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Biomass, composition and temporal dynamics of soil organisms of a silt loam soil under conventional and integrated management

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Abstract

Field plots under conventional (CF) or integrated (IF) farming and cropped to winter wheat were sampled in 1986 for various soil organisms. Organisms were assembled in functional groups, based on their main food source and life-history characteristics. Total biomass of soil organisms was, on average, 690 kg C ha^{-1} under CF and 907 kg C ha^{-1} under IF during the growing season. Bacteria constituted more than 90 %, fungi approximately 5 %, and protozoa less than 2 % of the total biomass. Nematodes and microarthropods were less important in terms of biomass C. Carbon flow through the protozoa was estimated to be 158 and 195 kg C ha^{-1} yr^{-1} in CF and IF, respectively, corresponding to 20 % of the estimated bacterial production in both conventional and integrated farming. Nitrogen mineralization by the protozoa was estimated to be 30.5 and 37.6 kg N ha^{-1} yr^{-1} in conventional and integrated farming, respectively. Nematodes were less important than protozoa in terms of direct C and N transfer. The direct contribution from microarthropods was insignificant. Results are discussed in terms of effects of the soil biota, in particular the soil fauna, on C and N transfer in arable soil.

Keywords: bacteria, fungi, protozoa, nematodes, mites, collembola, biomass, carbon, nitrogen, soil, conventional management, integrated management

Introduction

Several areas in the Netherlands are facing environmental problems due to contamination of groundwater by nitrate and pesticides, and due to deterioration of soil structure associated with the use of heavy machinery. Apart from causing environmental problems, conventional farming (CF) is associated with high costs of

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agrochemicals and machinery, constituting a high energy demand. Integrated farming (IF) has been suggested as a new direction to overcome many problems associated with CF (e.g. Vereijken, 1986). In integrated farming, reduction of input in terms of inorganic fertilizers, pesticides and, in some cases, soil tillage will initially decrease crop production. However, in economic terms this might, to a greater or lesser extent, be offset by lower costs (Vereijken, 1989).

For the development of integrated farming basic knowledge on biological mechanisms in the functioning of the soil – crop ecosystem is needed (Brussaard et al., 1988). The Dutch Programme on Soil Ecology of Arable Farming Systems has the objective to obtain such knowledge with respect to matching the nutrient supply by the soil and the nutrient demand by crops, and with respect to enhancement of the contribution of soil organisms to soil structure formation (Brussaard et al., 1988). Field studies include collection of data on biomass of microorganisms (bacteria and fungi) and fauna (protozoa, nematodes, collembola, mites).

The Dutch Programme on Soil Ecology of Arable Farming Systems started in 1985 and the data presented in this paper relate to winter wheat in 1986. Soil fauna was assembled in functional groups, as related to their main food source and life-history characteristics. The objective of the present paper is to present and discuss the dynamics of functional groups, in CF and IF, expressed as biomass carbon, with emphasis on the role of the soil microfauna (protozoa, nematodes) and microarthropods (mites, collembola). Biomass, activity and dynamics of the soil microflora have been analysed by Hassink et al. (submitted).

Materials and methods

Field research was carried out at the experimental farm 'Dr H. J. Lovinkhoeve' (Noordoostpolder, Netherlands), which was reclaimed from the sea in 1942. The soil is a calcareous marine silt loam, with a pH-KCl of 7.5, an organic matter (OM) content of 2.3-2.8 % and a total nitrogen (N) content of 0.09-0.14 %, both depending on the history of the various trial fields. The annual rainfall is 650-800 mm. Three different types of farm management are compared: CF, IF (both since 1985) and IF with minimum tillage (since 1986). The latter will not be discussed here. The site and farm management characteristics of CF and IF were described in detail by Kooistra et al. (1989).

In 1986, data were collected from winter wheat plots under conventional management and under integrated management. Conventional management was practiced on top soil with an organic matter content of 2.3 %, integrated management on top soil with an organic matter content of 2.8 %. On both plots a four-year rotation of winter wheat — sugar beet — spring barley — potatoes was started in autumn 1985, following a six-year rotation (conventional plot) or a six-year rotation plus two-year's ley (integrated plot) during 1953-1985. On both plots, winter wheat and sugar beet were cropped in 1984 and 1985, respectively. Integrated differed from conventional in reduction of N fertilizer application to 50-60 % of the recommended dosages (from 130-285 to 65-170 kg ha^{-1} yr^{-1}, depending on crop), in drastic reduction of pesticide applications (e.g. no soil fumigation with 1,3-

Table 1. Farm management at conventional (CF) and integrated (IF) farming at the Lovinkhoeve site preceding and during growth of winter wheat in 1985/1986 (after Kooistra et al., 1989).

Management	CF	IF
Tillage		
Autumn 1985	Plough Depth: 20 cm	Fixed-tine cultivator + lifting the soil without inversion Depth: 12 cm + 8 cm
Spring 1986 (seedbed)	Spring-tine cultivator Depth: superficial	Spring-tine cultivator Depth: superficial
Fertilizer		
N	200 kg ha^{-1} [a]	155 kg ha^{-1} [a]
Crop protection		
Weed control	Mainly chemical	Mainly mechanical
Pest control	Recommended dosages of pesticides (EPIPRE system)	Less pesticides
	Soil fumigation with 1,3-dichloropropene after harvest	No soil fumigation

[a] Including the amount of soil mineral N (0-100 cm) in early spring.

dichloropropene under integrated management) and in reduction of soil tillage (20-25 cm plough in conventional, 12-15 cm plough or cultivator in integrated); see Table 1. On each sampling date (18 April, 20 June, 30 July, 19 August and 18 November 1986) samples of the top 25 cm were taken from each of three subplots (3 m^2) on CF and IF, and analysed in two separate layers (0-10 and 10-25 cm). Details of the processing of samples, determination of numbers and calculation of biomass C are given below for each group of organisms considered in this paper. Physiological parameter values needed for the calculation of the contributions of faunal groups to the transfer of C and N were adopted from Hunt et al. (1987), unless stated otherwise.

Bacteria and fungi

Samples for estimating bacteria and fungi were taken from 10 bulked cores (diameter 2.5 cm), taken randomly in each subplot. Bacteria were counted in europium-chelate-stained soil smears using a Zeiss epifluorescence microscope (magnification × 1000) equipped with a HBO-50 mercury lamp. A 1:10 diluted soil suspension was homogenized in a blender for 30 seconds at full speed. Of the sus-

pension 10 μl were fixed on a microscope slide and stained with europium chelate solution for 2 hours (Anderson & Westmoreland, 1971). The slides were rinsed with 50 % ethanol, air-dried and mounted with Eukitt synthetic resin.

Bacteria were grouped into two size classes: length < approximately 1 μm, and length > 1 μm. A dry weight mass:volume ratio of 0.8 was assumed for bacterial biomass calculations and a carbon content of 40 % of the dry mass was used for calculating the total amount of carbon in the biomass (van Veen & Paul, 1979).

Fungal biomass was estimated by measurements of hyphal length and diameter using a Zeiss epifluorescence microscope (magnification × 100) equipped with a HBO-50 mercury lamp. Measurements were performed in agar films, made by mixing 1 ml of a 1:10 diluted soil suspension and 9 ml of agar, stained with fluorescent brightener No. F-6259 (Sigma, St. Louis, MD). After staining for 20 minutes the slides were rinsed with 50 % ethanol. A conversion factor of 0.33 (ratio between dry mass and wet volume) was used for biomass calculations and a carbon content of 40 % of the dry weight (van Veen & Paul, 1979).

N mineralization was determined by measuring the increase in mineral N after incubation of mixed and sieved soil samples at various temperatures for 5 weeks. Mineral N was measured after extraction with 1N KCl solution for 1 hour using a soil:water ratio of 1:2.5.

