovinkhoeve experimental farm is located near the village of Marknesse in the Noordoostpolder, a large polder that was reclaimed from the sea in 1942. The soil is a calcareous silt loam, pH (KCl) 7.3 and the organic matter content ranges from 2.2% in CONV to 2.8% in INT (Kooistra et al., 1989). Crop rotation was the same in both systems: winter wheat, sugar beet, spring barley and potatoes (Van Faassen and Lebbink, 1990).

At the Lovinkhoeve experimental farm, a conventional (CONV) and an integrated management system (INT) were practiced. Tillage in INT was less deep, fertilization was composed partly of organic manure and the total nitrogen input was 80% of that of CONV. The use of biocides was reduced, e.g. in contrast with CONV, no soil fumigation against cyst-nematodes was applied. The envisaged crop yield levels of INT were 80%- 90% of those of CONV and indeed such yields were achieved at the experimental site during 1988-1991 (Lebbink et al., 1994).

Sampling method.

All year round sampling was started in November 1989 after the potato harvest and winter wheat sowing and was continued on spring barley plots from November 1990 till November 1991. Sampling took place at 6 week intervals from two different subplots within the CONV and the INT fields. Different subplots were randomly chosen for each sampling occasion. Per subplot, four microarthropod samples from four distinct positions in and between the plant rows (to cover possible differences between rhizosphere and non-rhizosphere soil), were taken to a depth of 25 cm with a metal split corer of 6 cm diameter. Cores were divided in 2.5 cm layers and extracted in a high gradient extractor (Andrén, 1985; Brussaard et al., 1990). Collection cups contained a saturated solution of picric acid. Microarthropods were counted using a dissection microscope. Microarthropod biomass-C per hectare was calculated for each of the seven functional groups for the two management practices and for the 0-10 cm and the 10-25 cm soil layers separately. For the calculation of the individual biomass-C, the average dry weight per individual per functional group was derived from the average individual length per taxon constituting the functional groups (Edwards, 1967; Brussaard et al., 1990). Carbon content was estimated at 50 % of dry weight (Table 8).

Table 8: Average individual biomass-C per (microarthropod) functional group as derived from the average individual length per taxon (Edwards, 1967).

Functional group	Average individual biomass-C (µg)
Omnivorous Collembola	1.24
Cryptostigmata	0.38
Omnivorous non-cryptostigmatic mites	0.14
Bacterivorous mites	0.04
Predatory mites	1.18
Nematophagous mites	0.63
Predaceous Collembola	0.74

RESULTS

Microarthropod annual mean biomass-C

The average soil microarthropod biomass-C content of the soil (kg C $ha^{-1}cm^{-1}$ depth), divided over the upper (0-10 cm) and the lower soil layer (10-25 cm), the seven functional groups, the two sampling years and the two management systems used is given in Figure 14. Total average microarthropod biomass-C was a little higher in CONV (0.58 kg ha^{-1} vs. 0.55 kg ha^{-1}, 0-25 cm depth). In INT, no apparent differences

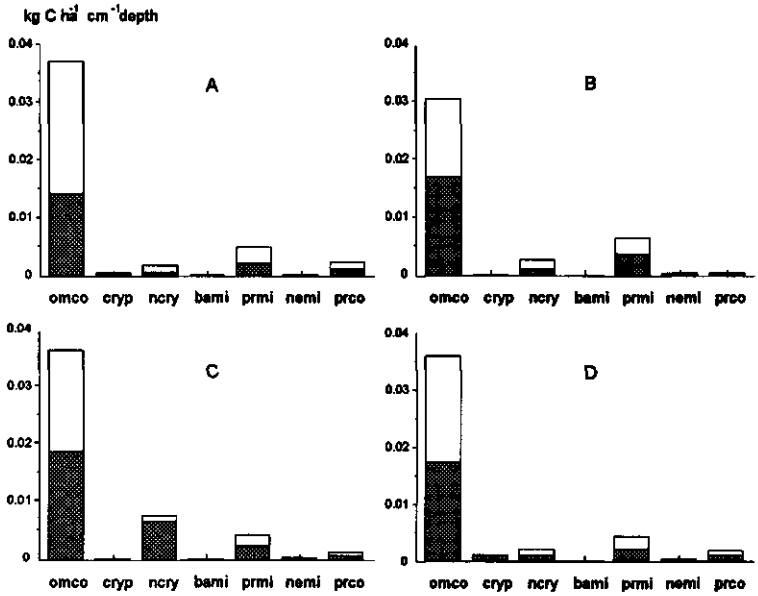


Fig. 14: Mean annual microarthropod biomass-C per functional group for the 0-10 cm (open bars) and the 10-25 cm soil layer (hatched bars) in 1990 and 1991: (A) conventional field (CONV), 1990; (B) integrated field (INT), 1990; (C) conventional field (CONV), 1991; (D) integrated field (INT), 1991 (omco: omnivorous Collembola; cryp: Cryptostigmata; ncry: omnivorous non-cryptostigmatic mites; bami: bacterivous mites; prmi: predatory mites; nemi: nematophagous mites; prco: predatory Collembola).

*Table 9: Results of ANOVA on the seven functional group data sets over two sampling years (1990 and 1991) in two management systems (conventional and integrated) in two soil layers (0-10 cm and 10-25 cm). Significance of the effects: - = no significance, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.*

Functional group	Source of variation			
	Depth	Management	Year	Year * Management
Omnivorous Collembola	-	-	-	-
Cryptostigmata	*	-	*	***
Omnivorous non-cryptostigmatic mites	*	-	-	-
Bacterivorous mites	-	**	-	-
Predatory mites	-	-	*	-
Nematophagous mites	*	-	-	-
Predatory Collembola	-	*	-	***

were found between the two sampling years, whereas in CONV, more omnivorous non-cryptostigmatic mites and less predatory mites were found in1991 than in 1990. In all cases, omnivorous Collembola were the dominant group among the microarthropods.

The results of an analysis of variance (ANOVA), including the factors depth, management system and year, indicated several effects on the composition of the microarthropod community (Table 9). The factor year represented not only the crop type, but also climatic factors. None of the factors significantly affected the most

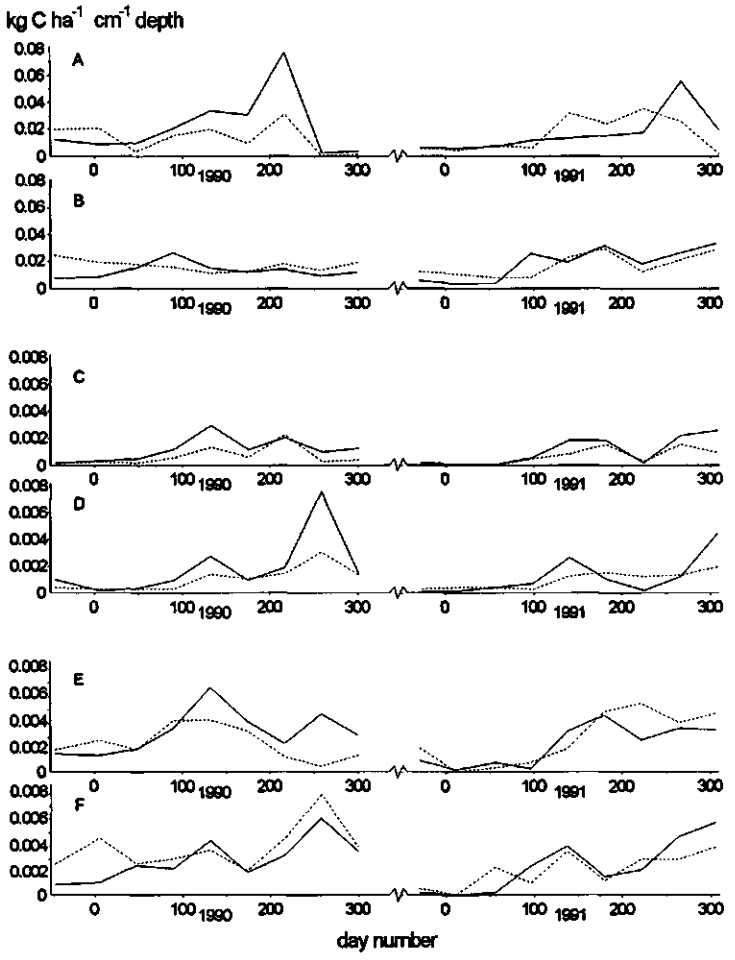


Fig. 15: Biomass-C dynamics of the three most abundant microarthropod functional groups in 1990 and 1991 in the 0-10 cm (solid lines) and the 10-25 cm soil layer (dotted lines): (A) omnivorous Collembola in conventional fields (CONV); (B) omnivorous Collembola in integrated fields (INT); (C) omnivorous non-cryptostigmatic mites in CONV; (D) omnivorous non-cryptostigmatic mites in INT; (E) predatory mites in CONV; (F) predatory mites in INT.

numerous group, the omnivorous Collembola. There were more Cryptostigmata in 1991 than in 1990. The biomass of the Cryptostigmata was significantly higher in the upper soil layer. Omnivorous non-cryptostigmatic mites showed a significantly higher biomass in the upper soil layer. Bacterivorous mite biomass was significantly higher in CONV.

Predatory mites biomass did not show an effect of the difference in management system or the depth layer, but was significantly higher in 1991 than in 1990. There was a significantly higher nematophagous mite biomass in the upper soil layer. Predatory Collembola were found in significantly higher quantities in CONV, though this was true only in 1990 (interaction between management and year).

Microarthropod dynamics

Dynamics of the three most abundant groups, i.e. omnivorous Collembola, omnivorous non-cryptostigmatic mites and predatory mites are presented in Figures 15A-15F. Omnivorous Collembola in the Lovinkhoeve soil consisted mainly of *Tullbergia* spec. and Onychiuridae and to a lesser extent of Sminthuridae, Entomobryidae and Isotomidae. The omnivorous non-cryptostigmatic mites consisted mainly of prostigmatic Pygmephoridae and Eupodidae. Predatory mites consisted almost completely of mesostigmatic Gamasina.

Although the annual mean biomass of these three groups did not differ between the two management systems studied (Table 9), the within-year dynamics of these groups showed considerable differences. The biomass-C of the omnivorous Collembola in INT was much less variable than in CONV (Figures 15A and 15B). The biomass in CONV showed a steep decline after day 240 (1 January designated day 1), when the soil had been fumigated, whereas in the same period in the following year, when no soil fumigation was applied, a relatively high level was maintained in CONV until the first cold spell.

In both INT and in CONV, the omnivorous non-cryptostigmatic mites showed a summertime peak (Figures 15C and 15D). In INT in 1990 this peak was followed by a much higher second peak in autumn. During the same period in CONV a clear dip was found. In the autumn of 1991 a dip in the biomass-C of the omnivorous non-cryptostigmatic mites was found in both INT and CONV.

Predatory mite dynamics (Figures 15E and 15F) showed a summertime peak in both systems and in both years. In CONV in 1991, however, numbers were increasing 6 weeks later than in 1990. Predatory mite biomass in CONV in 1990 had already declined after the summertime peak, but declined even further in the 10-25 cm layer after soil fumigation. In the autumn of 1990 the biomass-C of the predatory mites showed a peak in INT.

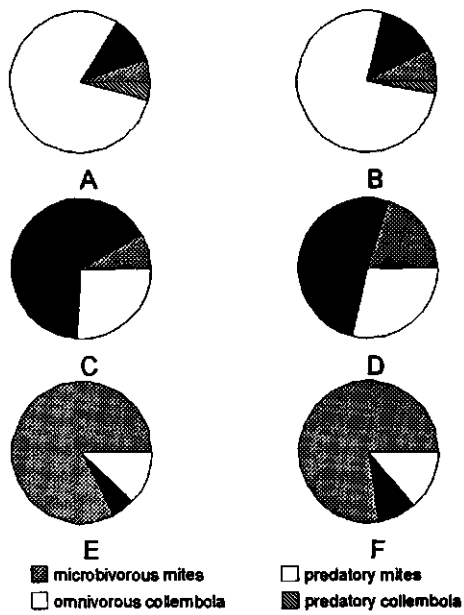


Fig. 16: Microarthropod biomass-C distribution in: (A) Lovinkhoeve (NL) conventional fields (average of 1990 and 1991 data); (B) Lovinkhoeve (NL) integrated fields (average of 1990 and 1991 data); (C) Kjettslinge (Sweden) high N-input barley field; (D) Kjettslinge (Sweden) no N-input barley field; (E) Horseshoe Bend (Georgia USA) conventional tillage field; (D) Horseshoe Bend (Georgia USA) no-tillage field (Kjettslinge data from Lagerlöf and Andrén ,1988; Andrén et al.,1990; Horseshoe Bend data from Hendrix et al., 1986).

Comparison with microarthropod populations in arable soil in Sweden and Georgia, USA.

The contribution of each functional group to the total microarthropod biomass-C in the Lovinkhoeve food webs was compared with corresponding percentages in the food webs described for the Kjettslinge experimental site in Sweden (Lagerlöf and Andrén, 1988, 1991; Andrén et al., 1990) and the Horseshoe Bend experimental site in Georgia, USA (Hendrix et al., 1987).

In Kjettslinge an arable farming system under inorganic N-fertilization was compared with a system without N-fertilizer addition. In Georgia an arable farming system with conventional tillage was compared with a no-tillage system. For the sake of comparison, functional groups were joined: predatory mites include nematophagous mites and microbivorous mites represent cryptostigmatic, omnivorous non-cryptostigmatic and bacterivorous mites. In both Lovinkhoeve systems, the largest proportion of the microarthropod biomass was formed by the omnivorous Collembola. The second largest group were the predatory mites, followed by the microbivorous mites (Figures 16A and 16B) . In the Kjettslinge food webs the contribution of the omnivorous Collembola was large, but not dominant and in

Horseshoe Bend it was relatively small. At Kjettslinge, the overall largest proportion was formed by the predatory mites, their biomass in the fields with fertilizer addition exceeding that in the fields without fertilizer addition (Figures 16C and 16D). At Horseshoe Bend, the microbivorous mites, that, like omnivorous Collembola, feed mainly on fungi and organic matter, formed the largest part of the biomass (Figures 16E and 16F).

The total contribution of the microarthropod biomass-C to the total soil biomass-C (below-ground plant biomass-C excluded) in the different soils was always relatively small (less than 0.3%)(Figures 17A and 17B). However, there were large differences between the sites and systems. Under no-tillage (Horseshoe Bend) the relative contribution of the microarthropods was much higher then under conventional tillage, although the total soil biomass-C showed much less difference.
This positive effect of reduced tillage was not reflected in the numbers of

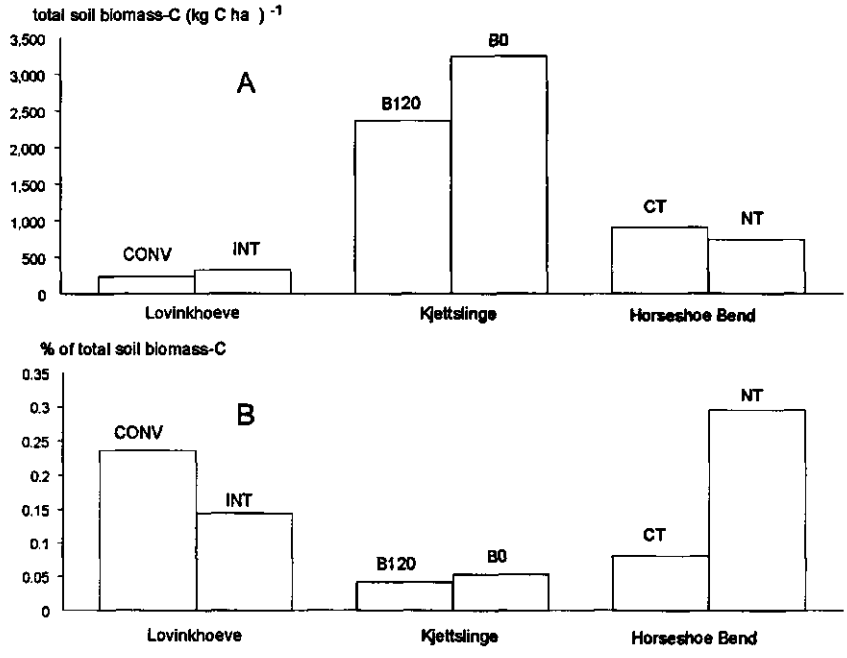


Fig. 17: Total soil biomass-C in kg ha (A) and relative contribution of microarthropods to the total soil biomass-C (B) in the Lovinkhoeve (NL)(1990 and 1991 data averaged); CONV: conventional farming system; INT: integrated farming system; Kjettslinge (Sweden); B120: high N-input barley field; B0: no N-input barley field; Horseshoe Bend (Georgia, USA); CT: conventional tillage system; NT: no tillage system. Lovinkhoeve and Kjettslinge data were based on samplings from the 0-25 cm layer, Horseshoe Bend data from the 0-15 cm layer. (Lovinkhoeve data from Zwart et al.(1994); Kjettslinge data from Lagerlöf and Andrén (1988) and Andrén et al.(1990); Horseshoe Bend data from Hendrix et al.(1986)).

microarthropods observed in the Lovinkhoeve systems. Microarthropod contribution to the soil biomass was smallest in Kjettslinge in both high and no N-input farming system, although the total faunal and microbial biomass was by far the highest of the three sites (approximately ten times higher than in the Lovinkhoeve fields).

