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C and N mineralisation in the decomposer food webs of a European forest transect

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Belowground processes are essential for the overall carbon and nitrogen fluxes in forests. Neither the functioning of the soil food web mediating these fluxes, nor its modulation by environmental factors is sufficiently understood. In this study the belowground carbon and nitrogen mineralisation of four European coniferous forest sites (northern Sweden to north-east France) with different climate and N depositional inputs was analysed by investigating the soil food webs using field observations and modelling. The soil fauna directly contributed 7–13% to C mineralisation, among which the testate amoebae (Protozoa) made the largest contribution. Microbial grazing was suggested to have an important indirect effect by stimulating bacterial turnover. Due to relatively high C:N ratios of their substrate, bacteria immobilized N, while the fauna i.e. testate amoebae, nematodes, microarthropods and enchytraeids, counteracted this N immobilisation.

Despite similar food web biomass, the sites differed with respect to food web structure and C and N flows. Model calculations suggested a significant influence of food web structure on soil ecosystem processes in addition to environmental factors and resource quality. Mineralisation rates were lowest at the low N input boreal site with a food web dominated by fungal pathways. Further south, as N availability increased, bacterial pathways became more important and the cycling of C and N was faster. The bioavailability of degradable C sources is suggested to be a limiting factor for microbial activity and overall mineralisation rates. In this respect, above- and belowground interactions e.g. transfers of labile C sources from the vegetation to the decomposer system deserve further attention.

Our study revealed the combined effects of climate and nutrient inputs to ecosystems and the subsequent changes in the structure and functioning of the systems. If decomposition, and therefore carbon loss, is stimulated as a consequence of structural and/or nutritional changes, resulting for example from continuous industrial N emission, the storage capacity of forest ecosystems could be altered.

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The amount of C and N stored in and released from forest ecosystems is an essential part of the global carbon (C) and nitrogen (N) cycle. The uncertainty in current estimates of these terrestrial fluxes results to a large extent from our limited understanding of the soil and the decomposition processes mediated by the soil organisms (Dufresne et al. 2002). The ecological understanding of the decomposer system and its contributions to biogeochemical cycling is essential to environmental management purposes and questions of global change (Currie 1999). In this study the C and N fluxes from the soil were derived from the contributions of the organisms involved. The decomposer food webs at four European coniferous forest sites were monitored

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and the biomasses of functional groups were assessed. Carbon and nitrogen mineralisation across and within the food webs were estimated using a numerical food web model (Hunt et al. 1987).

The four coniferous forests spanned a range of latitudes and climates along a European north-south transect extending from close to the polar circle to the north east of France (Persson et al. 2000a). Besides climate change, increased nitrogen deposition is an important aspect of global change (Nadelhoffer et al. 1999). In Europe nitrogen emission to the atmosphere remains elevated relative to pre-industrial levels. Since 1975, as the world population increased by 50%, the anthropogenic NO_x and NH_3 emissions through fossil combustion and food production have globally increased by 50% to 33 Tg N a^{-1} and 120% to 50 Tg N a^{-1}, respectively (Galloway 2001). Since many European forest ecosystems are N limited, the resulting atmospheric N deposition is expected to alter the C cycle (Currie 1999). In this context the study sites were chosen to be subject to different levels of atmospheric nitrogen deposition: a virtually unpolluted site was compared to sites with considerable loads of N input.

Climatic conditions and resource quality at each site were expected to change total mineralisation rates along the transect. It is not yet understood in what way these environmental factors may influence the decomposer food web, its total biomass, activity and/or its structure, and through this the soil mineralisation rates. Our first hypothesis therefore is that apart from direct influences of climate and resource quality on soil process rates, the food web biomass structure, e.g. the contribution of functional groups to the total food web biomass, affects the mineralisation rates (e.g. Moore 1994).