Protozoa

Soil sampling was similar to that for bacteria. Protozoa were enumerated by the most probable number (MPN) method after Darbyshire et al. (1974), using two-fold dilution series in Prescott and James' (P&J) medium (Prescott & James, 1955) and *Pseudomonas fluorescens* as food bacterium. Subsamples, containing 50 g of soil, were mixed thoroughly in 500 ml P&J and subsequently diluted in microtiter plates. The number of flagellates, amoebae and ciliates originally present in soil were estimated from MPN data using a GENSTAT computer programme. The C and N contents of flagellates and amoebae were estimated from the cell numbers using the following assumptions (Band, 1959; Heal, 1971; Sinclair et al., 1981; Frey et al., 1985; Hunt et al., 1987):

— cells were spherical with diameters of 3 and 7 μm for flagellates and amoebae, respectively;
— specific density = 1;
— dry mass = 20 % of wet mass;
— C content = 50 % of dry mass;
— C/N ratio = 7.

Nematodes

Three soil samples of approximately 120 g each were taken randomly per subplot with a drill (diameter 2.5 cm) and stored in closed jars at 4 °C until nematodes were isolated, within a few weeks after sampling. Nematodes were isolated from 100 g field moist soil by elutriation (Oostenbrink, 1960), allowed to move through a nema-

tode filter in 24 hours and stored in 150 ml demineralized water at 5 °C. Nematode suspensions were homogenized by bubbling air through the water and numbers were counted in triplicate in 2 ml suspension under a stereo microscope. Sixty specimens per sample were identified to variable taxonomic levels under a high power microscope. Taxa were combined to four different feeding categories (functional groups): bacterivorous, omnivorous, fungivorous and phytophagous nematodes. Results from 9 samples per plot were averaged. The average nematode density and taxonomic composition in the plough layer (0-25 cm) was calculated from the information on the two soil layers 0-10 and 10-25 cm.

Numbers per 100 g of field moist soil were multiplied by 3.25×10^7 for transformation to numbers per ha. Individual fresh mass of the representatives of functional groups was taken from Sohlenius & Sandor (1987). For transformation to amount of C per ha, numbers were multiplied by the specific mass of nematodes for each functional group assuming a carbon content of 10 % of the fresh mass (Jensen, 1984).

Microarthropods

Soil cores (6 cm diameter and 25 cm depth; three cores on each of three subplots on IF, two on each of three subplots on CF) were taken with a metal split-corer and transferred undisturbed to the laboratory in insulated containers. Five layers of 2.5 cm per core (0-2.5, 2.5-5, 7.5-10, 15-17.5 and 22.5-25 cm) were inverted and extracted intact for 10 days using a modified MacFadyen high-gradient system (Andrén, 1985). Microarthropods were collected in picric acid, sorted, mounted in Gisin's fluid (Gisin, 1960), identified to species or family level and counted. According to the literature (Walter, 1987; Moore et al., 1988; Walter et al., 1988) and our own observations seven functional groups were defined as: fungivorous collembola, predaceous collembola, bacterivorous mites, nematophagous mites, chewing mites (mainly Oribatida), piercing mites (mainly Prostigmata) and predaceous mites. Some groups are not distinguished as such in the literature and therefore deserve explanation. *Histiostoma litorale* is an anoetid mite with enlarged membraneous palps and chelicerae which rapidly move in and out of the liquid substrate, together facilitating an almost filter-feeding mode of food intake. The species may be mainly bacterivorous (Stammer, 1959) and constitutes the functional group bacterivorous mites. *Alliphis halleri* is a mesostigmatid mite which specializes on nematodes (Sardar & Murphy, 1987). This species largely constitutes the functional group nematophagous mites. Although collembola are generally considered fungivorous, many species are known to prey on nematodes as well (Walter, 1987). *Friesea mirabilis* is exceptional among collembola in that it is considered to be mainly predaceous (Petersen, 1971). This species constitutes the functional group predaceous collembola. Under the microscope (magnification 100×) the mean length per taxon was determined, from which the dry mass was calculated (Edwards, 1967) per taxon and per functional group. The amount of carbon per ha was calculated per functional group, depth (0-10 cm and 10-25 cm) and sampling date, using a C/N ratio of 8.

Results

The amounts of biomass C in the various functional groups on the five sampling dates are given in Figure 1, separately for CF and IF, and the layers 0-10 and 10-25 cm.

Bacteria and fungi

Bacteria constituted by far the largest biomass pool. Fungi only represented approximately 5 % of the microbial biomass. Both bacterial and fungal biomass were greater in IF than in CF (Fig. 1a), which is probably related to the higher organic matter content of IF (Table 2; Schnürer et al., 1985). No consistent pattern in the depth distribution of microbial biomass was apparent on CF, whereas on most dates relatively more microbial biomass was found in the top 10 cm than in the 10-25 cm layer of IF. This is probably related to the shallow (12 cm) tillage on IF with no inversion, as a result of which crop residues remained near the surface.

The fourth sampling date (19 August) coincided with the date of harvest at the end of a dry summer period which began in mid June (Fig. 2). The drought resulted in very low moisture contents of the top soil in both plots and probably led to the low microbial biomass on 19 August (Fig. 3; Elliott et al., 1984; Schnürer et al., 1986; Granatstein et al., 1987).

Assuming a turnover rate of 1.2 yr^{-1}, the bacterial production has been 751 kg C ha^{-1} on CF and 996 kg C ha^{-1} on IF.

Protozoa

At the Lovinkhoeve site the protozoan pool was 10.5 kg C ha^{-1} on CF and 13 kg C ha^{-1} on IF. In all cases amoebae had a higher biomass than flagellates (Fig. 1b). The number of ciliates was below the detection limit of the most probable number technique. There was no consistent pattern in the depth distribution on either CF or IF. Assuming steady-state, a population turnover rate of 6 yr^{-1}, and a yield of C of 40 %, the consumption of C by the protozoa in the top 25 cm was estimated to be 158 kg C ha^{-1} yr^{-1} on CF and 195 kg C ha^{-1} on IF. This corresponded to approximately 20 % of the bacterial production on CF and IF. Assuming a C:N ratio of bacteria of 4 and a C:N ratio of protozoa of 7, the protozoan contribution to the mineralization of N in the top 25 cm was estimated to be 30.5 and 37.6 kg N ha^{-1} yr^{-1} in CF and IF, respectively. Fig. 4 shows the potential nitrogen mineralization rates in the 0-25 cm layer, based on laboratory incubations. The rates range between 53 and 136 kg N ha^{-1} yr^{-1} on CF and between 113 and 265 kg N ha^{-1} yr^{-1} on IF. The estimates of the protozoan contribution to nitrogen mineralization hence range between 22.5 and 57.5 % on CF and between 14 and 33 % on IF.