DISCUSSION

Owing to the aims of the research program, the management systems practiced at the Lovinkhoeve had to differ in many aspects. Therefore, a separate evaluation of the different effects of these aspects on the dynamics of the microarthropod functional groups is not possible. However, we will discuss some of the aspects that may have affected the microarthropod dynamics as observed.

The 0.5% higher organic matter content of the soil in INT seemed to have no effect on the abundance of microarthropods. The input of fresh organic matter over the 4 year crop rotation was approximately the same for both systems (Van Faassen and Lebbink, 1994) and it might be that the microarthropod dynamics responded more to fresh organic matter (crop residues and green manure) than to the input of spent mushroom compost applied in INT only. Jagers op Akkerhuis et al. (1988) have indicated that in this type of moist, nutrient-rich soil, microbial decomposition of organic matter is very fast, making the input of fresh organic matter increasingly important to mesofauna dynamics. After the addition of organic matter in the form of spent mushroom compost, the numbers of omnivorous non-cryptostigmatic and predatory mites increased in INT in the autumn of 1990. This might have been mainly due to the introduction of mites together with the compost, because the numbers decreased rapidly afterwards.

The higher total nitrogen input in CONV coincided with a slightly higher total microarthropod biomass. This might indicate that a greater availability of nitrogen in the soil benefits not only the crop, but the total soil ecosystem. In Sweden, however, no noticeable effect of nitrogen fertilization on the collembolan populations was reported, although the N-fertilizer input difference between the two systems there was much more distinct, compared with the CONV and INT systems practiced at Lovinkhoeve (Lagerlöf and Andrén, 1991).

Reduced tillage probably affected the Cryptostigmata, since their biomass in the upper soil layer of INT, where organic matter content was increased, was much higher compared with the deeper layer. In Georgia no significant effect on the depth distribution of the microarthropods between the no-tillage and conventional tillage system was found. In both systems most mites were found in the top 0-5 cm zone, including the Cryptostigmata, that were proportionally much more abundant in these fields compared with the Lovinkhoeve fields (Perdue and Crossley, 1990).

The effect of the use of biocides could be found most clearly after fumigation of the soil with a nematocide in CONV at day 240 in 1990. All microarthropod populations decreased sharply, but numbers increased again within 12 weeks. This might be due to recolonization by organisms from the top 5 cm and from the lower

layers of the soil and rapid reproduction. In the top 5 cm the fumigation was less effective because of rapid volatilization of the fumigant. Live microarthropods were found here directly after soil fumigation, while little or none were found in the 5-25 cm zone (unpublished results).

Comparison of the microarthropod populations in the food webs of Kjettslinge, Horseshoe Bend and the Lovinkhoeve revealed no clear relation with the availability of food: the two webs in Sweden were quantitatively dominated by fungi (Andrén et al., 1990), whereas the Horseshoe Bend and the Lovinkhoeve webs were dominated by bacteria (Hendrix et al., 1986; Zwart et al., 1994). In the bacteria-dominated food webs mainly fungivorous microarthropods (Collembola and "microbivorous" mites) were found and in the fungi-dominated food webs, predators were found as the largest microarthropod group. Microarthropod community composition therefore has to be explained by other factors than food source availability.

The annual mean biomass-C of the three quantitatively most important groups (i.e. omnivorous Collembola, predatory mites and omnivorous non-cryptostigmatic mites) in the Lovinkhoeve soil was insensitive to differences in the management practice. Comparison of "eco-farmed" and conventionally farmed fields and grasslands in Austria also revealed that many of the investigated faunal groups, including microarthropods, did not differ statistically (Foissner, 1992). However, at the Lovinkhoeve the within-year dynamics of the three most abundant groups of microarthropods differed significantly between the management systems. The fact that these differences were not reflected in the mean annual biomass suggested that these groups of microarthropods were very well capable of recovering from the different, sometimes rather harsh management practices. This capability of rapid recovery requires a high growth rate after disturbances. Since disturbances often also affected many other groups of organisms, including the microarthropods food or prey, an omnivorous feeding mode might be an important trait to acquire sufficient food. One other possible factor enabling the microarthropods to recover quickly from harsh conditions is their ability to reproduce at any time of the season. This flexibility is characteristic of edaphic and hemiedaphic species (Petersen, 1980) and in all functional groups the majority of the life forms found in our experiment were indeed edaphic.

CHAPTER 5

RELATIONSHIPS OF SOIL MICROARTHROPOD BIOMASS WITH ORGANIC MATTER AND PORE SIZE DISTRIBUTION IN SOILS UNDER DIFFERENT LAND USE

SUMMARY

Soil microarthropods were sampled every three months for 1 year at 10 sites in the northern Netherlands, varying in soil type and land use. Microarthropods were divided into seven functional groups and biomass-C ha^{-1} was calculated for the top 10 cm soil layer. The four quantitatively principal functional groups were: Cryptostigmata, non-cryptostigmatic mites, predatory mites and omnivorous Collembola. Possible relationships between the mean annual biomass of these groups and soil type, land use or soil organic matter were studied. Microarthropod biomass was larger in sandy than in loamy soil, and generally larger in meadows than in wheat fields, the mineral layer of forest soils being intermediate. Non-cryptostigmatic mite, omnivorous Collembola and predatory mite biomass showed strong positive correlations. Cryptostigmatic mite biomass correlated with lower organic matter input quality, while omnivorous Collembola and non-cryptostigmatic mites showed a positive correlation to the amount of input. Omnivorous Collembola were negatively affected by a discontinuous input of organic matter to the soil. We found relationships between functional group biomass and either soil organic matter density fractions or soil pore size distribution only when the grassland sites were analyzed separately. Both analyses showed correlation patterns for Cryptostigmata to deviate from those of the other three main functional groups. Cryptostigmata showed a positive correlation with the lightest organic matter density fraction, while the non-cryptostigmatic mites and omnivorous Collembola were correlated to the heavier fractions. The Cryptostigmata correlated with the 6-90 μm pore size class, while the other three groups showed strong correlation to the 1.2-6 μm, as well as the largest (> 90 μm) pore size class. Both observations lead to the conclusion that omnivorous Collembola and non-cryptostigmatic mites are related to fungal growth (in the largest pores and on the heavy organic matter fraction), while the Cryptostigmata show a more detritivorous feeding mode.

INTRODUCTION

During the last decade, several studies have been performed in which the relationships of the community of soil microarthropods to ecosystem processes such as soil respiration and N mineralisation has been studied (Hunt et al., 1987; Lagerlöf and Andrén, 1988; Brussaard et al., 1990; Fromm et al., 1993). These studies revealed that the role of microarthropods varied strongly among sites.

In this study we identified the environmental factors that affect the occurrence and numbers of soil microarthropod functional groups to better assess their role in nutrient cycling and ecosystem functioning. Our study included both natural- (forest) and agro-ecosystems (arable fields and grasslands). The microarthropod community was described in terms of functional groups, according to Walter et al. (1988). This is a useful method when soil organic matter is taken as one of the prominent soil characteristics determining the occurrence and functioning of the microarthropods. First, because the way in which the different fractions of organic matter affect the microarthropods may depend on their trophic position, i.e. saprovorous, microbivorous or predatory. Secondly, effects of soil organic matter fractions on the functional groups of microarthropods can through functional group description be extrapolated in terms of nutrient flow rates.

The choice of the locations enabled an examination of (single or combined) effects of soil type and land use. These factors are main determinants of the composition and dynamics of the soil organic mater. Soil organic matter dynamics are a key process in ecosystem functioning and may vary strongly in time: for instance, input of spent mushroom compost in autumn, cattle or pig manure or slurry in spring, roots and root exudates during the growing season, crop residues after harvest and autumn litter fall in forests, alternating with periods without organic inputs. All these inputs have different chemical properties and different decomposition rates.

To use organic matter as a soil characteristic, it is necessary to distinguish between different components. The labile components of fresh organic matter are decomposed rapidly by microbes, and their effect on microarthropods is probably only transient. The more resistant or stabilized components will enter the active resident soil organic matter pool (Matus and Rodriguez, 1994) and may have a long-term effect on the microarthropod populations. Within the active resident soil organic matter, three different fractions, differing in decomposability and C/N ratio, can be obtained separately by density fractionation (Meijboom et al., 1995). The decomposition rate decreases with increasing density of the fraction (Hassink, 1995).

Apart from the organic matter inputs, habitable pore space in the soil may influence soil fauna population densities (Hassink et al., 1993). Habitable pore space is known to affect the abundance of bacteria, protozoa and nematodes. These faunal groups in turn affect nitrogen mineralisation (Postma and Van Veen, 1990; Rutherford and Juma, 1992; Hassink et al., 1993; Brussaard and Van Faassen, 1994). Microarthropods, with wider bodies, may interact with larger pore sizes than

the microflora and -fauna. Differences in microarthropod (mainly Collembola) densities, associated with differences in habitable pore space have been found between coarse and fine-textured soils (Choudhuri, 1961; Naglitsch, 1966; Van de Bund, 1970, 1980) and within a single soil type as a result of soil compaction (Chappell et al., 1971; Didden, 1987; Heisler, 1991; Heisler and Kaiser, 1995; Kopeszki and Trockner, 1994). As functional groups of microarthropods have different mean body widths, we hypothesized correlations with corresponding pore size classes.

Our aim was to establish how the composition of the microarthropod community (i.e. the distribution of the microarthropod biomass among the different functional groups) is affected by:

1. soil type and land use in general,
2. the quality, the amount and the dynamics of the organic matter input,
3. the density fractions of the resident soil organic matter,
4. pore space distribution in the soil.

MATERIALS AND METHODS

Site description

The sites selected were a forest, a wheat field and a grassland on sandy soil and on loamy soil, two grassland sites on loamy sand (one artificially compacted (VII) and one reference site (VIII)), a grassland on clay and a wheat field on reclaimed sandy peat, all located in the northern part of the Netherlands. Both wheat fields were part of a crop rotation. Table 10 shows the main characteristics

Table 10: Study site characteristics (SOM: soil organic matter)

Code	Location	Soil type	Land use	SOM (% w/w)	pH-KCl	N applied (kg N/ha)
I	Tynaarlo	sand	grassland	11.4	4.2	280
II	Tynaarlo	sand	winter wheat	7.5	6.2	100
III	Tynaarlo	sand	oak-birch forest	8.9	3.3	-
IV	Lelystad	loam	grassland	4.8	6.7	> 280
V	Marknesse	loam	winter wheat	2.9	6.6	100
VI	Marknesse	loam	poplar forest	4.4	6.3	-
VII	Wieringermeer	loamy sand (compacted)	grassland	4.7	6.7	200
VIII	Wieringermeer	loamy sand (reference)	grassland	4.5	6.7	200
IX	Finsterwolde	clay	grassland	5.2	6.8	300
X	Valthermond	reclaimed sandy peat	winter wheat	4.0	5.1	-

of the ten different sites with respect to soil type, land use, soil organic matter content, pH, and nitrogen amendment.

Sampling

The ten sites were sampled on March 23, June 9, September 9 and December 1, 1992. Samples were taken from the top soil of three different subplots (pseudo-replicates). Per subplot one microarthropod sample was taken to a depth of 15 cm with a metal split corer of 6 cm diameter. Cores were divided into 2.5 cm layers and the 0-2.5 cm, the 2.5 - 5 cm and the 7.5-10 cm layer were extracted in a high gradient extractor (Andrén, 1985). Collection vials contained a saturated solution of picric acid. Microarthropods were counted using a dissection microscope and divided into seven functional groups (Brussaard et al., 1990). These seven groups were: predatory mites (mainly Mesostigmata), Cryptostigmata, non-cryptostigmatic mites (mainly Prostigmata), nematophagous mites (*Alliphis halleri* (G. and R. Canestrini 1881)), bacterivorous mites (predominantly *Histiostoma litorale* (Oudemans 1914)), predatory Collembola and omnivorous Collembola. To calculate microarthropod biomass-C, the average dry weight per individual per functional group was derived from the average individual length per taxon constituting a functional group. Carbon content of the biomass was estimated at 50% of dry weight (Didden et al., 1994).

Size and density fractionation of organic matter

Soil chemical and physical analyses were executed with three replications on soil samples from the March sampling only, because these factors are not expected to vary greatly over the year. To separate the organic matter from the mineral components of the soil, field moist soil samples (250 g) were wet-sieved over 250 µm and 150 µm mesh sieves. The samples were placed on the top sieve and washed with tap water. The macroaggregates were destroyed by pushing the soil through the top sieve during the washing procedure until the water passing the sieve became clear. The material present on both sieves was pooled and washed into a bucket. The material in the bucket was swirled and the organic matter was separated from the mineral material by decantation. The organic material was poured into a small tray with a 150 µm mesh sieve at the bottom and sides of 10 cm height. The mineral material was retained at the bottom of the bucket. Swirling and decantation was repeated several times until there were no more visible organic particles left in the mineral fraction. The mineral fraction was discarded.

The organic material was fractionated in Ludox TM. Ludox® is an aqueous colloidal dispersion of silica particles. The tray containing the organic material was placed in Ludox® with a density of 1.37 g cm^{-3}, and was stirred several times. The floating fraction was collected and placed in a similar tray that was placed in

Ludox® with a density of 1.13 g cm^{-3}. Mixing was repeated until the quantity of the floating material became negligible. The organic matter, placed into the 1.13 g cm^{-3} Ludox® was also separated into a floating and a sinking fraction. Finally, three fractions were obtained: a light fraction with a density <1.13 g cm^{-3}, an intermediate fraction with a density between 1.13 and 1.37 g cm^{-3}, and a heavy fraction with a density >1.37 g cm^{-3}. The three fractions were washed with tap water and dried. A more extensive description of the procedure and the characteristics of the Ludox® is given by Meijboom et al. (1995). Its importance to the decomposition processes lies in the finding that the light fraction is the most "active", i.e. it has the highest decomposition rate, followed by the intermediate and the heavy fraction (Hassink, 1994). Fractionation yields only the active soil organic matter; the size fraction <150 µm, that passes the sieve, is considered the passive pool of organic matter that forms part of micro-aggregates and has a much lower decomposition rate (Hassink, 1995).

The N content of the density fractions was determined according to Deys (1961) after destruction with sulfuric acid. Organic C was determined by treating the samples with dichromate H_2SO_4 according to Kurmies (Mebius, 1960).

Soluble C was determined by shaking 20 g of soil with 80 ml of 0.5 M K_2SO_4 for 1 h. Soluble C in the extract was measured using a dry oxidation method; 30 ml of the K_2SO_4 -solution was injected in an analyzer for total organic C (TOC-500 Shimadzu), equipped with a furnace to reach 680°C and an infrared CO_2 analyzer.

Pore size distribution

The relationship between soil water potential and moisture content was determined according to Klute (1986) in undisturbed soil samples from the 2.5- 7.5 cm layer. The effective pore neck diameter (d) was estimated from the water retention curve as

$$d = 2r = -30.0 * 10^{-6} h^{-1}$$

where h = pressure head, r = radius of curvature of capillary pore. This equation was derived for a water temperature of 15 °C (Vargas and Hattori, 1986). The corresponding pF values can be obtained by taking the logarithm of the absolute value of the pressure head: $pF = {}^{10}\log [h]$. The pore volumes corresponding with the different pore neck diameters can then be calculated from the retention curve. In this study pore sizes were divided into 4 different classes: p1: < 1.2 µm, p2: 1.2-6 µm, p3: 6- 90 µm and pmax: > 90 µm.