According to Parmelee (1995) major changes in environmental conditions are accompanied by marked shifts in the composition of the soil microbial community. In the context of the study presented here we expected a shift from a fungal-based food web with slow turnover rates in the North and bacterial-based food webs with fast turnover rates at the more southern sites. Presently no consistent theory is available on the contribution of specific faunal groups to total mineralisation since comparative studies along depositional patterns and on this spatial scale are rare. In particular, the negligence of testate amoebae seems to be critical, because this group on the one hand positively responds to increases in N availability and, on the other hand, is intimately involved in microbial N cycling (Foissner 1994). Our second hypothesis therefore is that the relative importance of testate amoebae to total fluxes will increase with increasing N deposition. Finally, the enchytraeid species *Cognettia sphagnetorum* (Vejdovsky) has proven to be a keystone species in boreal forests (Huhta et al. 1998). We thus hypothesised Enchytraeidae to be of particularly large importance to mineralisation at the boreal site.

To test these three hypotheses, the major taxa within the decomposer food webs of the four coniferous forest sites were identified, biomasses were assessed and species or taxonomic units were united into functional groups (Moore et al. 1988). Then a food web model (Hunt et al. 1987, De Ruiter et al. 1994) was applied to each site to estimate C and N flux across and within the decomposer food web. The estimates of total C and N mineralisation calculated by the food web model were compared with those extrapolated from laboratory incubation studies on soils from the same sites (Persson et al. 2000b, c).

Methods

Description of study sites

The study sites were selected to form a north-south-transect of European coniferous forests: N-SE (northern Sweden, Åheden), S-SE (southern Sweden, Skogaby), DE (Germany, Waldstein) and FR (France, Aubure; Table 1). The sites were chosen to lie on a latitudinal gradient and to be subject to different levels of nitrogen (N) deposition. They form part of a larger network of forest sites that were studied within the European project CANIF (carbon and nitrogen cycling in forest ecosystems, Schulze 2000). The litter at all sites consisted almost entirely of *Picea abies* (L.) Karst. needles, except for the northern Swedish forest site that is a mixed stand of spruce, pine and occasional birch trees. Nutrient status was usually richer in the needle litter of central European sites. A detailed description of the sites and their history can be found in Persson et al. (2000a).

Along the three southern sites the increasing altitude towards the south counteracts the climatic gradient. S-SE, the youngest site, lies on the lowest altitude having the highest mean annual temperature and precipitation. The two more southern sites DE and FR lie on high altitudes resulting in lower mean annual temperatures (Table 1). The boreal site in northern Sweden, N-SE, differs from the others with respect to its boreal climate and the nearly total absence of N deposition (2 kg ha^{-1} a^{-1}; Table 1). S-SE and FR receive intermediate levels of nitrogen via the atmosphere (15–16 kg ha^{-1} a^{-1}), while DE is subject to the highest amount of atmospheric N deposition (20 kg ha^{-1} a^{-1}).

Sampling scheme and sample treatment

Soil samples were collected at all four sites at four sampling dates within a 2 to 4 week period: (i) October/November 1996, (ii) May/June 1997, (iii) September 1997, and (iv) March/April 1998. At each time, between 80 and 110 samples (soil corer: Ø 5 cm) of the organic layer (LFH) were taken at each site.

Table 1. Characteristics of the four study sites (from data given in Persson et al. 2000c); site abbreviations: N-SE = northern Sweden, Åheden; S-SE = southern Sweden, Skogaby; DE = Germany, Waldstein; and FR = France, Aubure.

	N-SE	S-SE	DE	FR
total N deposition (kg N ha^{-1} a^{-1})	2	16	20	15
latitude, longitude	64°13′ N, 19°30′ E	56°33′ N, 13°13′ E	50°12′ N, 11°53′ E	48°12′ N, 07°11′ E
climate	boreal	humid oceanic	humid continental	humid oceanic
altitude a.s.l. (m)	175	95–115	700	1050
mean annual air temperature (°C)	1.0	7.6	5.5	5.4
mean annual precipitation (mm)	488	1237	890	1192
dominant tree species	*Pinus sylvestris*, *Picea abies*, *Betula pendula*	*Picea abies*	*Picea abies*	*Picea abies*
understorey vegetation	dense layer of forest, mosses, dwarf-shrubs	occasional mosses	dense field layer of grasses and dwarf-shrubs	patches of grass and fern
site history	unmanaged, virtually undisturbed site	2nd generation, planted, former grazed *Calluna* heathland	planted	planted, former grazed declining fir forest
stand age (a)	183	36	145	95
C:N-ratio LFH layer	39	29	22	26
organic layer C (10^{-3} kg C ha^{-1})	22.6	27.9	38.9	29.5
pH (H_2O) FH layer	3.9	4.1	3.7	3.5
soil type	regosol	haplic podsol	cambic podsol	dystric cambisol