Nematodes

At the Lovinkhoeve site the nematode pool represented approximately 0.9 kg C

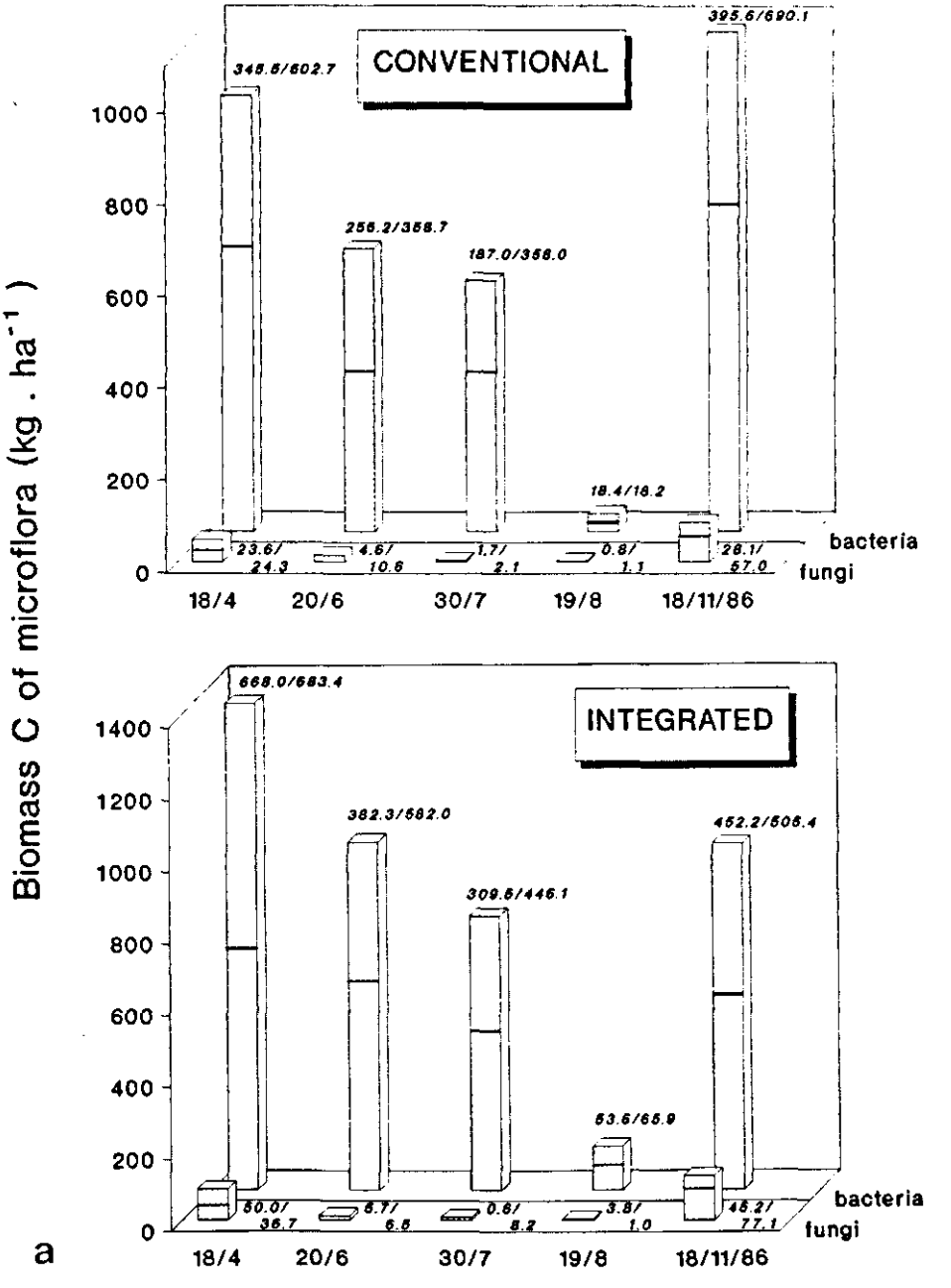

Fig. 1. Biomass C of various functional groups of soil organisms on winter wheat plots under conventional or integrated management in 1986. Figures near bars represent biomass C in the 0-10 (upper parts of bars) and 10-25 cm (lower parts of bars) layers, respectively. (a) Bacteria and fungi. Mind different scales of Y-axes.

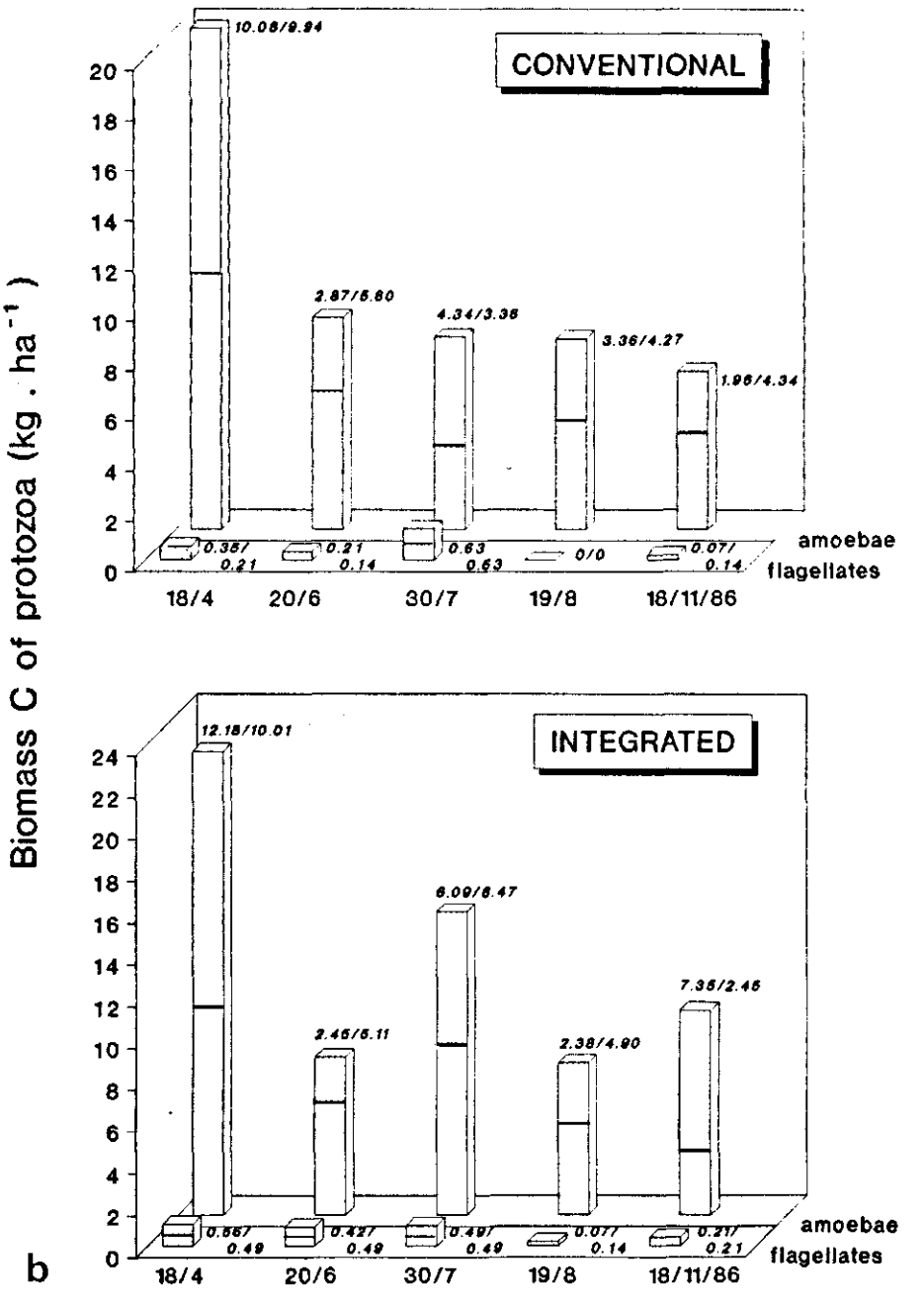

Fig. 1 continued. (b) Protozoa. Mind different scales of Y-axes.