Statistical methods

Because the distribution of the microarthropod functional group biomass was skewed in all cases, biomass-C values were log-transformed before further analysis. Analysis of variance was applied to the transformed biomass-C values of the seven functional groups on the effects of sampling date, soil type and land use. To obtain realistic annual mean values, the transformed biomass-C values were averaged and subsequently re-transformed. Student's *t*-test was used to test the differences when ANOVA could not be used (Siegel, 1956). Correlation matrices were obtained by the Genstat 5 (Release 3.1) procedure Correlate. The Spearman rank correlation coefficient was used as a non-parametric measure of correlation (Siegel, 1956).

RESULTS

Microarthropod biomass distribution at the ten sites

In all sites, omnivorous Collembola formed the most abundant functional group of microarthropods (Table 11). Other main functional groups were the predatory mites and the microbivorous/saprovorous cryptostigmatic mites and microbivorous non-cryptostigmatic mites. On average, total microarthropod biomass was largest in the grasslands, smallest in the wheat fields and intermediate in the mineral layer of the forests. Annual mean biomass of predatory Collembola and bacterivorous and nematophagous mites was too low to lead to any relevant statistical results.

Table 11: Retransformed annual mean of ^{10}log of biomass-C (kg C ha^{-1}, 0-10cm) of seven microarthropod functional groups at ten sampling sites. Sampling site codes: see Table 10.

Site code	Predatory mites	Crypto-stigmatic mites	Non-cryptostig-matic mites	Nemato-phagous mites	Bacteri-vorous mites	Predatory collembola	Omnivorous collembola	Total
I	0.11341	0.01086	0.10543	0	0	0.01397	0.76073	1.00440
II	0.02791	0.00958	0.01268	0.00001	0	0.00035	0.04025	0.09077
III	0.07409	0.13967	0.02737	0.00007	0.00042	0.00260	0.38083	0.62505
IV	0.02369	0.00278	0.01681	0	0	0	0.35596	0.39923
V	0.02752	0.00164	0.01628	0.00048	0.00096	0.00056	0.09090	0.13834
VI	0.04067	0.01693	0.01067	0.00019	0.00036	0.00049	0.14238	0.21167
VII	0.06478	0.04301	0.02715	0.00012	0	0	0.20396	0.33901
VIII	0.04741	0.03310	0.04398	0.00004	0.00048	0.00021	0.27163	0.39684
IX	0.02303	0.01121	0.00940	0.00003	0.00078	0.00127	0.04682	0.09253
X	0.04845	0.01991	0.01570	0	0.00126	0.00021	0.08232	0.16785

All available data (microarthropod biomass and soil characteristics measured: pH, mineralized N, soil biomass, organic matter, soluble C) from the 10 sites were tested together in a multiple correlation analysis, but the only significant correlations found, were among the microarthropod functional groups: predatory mites were significantly correlated to both non-cryptostigmatic mites and omnivorous Collembola and non-cryptostigmatic mites and omnivorous Collembola were also correlated (Table 12: relevant fragment of the complete multiple correlation matrix).

Table 12: Correlation between the four largest microarthropod functional groups (average biomass-C in kg ha^{-1}y^{-1}); underlined values: significant correlations (P < 0.05).

Predatory mites (prmi)	1.0000			
Cryptostigmata (cryp)	0.3998	1.0000		
Non-cryptostigmatic mites (ncry)	0.8262	0.0861	1.0000	
Omnivorous Collembola (omco)	0.7857	0.1857	0.8670	1.0000
	Predatory mites	Cryptostigmatic mites	Non-cryptostigmatic mites	Omnivorous collembola

*Table 13: ANOVA on the log-transformed microarthropod data from three types of land use and two soil types (sites I-IV; - : no significant effect; * : P < 0.05; ** : P < 0.01; *** : P < 0.001).*

	Land use	Soil type	Land use * Soil type	Time	Land use * Time	Soil type * Time
Predatory mites (prmi)	-	**	*	-	-	-
Cryptostigmatic mites (cryp)	***	***	***	**	***	**
Non-cryptostigmatic mites (ncry)	*	*	*	-	*	*
Omnivorous Collembola (omco)	**	-	-	-	-	-
Total microarthropods	**	*	-	-	*	*

Effects of land use and soil type on microarthropod functional group biomass

ANOVA on the transformed biomass-C values of the Tynaarlo and the Lelystad/Marknesse sites (I to VI), covering two soil types and three land use types, showed an effect of type of land use on the microarthropod biomass (Table 13) of the dominant functional groups (grassland>forest>wheat field), with the exception of the predatory mites. Soil type had a significant effect on all mite groups

(sand>loam), but not on the omnivorous Collembola. Interaction between soil type and land use was found in all functional groups, except in omnivorous Collembola and total microarthropod biomass. This implies the presence of other factors, causing a changing land use effect in different soils and vice versa.

Effects of the quality, the amount and the dynamics of the organic matter input on microarthropod functional group biomass

We analyzed the microarthropod biomass in relation to the mean annual inputs of fresh organic matter (crop residues, roots, litter and manure) to the three different land use types, and in relation to the 'humification factor' (i.e. the fraction of the residues remaining in the soil after a period of one year), which is an index of the quality of the organic matter (Table 14).

Table 14: Estimated annual organic matter input to the mineral soil in kg dry matter ha^{-1} y^{-1} (Wolf and Janssen, 1991; Van Faassen and Lebbink, 1994).

	C input (kg C/ha/year)	Humification factor (kg C/kg C)	SOM remaining after one year (= flux) (kg C/ha/year)	SOM pool (kg C/ha)
Grassland	3890		1500	75000
- litter		0.39		
- roots		0.45		
Wheat field (crop rotation average)	1480		592	29600
- straw		0.39		
- roots		0.45		
Deciduous forest (mineral soil)			870	43500
- input from the litter		0.98	(472)	
- fine roots	249	0.45	(112)	
- stumps and big roots	249	0.87	(286)	

Table 15 qualitatively lists the different sites by land use, organic matter input quality, input amount and input frequency, i.e. continuous (all year round) vs. discontinuous (in the growing season only). By means of Student's *t* test (Siegel, 1956), we tested the differences between the (weighted) mean annual biomass of the four dominant microarthropod functional groups of grassland and wheat against forest (effect of input quality). We found a significant difference at the 5% probability level only for the Cryptostigmata (grassland and wheat < forest). We did the same test for grassland soil against forest and wheat field soil (effect of input

amount) and found a significant effect on the non-cryptostigmatic mites and the omnivorous Collembola (grassland > forest and wheat).We then tested the

Table 15: Comparative site classification by organic matter regime and the soil microarthropod functional groups that are affected by specific regime parameters.

Sites (code)	Land use in 1992	Input quality	Input amount	Input frequency
I	grass	high	high	continuous
II	wheat	high	low	discontinuous
III	forest	low	low	continuous
IV	grass	high	high	continuous
V	wheat	high	low	discontinuous
VI	forest	low	low	continuous
VII	grass	high	high	continuous
VIII	grass	high	high	continuous
IX	grass	high	high	continuous
X	wheat	high	low	discontinuous
Effects (Student's t test; $P < 0.05$) found on:				
		Cryptostigmatic mites	Non-cryptostigmatic mites and omnivorous Collembola	Cryptostigmatic mites

forest and the grassland against the wheat (effect of input frequency), and only found an effect on the omnivorous Collembola (grassland and forest > wheat).

Effects of active soil organic matter characteristics on microarthropod functional group biomass

Density fractionation of the active soil organic matter revealed significant differences in the contribution of the three fractions separated among the ten sites (Figure 17). The three fractions separated showed different C/N ratios as well (Table 16). Using multiple correlation analysis we examined possible relationships between the microarthropod population sizes, the dry weight of the three density fractions and the total organic matter. No correlation of the microarthropod functional group biomass with the total resident organic matter content of the soil or with the dry weight of the three density fractions was found when all ten sites were taken into account. Neither was there any correlation between the C/N ratio of the organic matter and the microarthropod functional groups biomass-C, except for a weak correlation with the Cryptostigmata.

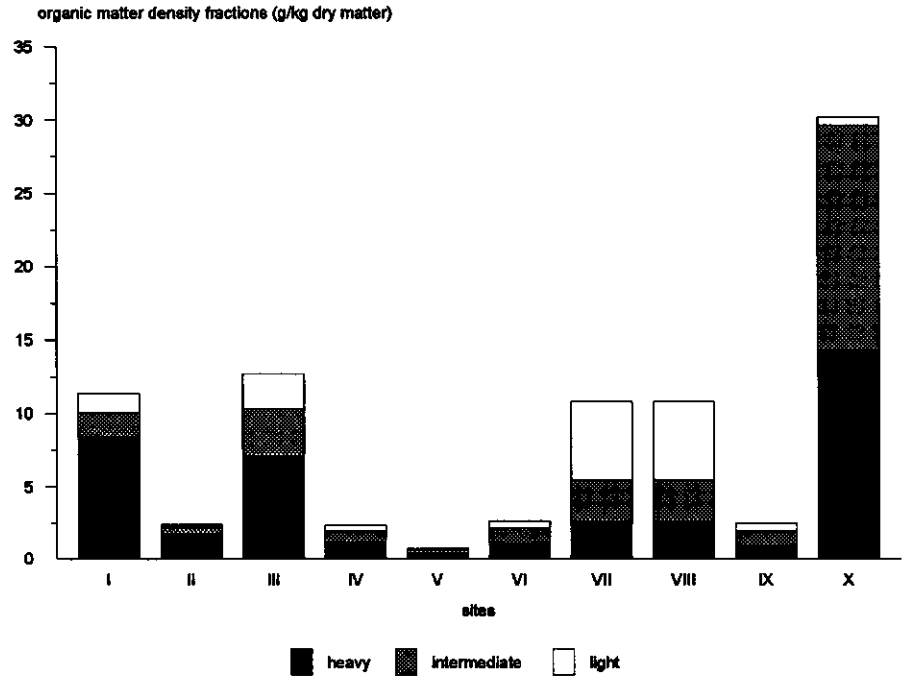


Fig. 18: Soil organic matter density fractions. Sampling site codes: see Table 10.

Table 16: C/N ratios of soil organic matter density fractions (different superscript letters: different means at $P < 0.05$).

Sites (code)	Land use in 1992	Light fraction	Intermediate fraction	Heavy fraction	Weighted mean
I	grass	23.0	21.9	17.6	18.85
II	wheat	19.1	19.2	17.5	17.91
III	forest	25.2	25.5	28.0	26.84
IV	grass	22.5	19.8	18.4	19.58
V	wheat	19.7	19.2	17.5	18.39
VI	forest	25.4	19.6	16.5	19.35
VII	grass	23.2	21.6	19.5	21.89
VIII	grass	23.2	21.6	19.5	21.89
IX	grass	21.0	14.9	13.7	15.74
X	wheat	19.4	19.2	17.5	18.40
Mean		22.2[a]	20.3[ab]	18.6[b]	

Table 17: Correlation between dry weight of density fractions of the grassland soil organic matter and microarthropod biomass-C (underlined values: significant correlation (P < 0.05)).

	Light fraction	Intermediate fraction	Heavy fraction	Predatory mites	Crypto-stigmatic mites	Non-crypto-stigmatic mites	Omnivorous Collembola
Light fraction	1.0000						
Intermediate fraction	0.9884	1.0000					
Heavy fraction	-0.0267	0.1201	1.0000				
Predatory mites	0.2077	0.3467	0.9584	1.0000			
Cryptostigmatic mites	0.9634	0.9499	-0.0869	0.1744	1.0000		
Non-cryptostigmatic mites	0.1838	0.3216	0.9627	0.9445	0.0769	1.0000	
Omnivorous Collembola	-0.1379	-0.0286	0.8637	0.7693	-0.2988	0.8597	1.0000

The relative size of either of the three organic matter density fractions did not show any significant correlation with land use (Spearman Rank Correlation Coefficient) or with any of the soil pore size classes, probably due to the fact that differences between sites with respect to soil organic matter were extremely large. For this reason we repeated the multiple correlation analysis for the five grassland soils (high organic matter content) separately.

No correlation between the biomass of the four dominant microarthropod functional groups and the total organic matter content of the soil was found, even when only the grassland soils were analyzed. However, strong correlations were found between microarthropod functional group biomass-C and soil organic matter density fractions (Table 17): the Cryptostigmata showed a significant correlation to the light fraction and the intermediate fraction. The predatory mites and the non-cryptostigmatic mites were significantly correlated to the heavy fraction of the soil organic matter. Also the omnivorous Collembola were strongly, yet not significantly, correlated to this heavy fraction.

No correlation between the quality of the organic matter, as derived from the C/N ratio of the Ludox fractions was found for the predatory mites, the non-cryptostigmatic mites or the omnivorous Collembola, due to significant correlations between the C/N ratios of the three density fractions.

Effects of pore size distribution on microarthropod functional group biomass

No correlation between microarthropod functional group biomass and the pore size distribution was found, when all ten sites were taken into account. In correspondence to the organic matter density fractionation study, we therefore concentrated on the grassland sites only, to avoid the variation caused by the

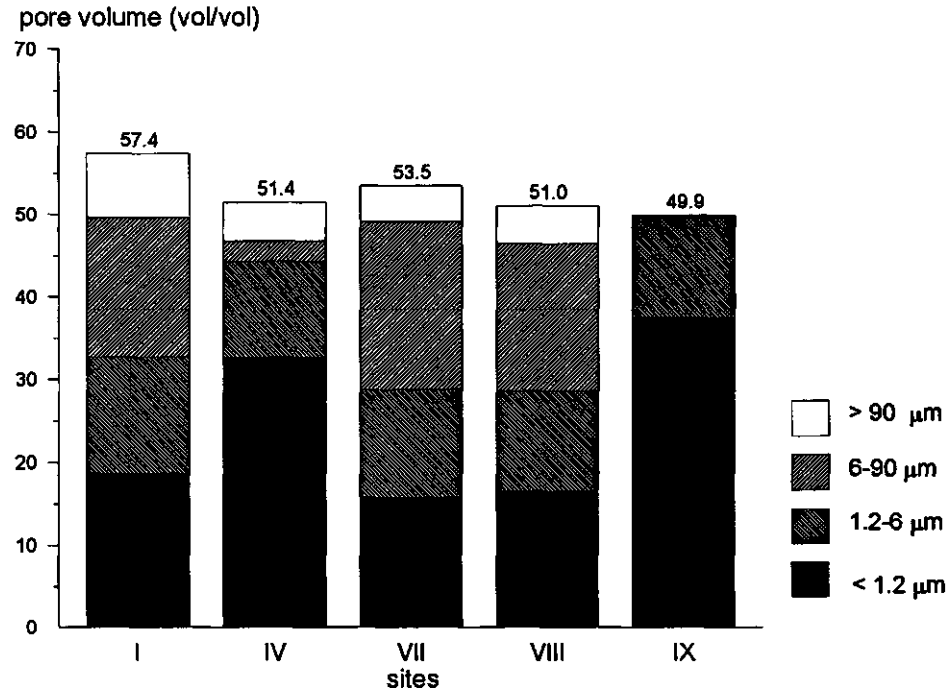


Fig. 18: Soil pore size distribution at five grassland sites. Sampling site codes: see Table 10.

Table 18: Correlation between grassland soil pore volume and microarthropod biomass (pore volume classes: p1: < 1.2 µm, p2: 1.2- 6 µm, p3: 6- 90 µm, pmax: > 90 µm); underlined values: significant correlation (P < 0.05).

	p1	p2	p3	pmax	Predatory mites	Crypto-stigmatic mites	Non-crypto-stigmatic mites	Omnivorous Collembola
p1	1.0000							
p2	-0.5077	1.0000						
p3	-0.9943	0.5566	1.0000					
pmax	-0.6774	0.5856	0.6310	1.0000				
Predatory mites	-0.6992	0.8050	0.6974	0.8030	1.0000			
Cryptostigmatic mites	-0.7150	-0.0590	0.7211	0.0222	0.1744	1.0000		
Non-crypto-stigmatic mites	-0.6992	0.9290	0.7132	0.8205	0.9445	0.0769	1.0000	
Omnivorous Collembola	-0.4490	0.7466	0.4267	0.9182	0.7693	-0.2988	0.8597	1.0000

different land use. Pore size distribution of the five grassland sites is shown in Figure 19. The two Wieringermeer sites are of the same soil type, but have a different pore size distribution due to artificial soil compaction (sites VII and VIII).