At the first sampling occasion 10 bulk samples were obtained at each site by merging 10 single soil cores per sample (procedure see below). An additional 10 soil cores were drawn to determine a site-specific mass-to-area ratio of the organic layer. After material had been taken out for the extraction of microarthropods, the 10 bulk samples were bulked again in pairs to deliver 5 bulk samples for the remaining measurements. This scheme results in 10 and 5 samples of organic layer per site.

For the subsequent sampling times (samplings 2–4) the sampling scheme was slightly altered. Eight bulk samples were obtained by merging 7–10 single soil cores per sample. An additional 24 single soil cores were drawn and treated separately. Of these single soil cores 8 in each case were used to extract Nematoda, Enchytraeidae and Microarthropoda. From all cores site-specific mass-to-area ratios were obtained prior to animal extraction. All other measurements were made with material from the bulk samples. This scheme results in 8 replicate samples of organic layer per site and sampling time.

In the laboratory the single soil cores for faunal extractions were separated from living plants (moss etc.). All fauna extractions started within 3 days after sampling. The bulk samples were mixed by hand, and larger pieces of wood, twigs, cones and living plant material were removed. Material for testate amoebae enumeration was fixed within two days after sampling. Prior to microbial analyses the material was sieved using a 4 mm mesh. The samples were stored in the dark at 4°C in polyethylene bags.

Food web modelling

The food web approach of Hunt et al. (1987) was used to calculate C and N mineralisation by the below ground community (for detailed description and model formulations see O'Neill 1969, Hunt et al. 1987, De Ruiter et al. 1993b). The major taxa within the decomposer food webs were identified, biomasses were assessed and species or taxonomic units were united into functional groups (Moore et al. 1988, Table 2). Energy flow descriptions of the food web were constructed, in which the feeding rates were calculated from the observed site-specific population sizes (biomasses), and death rates and energy conversion efficiencies were taken from the literature (Table 2, but see Physiological parameters below). Annual feeding rates were calculated assuming that the annual average production of the organisms balances the rate of loss through natural death and predation. Calculations of feeding rates started with the top predators, which suffer only from natural death, and proceeded working backwards to the lowest trophic level. If a predator was considered to feed on more than one prey type, then both the preference of the predator for a given prey and the relative population sizes of the prey types were taken into account using a matrix of feeding preferences. Additionally to the prey preferences published (Hunt et al. 1987) the group of panphytophagous testate amoebae was considered to be primarily bacteria feeding, to graze on fungi to a lesser extent and to use detritus as a minor food source (Bonnet 1964, Schönborn 1978, Laminger et al. 1980, Meisterfeld 1987). The term 'panphytophagous' was originally coined by Luxton (1972)