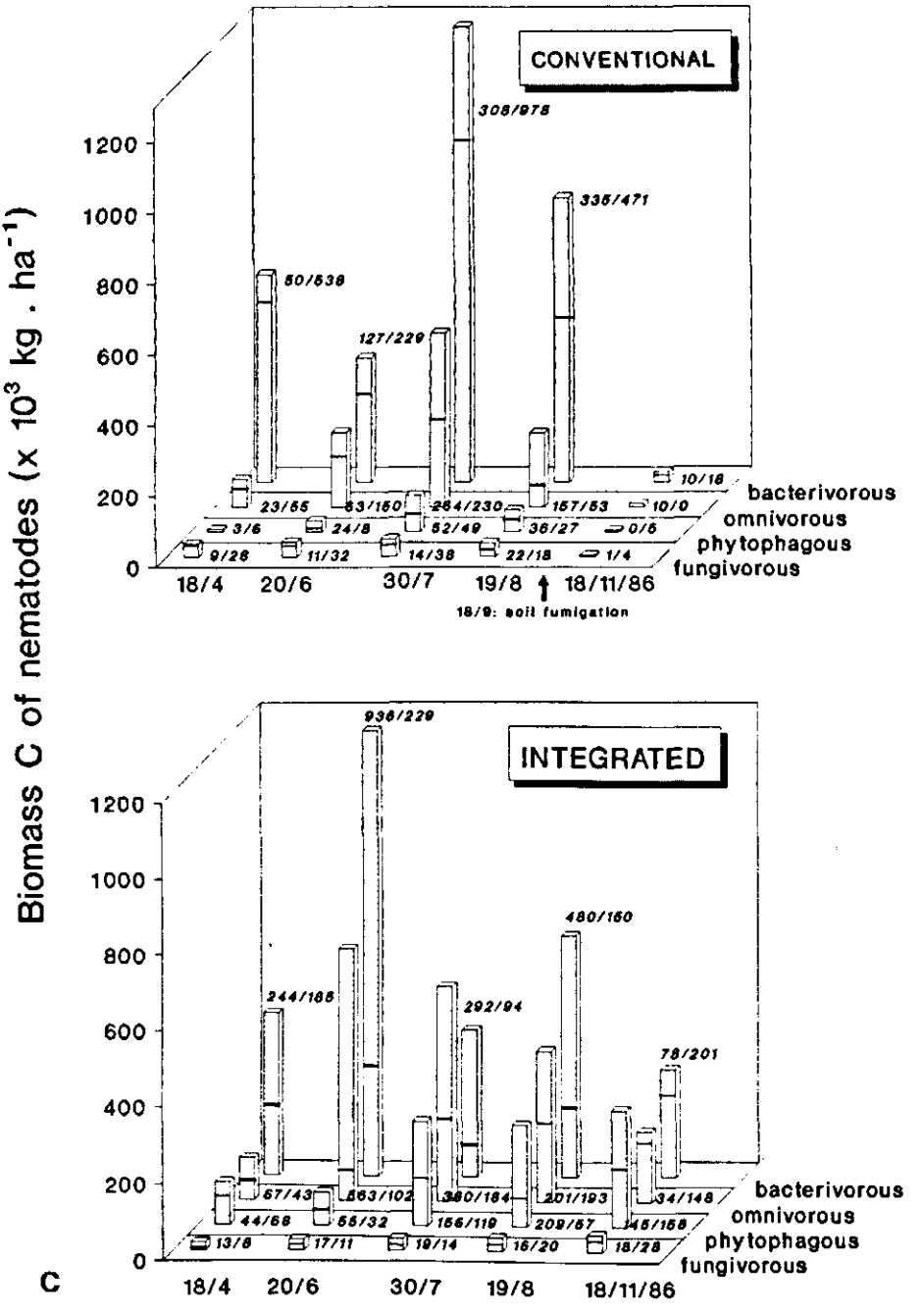

Fig. 1 continued. (c) Nematodes.

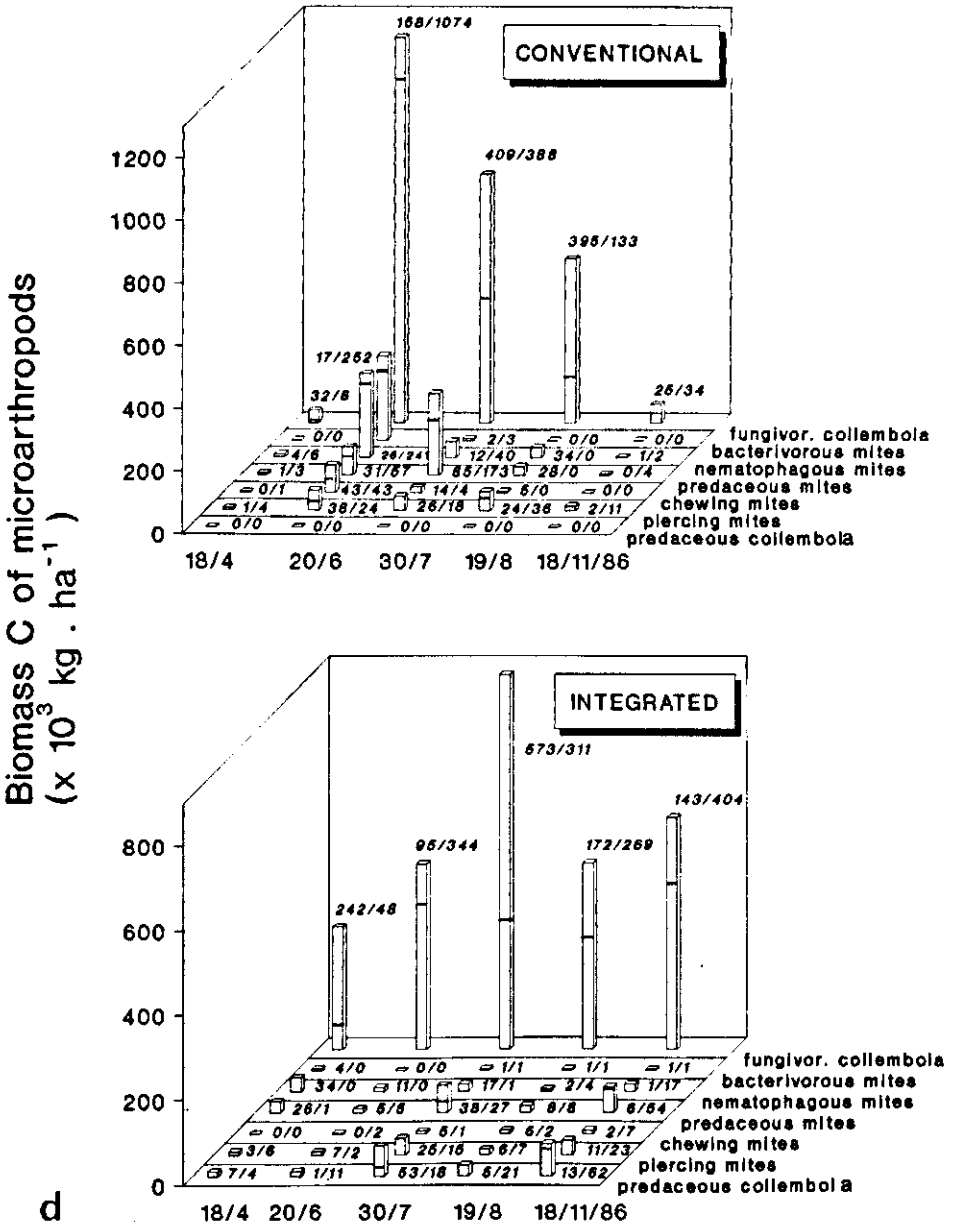

Fig. 1 continued. (d) Microarthropods. 'Chewing mites' mainly refers to Oribatida, 'piercing mites' to Prostigmata. Mind different scales of Y-axes.

Table 2. Organic matter content (%) and input of organic matter (kg ha^{-1}) immediately prior to and during growth of winter wheat at the Lovinkhoeve site, at conventional (CF) and integrated (IF) farming in 1986. SDOM = stable dead organic matter.