From Table 18 we can conclude that the smallest pore size category (< 1.2 μm) in grassland soil is negatively correlated to all the microarthropod functional groups, whereas the 1.2-6 μm pore size class, as well as the largest pore size class (> 90 μm) are positively correlated to three of the dominant functional groups. For the Cryptostigmata the strongest, though not significant, correlation is found with the 6-90 μm size class.

DISCUSSION

Microarthropod functional group biomass at the ten sites

In all sites, omnivorous Collembola formed the functional group that contributed most to the microarthropod biomass-C in arable fields, as was found in earlier field samplings (House and Parmelee, 1985; Vreeken-Buijs et al., 1994; Lagerlöf and Andrén, 1988; Andrén et al., 1990). Cryptostigmata have been found before to be the dominant group in litter layers of forests and other natural, undisturbed soils (forests: a. o. Alejnikova, 1965; Sgardelis and Usher, 1994; prairie: Hunt et al., 1987) as well as in the mineral layer of forest soils.

Grassland soil contained the highest microarthropod biomass, supporting the assumption that grasslands and other perennial crops offer more suitable conditions to microarthropods, compared to arable fields (Alejnikova, 1965; Lagerlöf and Andrén, 1991). In these soils, the soil microflora, the main primary food source of the microarthropods, is stimulated by continuous inputs of organic matter from litter, roots and often manure all year round. The absence of soil tillage constitutes the main difference between annual and perennial crops. Disruption of the soil structure by ploughing causes a decrease in the abundance of the total microarthropod community (Van de Bund, 1970; Lagerlöf and Andrén, 1991). In soils under root and tuber crops, perturbation of the soil is even more intense, resulting in an even more impoverished microarthropod fauna (Jagers op Akkerhuis et al., 1988; Röske, 1993).

Presence of bacterivorous, as well as nematophagous mites seems to be more related to specific, early stages of organic matter decomposition, than to land use or soil characteristics and both groups are found in high numbers only very locally (Vreeken-Buijs and Brussaard, 1996). This explains why their mean annual biomass, as derived from bulk soil samplings, was found to be very low. Therefore, these two groups were not included in the study of relationships with soil characteristics.

Strong correlations were found between the predatory mites and both non-cryptostigmatic mites and omnivorous Collembola. These correlations might indicate a dependency of predatory mite density on the population density of non-cryptostigmatic mites or omnivorous Collembola or both. A discrimination cannot be made because these two microbivorous groups also show a very strong mutual correlation. The correlations found support the evidence that under field conditions population densities of these microbivorous groups are controlled by predation (Vreeken-Buijs and Brussaard, 1996). The strong correlation between the non-cryptostigmatic mites and the omnivorous Collembola is probably caused by their common feeding preference, i.e. predominantly browsing of the fungal biomass (Edwards, 1967; Siepel, 1994). In other aspects these two groups are very different (average body weight, food conversion efficiencies, life strategy). Cryptostigmata biomass showed no correlation to the predatory mite biomass, indicating that at least the mobile instars of this group in general will not be an important prey to the predatory mites, probably due to their armored cuticle.

The statistical "noise" caused by the large differences in land use and soil type probably caused the absence of any significant correlation with soil characteristics like soil pH, organic matter content or N mineralisation, though Alejnikova (1965) had found a positive effect of the humus content of the soil on total microarthropod abundances, in corn and wheat, but no clear effect in perennial crops.

Effects of land use and soil type on microarthropod functional group biomass

In general, microarthropod biomass was higher in sandy soils than in loamy soils and higher in grasslands than in wheat, with the mineral layer of forests intermediate, but significant interactions between land use and soil type for the three mite functional groups were found. These interactions may be caused by secondary differences between the sandy and the loamy sites, like soil age, age of the grassland (years after sowing), tree species in the forest or effects of biocide treatment in the wheat fields.

The effect of soil type on the biomass of the mite functional groups indicates an effect of habitable pore space or physical protection against predation. The much larger variation in body size within the omnivorous Collembola group, relative to the mite functional groups, may have obscured the soil type effect on this specific functional group. Perhaps a body size or a life form classification (Gisin, 1943) would have been more suitable here. Effects of soil pore size, measured by bulk density differences, on the body length of Collembola were found by Van Amelsvoort et al. (1988). To support this idea, other soils, with similar pore size distribution, but different in other characteristics (e. g. soil pH) should be examined.

Site comparison, based on the classification according to land use and amount, quality and frequency of the inputs, gave insight into how land use

affected the three microbivorous microarthropod groups (Table 15). First, large cryptostigmatic mite biomass coincided with low N organic matter input, probably because in a high N input environment, competition by the other microbivorous groups, with on average higher fecundity and development rate may be limiting the cryptostigmatic mite numbers. Secondly, high amounts of organic matter input agreed with high amounts of non-cryptostigmatic mites and omnivorous Collembola, indicating a quantitative effect on these groups of increased energy input to the soil, and thirdly, omnivorous Collembola seemed to profit from a continuous input of organic matter to the soil, in the grassland soil as well as in the forest soil. Collembola may be more dependent than other groups on a continuous application of fresh organic matter, since some of the most abundant species have been shown to forage specifically on actively-growing hyphae (Moore et al., 1987).

Predatory mites were not affected by land use, though probably depend more on their prey densities rather then on the soil organic matter. Comparable results of the effects of land use on the abundance of Collembola and a lesser effect of soil type were found on a landscape scale sampling (total sampling area 143 ha) by Fromm et al. (1993). In the same study only a weak correlation of Collembola with the total C content of the soil was found.

Since no significant correlations were found between microarthropod functional group biomass and either soil pore size distribution or organic matter density fractionation, while these same correlations could be found when only the grassland sites were analyzed , we may conclude, that land use and all its implications had an over-ruling effect over soil and resident organic matter characteristics regarding microarthropod functional group biomass (Fromm et al., 1993).

To discern any patterns in microarthropod distribution independent of land use, further analysis of the characteristics of only the grassland soils seemed useful.

Effect of active organic matter characteristics on microarthropod functional group biomass in grassland soils

The strong correlation of Cryptostigmata with the light and the intermediate density fraction of the grassland soil organic matter, indicate that they feed mainly on the least decomposed, low quality organic matter. In this low C/N material we assume that the fungal community is not yet fully developed. The non-cryptostigmatic mites and the omnivorous Collembola were correlated to the heavier fractions, indicating that they feed on the fungi that are associated with these fractions. The results confirm those of Van Amelsvoort et al. (1988): the euedaphic life forms, dominating the grassland soil collembolan population, feed on low quality food, as opposed to the more mobile hemiedaphic and euedaphic species, that selectively forage on higher quality fungi, but more detailed studies are needed to further reveal the nature of the relationship between the dominant

microarthropod functional groups and the three soil organic matter fractions separated.

Effects of pore size distribution on microarthropod functional group biomass in grassland soil

Regarding the pore size distribution at the five grassland sites, a negative correlation of the pore size class < 1.2 µm to all four microarthropod functional groups was found. This pore size class, that is too small for microarthropods to penetrate, is positively correlated to the bacterial biomass (Hassink, 1994). It indicates that microbivorous mites are only able to forage on unprotected bacterial colonies, growing on fresh organic matter input such as roots, litter or crop residues. The correlation of the non-cryptostigmatic mites with the second smallest pore size category (1.2-6 µm) can not be explained by body size, because the smallest estimated body width of the Prostigmata (the dominant group within

Table 19: Average weight, length and estimated body width of four soil microarthropod functional groups (after Edwards (1967) and Vreeken-Buijs et al.(1993)).

functional group	average live body weight (µg)	estimated average body length (mm)	average specific density	estimated average body width (µm)
predatory mites	5.476	0.446	1.035	123
cryptostigmatic mites	1.176	0.215	1.062	81
non-cryptostigmatic mites	0.649	0.224	1.038	60
omnivorous collembola	7.75	0.690	1.042	117

the non-cryptostigmatic mites) is ca. 60 µm (Table 19). Egg protection may be the explanation: this generally *r*-strategic group has a relatively high fecundity, so protection against egg predation will have a relatively large effect. Finally, all three interrelated functional groups correlated with the largest pore size category (> 90 µm). Visser (1985) and Anderson et al. (1984) suggested that fungal growth is greatest in soils with pore sizes, large enough to allow fungal sporulation. This could explain why not only the larger (predatory) mites, but also the groups with on average much smaller body size (non-cryptostigmatic mites) correlate with the largest pore size category. Cryptostigmata were not correlated to these large soil pores, probably because this group is partly saprovorous. Maybe also their hard exoskeletons permit some burrowing activity, enabling cryptostigmatic mites to create soil pores of their own.

CHAPTER 6

GENERAL DISCUSSION

Introduction

The experiments and field studies I have conducted, allowed me to evaluate the importance of the microarthropods in the functioning of the soil ecosystem of agricultural fields. At first sight, no direct effect of the microarthropod community has been assessed, neither on the decomposition of organic matter, nor on the mineralization of nitrogen. However, some interesting conclusions can be drawn in respect to indirect effects of microarthopod functional groups, as well as to their spatial and temporal habitat differentiation in the context of the below-ground food web.

Effect of microarthropods on decomposition of organic matter

The results of the litterbag experiment described in Chapter 3 led to the conclusion that in a complete and undisturbed food web, there is an inhibiting effect on litter decomposition by fungivorous browsers, which is compensated by the stimulating effect of fungivorous grazers, but only if the population densities of these groups are controlled by the predator population. This situation changes, if for some reason the predation pressure is lifted. Then, overgrazing of the fungal population by Prostigmata and Collembola may result in a decreased decomposition rate. This probably happened in the fine mesh litterbags in Chapter 3. A reduced predation pressure will have relatively more effect on groups with a high reproduction capacity, like for instance Prostigmata and Collembola. An additional cause to the rapid density increase that occurred in the absence of egg predation is the ability of Collembola to synchronize their egg deposition.

As for the development of sustainable agricultural ecosystems, the increased input of fresh organic matter, rather than a slightly increased organic matter content of the soil (Chapter 4), seems to be the only important consequence of "integrated" management of agricultural fields for microarthropods. Soil fumigation only has a temporal effect on the functional group biomass, although a lasting effect on species diversity should not be excluded.

Soil fauna and the mineralization of nitrogen

In the experiments described in this thesis, the direct quantitative effect of microbivorous microarthropod groups on nitrogen mineralization is always lower or unmeasurable, compared to that of protozoa or nematodes. This is not related to the individual mineralization efficiency of the microarthropods, which is in most cases superior to that of the microfaunal groups, but caused by much lower biomass and biomass production rate of microarthropods (Chapter 2). Only in situations in which the production capacity of microbivorous microfaunal groups is reduced in some way, like when the production of the microbial biomass has decreased due to the reduced decomposability of the organic matter (e.g. in "old" organic matter), we tend to expect a measurable direct effect of the microbivorous microarthropods. Like the decomposition, the net mineralization of nitrogen is reduced under nitrogen limited conditions in case of overgrazing by microbivorous microarthropods, caused by the absence of predators.

Local characteristics of the soil (acidity, mineral content, amount and quality of the soil organic matter) not only determine the composition of the primary decomposer community, but also which faunal group will have the largest direct effect on the mineralization. However, different faunal groups affect nitrogen mineralization by different mechanisms. In forests, for example, in the litter layer, that consists of large fragments of leaf material, fragmenting macroarthropods and the larger microarthropods, like surface dwelling Collembola, affect the mineralization by increasing the litter surface and thereby the exposure to saprophytic fungi (Teuben and Roelofsma, 1990). Another example of such a mineralization affecting mechanism is presented by the later stages of the decomposition of low N litter, where fungal grazers mobilizing N from cell walls of senescent fungal hyphae will enhance mineralization (Siepel and Van Wieren, 1990). Additionally, in easy decomposable, high N organic matter, like lucerne meal, only the most effective bacterial grazers, the protozoa, which are able to reach almost every soil pore, affect the mineralization of nitrogen to a measurable degree (Chapter 2). Since nitrogen in this situation is not limiting microbial growth, the effect of any other, less efficient, grazers on the net mineralization of nitrogen will not be measurable.

Functional groups and habitat classification

In this thesis all organisms were grouped in functional groups or guilds, as opposed to taxonomic classification, because the function of the organisms in the soil food web is linked to their resource exploitation. In practice, functional and taxonomic classification often largely coincide. Therefore, taxonomic knowledge should not be neglected. As was already stated in the introduction of this thesis, the classification in functional groups of the soil fauna, especially the microarthropods, by their mouth part morphology has many drawbacks because linkage to resource

utilization is uncertain to some extent, but as a tool it has functioned satisfactory. A truly reliable classification can only be made after the much more time consuming species identification of every specimen found in a soil sample, and, in case of detritivores/microbivores, a subsequent analysis of the gut enzyme activity after Siepel and De Ruiter- Dijkman (1993) or in case of supposed predators either gut content analysis or prey selection behavior experiments as in Walter and Ikonen (1989).

Faber's concept of "leagues" (1991) for functional groups that share not only a mutual mode of resource utilization, but also inhabit a specific stratum of the (forest) soil, is not adequate in the agricultural soil, due to the absence of micro-stratification. Also, in a relatively static situation like a coniferous forest soil, the thickness, as well as the nutritional status of the different soil strata (L, F and H layer) does not show much variation over the year, even though the actual organic matter moves through the profile. In an agricultural field however, soil conditions vary enormously over the year. Depending on the management practice and the crop, in the winter fields often do not have a vegetation cover, nor is there a rhizosphere: the other, very important source of carbon for the soil ecosystem. This means that temperatures vary more severely, causing changes in the soil structure due to freeze-thaw effects, in addition to the disruption of the soil structure by plowing in the autumn. The most important factor for the microarthropod community is probably that the input of organic matter occurs at very distinct moments: by addition of manure, and also at harvest, when, depending on the crop, the root system is left in situ to decompose, or crop residues, as for instance straw, corn stalks, beet leaves or potato plants are left on the field or will be plowed under on a later occasion.

Observations in this thesis have therefore led to a food web differentiation, specific for cultured soils:

1. The food web of fresh organic matter, based on bacteria and perhaps sugar digesting fungi (Figure 20A).
2. The food web of the resident older organic matter, that is based on bacteria and fungi, that have a much lower production rate (Figure 20B).
3. The food web of the rhizosphere, based on mycorrhizal fungi as well as on saprotrophic fungi and bacteria, that live on root exudates and senescent root material.

These three food webs are separated in time and in space: the fresh organic matter food web (1) exists only shortly after input of fresh organic matter and will transpose into the "old" organic matter food web (2) in time. The rhizosphere community (3) only exists as long as annual crops are growing and will disappear in the winter season, unless a green manure has been sown under (Figure 21). In perennial crops and meadows the rhizosphere food web will be maintained all year round.

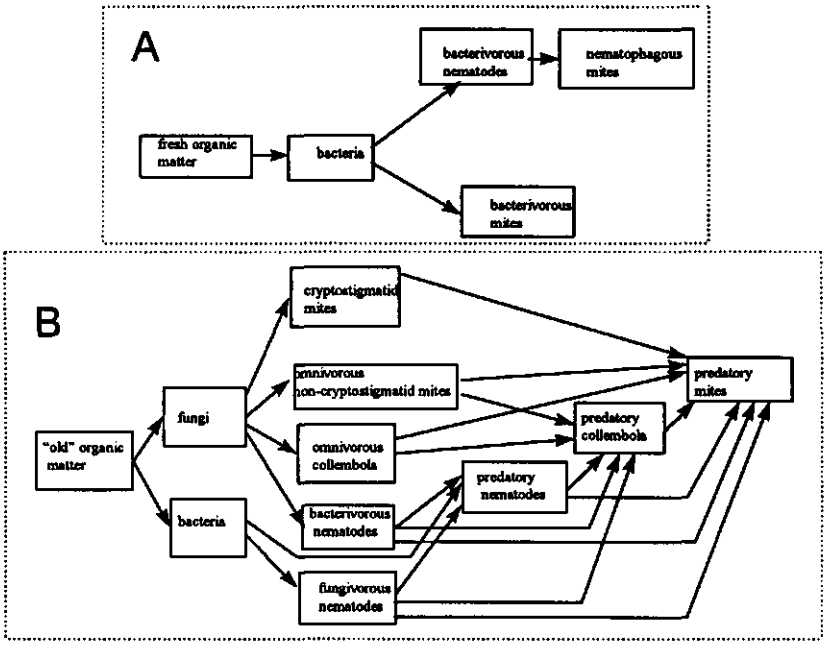


Fig. 20: Simplified diagrams of the below-ground detrital food webs. A: the food web connected to the fresh organic matter and B: the food-web connected to the "old" organic matter (protozoa not included).