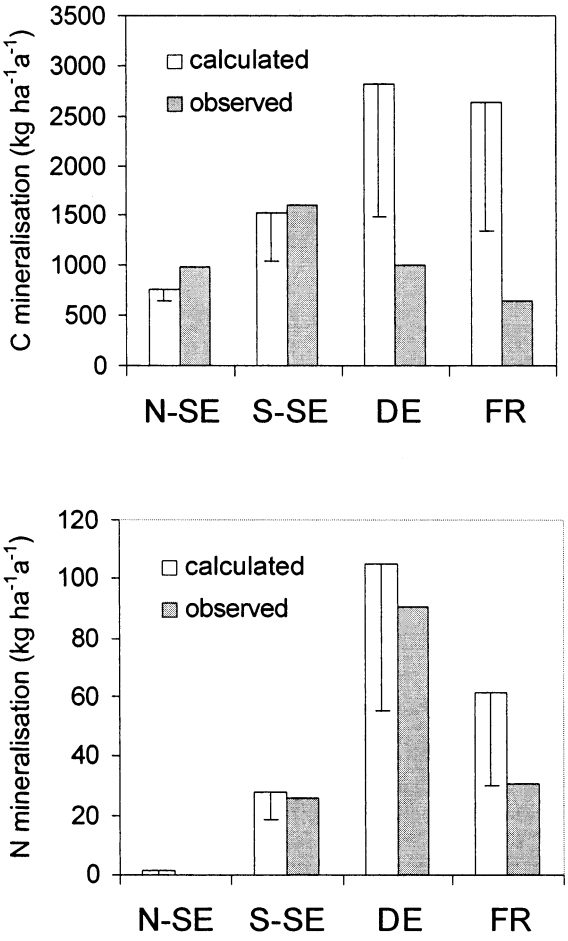

Fig. 1. Estimates of C and N mineralisation rates at the different sites obtained using the food web model ("calculated") and laboratory incubations of soil cores ("observed"). Laboratory incubation data are taken from Persson et al. (2000a, b). (A): C mineralisation (kg ha^{-1} a^{-1}); (B): N mineralisation (kg ha^{-1} a^{-1}). Whiskers on columns represent standard deviation (see Table 1 for site abbreviations).

and is used for functional groups that are both, detritivorous and microbivorous. C and N mineralisation rates for each functional group were calculated from feeding rates and estimates of the C:N ratio of the functional groups (Table 2).

Biomass and organic C pool

Soil microbial carbon and nitrogen were determined using the fumigation-extraction-method (Brookes et al. 1985, Vance et al. 1987). Since this method does not distinguish bacterial from fungal biomass additional measurements were undertaken with material collected at the 4th sampling time. Bacterial biomass was measured using automatic confocal laser-scanning microscopy picture analysis (Bloem et al. 1997). To estimate fungal biomass the ergosterol content (ergosterol/fungal dry weight: 5.1 mg/g) was determined using HPLC analysis (Djajakirana et al. 1996). It was assumed that the site-specific bacterial-to-fungal-biomass-ratio remained constant at the four sampling times.

Testate amoebae (Protozoa) were counted at the species level. Direct observation and enumeration (inverse microscopy) in aqueous suspensions after aniline blue staining allowed differentiation of shells filled with cytoplasm and empty shells (Aescht and Foissner 1992, modified). Species were allocated to 5 size classes for biomass calculation. Each size class was assigned a biomass conversion factor considering values from the literature (Volz 1951, Schönborn 1975, 1977, 1981, 1982, 1986, Lousier and Parkinson 1984, Lousier 1985, Wanner 1991) and estimates calculated using measurements of cell length, width and height of at least 10 specimens and an ellipsoid formula (Heal 1965, Schönborn 1977). Testate amoebae species were assembled into two feeding groups: panphytophagous and predaceous species. The latter group comprised of the genera *Nebela* Leidy and *Heleopera* Leidy (Bonnet 1964 in Coûteaux 1976, Laminger 1980).

A modified O'Connor-wet-funnel-extraction followed by milk-filter-cleaning (s'Jakobs and van Bezooijen 1984) was used to extract Nematoda. Nematodes of sampling occasions 1–3 were counted alive without further taxonomic determination. Nematodes of the 4th sampling occasion were counted on genus level (distinguishing juveniles from adults) and assembled into feeding groups (Yeates et al. 1993). Nematode biomass was calculated from genus specific abundances using conversion factors from the literature (Berg 1997, Ekschmitt et al. 1999) or from own calculations using the formula from Andrássy (1956) and length and width estimates from Bongers (1994).

Microarthropods were extracted by means of the high-gradient-canister method (Macfadyen 1953, Kempson et al. 1963, Wolters 1983). Collembola were counted at species level and aggregated into two feeding groups. The genus *Frisea* Dalla Torre was considered as predaceous, the remaining genera were categorized as panphytophagous. Body size measures were taken from the literature (Gisin 1960, Palissa 1964, Tanaka 1970, Petersen 1975, Fjellberg 1980, 1998, Zimdars and Dunger 1994, Jordana et al. 1997, Pomorski 1998). Collembola biomass was then calculated using the formula given by Persson and Lohm (1977), treating juveniles and adults separately. Acari were also counted at species level and sorted into two feeding groups (Luxton 1972, Walter and Proctor 1999): panphytophagous (juvenile and adult Cryptostigmata, Astigmata, Prostigmata and unidentified juveniles) and predaceous (juvenile and adult Mesostigmata) Acari. Length and width of a particular species were either taken from the literature (Sellnick 1928, Willmann 1931, Giljarov and Krivolutsky 1975, Berg et al. 1990, Wunderle et al.