	CF	IF
Organic matter content (%)		
Depth (cm): 0-10	2.09	2.67
Depth (cm): 10-25	2.12	2.81
Input of organic matter (kg ha^{-1})		
Previous crop[1]	500	4500
Exudation from wheat[2]	1940	1900
Degradation of SDOM[3]	1370	1750
Total	3810	8150
Total carbon (50 %)	1905	4075

[1] Sugar beet, input was different for CF and IF: CF obtained roots only, whereas IF also obtained leaves.
[2] Assumed to be 10 % of primary production (Woldendorp, 1981).
[3] Degradation of SDOM assumed to be 2 % per year (Kortleven, 1963); CF < IF, because of somewhat higher organic matter content in IF plots.

ha^{-1} in CF and 1.2 kg C ha^{-1} in IF. The nematode fauna was dominated by bacterivores and omnivores on CF, while on IF phytophagous nematodes were almost as abundant as omnivores (Fig. 1c). Because omnivorous nematodes, mainly consisting of Dorylaimida, are considered to feed largely on bacteria, bacteria were the main food source for the nematodes. There was a marked difference between CF and IF in the depth distribution of bacterivores and, to a lesser extent, fungivores, their numbers being higher in the top 10 cm in IF and in the 10-25 cm layer in CF, whereas in both CF and IF numbers of phytophagous and omnivorous nematodes were highest in the upper soil layer. The bacterivores were dominated by Rhabditidae, which are indicative of degrading fresh organic matter under moist conditions (Southey, 1982). Their depth distribution reflected the distribution of residues of the previous crop as affected by soil tillage: shallow without soil inversion under IF and ploughed down under CF (Table 1). Rhabditidae and the also bacterivorous Monhysterida showed considerable fluctuations in numbers (data not shown). The other taxa fluctuated either with a smaller amplitude (fungivores) or increased gradually in number parallel to crop development (bacterivorous Cephalobidae and Panagrolaimidae, and phytophagous nematodes). Soil fumigation in autumn wiped out the nematode fauna almost completely, irrespective of taxon.

Although differently distributed over the two soil layers sampled, bacterivores and fungivores under IF were not different in biomass from those under CF. Phytophagous nematodes (mainly *Paratylenchus* and *Rotylenchus/Helicotylenchus*) and omnivores, however, were more abundant under IF throughout the 1986 sea-

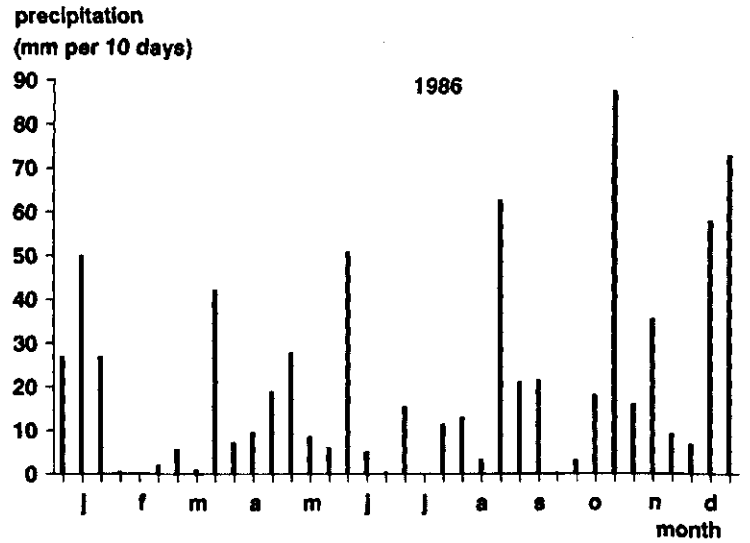

Fig. 2. Precipitation at the Lovinkhoeve experimental farm during 1986.

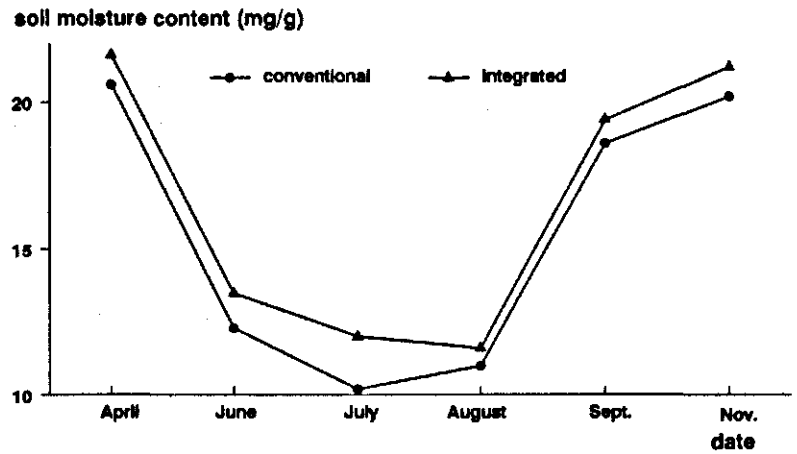

Fig. 3. Soil moisture content of the top 25 cm of the conventional and the integrated plot during 1986.

son. Assuming a population turnover rate of 10 yr^{-1} (Sohlenius et al., 1988), an assimilation efficiency of 0.6 and a production efficiency of 0.37, the consumption of C by the nematodes was estimated to be 40.5 kg C ha^{-1} yr^{-1} on CF and 54.1 kg C on IF in the top 25 cm, which corresponds to 5.4 % of the bacterial production on CF and IF.

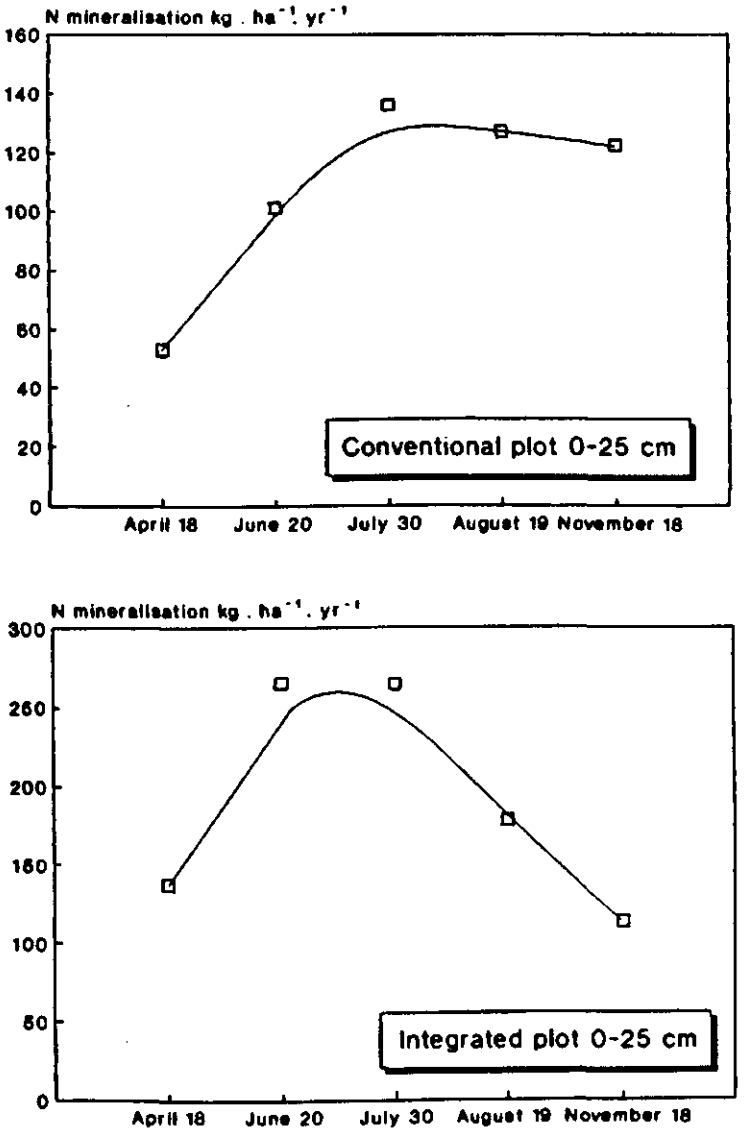

Fig. 4. Potential nitrogen mineralization rates during 1986. Mind the different scales of the Y-axes.