Although I cannot give any proof concerning the diversity of the bacteria, the species composition of the microarthropod community of the fresh organic matter food web, as opposed to the "old" organic matter food web differs remarkably. Results from the litterbag experiment show, that the fresh detritus food web is characterized by phoretic species, that can exploit the locally abundant sources of bacteria and bacterivorous nematodes, that have developed within days after the introduction of the litter. After the population density of the bacteria and the bacterivorous nematodes has decreased due to depletion of the highly decomposable, energy-rich substances in the litter, these microarthropods disappear: they form non-feeding hypopi, that await passing carrier organisms, that may transport them to new food sources, or go into dormancy. It is also remarkable, that in the fresh organic matter specialist feeders are found, while in the "old" organic matter the omnivorous feeding mode prevails. For instance, in the fresh organic matter, the specialist nematode feeding mite *Alliphis halleri* is found in far higher densities, than in the surrounding soil (Chapter 3). In grassland soil, which is mostly rhizosphere soil in which a rich variety of nematode prey is available all year round, very few specialist nematophagous microarthropods are

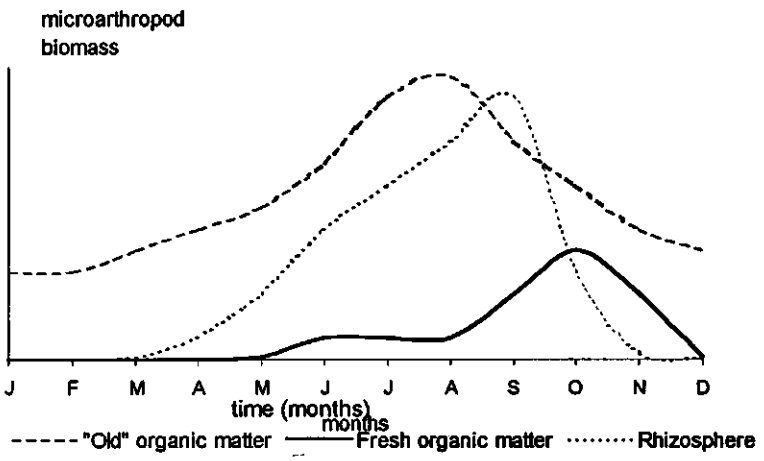


Fig. 20: Conceptual representation of the dynamics of the total microarthropod biomass of the three separate food webs in a wheat field soil.

found, but instead large numbers of a variety of predominantly general predacious Acari were counted (Chapter 5).

An indication of the existence of the fresh organic matter food web under field conditions can be found in the data gathered by Bloem et al. (1994). Weekly monitoring of the microbial biomass and the nitrogen mineralization in two differently managed wheat fields at the Lovinkhoeve site disclosed a dip in nitrogen mineralization as well as a peak in microbial and amoebal biomass right after harvest and skim plowing. In the "conventional" plot the effect on the mineralization was increased by a soil fumigation, that killed all nematodes, including the large population of potentially mineralizing bacterivorous nematodes, resulting in a net immobilization of nitrogen. After only a few weeks the easily decomposable litter components had depleted and thereby the temporary dominance of the fresh organic matter food web over the "old" organic matter food web. In Figures 20A and 20B the protozoa are not represented to keep the diagrams surveyable, but from the data by Bloem et al. (1994) we may deduce that especially the amoebae play an important part in the fresh organic matter food web. Their role is probably also considerable in the "old" organic matter web, as well as in the rhizosphere food web (Kuikman et al., 1990).

My concept of food web differentiation may also give new incentives to the integration of two important N-mineralization models, i.e. the model based on the organic matter (Van Faassen and Lebbink, 1994) and the food web model based on the biomass of soil organisms (De Ruiter and Van Faassen, 1994). Maybe it will be possible, after complementary study, to link the fresh organic matter food web to

the "easily decomposable plant material" pool (DPM) and the "old" organic matter food web to the resistant plant material pool (RPM). This combination might improve the predictability value of nitrogen mineralization model calculations.

Food web interactions

The level at which different functional and taxonomic groups interact with each other is spatially limited, due to the different pore sizes the groups are restricted to (Elliott and Coleman, 1988). No trophic interaction exists between seemingly "connected" groups, like for instance bacteria and nematodes, protozoa and microarthropods, or bacteria and bacterivorous mites, only tenths of millimeters apart, when each organism inhabits soil pores matching their body width. This may also partly explain, why protozoa and bacterivorous mites did not show any competition for food in the experiment described in Chapter 2. Therefore, competition is only probable between groups of, more or less, corresponding body width.

Bacteria not only escape from being grazed by inhabiting soil pores between 0.2 and 1.2 µm, but also by adsorption to or coating by clay and silt particles (Hassink et al., 1997). Although the ecosystem of the Lovinkhoeve soil that was studied, was almost completely bacterial based, bacterivorous mites were rare, for these mites are only able to exploit large and easily accessible bacterial colonies, while the bulk of the bacteria inhabits the smallest soil pores (Chapter 5). Therefore, the most important bacterial grazers are protozoa and bacterivorous nematodes. Protozoa are possibly a food source for the omnivorous Collembola in the Lovinkhoeve soil, while nematodes may fall prey to general predators among the mites (Zwart et al., 1994). Correlation matrices in Chapter 5 of the biomass annual means of field samplings show a positive correlation between omnivorous Collembola and non-cryptostigmatic mites, indicating that any competition within the second trophic level has no impact on the annual mean biomass. In that case a negative correlation would be expected in stead. The correlation of these two partly omnivorous groups of microarthropods with predatory mites, could indicate a trophic relationship, as well as a possible shared prey: nematodes.

For the top-down/ bottom-up debate some interesting points of thought can be distilled from the results of the litterbag experiment (Chapter 3). In the "fresh organic matter food web", a top down effect of the nematophagous mite *Alliphis halleri* on bacterivorous nematodes, as has been found in the microcosm experiment of Brussaard et al. (1995), could not be assessed statistically significantly in the litterbags. This can be caused by the very high level of primary productivity of the bacteria in this fresh material and/or by immigration of bacterivorous nematodes from the surrounding soil, compensating the loss due to predation. Such an influx can of course not be witnessed in a microcosm. The incapability of bacterivorous mites to reduce the bacterial biomass, was assessed in Chapter 2. The interaction strength of the above mentioned trophic interactions, expressed as the

per capita effect on the predator, c. q. prey as calculated by De Ruiter et al. (1995) using Lovinkhoeve field data, showed opposite effects, albeit only small ones. In the succeeding, less productive, decomposition phase, that is dominated by fungi instead of bacteria, several top-down effects (Yodzis, 1988) could be noticed: predatory mites positively affected fungal growth and subsequently decomposition rate by controlling the numbers of fungal browsing mites and omnivorous collembolans. Predation by predatory mites on fungivorous microarthropods positively affected the numbers of fungivorous nematodes, that competed for the same food source as the fungivorous mites and collembolans. It showed, that resource availability (fungal biomass) controlled the densities of the fungivorous mites and Collembola, that competed with the nematophagous nematodes for the same resource (bottom-up), while on the other hand predation by predatory mites kept the numbers of fungivorous mites and collembolans down (top-down) to the benefit of the fungivorous nematodes. Perhaps these nematodes were a less likely prey for the predatory mites, since they could make use of smaller soil pores. These tri-trophic effects, as witnessed in the litterbag experiment, were not within the scope of the interaction strength calculations by De Ruiter et al. (1995).

Impact of the resolution level on the interpretation of experimental results

Gnotobiotic microcosm experiments demand extreme precautions considering the sterility of the soil material used. It requires soil treatments, like high doses of gamma-rays, heat or microwave treatment or freeze-thaw treatment, each of which disturbs the soil chemical and physical characteristics in a different way. Possible effects of these treatments are the increase in mineralization of nitrogen, the inhibition of nitrification, a changed water retention capacity and changes in the decomposability of the organic matter, due to chemical reactions resulting from high temperatures. The inoculated fauna should be free of microorganisms as well. This type of experiments should therefore be restricted to comparative studies only. Even then, secondary effects, that may be important in the natural situation will be missed due to the absence of other connected functional groups. Migration of organisms is restricted. Extrapolation of microcosm results to simulation models of the (undisturbed) field situation are therefore hardly ever possible.

Litterbags are a more appropriate tool to study microarthropods under natural circumstances. However, litterbag experiments require long time incubation, lots of replications, careful handling upon exhuming and correction procedures concerning possible pollution with mineral soil or other intrusions, like roots. As pointed out in Chapter 3 of this thesis, a check on the exclusion of microarthropods in fine mesh litterbags is always indispensable. The major problem of litterbag experiments is to find the optimal excluding mesh size, one that both excludes all microarthropods and allows fungal ingrowth and the colonization by nematodes and protozoa, while keeping the moisture content at the same level as in

the control bags. Too wide meshes in the control bags will allow small fragments of litter material to fall through, and in the presence of earthworms active transportation of litter fragments from the litterbag can occur. Litterbags can only be used to study the breakdown of more or less fresh organic debris. They are unsuitable to study faunal interactions within the food web, that is based on the old, resident soil organic matter, because in the natural situation this material is practically inseparable from the inorganic soil components.

Field observations by soil sampling are the most direct way to collect data on the distribution of microarthropods at a distinct time and place. Regarding the division of the soil food web in three separate webs, it is obvious, that in our climate the "old" organic matter food web can be sampled most reliably in a year round sampling scheme. The same holds for the rhizosphere food web in perennial crops, because it maintains a considerable biomass all year round. The emergence of the fresh organic matter food web on the other hand, can easily be missed in a long interval sampling scheme (six weeks or more, see Chapter 4). For species or functional groups with a very low density on an annual mean basis, drawing conclusions on the basis of a limited number of random field samplings, is hazardous.

Life history tactics of microarthropods in agricultural ecosystems

The largest microarthropod functional groups in Dutch agricultural fields and grasslands, dominating the "old" organic matter food web and the rhizosphere food web both in density and in annual mean biomass, are the omnivorous Collembola, the non-cryptostigmatic mites (mainly Prostigmata) and the predatory mites. Omnivory is the trait they have in common, it therefore seems obligatory in a dynamic environment.

Life-history tactics that are connected to such a varying biotope, are sexual reproduction to maintain a population and arrhenotoky (unfertilized eggs hatch into males, and fertilized eggs become females) to establish a population (Siepel, 1994). However, deeper in the soil profile, the variability of the biotope is less than in the top soil layer. In euedaphic Collembola, that represent a large part of the omnivorous Collembola in the agro-ecosystem, thelytoky (asexual reproduction of females giving female offspring, resulting in clones) seems much more prominent. Arrhenotoky is the trait more prominent in the non-cryptostigmatic mites: it was found among the Pyemotidae, Pygmephoridae, most Tarsonemidae, some Scutacaridae and the Tetranychinae. Arrhenotoky is advantageous in a colonization process: one unfertilized female in a new habitat can produce male offspring and thereupon, after mating, female offspring. Amphytoky, a combination of thelytoky and arrhenotoky, was observed in several species of *Tarsonemus*. Arrhenotoky also occurs among the Mesostigmata (predatory mites).

Semelparity (oviposition concentrated at a single specific moment), as well as seasonal iteroparity (oviposition in a specific season), is common among the

microarthropods of the agricultural field. The collembolan *Folsomia candida* combines a short development time with a relatively large batch size, which increases its chances in a colonization process (Hutson, 1978). Together with synchronized egg deposition it explains the high colonization rate of the fine mesh litterbags in Chapter 3.

Phoresy is a trait, connected to mites, characteristic of the fresh organic matter food web. It helps specialist feeders, that are depending on specific habitats for their food source. Due to the limitations, both in time and in space, of their habitat, they can only survive and explore new food sources, when they can disperse over considerable distances by air currents (anemochory) or by carrier-unspecific phoresy. Both nematophagous mites (*Alliphis halleri*) and bacterivous mites (*Histiostoma litorale*) are capable of phoresy. These groups were the first to colonize the straw litterbags in Chapter 3. Both are depending on the relatively short period of bacterial domination in litter decomposition. When bacterial production drops, so do the bacterivorous nematodes, and both *A. halleri* and *H. litorale* form adaptations, with which they cling to accidentally passing arthropods, like Coleoptera.

In general, all traits, related to a dynamic environment and discontinuous sources of food (arrhenotoky, seasonal iteroparity, short development time, phoresy) are common among the soil microarthropods of agricultural fields. These life history traits help to explain why the mean annual biomass of the three largest groups showed no significant difference between the conventional and the integrated management system, while the within year dynamics differed considerably. An exception should be made for most euedaphic species, that live at such depths, that the variation in the environmental conditions is only limited. These groups also managed to survive soil fumigation and recolonize the higher soil layers even in autumn (Chapter 4). The varying conditions also provided little opportunity for the settlement of population of most cryptostigmatic (oribatid) mite species, the dominant group in natural soils, but rare in Dutch agricultural fields.

Concluding remarks

1. In undisturbed situations, negative effects on the decomposition of organic matter of microarthropods balance positive effects of microarthropods.
2. Top- down control of predatory mites on fungal browsing microarthropods and collembolans precludes the negative effects of overgrazing on litter decomposition. Among the microarthropod community, tri-trophic interactions are most important in respect to litter decomposition and nitrogen mineralization.
3. Only the most efficient microbial grazers will directly affect nitrogen mineralization. In most cases these are not microarthropods, but protozoa and nematodes.

4. The soil food web of agro-ecosystems can be divided into three spatially and temporally separate webs, based on three different carbon sources: the fresh organic matter web, the "old" organic matter web and the rhizosphere food web.
5. Food web interactions are limited by the soil pore size distribution: grazing and predation by microarthropods will only occur in the larger soil pores; competition can only exist between groups or species of comparable body width.
6. Field samplings are useful in studying the "old" organic matter and the rhizosphere food webs and litterbags are a good tool in studying the fresh organic matter food web.
7. Agricultural land use directs the distribution of the main life history tactics of the microarthropods of the "old" organic matter food web towards omnivory, sexual reproduction and/or arhenotoky and semelparity and/or seasonal iteroparity. The fresh organic matter food web is characterized by highly phoretic specialists.

REFERENCES

Alejnikova, M. M. (1965) Die Bodenfauna des Mittleren Wolgalandes und ihre regionalen Besonderheten. Pedobiologia 5: 17-49.

Alphei, J., Bonkowski, M., Scheu, S. (1996) Protozoa, Nematoda and Lumbricidae in the rhizosphere of *Hordelymus europaeus* (Poaceae): faunal interactions, response of microorganisms and effects on plant growth. Oecologia 106: 111-126.

Anderson, J. M (1973) The breakdown and decomposition of Sweet Chestnut (*Castanea sativa* Mill.) and Beech (*Fagus sylvatica* L.) leaf litter in two deciduous woodlands. I. Breakdown, leaching and decomposition. Oecologia 12: 251-274.

Anderson, J. M. (1988) Spatiotemporal effects of invertebrates on soil processes. Biol. Fertil. Soils 6: 216-227.

Anderson, R.. V., Coleman, D. C., Cole, C. V. (1981) Effects of saprotrophic grazing on net mineralization. In: Clark, F. E., Rosswall, T. (Eds.) Terrestrial nitrogen cycles. Ecol. Bull. 33, 201-216.

Anderson, R.. V., Elliott, E. T., McClellan, J. F., Coleman, D. C., Cole, C.V., Hunt, H. W. (1978) Trophic interactions in soils as they affect energy and nutrient dynamics. III. Biotic interactions of bacteria, amoebae, and nematodes. Microb. Ecol. 4, 361-371.

Anderson, R.. V., Ingham, R.. E., Trofymov, J. A. ,Coleman, D. C. (1984) Soil mesofaunal distribution in relation to habital types in a shortgrass prairie. Pedobiologia 26: 257-261.

Andrén, O. (1985) Microcomputer-controlled extractor for soil microarthropods Soil Biol. Biochem. 17: 27-30.

Andrén, O. (1987) Decomposition of shoot and root litter of barley, lucerne and meadow fescue under field conditions. Swedish J. Agric. Res. 17: 113-122.

Andrén, O., Lindberg, T., Bostrom, U., Clarholm, M., Hansson, A.-C., Johansson, G., Lagerlöf, J., Paustian, K., Persson, J., Petterson, R. (1990) Organic carbon and nitrogen flows. In: Andrén, O., Lindberg, T., Paustian, K. and Rosswall, T. (Eds.) Ecology of arable land - organisms, carbon and nitrogen-cycling. Ecol. Bull., 40: 85-126.