Assuming a C:N ratio of bacteria of 4 and a C:N ratio of nematodes of 10, the nematode contribution to the mineralization of N in the top 25 cm was estimated to be 2.0 and 2.7 kg N ha^{-1} yr^{-1}, respectively. The estimates of the nematode contribution to nitrogen mineralization (Fig. 4) hence range between 1.5 and 3.8 % on CF and between 1.0 and 2.4 % on IF.

Microarthropods

Microarthropods (mites and collembola) constituted a small fraction of the total biomass at the Lovinkhoeve site on both CF and IF. It would seem, however, that the soil fumigation in autumn on CF has had marked side-effects on the microarthropods.

Microarthropods were dominated by fungivorous collembola. They showed no consistent pattern in depth distribution, except for the nematophagous mites, which reflected the distribution of the nematodes (Fig. 1c, d). Although the differences in biomass of functional groups between CF and IF were not large, there were marked differences between the abundances of various taxa (Table 3), some of which constitute separate functional groups as mentioned in the M&M section. Based on their low biomass, generally low turnover rates and low assimilation efficiencies, the microarthropods had little direct contribution to C and N transfer on CF or IF.

Table 3. The 12 most abundant taxa of mites and collembola from the layers 0-5, 7.5-10, 15-17.5 and 22.5-25 cm below the surface of CF and IF. Sums of six soil cores (diameter 6 cm) per date per field. For numbers per m² multiply by 59.

Taxon		18 Apr	19 Jun	30 Jul	19 Aug	18 Nov	Total
Associated with CF							
Hypogastrura denticulata	CF	0	25	137	251	21	434
	IF	0	6	2	1	0	9
Arctoseius cetratus	CF	0	71	63	20	0	154
	IF	0	3	1	0	1	5
Histiostoma litorale	CF	4	501	59	9	0	573
	IF	24	11	23	11	21	90
Folsomia candida	CF	2	237	68	38	6	351
	IF	18	9	16	4	18	65
Tarsonemidae	CF	4	8	23	60	17	113
	IF	2	1	10	4	11	28
Alliphis halleri	CF	8	150	34	39	2	233
	IF	40	13	20	5	10	88
Pyemotidae	CF	10	144	80	196	23	453
	IF	7	20	88	34	89	238
Eupodidae	CF	1	100	55	27	3	186
	IF	5	11	52	13	21	102
Associated with IF							
Onychiurus armatus	CF	6	21	61	4	0	92
	IF	34	47	170	31	56	291
Tullbergia krausbaueri	CF	3	16	16	46	8	89
	IF	16	15	115	99	151	396
T. quadrispina	CF	1	0	0	0	0	1
	IF	24	2	16	19	45	106
Friesea mirabilis	CF	0	0	0	0	0	0
	IF	9	4	55	8	35	111

Discussion

Our results will be briefly discussed by comparison with the literature. Subsequently, a more elaborate discussion follows on the structure and functioning of the soil ecosystem under conventional and integrated farming at the Lovinkhoeve site.

Comparison with the literature

Our biomass C estimates of all groups collected at the Lovinkhoeve site were within the range published in the literature (Table 4) and our estimates of C and N transfer by the fauna agree with those published in the literature (Hendrix et al., 1986, 1987; Ingham et al., 1986; Hunt et al., 1987; Sohlenius et al., 1988; Andrén et al., 1990). Fungal biomass was low at the Lovinkhoeve site, in contrast to the Kjettslinge site (Table 4) although the methods of biomass determination used were the same. The

Table 4. Total organism biomass carbon and biomass of microfloral and faunal groups as percentages of total biomass carbon in arable soils at different sites under different management systems (n.d. = not determined).

	A		B	C	D		E		F	
	CF	IF			CT	NT	BO	B120	SM	NT
Total biomass carbon (kg C ha⁻¹)	690	907	609	554	910	740	2360	3050	235	273
Organisms (%)										
Bacteria	93.59	91.47	75.3	47.6	76	59.5	29.7	29.5	99	99
Fungi	4.46	5.18			16.5	21.5	63.6	68.9		
Protozoa	1.52	1.43	24.6	52.3	5.5	5.4	5.9	1.0	0.6	0.6
Nematodes	0.13	0.13	0.01	0.00	0.22	0.14	0.05	0.03	0.3	0.3
Microarthropods	0.11	0.07	0.06	0.03	0.08	0.27	0.02	0.01	0.06	0.09
Macroarthropods	0.04	0.00	n.d.	n.d.	0.01	0.03	0.05	0.01	n.d.	n.d.
Enchytraeids	0.11	0.06	n.d.	n.d.	0.03	0.07	0.18	0.12	n.d.	n.d.
Earthworms	0.00	1.65	n.d.	n.d.	2.2	13.5	0.47	0.45	n.d.	n.d.

A. Lovinkhoeve site, The Netherlands, Typic Fluvaquent, silt loam, 0-25 cm, spring/summer, winter wheat.
B. Ellerslie, Alberta, Canada, Black Chernozem, silt clay loam, 0-10 cm, barley, summer/autumn (Rutherford & Juma, 1989).
C. Breton, Alberta, Canada, Gray Luvisol, silt loam, 0-10 cm, barley, summer/autumn (Rutherford & Juma, 1989).
D. Horse Shoe Bend site, Athens, Georgia, USA, Hiwassi loam, Typic Rhodudult, sandy clay loam, 0-15 cm, winter/spring, grain/rye (Hendrix et al., 1986; 1987).
E. Kjettslinge site, Sweden, mixed, frigid Haplaquoll, loam, 0-27 cm, barley, 1982-1983 (Andrén et al., 1988; Andrén et al., 1990).
F. Akron, Colorado, USA, Mollisol, 0-10 cm, fallow/wheat, summer (Elliott et al., 1984).
CF = conventional management, IF = integrated management, CT = conventional tillage, NT = no tillage, BO = no N-fertilizer, B120 = 120 kg N fertilizer ha⁻¹, SM = stubble mulch.

low biomass of fungivores at the Lovinkhoeve site (Fig. 1) is consistent with the low biomass of fungi. Although it is generally assumed that microorganisms disperse well, this may not hold for many fungi (cf. Christensen, 1989) and the low fungal biomass may reflect the recent reclamation of the Lovinkhoeve site (1942) from the sea. The rather high pH of the soil (pH-KCl 7.5) is not conducive to a high fungal biomass, either. Hendrix et al. (1986, 1987) hypothesized that changing from conventional tillage to no-tillage would result in a relatively higher biomass of fungi and fungivorous animals. Data from both the Lovinkhoeve and the Horse Shoe Bend sites, however, so far indicate that bacteria remain to be the most important decomposers under various types of soil management. Amoebae were higher in biomass than flagellates which was also found in Sweden by Clarholm (1989).