Andrén, O., Schnürer, J. (1985) Barley straw decomposition with varied levels of microbial grazing by *Folsomia fimetaria* (L.) (Collembola, Isotomidae). Oecologia 68: 57-62.

Beare, M. H., Parmelee, R. W., Hendrix, P. F., Cheng, W., Coleman, D. C., Crossley Jr., D. A. (1992) Microbial and faunal interactions and effects on litter nitrogen and decomposition in agroecosystems. Ecol. Monogr. 62: 569-591.

Blair, J. M., Crossley Jr., D. A., Callaham, L. C. (1992) Effects of litter quality and microarthropods on N dynamics and retention of exogenous ^{15}N in decomposing litter. Biol. Fertil. Soils 12: 241-252.

Bloem, J., Bolhuis, P. (1990) Microscopic counting of soil bacteria and fungi using europium chelate and fluorescent brightener. Institute for Soil Fertility Research, Haren, Netherlands.

Bloem, J., De Ruiter, P. C., Koopman, G. J., Lebbink, G., Brussaard, L. (1992) Microbial numbers and activity in dried and rewetted arable soil under integrated and conventional management. Soil Biol. Biochem. 24: 655-665.

Bloem, J., Lebbink, G., Zwart, K. B., Bouwman, L. A., Burgers, S. L. G. E., De Vos, J. A., De Ruiter, P. C. (1994) Dynamics of microorganisms and nitrogen mineralisation in winter wheat fields under conventional and integrated management. Agric. Ecosyst. Environ. 51: 129-144.

Boersma, O. H., Kooistra, M. J. (1994) Differences in soil structure of silt loam Typic Fluvaquents under various agricultural management practices. Agric. Ecosyst. Environ. 51: 21-42.

Bouwman, L. A., Bloem, J., Van den Boogert, P. H. J. F., Bremer, F., Hoenderboom, G. H. J., De Ruiter P. C. (1994) Short-term and long-term effects of bacterivorous nematodes and nematophagous fungi on carbon and nitrogen mineralization in microcosms. Biol. Fertil. Soils 17: 249-256.

Bouwman, L. A., Zwart, K. B. (1994) The ecology of bacterivorous protozoa and nematodes in arable soil. Agric. Ecosyst. Environ. 51: 145-160.

Brussaard L., Bouwman L. A., Geurs M., Hassink J. and Zwart K. B. (1990) Biomass, composition and temporal dynamics of soil organisms of a silt loam soil under conventional and integrated management. Neth. J. Agric. Sc. 38: 283-302.

Brussaard, L., Juma, N. G. (1996) Organisms and humus in soils. In: A Piccolo (Ed.) Humic substances in terrestrial ecosystems. Elsevier. pp. 329-359.

Brussaard, L., Kools, J. P., Bouwman, L.A., De Ruiter, P.C. (1991) Population dynamics and nitrogen mineralization rates in soil as influenced by bacterial grazing nematodes and mites. In: Veeresh, G. K., Rajagopal, D., Viraktamath C. A. (Eds.) Advances in management and conservation of soil fauna. Oxford & I. B. H. Publishing Company Pvt. Ltd., New Delhi.. pp. 517-523.

Brussaard, L., Noordhuis, R., Geurs, M., Bouwman, L. A. (1995) Nitrogen mineralization in soil in microcosms with or without bacterivorous nematodes and nematophagous mites. Acta Zool. Fennica 196: 15-21.

Brussaard, L. , Van Faassen, H. G. (1994) Effects of compaction on soil biota and biological processes. In: Soane, B. D., and Van Ouwerkerk, C. (Eds) Soil compaction in crop production. Elsevier Science BV. pp. 215-235.

Brussaard, L., Van Veen, J. A., Kooistra, M. J., Lebbink, G. (1988) The Dutch Programme on Soil Ecology of Arable Farming systems I: Objectives, approach and some preliminary results. Ecol. Bull. 39: 35-40.

Chappell, H. G., Ainsworth, J. F., Cameron, R. A. D., Redfern, M. (1971) The effect of trampling on a chalk grassland ecosystem. J. Appl. Ecology 8: 869-882.

Choudhuri, D. K. (1961) Effects of soil structure on Collembola. Science and Culture 27: 494-495.

Coleman, D. C. (1986) The role of microfloral and faunal interactions in affecting soil processes. In:. Mitchell, M. J., and Nakas, J. P. (Eds.) Microfaunal and faunal interactions in natural and agro-ecosystems. Developments in Biogeochemistry. Martinus Nijhoff, Dordrecht. pp. 317-348.

Crossley Jr., D. A., Mueller, B. R., Perdue, J. C. (1992) Biodiversity of microarthropods in agricultural soils: relations to processes. Agric. Ecosyst. Environ. 40: 37-46.

Darbyshire, J. F., Wheatley, R. E., Greaves, M. P., Inkson, R. H. E. (1974) A rapid method for estimating bacterial and protozoan numbers in soil. Rev. Ecol. Biol. du Sol 11, 465-475.

De Ruiter, P. C., Bloem, J., Bouwman, L. A., Didden, W. A. M., Hoenderboom, G. H. J., Lebbink, G., Marinissen, J. C. Y., De Vos, J. A., Vreeken-Buijs, M. J., Zwart, K. B., Brussaard, L. (1994) Simulation of dynamics of nitrogen mineralisation in the belowground food webs of two arable farming systems. Agric. Ecosyst. Environ. 51: 199-208.

De Ruiter, P. C., Moore, J. C., Zwart, K. B., Bouwman, L. A., Hassink, J., Bloem, J., De Vos, J. A., Marinissen, J. C. Y., Didden, W. A. M., Lebbink, G., Brussaard, L. (1993a) Simulation of nitrogen mineralization in below-ground food webs of two winter wheat fields. J. Appl. Ecology 30: 95-106.

De Ruiter, P. C., Neutel, A.- M., Moore, J. C. (1995) Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269: 1257-1260.

De Ruiter, P. C., Van Faassen, H. G. (1994) A comparison between an organic matter dynamics model and a food web model simulating nitrogen mineralization in agro-ecosystems. Eur. J. Agron. 3: 347-354.

De Ruiter, P. C., Van Veen, J. A., Moore, J. C., Brussaard, L., Hunt, H. W. (1993b) Calculation of nitrogen mineralization in soil food webs. Plant and Soil 157, 263-273.

De Vos, J. A., Raats, P. A. C. (1994) Macroscopic soil physical processes considered within an agronomical and soil biological context. Agric. Ecosyst. Environ. 51: 43-74.

Deys, W. B. (1961) The determination of total nitrogen in herbage samples (in Dutch). Mededelingen 89,90. Institute for Biological and Chemical Research, Wageningen.

Didden, W. A. M. (1987) Reactions of *Onychiurus fimetarus* (Collembola) to loose and compact soil. Pedobiologia 30: 93-100.

Didden, W. A. M., Marinissen, J. C. Y., Vreeken-Buijs, M. J., De Fluiter, R., Geurs, M., Brussaard, L. (1994) Soil meso- and macrofauna in two agricultural

systems; factors affecting population dynamics and evaluation of their role in carbon and nitrogen dynamics. Agric. Ecosyst. Environ. 51: 171-186.

Edwards, C. A. (1967) Relationships between weight, volumes and numbers of soil animals. In: Graff, O. and Satchell, J. J. (Eds.) Progress in Soil Biology. Proc. Coll. Dynamics of Soil Communities, Braunschweig-Völkenrode, 5-10 Sept. 1966. North Holland Publishing Company, Amsterdam. pp. 585-591.

Eitminaviciüté, I., Bagdanaviciené, Z., Kadyté, B., Lazauskiené, L., Sukackiené, I. (1976) Characteristic successions of microorganisms and soil invertebrates in the decomposition process of straw and lupine. Pedobiologia 16: 106-115.

Elkins, N. Z., Whitford, W. G. (1982) The role of microarthropods and nematodes in decomposition in a semi - arid ecosystem. Oecologia 55: 303-310.

Elliott, E. T., Coleman, D. C. (1988) Let the soil work for us. Ecological Bulletins 39: 23-32.

Elliott, E. T., Hunt, H. W., Walter, D. E. (1988) Detrital food web interactions in North American grassland ecosystems. Agric. Ecosyst. Environ. 24: 41-56.

Evans, G. O. (1955) Identification of terrestrial mites. In: McE. Kevan, D. K. (Ed.) Soil Zoology. Prov. Univ. of Nottingham Second Easter School in Agric. Science. Butterworth Sc. Publ., London. pp. 55-61.

Faber, J. H. (1991) Functional classification of soil fauna: a new approach. Oikos 62: 110-117.

Foissner, W., 1992. Comparative studies on the soil life in ecofarmed and conventionally farmed fields and grasslands of Austria. Agric. Ecosyst. Environ., 40: 207-218.

Foster, R. C., Dormaar, J. F. (1991) Bacteria-grazing amoebae in situ in the rhizosphere. Biol. Fertil. Soils 11: 83-87.

Fromm, H., Winter, K., Filser, J., Hantschel, R. and Beese, F. (1993) The influence of soil type and cultivation system on the spatial distributions of the soil fauna and micro-organisms and their interactions. Geoderma 60: 109-118.

Gisin, H. (1943) Öekologie und Lebensgemeinschaften der Collembolen im Schweizerischem Exkursionsgebiet Basels. Rev. Suisse Zool. 50: 131-224.

Griffiths, B. S., Caul, S. (1993) Migration of bacterial-feeding nematodes, but not protozoa, to decomposing grass residues. Biol. Fertil. Soils 15: 201-207.

Hanlon, R. D. G., Anderson, J. M. (1979) The effects of collembola grazing on microbial activity in decomposing leaf litter. Oecologia 38: 93-99.

Hassink, J. (1994) Effect of soil texture on the size of the microbial biomass and on the amount of C and N mineralized per unit of microbial biomass in Dutch grassland soils. Soil Biol. Bioch. 26: 1573-1581.

Hassink, J. (1995) Decomposition rate constants of size and density fractions of soil organic matter. Soil Sc. Soc. of America J. 59: 1631-1635.

Hassink, J., Bouwman L. A., Zwart K. B., Brussaard L. (1993) Relationships between habitable pore space, soil biota and mineralization rates in grassland soils. Soil Biol. Bioch. 25: 47-55.

Hassink, J., Matus, F. J., Chenu, C., Dalenberg, J. W. (1997) Interactions between soil biota, soil organic matter, and soil structure. In: Brussaard, L., and

Ferrera-Cerrato, R (Eds.) Soil ecology in sustainable agricultural systems. Lewis/CRC Press. pp. 15-35.

Heisler, C. (1991) Einfluss von Gefügeschäden infolge mechanischer Belastungen auf die Springschwanz-Besiedelung einer Konventionell Bewirtschafteten Ackerfläche (Collembola). Entomologische Gener. 16, 39-52.

Heisler, C., Kaiser, E.-A. (1995) Influence of agricultural traffic and crop management on collembola and microbial biomass in arable soil. Biol. Fertil. Soils 19: 159-165.

Hendrix, P. F., Parmelee, R. W. (1985) Decomposition, nutrient loss and microarthropod densities in herbicide-treated grass litter in a Georgia Piedmont agroecosystem. Soil. Biol. Biochem. 17: 421-428.

Hendrix, P. F., Parmelee, R. W., Crossley Jr., D. A., Coleman, D. C., Odum, E. P., Groffman, P.M. (1986). Detritus food webs in conventional and no-tillage agroecosystems. Bioscience 36: 374-380.

House G. J., Parmelee, R. W. (1985) Comparison of soil arthropods and earthworms from a conventional and no-tillage agroecosystems. Soil and Tillage Research 5, 351-360.

House, G. J., Stinner, R. E. (1987) Decomposition of plant residues in no-tillage agroecosystems: Influence of litterbag mesh size and soil arthropods. Pedobiologia 30: 351-360.

House, G. J., Worsham, A. D., Sheets, T. J., Stinner, R. E. (1987) Herbicide effects on soil arthropod dynamics and wheat straw decomposition in a North Carolina no-tillage agroecosystem. Biol. Fertil. Soils 4: 109-114.

Huhta, V., Wright, D. H., Coleman, D. C. (1989) Characteristics of defaunated soil. I. A comparison of three techniques applied to two different forest soils. Pedobiologia 33: 417-42.

Hunt, H. W., Coleman, D. C., Cole, C. V., Ingham, R. E., Elliott, E. T., Woods, L. E. (1984) Simulation model of a food web with bacteria, amoebae and nematodes in soil. In: Klug, M. J. and Reddy, C.A. (Eds.) Current perspectives in microbial ecology. American Society of Microbiologists, Washington, DC. pp. 346-352.

Hunt, H. W., Coleman, D. C., Ingham, E. R., Ingham, R. E., Elliott, E. T., Moore, J. C., Rose, S. L., Reid, C. P. P., Morley, C. R. (1987) The detrital food web in a shortgrass prairie. Biol. Fertil. Soils 3: 57-68.

Hunt, H. W., Elliott, E. T., Walter, D. E. (1989) Inferring trophic transfers from pulse dynamics in detrital food webs. Plant and Soil 115: 247-259.

Hutson, B. R. (1978) Influence of pH, temperature and salinity on the fecundity and longevity of four species of Collembola. Pedobiologia 18: 163-179.

Jagers op Akkerhuis, G. A. J. M., De Ley, F., Zwetsloot, H. J. C., Ponge, J.-F., Brussaard, L. (1988) Soil microarthropods (Acari and Collembola) in two crop rotations on a heavy marine clay soil. Rev. Ecol. Biol. Sol 25: 175-202.

Klute, A. (1986) Water retention: laboratory methods. In: Klute, A. (Ed.) Methods of Soil Analysis Part I. Physical and Mineralogical Methods. Agronomy Monograph No. 9. American Society of Agronomy, Madison.

Kooistra, M. J., Lebbink, G., Brussaard, L. (1989) The Dutch Programme on Soil Ecology of Arable Farming Systems 2: Geogenesis, agricultural history, field site characteristics and present farming systems at the Lovinkhoeve experimental farm. Agric. Ecosyst. Environ. 27: 463-469.

Kopeszki, H., Trockner, V. (1994) Auswirkungen des Skibetriebs auf die Collembolenfauna einer alpinen Wiese im Grödental (Südtirol). Zool. Anzeigungen 233: 221-239.

Kuikman, P. J., Jansen, A. G., Van Veen, J. A., Zehnder, A. J. B. (1990). Protozoan predation and the turnover of soil organic carbon and nitrogen in the presence of plants. Biol. Fert. Soils 10: 22-28.

Lagerlöf, J., Andrén, O. (1985) Succession and activity of microarthropods and enchytraeids during barley straw decomposition. Pedobiologia 28: 343-357.

Lagerlöf, J., Andrén, O. (1988) Abundance and activity of soil mites (Acari) in four cropping systems. Pedobiologia 32: 129-145.

Lagerlöf, J., Andrén, O. (1991) Abundance and activity of Collembola, Protrura and Diplura (Insecta, Apterygota) in four cropping systems. Pedobiologia 35: 337-350.

Larink, O. (1997) Springtails and mites: important knots in the food web of soils. In: Benckiser, G. (Ed.) Fauna of soil ecosystems. Marcel Dekker Inc. New York. pp. 225-264.

Lebbink, G., Van Faassen, H. G., Van Ouwerkerk, C., Brussaard, L. (1994) The Dutch Programme on Soil Ecology of Arable Farming Systems: Farm management, monitoring programme and general results. Agric. Ecosyst. Environ. 51: 7-20.

Lee, Q., Widden, P. (1996) *Folsomia candida*, a "fungivorous" collembolan, feeds preferentially on nematodes rather than soil fungi. Soil Biol. Biochem. 28: 689-690.

Leonard, M, J., Anderson, J. M. (1991) Grazing interactions between a collembolan and fungi in a leaf litter matrix. Pedobiologia 35: 239-246.

Marinissen, J. C. Y. (1994) Earthworm populations and stability of soil structure in a silt loam of a recently reclaimed polder in the Netherlands. Agric. Ecosyst. Environ. 51: 75-88.

Martikainen, E., Huhta, V. (1990) Interactions between nematodes and predatory mites in raw humus soil: a microcosm experiment. Rev. Ecol. Biol. Sol 27: 13-20.

Matus, F. J., Rodriguez, J. (1994) A simple model for estimating the contribution of nitrogen mineralization to the nitrogen supply of crops from a stabilized pool of organic matter and recent organic matter input. Plant and Soil 162: 259-271.

Mebius, L. J. (1960) A rapid method for the determination of organic carbon in soil. Analitica Chimica Acta 22: 120-124.

Meijboom, F., Hassink, J., Van Noordwijk, M. (1995) Density fractionation of soil organic matter using silica suspensions. Soil Biol. Biochem. 27: 1109-1111.

Moore, J. C., Ingham, E. R., Coleman, D. C. (1987) Inter-and intraspecific feeding selectivity of *Folsomia candida* (Willem) (Collembola, Isotomidae) on fungi. Biol. Fertil. Soils 5: 6-12.

Moore, J. C., Walter, D. E., Hunt, H. W. (1988) Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. Ann. Rev. Entomol. 33: 419-439.

Mueller, B. R., Beare, M. H., Crossley Jr., D. A. (1990) Soil mites in detrital food webs of conventional and no-tillage agroecosystems. Pedobiologia 34: 389-401.

Naglitsch. F. (1966) Über Veränderungen der Zusammensetzung der Mesofauna während der rotte organischen Substanzen in Boden. Pedobiologia 6: 178-194.

Olsen, J. S. (1963) Energy storage and balance of producers and decomposers in ecological systems. Ecology 44: 322-331

O'Neill, R. V. (1969) Indirect estimation of energy fluxes in animal food webs. J. Theor. Biol. 22: 284-290.

Page, F. C. (1988) A new key to the freshwater and soil Gymnamoebae. Freshwater Biological Association, Ambleside, UK.

Perdue, J. C., Crossley Jr., D. A., 1990. Vertical distribution of soil mites (Acari) in conventional and no-tillage agricultural systems. Biol. Fertil. Soils 9: 135-138.

Persson, T. (1983) Influence of soil animals on nitrogen mineralisation in a northern Scots pine forest. In: Lebrun, Ph. et al. (Eds.), New Trends in Soil Biology. Dieu-Brichart, Ottignies-Louvain-la-Neuve. pp. 117-126.

Persson, T. (1989) Role of soil animals in C and N mineralisation. Plant and Soil 115: 241-245.

Petersen, H. (1980) Population dynamics and metabolic characterization of Collembola species in a beech forest system. In: Dindal, D. (Ed.) Soil biology as related to land use practices. pp. 806-833.

Postma, J., Van Veen, J. A. (1990) Habitable pore space and population dynamics of *Rhizobium leguminosarium* Biovar Trifolii introduces into soil. Microbial Ecology 19: 149-161.

Röske, H. (1993) Untersuchung und Simulation der zeitlichen Dynamik von Collembolen auf verschiedenen Ackerstandorten. Dissertation. Technischen Universität Carolo-Wilhelmina, Braunschweig.

Rutherford, P. M., Juma, N. G. (1992) Influence of texture on habitable pore space and bacterial-protozoan populations in soil. Biol. Fertil. Soils 12: 221-227.

Santos, P. F., Phillips, J., Whitford, W. G. (1981). The role of mites and nematodes in early stages of buried litter decomposition in a desert. Ecology 62: 664-669.

Santos, P. F., Whitford, W. G. (1981) The effects of microarthropods on litter decomposition in a Chihuahuan desert ecosystem. Ecology 62: 654-663.

Sardar, M. A., Murphy, P. (1987) Feeding tests of grassland soil-inhabiting Gamasine predators. Acarologia 28: 117-121.

Scholle, G., Joergensen, R. G., Schaefer, M., Wolters, V. (1993) Hexosamines in the organic layer of two beech forest soils: effects of mesofauna exclusion. Biol. Fertil. Soils 15: 301-307.

Scholle, G., Wolters, V., Joergensen, R. G. (1992) Effects of mesofauna exclusion on the microbial biomass in two moder profiles. Biol. Fertil. Soils 12: 253-260.

Schoonderbeek,. D., Schoute, J. F. Th. (1994) Root and root-soil contact of winter wheat in relation to macroporosity. Agric. Ecosyst. Environ. 51: 89-98.

Seastedt, T. R. (1984) The role of microarthropods in decomposition and mineralization processes. Ann. Rev. Entomol. 29: 25-46.

Sgardelis S. P., Usher, M. B. (1994) Responses of soil Cryptostigmata across the boundary between a farm woodland and an arable field. Pedobiologia 38: 36-49.

Siegel S. (1956) Nonparametric statistics for the behavioural sciences. McGraw-Hill, Kogakusha.

Siepel, H. (1990) Decomposition of leaves of *Avenella flexuosa* and microarthropod succession in grazed and ungrazed grasslands. I. Succession of microarthropods. Pedobiologia 34: 19-30.

Siepel, H. (1994) Life-history tactics of soil microarthropods. Biol. Fertil. Soils 18: 263-278.

Siepel, H., De Ruiter-Dijkman, E. M. (1993) Feeding guilds of orabitid mites based on their carbohydrase activities. Soil Biol. Biochem. 25: 1491-1497.

Siepel, H., Maaskamp, F. (1994) Mites of different feeding guilds affect decomposition of organic matter. Soil Biol. Biochem. 26: 1389-1394.

Siepel, H., Van de Bund, C. F. (1988) The influence of management practices on the microarthropod community of grassland. Pedobiologia 31: 339-354.

Siepel, H., Van Wieren, S. E. (1990) Decomposition of leaves of *Avanella flexuosa* and microarthropod succession in grazed and ungrazed grasslands. II. Chemical data and comparison of decomposition rates. Pedobiologia 34: 31-36.

Singh, K. P., Shekhar, C. (1989) Concentrations and release patterns of nutrients (N, P and K) during decomposition of maize and wheat roots in a seasonally-dry tropical region. Soil Biol. Biochem. 21: 81-85.

Sohlenius, B. (1973) Structure and dynamics of populations of *Rhabditis* (Nematoda: Rhabditidae) from forest soil. Pedobiologia 13: 368-375.

Sohlenius, B., Boström, S. (1984) Colonization, population development and metabolic activity of nematodes in buried barley straw. Pedobiologia 27: 67-78.

Stout, J. D. (1980) The role of protozoa in nutrient cycling and energy flow. Adv. Microb. Ecol. 4: 1-50.

Swinnen, J. (1994) Rhizodeposition and turnover of root-derived organic material in barley and wheat under conventional and integrated management. Agric. Ecosyst. Environ. 51: 115-128.

Teuben, A., Roelofsma, T. A. P. J. (1990) Dynamic interactions between functional groups of soil arthropods and microorganisms during decomposition of coniferous litter in microcosm experiments. Biol. Fertil. Soils 9: 145-151.

Van Amelsvoort, P. A. M., Van Dongen, M., Van der Werff, P.A. (1988) The impact of Collembola on humification and mineralisation of organic matter. Pedobiologia 31: 103-111.

Van de Bund, C. F. (1970) Influence of crop and tillage on mites and springtails in arable soil. . Neth. J. Agric. Sc. 18: 308-314.

Van de Bund, C. F. (1980) Mesofauna of arable soil. In: Minks, A. K. and Gruys, P., (Eds.) Integrated control of pests in the Netherlands. Pudoc, Wageningen. pp. 87-92.

Van der Drift, J., Jansen, E. (1977) Grazing of springtails on hyphal mats and its influence on fungal growth and respiration. Ecol. Bull. 25: 203-209.

Van Faassen, H. G., Lebbink, G. (1990) Nitrogen cycling in high-input versus reduced-input arable farming. Neth. J. Agric. Sc. 38, 265-282.

Van Faassen, H. G., Lebbink, G. (1994) Organic matter and nitrogen dynamics in conventional versus integrated arable farming. Agric. Ecosyst. Environ. 51: 209-226.

Van Noordwijk, M., Brouwer, G., Koning, H., Meijboom, F. W., Grzebisz, W. (1994) Production and decay of structural root material of winter wheat and sugar beet in conventional and integrated cropping systems. Agric. Ecosyst. Environ. 51: 99-114.

Vargas, R., Hattori, T. (1986) Protozoan predation of bacterial cells in soil aggregates. FEMS Microbiol. Ecol. 38: 233-242.

Verhoef, H. A. (1996) The role of soil microcosms in the study of ecosystem processes. Ecology 77: 685-690.

Verhoef, H. A., Brussaard, L. (1990) Decomposition and nitrogen mineralisation in natural and agro-ecosystems; the contribution of soil animals. Biogeochemistry 11: 175-211.

Vierveijzer, H. C., Lepelaar, A., Dijkstra, J. (1979) Analysemethoden voor grond, rioolslib, gewas en vloeistof. Institute for Soil Fertility Research, Haren, Netherlands.

Visser, S. (1985) Role of soil invertebrates in determining the decomposition of soil microbial communities. In: Fitter, A. H. (Ed.) Ecological interactions in soil. Blackwell, Oxford. pp. 297-317.

Vos, E. C., Kooistra, M. J. (1994) The effect of soil structure differences in a silt loam soil under various farm management systems on physical properties and simulated land qualities. Agric. Ecosyst. Environ. 51: 227-238.

Vreeken-Buijs, M. J. and Brussaard L. (1996) Soil mesofauna dynamics, wheat residue decomposition and nitrogen mineralization in buried litterbags. Biol. Fertil. Soils 23: 374-381.

Vreeken-Buijs M. J., Geurs M., De Ruiter P.C. and Brussaard L. (1994) Microarthropod biomass-C dynamics in the below ground food webs of two arable farming systems. Agric. Ecosyst. Environ. 51: 161-170.

Vreeken-Buijs M. J., Geurs M., De Ruiter P.C. and Brussaard L. (1997) the effects of bacterivorous mites and amoebae on mineralization in a detrital based below-ground food web; microcosm experiment and simulation of interactions. Pedobiologia 41: 481-493.

Walter, D. E. (1987) Trophic behaviour of 'mycophagous' microarthropods. Ecology 68: 226-229.

Walter D. E., Hudgens, R. A. (1986) Consumption of nematodes by fungivorous mites, *Tyrophagus* spp. (Acarina: Astigmata: Acaridae). Oecologia 70: 357-361.

Walter, D. E., Hunt, H. W., Elliott, E. T. (1988) Guilds or functional groups? An analysis of predatory arthropods from a shortgrass steppe soil. Pedobiologia 31: 247-260.

Walter, D. E., Ikonen, E. K. (1989) Taxonomy and behaviour in nematophagous arthropods. J. Nematology 21: 315-327.

Wessén, B., Berg, B. (1986) Long-term decomposition of barley-straw: chemical changes and ingrowth of fungal mycelium. Soil. Biol. Biochem. 18: 53-59.

Wolf, J., Janssen, L. H. J. M. (1991) Effects of changing land use in the Netherlands on net carbon fixation. Neth. J. Agric. Sc. 39: 237-246.

Woods, L. E., Cole, C.V., Elliott, E. T., Anderson, R. V., Coleman, D. C. (1982) Nitrogen transformations in soil as affected by bacterial-microfaunal interactions. Soil Biol. Biochem. 14: 93-98.

Yodzis, P. (1988) The indeterminancy of ecological interactions, as perceived through perturbation experiments. Ecology 69: 508-515.

Zwart, K. B., Brussaard, L. (1991) Soil fauna and cereal crops. In: Firbank, Carter, Darbyshire and Potts (Eds.) The ecology of temperate cereal fields. Blackwell Sci. Publ. Oxford. pp. 139-168.

Zwart, K. B., Burgers, S. L. G. E., Bloem, J., Bouwman, L. A., Brussaard, L., Lebbink, G., Didden, W. A. M., Marinissen, J. C. Y., Vreeken-Buijs, M. J., De Ruiter, P. C. (1994) Population dynamics in the belowground food webs in two different agricultural systems. Agric. Ecosyst. Environ. 51: 187-198.

SUMMARY

Soil microarthropods are all free-living mites and collembolans, living in the soil. The study presented in this thesis formed part of the Dutch Programme on Soil Ecology of Arable Farming Systems, an integrated multidisciplinary research programme, focused on the functioning of two differently managed agro-ecosystems: a conventional and an "integrated" system. To understand the mechanisms that control litter decomposition and mineralization of nutrients, knowledge of the role of the microarthropods in the soil food web is indispensable. In this thesis I have studied the effect of microarthropods on the decomposition of organic matter and the mineralization of nitrogen in arable soil. A reliable outlook on the subject could only be achieved, however, by including in the research all possible relationships with other organisms in the soil food web. Therefore, the soil fauna is classified into functional groups: organisms that share a common resource and a common mode of resource utilization. Microarthropod functional groups are: predatory mites, predatory Collembola, nematophagous mites, omnivorous Collembola, Cryptostigmata, non-cryptostigmatic mites and bacterivorous mites. Food web interactions and the effect of microarthropods on decomposition and mineralization were studied at three different resolution levels.

In a microcosm experiment, the separate and combined effects of an amoeba (*Acanthamoeba* spec.) and a bacterivorous mite (*Histiostoma litorale*) on C- and N mineralization were studied with sterilized silt loam soil, reinoculated with a bacterial solution and with lucerne meal as substrate for the microbes. The aim of the experiment was to separate the direct contribution of the mites to the mineralization from possible indirect effects, such as enhancement of microbial grazing by protozoa. In spite of some problems with the gnotobiosis of the microcosms it was evident from the results that the amoebae enhanced nitrogen mineralization whereas mites had no measurable direct or indirect effect on the nitrogen mineralisation. No grazing effects on the microbial activity were found, since there were no significant differences in the oxygen consumption between the separate treatments.

In a litterbag experiment, the effect of soil microarthropods and enchytraeids on the decomposition of buried wheat straw was studied by selective admission and exclusion. Litterbags with 20 μm mesh size did not exclude nematodes, but did keep out microarthropods until after 27 weeks of incubation, when a major colonization, mainly by fungivorous Collembola and mites, occurred. When litterbags with a complete microarthropod community were compared to litterbags with strongly reduced microarthropod numbers, no differences between decomposition rates were found. In colonized fine mesh bags, a reduced decomposition rate was found compared to the coarse mesh litterbags, probably due to overgrazing of the fungal population by large numbers of fungivorous

microarthropods; these large numbers were probably the result of absence of predators. The results indicated that the decomposition rate is predator-controlled. Extraction of microarthropods as well as enchytraeids and nematodes from the coarse mesh litterbags showed a distinct succession during decomposition. The process was dominated in the first phase by bacterivorous nematodes, nematophagous and bacterivorous mites, and in the later phase by fungivorous nematodes, fungivorous and omnivorous mites and Collembola, and predatory mites. This succession is indicative for a transition from bacterial to fungal dominated decomposition of the buried organic matter.

Microarthropod population dynamics in arable soil were observed in a two year soil sampling scheme in a conventional and an integrated wheat field as part of the Dutch programme on Soil Ecology of Arable Farming Systems. The most abundant functional groups were omnivorous Collembola, omnivorous non-cryptostigmatic mites and predatory mites. Management practice affected the dynamics of most groups, especially soil fumigation, but these effects could not be observed from average yearly biomass values. In the food webs studied in the Netherlands (Lovinkhoeve), in Sweden (Kjettslinge) and in Georgia, USA (Horseshoe Bend), dependence of the abundance of the microarthropods on their food source could not be identified from the annual mean biomass of both. The sampling results further indicated that the microarthropod populations were able to recover rapidly from harsh management practices.

In a comparative field sampling program, soil microarthropods were sampled every three months for one year at ten sites in the northern Netherlands, varying in soil type and land use. Biomass-C $ha^{-1}$of the seven functional groups of microarthropods was calculated for the top 10 cm soil layer. Here, the four overall principal functional groups were: cryptostigmatic mites, non-cryptostigmatic mites, predatory mites and omnivorous collembolans. Possible relations between the mean annual biomass of these groups and soil type, land use or soil organic matter were studied. Microarthropod biomass was larger in sandy than in loamy soil, and generally larger in meadows than in wheat fields, the mineral layer of forest soils being intermediate. Non-cryptostigmatic mite, omnivorous Collembola and predatory mite biomass showed strong positive correlations. Cryptostigmatic mite biomass correlated with lower organic matter input quality, while omnivorous Collembola and non-cryptostigmatic mites showed a positive correlation to the amount of input. Omnivorous Collembola were negatively affected by a discontinuous input of organic matter to the soil. Relationships between functional group biomass and either soil organic matter density fractions or soil pore size distribution were only found, when the grassland sites were analyzed separately. Both analyses showed correlation patterns for Cryptostigmata to deviate from those of the other three main functional groups. Cryptostigmata showed a positive correlation with the lightest organic matter density fraction, while the non-cryptostigmatic mites and omnivorous Collembola were correlated to the heavier fractions. The Cryptostigmata correlated with the 6-90 µm pore size class, while the other three groups showed strong correlation to the 1.2-6 µm size class and the largest (> 90 µm) size class. Both observations lead to the conclusion, that

omnivorous Collembola and non-cryptostigmatic mites are related to fungal growth (in the largest pores and on the heavy organic matter fraction), while the Cryptostigmata show a more saprovorous feeding mode.