Structure of the soil ecosystem in CF and IF

In this study, integrated farming (IF) differed in three important aspects from conventional farming (CF) and the results will be discussed in the context of those differences:

1. The IF plot had a higher *organic matter content* and received more *crop residues* than the CF plot. The higher bacterial and fungal biomass on IF reflects these differences.
2. The relatively higher amount of microbial biomass in the top 10 cm than in the 10-25 cm layer on IF is associated with the shallow, non-inversion *tillage* on IF, which kept crop residues in the top layer. The absence of such a difference on CF is associated with the more even distribution of crop residues in the top 25 cm by ploughing. The higher biomass of bacterivorous nematodes in the top 10 cm on IF, as compared with the 10-25 cm layer, is consistent with the depth distribution of the bacterial biomass on IF. Although no clear pattern in the depth distribution of the bacterial biomass on CF was apparent, the higher biomass of bacterivorous nematodes in the 10-25 cm layer on CF, as compared with the top 10 cm, is not at variance with the soil tillage (ploughing down of crop residues) on CF. The depth distribution of nematophagous mites is consistent with that of the most abundant nematodes, the bacterivores.
3. Considerably less *pesticides* were applied on IF than on CF, the most important difference being the omission of soil fumigation on IF. Soil fumigation on CF was directed against phytophagous nematodes, in particular potato cyst nematodes. This treatment, however, also wiped out other nematode groups and may have been among the causes by which microarthropods were decreased on the last sampling date on CF. Phytophagous nematodes were, however, lower in biomass on CF than on IF throughout the season and not only following soil fumigation. This may relate to a long-term effect of soil fumigation. Phytophagous nematodes have relatively long generation times and will hence recover more slowly from soil disinfestations than other nematodes.

The organisms of most of the functional groups were not identified to the genus or species level. In the few cases where this was done, however (microarthropods), marked qualitative and quantitative differences between the fauna on CF and IF be-

came apparent (Table 3). Statistical analysis of the biomass dynamics of functional groups of the microflora, defined according to their ability to decompose a range of chemicals, showed that the characteristics of the microfloral populations changed considerably in time in both CF and IF, the differences within plots generally being greater than between plots (Hassink et al., submitted). Taking bacteria and fungi as two functional groups, Moore et al. (1990) designed food webs of CF and IF plots on the basis of the functional groups defined in this paper and they statistically analysed the food webs to identify patterns in the way species interact. The food web in CF differs from that in IF by the absence of predaceous collembola and by the near non-existence of the phytophagous nematodes. The analysis showed that the webs can be compartmented into a bacterial and a fungal channel, the degree of compartmentalisation depending on farm management: under integrated management consumers of fungi were separated in time from consumers of bacteria, as were fungi and bacteria themselves, whereas little separation was observed under conventional management (Moore et al., 1990).

Hence, the available evidence indicates that the structure of the soil ecosystem shows considerable differences between CF and IF, both in depth and in time. These differences are associated with the main differences in management.

Functioning of the soil ecosystem under CF and IF

At first sight, despite the differences in structure of the soil ecosystems under CF and IF, there seems to be remarkable similarity in their functioning. The ratio CF:IF for organic matter content, bacterial biomass, protozoan biomass and bacterivorous plus omnivorous nematodes in the 0-25 cm layer was approximately 0.8 in all cases; the estimated protozoan consumption of C corresponded to 20 % of the estimated bacterial production in both CF and IF; the estimated nematode consumption of C corresponded to 5.4 % of the estimated bacterial production in both CF and IF. Based on our estimates of the faunal contribution to the C and N transfer, protozoa were quantitatively important as were, to a lesser extent, nematodes. Yet, the validity of estimates made by us and others of the contribution of the soil biota to the transfer of C and N, although based on the best available knowledge, may be limited by various factors:

1. The steady-state assumption. Calculations of rates of C and N transfer are based on average biomass of functional groups. The biomass, however, is fluctuating (Fig. 1) and so are the transfer rates of C and N by various groups of soil organisms. The timing of mineralization is crucial for the improvement of the nutrient use efficiency and more realistic modelling of transfer rates, and comparison between CF and IF is needed.
2. Not only *when* nutrients become available (synchronization of supply by the soil and demand by the plant) but also *where* they become available is important (synlocalization of supply by the soil and rooting by the plant). Simulation modelling has shown that disproportionally more material flow occurred in the upper 10 cm than in the 10-25 cm layer in IF, whereas no such difference occurred in CF (Moore et al., 1990).

3. The reliability of physiological parameters. Because assessment of physiological parameters is tedious, we relied on published values, e.g. those listed by Hunt et al. (1987). To mention only one example, turnover rates of populations are in fact nominal death rates, i.e. the inverses of the mean life spans of organisms dying because of physiological ageing. This may be realistic for protozoa, but not for nematodes and most of the other functional groups because predators contribute considerably to their death rates. For nematodes, turnover rates and, thereby, their contribution to C and N transfer, may be four times higher than assumed hitherto, because nematophagous fungi are an important death factor (Bouwman, unpublished results). Moreover, and perhaps more important in terms of comparing CF and IF, turnover rates of a functional group may be different under different management systems, e.g. depending on the quality of the added organic materials.
4. Indirect effects of the soil fauna. Indirect effects include faunal stimulation of the microflora by comminution of organic residues and enhancing the specific metabolic activity of microbial cells that escape grazing by microbivores. Evidence of such effects has been reviewed by e.g. Seastedt (1984), Moore et al. (1988), Verhoef & Brussaard (1990), and Zwart & Brussaard (1990). Indirect contributions of the fauna to C and N transfer are calculated as part of the contribution of the microflora. If such indirect effects are quantitatively important, the contribution of the fauna to C and N transfer is underestimated. Interpretation of indirect effects is, however, hampered by a lack of causal insight in the mechanisms involved. Such insight is needed to appropriately fit saprovorous animals such as enchytraeids, earthworms and various macroarthropods (Table 4) into current detritus-based food webs.

To conclude, the structure of the soil ecosystem and, given the right level of observation, the functioning of the soil ecosystem differed between CF and IF as related to the different management practices. To the extent that our knowledge of the structure and functioning of agro-ecosystems increases, our understanding will increase on how to manage the soil biota towards a higher efficiency in integrated farming, i.e. to let the soil work for us sensu Elliott & Coleman (1988). The abovementioned limitations to our understanding and, hence, to our management skills, have defined the scope of our current research.

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References

Anderson, J. R. & D. Westmoreland, 1971. Direct counts of soil organisms using a fluorescent brightener and a europium chelate. *Soil Biology and Biochemistry* 3: 85-87.

Andrén, O., 1985. Microcomputer-controlled extractor for soil microarthropods. *Soil Biology and Biochemistry* 17: 27-30.

Andrén, O., K. Paustian & T. Rosswall, 1988. Soil biotic interactions in the functioning of agroecosystems. *Agriculture, Ecosystems and Environment* 24: 57-67.

Andrén, O., T. Lindberg, U. Boström, M. Clarholm, A.-C. Hansson, G. Johansson, J. Lagerlöf, K. Paustian, J. Persson, R. Petterson, J. Schnürer, B. Sohlenius & M. Wivstad, 1990. Organic carbon and nitrogen flows. In: O. Andrén, T. Lindberg, K. Paustian & T. Rosswall (Eds), Ecology of arable land — organisms, carbon and nitrogen-cycling. *Ecological Bulletins* 40: 85-126.

Band, R. N., 1959. Nutritional and related biological studies on the free-living soil amoeba, *Hartmannella rhysodes*. *Journal of General Microbiology* 21: 80-95.

Brussaard, L., J. A. van Veen, M. J. Kooistra & G. Lebbink, 1988. The Dutch programme on soil ecology of arable farming systems. I. Objectives, approach and some preliminary results. *Ecological Bulletins* 39: 35-40.

Christensen, M., 1989. A view of fungal ecology. *Mycologia* 81: 1-19.

Charholm, M., 1989. Effects of plant-bacterial-amoebal interactions on plant uptake of nitrogen under field conditions. *Biology and Fertility of Soils* 8: 373-378.