Although in none of my experiments a significant effect of the microarthropod community as a whole on the decomposition of litter or the mineralization of nitrogen, either positive or negative, could be assessed, a number of conclusions on the ecology of the microarthropod functional groups, their mutual relationships, as well as their relationships with other faunal groups in arable soil can be drawn:

1. In undisturbed situations, negative effects of microarthropods on the decomposition of organic matter are balanced by positive effects.
2. Top- down control of predatory mites on fungal browsing microarthropods and collembolans precludes the negative effects of overgrazing on litter decomposition. Among the microarthropod community, tri-trophic interactions are most important in respect to litter decomposition and nitrogen mineralization.
3. Only the most efficient microbial grazers will directly affect nitrogen mineralization. In most cases these are not microarthropods, but protozoa and nematodes.
4. Food web interactions are limited by the soil pore size distribution: grazing and predation by microarthropods will only occur in the larger soil pores; competition can only exist between groups or species of comparable body width.
5. The soil food web of agro-ecosystems can be divided into three spatially and temporally separate webs, based on three different carbon sources: the fresh organic matter web, the "old" organic matter web and the rhizosphere food web.
6. Agricultural land use directs the distribution of the main life history tactics of the microarthropods of the "old" organic matter food web towards omnivory, sexual reproduction and/or arrhenotoky and semelparity and/or seasonal iteroparity. The fresh organic matter food web is characterized by highly phoretic specialists.
7. Field samplings are useful in studying the "old" organic matter and the rhizosphere food webs and litterbags are a good tool in studying the fresh organic matter food web.

SAMENVATTING

Onder bodemmicroarthropoden worden in dit proefschrift alle vrij-levende mijten en springstaarten (collembolen) verstaan die onze bodem bevolken. Om de mechanismen te begrijpen, die de afbraak van organische stof en de mineralisatie van nutriënten beinvloeden, is kennis van de rol van de microarthropoden in het voedselweb onontbeerlijk. Het hier gepresenteerde onderzoek maakt deel uit van het "Dutch Programme on Soil Ecology of Arable Farming Systems", een geïntegreerd multidisciplinair onderzoeksprogramma, gericht op het functioneren van twee verschillend beheerde agroecosystemen: een conventioneel systeem en een zogenaamd geïntegreerd systeem. In dit kader heb ik het effect bestudeerd van microarthropoden op de afbraak van organische stof en de mineralisatie van stikstof in landbouwgrond. Ik kon hierin echter alleen een betrouwbaar inzicht krijgen, als ik hierbij ook alle relaties met andere faunagroepen in het ondergrondse voedselweb in ogenschouw nam. Voor dit doel is de bodemfauna onderverdeeld in functionele groepen: organismen met een gemeenschappelijke voedselbron en een gemeenschappelijke manier van voedselverwerking. De microarthropoden zijn onderverdeeld in zeven functionele groepen: predatore mijten, predatore springstaarten, nematode-etende mijten, omnivore springstaarten, cryptostigmate mijten, niet-cryptostigmate mijten en bacterie-etende mijten. Deze voedselweb-interacties en mogelijke effecten van microarthropoden op afbraak en mineralisatie heb ik onderzocht op drie verschillende abstractieniveau's.

In een microcosmos-experiment werden de afzonderlijke en de gecombineerde effecten van een amoebe (*Acanthamoeba* spec.) en een bacterivore mijt (*Histiostoma litorale*) op de C- en N-mineralisatie onderzocht in gesteriliseerde zavelgrond, die opgeënt was met een bacteriesuspensie en waaraan luzernemeel was toegevoegd als substraat voor de microben. Doel van het onderzoek was om de directe bijdrage van de mijten aan de N-mineralisatie te scheiden van mogelijke indirecte effecten, zoals een stimulering van de begrazing door de protozoën op de bacteriën Ondanks problemen met de gnotobiosis van de microcosmospotten, maakten de resultaten duidelijk dat de amoeben de stikstofmineralisatie stimuleerden, terwijl de mijten hier geen meetbaar direct of indirect effect op uitoefenden. Er kon geen begrazingseffect worden aangetoond op de microbiële activiteit, omdat er geen significant verschil in zuurstofconsumptie was tussen de verschillende behandelingen.

In een experiment met strooiselzakjes werd door middel van selectieve uitsluiting en toelating het effect van bodemmicroarthropoden en potwormen op de afbraak van ondergeploegd tarwestro onderzocht. Strooiselzakjes met een maaswijdte van 20 µm sloten geen nematoden uit, maar wel de microarthropoden. Echter, 27 weken na de start van de incubatie trad er op grote schaal kolonisatie van deze zakjes op met voornamelijk schimmel-etende springstaarten en mijten. Als

de controlezakjes, met een volledige microarthropoden-gemeenschap, werden vergeleken met de fijnmazige zakjes met een sterk gereduceerde gemeenschap, was er geen verschil te vinden in afbraaksnelheid. In de massaal gekoloniseerde fijnmazige zakjes werd echter een afname in afbraaksnelheid gevonden vergeleken met de grofmazige zakjes, die in de eerste waarschijnlijk veroorzaakt werd door overbegrazing van de schimmelpopulatie door de grote aantallen fungivore microarthropoden. Deze sterke populatiegroei was waarschijnlijk het gevolg van de afwezigheid van predatoren. Deze resultaten tonen een regulering van de organische stof afbraak aan door de predatoren, m. n. predatore mijten. De uit de grove strooiselzakjes verzamelde microarthropoden, vertoonden evenals de potwormen en de nematoden een duidelijke opeenvolging gedurende het afbraakproces. De eerste fase van de afbraak werd gekenmerkt door bacterie-etende nematoden, nematode-etende mijten, en bacterie-etende mijten en de latere fase door schimmel-etende nematoden, schimmel-etende en omnivore mijten en -springstaarten en roofmijten. Deze successie is kenmerkend voor de overgang van bacterieel gedomineerde naar schimmel-gedomineerde afbraak van ondergeploegde oogstresten.

Als onderdeel van het "Dutch Programme on Soil Ecology of Arable Farming Systems" is door middel van een tweejarig bemonsteringsprogramma onderzoek gedaan naar de dynamiek van de microarthropoden-gemeenschap in de bodem van een conventioneel en een geïntegreerd beheerd tarweveld. De meest voorkomende groepen waren de omnivore springstaarten, de omnivore niet-cryptostigmate mijten en de predatore mijten. De wijze van beheer beïnvloedde de dynamiek van de meeste groepen, met name de bodemontsmetting, maar deze effecten werden niet weerspiegeld door de jaarlijkse gemiddelden van de berekende biomassa's. In geen van de drie agrarische bodemvoedselwebben die beschreven zijn (Nederland: Lovinkhoeve, Zweden: Kjettslinge en Georgia, VS: Horseshoe Bend), kon een relatie tussen de microarthropoden-dichtheden en de dichtheid van hun voedsel worden afgeleid uit de gemiddelde jaarlijkse biomassa van beide. Verder toonden de bemonsteringsresultaten aan dat de microarthropoden-biomassa zich snel kon herstellen van zelfs de meest ingrijpende landbouwkundige maatregelen.

In een vergelijkend veldbemonsteringsprogramma werden iedere drie maanden op tien locaties in Noord-Nederland, die zowel in bodemtype als in grondgebruik verschilden, microarthropoden bemonsterd. Voor de zeven functionele groepen microarthropoden werd voor de bovenste 10 cm de hoeveelheid biomassa-C ha^{-1} berekend. De vier belangrijkste functionele groepen waren hier de cryptostigmate mijten, de niet-cryptostigmate mijten, de roofmijten en de omnivore springstaarten. Onderzocht werden mogelijke relaties tussen bodemtype, landgebruik, organische stof-dynamiek en het jaarlijks gemiddelde van de biomassa-C van deze functionele groepen. De microarthropoden-biomassa was groter in zandgrond dan in zavel en gewoonlijk groter in grasland dan in tarwe-akkers, terwijl de waarden voor de minerale laag van de bosbodem hier tussen in lagen. De biomassa's van niet-cryptostigmate mijten, omnivore springstaarten en roofmijten waren sterk onderling gecorreleerd. De biomassa van cryptostigmate

mijten correleerde met een kwalitatief mindere organische stof- toevoer, terwijl omnivore collembolen en niet-cryptostigmate mijten positief gecorreleerd waren met de hoeveelheid organische stof input. Omnivore springstaarten werden negatief beïnvloed door een discontinue toevoer van organische stof. Een relatie tussen de biomassa's van de functionele groepen en de bodemorganische stof-fracties, dan wel de poriegrootte-verdeling in de grond kon alleen worden gevonden als de graslandlocaties afzonderlijk werden geanalyseerd. Beide analyses toonden een afwijkend correlatiepatroon aan voor de cryptostigmate mijten, vergeleken met de andere drie belangrijke functionele groepen. Cryptostigmate mijten waren positief gecorreleerd met de lichtste organische stof fractie, terwijl de niet-cryptostigmate mijten en de omnivore collembolen gecorreleerd waren met de zwaardere fracties. De cryptostigmate mijten waren gecorreleerd met de 6-90 µm poriegrootte-klasse, maar de andere drie groepen waren juist gecorreleerd met de 1.2-6 µm en de grootste (>90 µm) klasse. Beide waarnemingen leidden tot de conclusie, dat het voorkomen van omnivore springstaarten en niet-cryptostigmate mijten samenhing met schimmelgroei (in de grotere poriën en op de zware organische stof fractie), maar dat de cryptostigmate mijten in deze grond voornamelijk saprotroof waren.

Hoewel ik in geen van mijn experimenten een significant effect, positief noch negatief, van de microarthropoden in het algemeen op de afbraak van organische stof of de mineralisatie van stikstof kon vaststellen, zijn er toch een aantal conclusies die ik kan trekken met betrekking tot de ecologie van de functionele groepen van microarthropoden, dat wil zeggen, hun onderlinge relaties en de relaties met andere functionele groepen binnen het bodemvoedselweb:

1. In ongestoorde situaties heffen de negatieve effecten van microarthropoden de positieve effecten van microarthropoden op de afbraak van organische stof op.
2. "Top-down" regulering door roofmijten van de schimmel-"browsende" mijten en springstaarten voorkomt negatieve effecten op de strooiselafbraak als gevolg van overbegrazing.
3. Alleen de meest effectieve bacteriële begrazers zijn in staat een direkt effect uit te oefenen op de stikstofmineralisatie. In de meeste gevallen zijn dit niet de microarthropoden, maar in de eerste plaats de protozoën en in de tweede plaats de nematoden.
4. Voedselweb-interacties worden beperkt door de poriegrootte-verdeling: zowel begrazing als predatie door microarthropoden kan alleen plaatsvinden in de grotere poriën; concurrentie bestaat alleen tussen groepen van vergelijkbare lichaamsgrootte.
5. Het bodemvoedselweb van agro-ecosystemen kan verdeeld worden in drie afzonderlijke, in ruimte en tijd van elkaar gescheiden voedselwebben, gebaseerd op drie verschillende koolstof- of energiebronnen: een verse organische stof-voedselweb, een "oude" organische stof-voedselweb en een rhizosfeer-voedselweb.

6. Akkerbouw leidt in de bodem in het "oude" organische stof-voedselweb tot dominantie van die microarthropoden, waarvan de overlevingsstrategieën gekenmerkt worden door omnivorie, geslachtelijke voortplanting en/of arrhenotokie en semelpariteit en/of seizoensgebonden iteropariteit. Het verse organische stof-voedsel web wordt daarentegen gekenmerkt door microarthropoden die foresie paren aan een gespecialiseerde voedselkeuze.
7. Veldbemonsteringen zijn vooral van nut bij de bestudering van het "oude" organische stof-voedselweb en het rhizosfeer-voedselweb, terwijl strooiselzakjes juist een goed instrument zijn om het verse organische stof-voedselweb te onderzoeken.

DANKWOORD

Toen ik in september 1990 als AIO begon bij de afdeling Bodembiologie van het Instituut voor Bodem-vruchtbaarheid, had ik alleen wat kennis over sluipwespen en hun oecologie en wat bodemkundige kennis in huis. Alleen dankzij de steun van al mijn collega's in Haren, heb ik dit promotieonderzoek tot een goed einde kunnen brengen. In de allereerste plaats gaat daarbij mijn dank uit naar Lijbert Brussaard, promotor en begeleider, die mij al die jaren gestimuleerd heeft en van wie ik zeer veel heb geleerd aangaande alle aspecten van de wetenschapsbeoefening, van proefopzet tot publicatie. Peter de Ruiter heeft mij mentaal vaak een steuntje in de rug gegeven. Ook zijn heldere commentaar op mijn manuscripten was voor mij van grote waarde. Veel dank ben ik ook verschuldigd aan al de medewerkers en oud-medewerkers van de afdeling, met name Monique Geurs, An Vos, Guido Hoenderboom, Meint Veninga, Edy Biewenga, Henk Velvis, Popko Bolhuis, Marieke Wolters, Kees Verhagen, Bert van der Boom en Willem Willems, die ieder op hun eigen manier mij geholpen hebben met de soms schier eindeloze hoeveelheden monsters die geteld moesten worden of door mij op geduldige wijze de nodige laboratorium- of computertechnieken aan te leren, maar meest van al door de gezellige en vriendschappelijke sfeer die zij binnen onze afdeling wisten te onderhouden, ondanks alle perikelen, waar het Instituut mee kampte.

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Arie, mijn man, die in deze jaren een flink deel van zijn vrije tijd op zag gaan aan huishoudelijke taken en Tiny Bekkema, onze trouwe oppas, die vijf jaar lang onze drie kinderen onder haar hoede nam als zij uit school of uit de crèche kwamen en die altijd bereid was om ons op onverwachte momenten uit de brand te helpen, zoals wanneer wij niet op tijd thuis konden zijn of de kinderen om welke reden dan ook niet naar school konden. Als laatste dank ik Hilde, Roel en Karin, onze kinderen, voor de manier waarop ze zich hebben aangepast aan een moeder, die bijna altijd weg was in de plaats van een moeder, die bijna altijd thuis was.

Lest best, Sasha bedankt, hè.

Den Haag, 6 april 1998

CURRICULUM VITAE

Madelein Buijs werd op 15 mei 1957 geboren in Den Haag. Na de eerste zes jaar in Voorburg gewoond te hebben, bracht zij haar gehele schooltijd door in Den Haag. waar zij aan de Thorbecke-scholengemeenschap het atheneum-diploma behaalde. In 1975 begon zij haar studie Biologie aan de Rijksuniversiteit Leiden, waar ze in 1981 afstudeerde met als hoofdvak Dieroecologie, op aut-oecologisch onderzoek aan sluipwespen. In 1980 trouwde zij met Arie Vreeken, geoloog, die in 1981 uitgezonden werd naar Jakarta, Indonesië. Door contacten te leggen via het Rijksherbarium te Leiden met in Indonesië werkzame Nederlandse biologen heeft zij daar ervaring kunnen opdoen met botanisch veldwerk in het tropenbos.

Na omzwervingen via Tunesië en Drenthe en uitbreiding van het gezin met Hilde, Roel en Karin, kwam zij in september 1990 als AIO in dienst bij de Landbouwuniversiteit Wageningen, die haar detacheerde bij het Instituut voor Bodemvruchtbaarheid, later AB-DLO, te Haren, Groningen. Als onderdeel van het Lovinkhoeve-project nam zij daar als onderdeel van het voedselweb onderzoek de mijten en springstaarten voor haar rekening. In juni 1993 nam zij tevens het bodemfauna- gedeelte van het CLIMEX- project over van haar promotor, prof. dr. L. Brussaard, die toen het Instituut verliet. CLIMEX was een internationaal onderzoeksproject naar de effecten van verhoging van de atmosferische temperatuur en het CO_2-gehalte op een compleet en ongestoord bosecosysteem in Zuid-Noorwegen. In 1995 eindigde het dienstverband als AIO, waarna zij nog van januari 1996 tot januari 1997 als toegevoegd onderzoeker verbonden was aan de leerstoelgroep Bodembiologie van de Landbouwuniversiteit in Wageningen als projectleider van de tweede fase van het bodemfauna-gedeelte van CLIMEX.