Darbyshire, J. F., R. E. Wheatley, M. P. Greaves & R. H. E. Inkson, 1974. A rapid method for estimating bacterial and protozoan numbers in soil. *Révue d'Écologie et de Biologie du Sol* 11: 465-475.

Edwards, C. A., 1967. Relationships between weight, volumes and numbers of soil animals. In: O. Graff & J. J. Satchell (Eds), Progress in soil biology, p. 585-591. Proc. Coll. Dynamics of Soil Communities. North Holland Publishing Company, Amsterdam.

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

Elliott, E. T., K. Horton, J. C. Moore, D. C. Coleman & C. V. Cole, 1984. Mineralization dynamics in fallow dryland wheat plots, Colorado. *Plant and Soil* 76: 149-155.

Frey, J. S., J. F. McClellan, E. R. Ingham & D. C. Coleman, 1985. Filter-out-grazers (FOG): a filtration experiment for separating protozoan grazers in soil. *Biology and Fertility of Soils* 1: 73-79.

Gisin, H., 1960. Collembolenfauna Europas. Muséum d'Histoire Naturelle, Genève.

Granatstein, D. M., D. F. Bezdicek, V. L. Cochran, L. F. Elliott & J. Hammel, 1987. Long-term tillage and rotation effects on soil microbial biomass, carbon and nitrogen. *Biology and Fertility of Soils* 5: 265-270.

Heal, O. W., 1971. Protozoa. In: J. Phillipson (Ed.), Methods of study in quantitative soil ecology: population, production and energy flow. IBP Handbook No 18, p. 51-71. Blackwell Scientific Publications, Oxford/Edinburgh.

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

Hendrix, P. F., D. A. Crossley Jr., D. C. Coleman, R. W. Parmelee & M. H. Beare, 1987. Carbon dynamics in soil microbes and fauna in conventional and no-tillage agroecosystems. *INTECOL Bulletin* 15: 59-63.

Hunt, H. W., D. C. Coleman, E. R. Ingham, R. E. Ingham, E. T. Elliott, J. C. Moore, S. L. Rose, C. P. P. Reid & C. R. Morley, 1987. The detrital food web in a shortgrass prairie. *Biology and Fertility of Soils* 3: 57-68.

Ingham, E. R., J. A. Trofymow, R. N. Ames, H. W. Hunt, C. R. Morley, J. C. Moore & D. C. Coleman, 1986a. Trophic interactions and nitrogen cycling in a semi-arid grassland soil. I. Seasonal dynamics of the natural populations, their interactions and effects on nitrogen cycling. *Journal of Applied Ecology* 23: 597-614.

Ingham, E. R., J. A. Trofymow, R. N. Ames, H. W. Hunt, C. R. Morley, J. C. Moore & D. C. Coleman, 1986b. Trophic interactions and nitrogen cycling in a semi-arid grassland soil. II. System responses to removal of different groups of soil microbes or fauna. *Journal of Applied Ecology* 23: 615-630.

Jensen, P., 1984. Measuring carbon content in nematodes. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 38: 83-86.

Kooistra, M. J., G. Lebbink & L. Brussaard, 1989. The Dutch programme on soil ecology of arable farming systems. II. Geogenesis, agricultural history, field site characteristics and present farming systems at the Lovinkhoeve experimental farm. *Agriculture, Ecosystems and Environment* 27: 361-387.

Kortleven, J. K., 1963. Quantitative aspects of humus formation and humus degradation. (In Dutch). Verslagen Landbouwkundige Onderzoekingen 69.1, 109 pp.

Moore, J. C., D. E. Walter & H. W. Hunt, 1988. Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. *Annual Review of Entomology* 33: 419-439.

Moore, J. C., H. J. C. Zwetsloot & P. C. de Ruiter, 1990. Statistical analysis and simulation modelling of the belowground food webs of two winter wheat management practices. *Netherlands Journal of Agricultural Science* 38: 303-316.

Oostenbrink, M., 1960. Estimating nematode populations by some selected methods. In: J. N. Sasser & W. R. Jenkins (Eds), Nematology, p. 196-205. University of North Carolina Press, Columbia.

Petersen, H., 1971. Collembolernes ernaeringbiologi og dennes økologiske betydning. *Entomologiske Meddelelser* 39: 97-118.

Prescott, D. M. & T. W. James, 1955. Culturing of *Amoeba proteus* on *Tetrahymena*. *Experimental Cell Research* 8: 256-258.

Rutherford, P. M. & N. G. Juma, 1989. Dynamics of microbial biomass and soil fauna in two contrasting soils cropped to barley (*Hordeum vulgare* L.). *Biology and Fertility of Soils* 8: 144-153.

Sardar, M. A. & P. W. Murphy, 1987. Feeding tests of grassland soil-inhabiting gamasine predators. *Acarologia* 18: 117-121.

Schnürer, J., M. Clarholm & T. Rosswall, 1985. Microbial biomass and activity in an agricultural soil with different organic matter contents. *Soil Biology & Biochemistry* 17: 611-618.

Schnürer, J., M. Clarholm, M. Boström & T. Rosswall, 1986. Effects of moisture on soil microorganisms and nematodes: a field experiment. *Microbial Ecology* 12: 217-230.

Seastedt, T. R., 1984. The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology* 29: 25-46.

Sinclair, M. J., J. F. McClellan, J. L. Sinclair & D. C. Coleman, 1981. Yield constant for *Acanthamoeba polyphaga* in batch and continuous culture. *Journal of Protozoology* 28: 479-483.

Sohlenius, B. & A. Sandor, 1987. Vertical distribution of nematodes in arable soil under grass (*Festuca pratensis*) and barley (*Hordeum distichum*). *Biology and Fertility of Soils* 3: 19-25.

Sohlenius, B., S. Boström & A. Sandor, 1988. Carbon and nitrogen budgets of nematodes in arable soil. *Biology and Fertility of Soils* 6: 1-8.

Southey, J. F., 1982. Some free-living nematodes found in plant material and soil samples. In: J. F. Southey (Ed), Plant Nematology, p. 246-247. Ministry of Agriculture, Fisheries and Food, Her Majesty's Stationery Office, London.

Stammer, H.-J., 1959. Beiträge zur Systematik und Ökologie Mitteleuropäischer Acarina. Band I: Tyroglyphidae und Tarsonemini. Akademische Verlagsgesellschaft Geest und Portig, Leipzig, 384 pp.

Veen J. A. van & E. A. Paul, 1979. Conversion of biovolume measurements of soil organisms, grown under various moisture tensions, to biomass and their nutrient content. *Applied and Environmental Microbiology* 37: 686-692.

Vereijken, P., 1986. From conventional to integrated agriculture. *Netherlands Journal of Agricultural Science* 34: 387-393.

Vereijken, P., 1989. From integrated control to integrated farming, an experimental approach. *Agriculture, Ecosystems and Environment* 26: 37-43.

Verhoef, H. A. & L. Brussaard, 1990. Decomposition in natural and agro-ecosystems; the contribution of soil animals. *Biogeochemistry* (in press).

Walter, D. E., 1987. Trophic behavior of 'mycophagous' microarthropods. *Ecology* 68: 226-229.

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

Woldendorp, J. W., 1981. Nutrients in the rhizosphere. Proceedings of the 16th Colloquium of the International Potash Institute, p. 99-125. International Potash Institute, Bern.

Zwart, K. B. & L. Brussaard, 1990. Soil fauna and cereal crops. In: L. G. Firbank, N. Carter, J. F. Darbyshire & G. R. Potts (Eds), The ecology of temperate cereal fields. Proceedings of an AAB/BES Symposium, 3-5 April 1990, Cambridge, UK (in press).