Table 2. Physiological parameters for each functional group. Assimilation and production efficiencies (*a* and *p*) taken from Andrén et al. (1990) and C:N-ratios (*C:N*) from Hunt et al. (1987) if not stated otherwise. Basic death rates (at 10°C) were obtained from Hunt et al. (1987) and De Ruiter et al. (1993a) and adapted according to temperature and moisture regime of the specific sites (see Table 1 for site abbreviations and section on methods for details).

	a	*p*	*C:N*	death rate (a^{-1})			
				N-SE	S-SE	DE	FR
microflora							
Bacteria	1.00[a]	0.30[a]	4	0.4	0.7	0.6	0.6
Fungi	1.00[a]	0.30[a]	10	0.4	0.7	0.6	0.6
microfauna							
Testate amoebae							
panphytophagous	0.70	0.43	7	2.0	3.6	3.0	3.0
predaceous	0.70	0.43	7	2.0	3.6	3.0	3.0
Nematoda							
bacterivorous	0.30	0.40	5[b]	0.9	1.6	1.4	1.3
fungivorous	0.30	0.40	5[b]	0.6	1.1	1.0	1.0
omnivorous	0.60	0.33	5[b]	1.5	2.6	2.2	2.2
predaceous	0.60	0.33	5[b]	0.5	1.0	0.8	0.8
mesofauna							
Acari							
panphytophagous	0.25	0.40	5.5[b]	0.6	1.1	0.9	0.9
predaceous	0.80	0.30	8	0.6	1.1	0.9	0.9
Collembola							
panphytophagous	0.25	0.40	8	0.6	1.1	0.9	0.9
predaceous	0.80	0.30	8	0.6	1.1	0.9	0.9
Enchytraeidae	0.25	0.40	5[c]	1.7	3.0	2.5	2.5

[a] Hunt et al. (1987).
[b] Persson (1983).
[c] De Ruiter et al. (1993a).

1990, Beck and Woas 1991) or measured on 3–10 specimens. Biomass was then calculated using the formulae given by Persson and Lohm (1977). Nymphs and adults were treated separately in the biomass calculations to account for the species-specific smaller size of juvenile Acari.

Enchytraeidae were extracted using a modified O'Connor-wet-funnel method (O'Connor 1955). Enchytraeidae were counted alive without further taxonomic determination. Their biomass was calculated from abundances using a conversion factor (Heal 1967, Persson and Lohm 1977, Petersen and Luxton 1982, Dunger and Fiedler 1989, Górny and Grüm 1993, Berg 1997).

The size of the detritus pool (LFH layer) at each site was calculated from the mass-to-area ratios. Since naturally occurring organic matter is a mixture of degradable and recalcitrant substances (Tezuka 1990) it cannot be assumed that the entire C pool is equally available to primary decomposers. Instead it was assumed that only 20% of the total detritus pool is realizable for the decomposer organisms. This assumption is supported by the mean residence time of carbon (MRT) in the LF-layer. The MRT at the sites was estimated to be 5–6 years in measurements making use of the ^{14}C-signature of the material (Harrison et al. 2000).

Physiological parameters

Several physiological parameters are required to calculate the feeding rates and the concomitant C and N mineralisation rates: the average C:N-ratio of the tissue of the functional groups, their death rate, and their assimilation and production efficiencies (Table 2).

The nominal death rate used in the food web model is defined by Hunt et al. (1987) as the inverse of the maximal life span observed under ideal laboratory conditions. Since the death rates given in the literature refer to a temperature of 10°C (De Ruiter et al. 1993a) they had to be adapted to the specific climatic conditions of a given site. Instead of simply using a Q_{10} factor to take temperature into account, we used correction factors that also consider moisture from Persson et al. (2000b, c). Persson et al. (2000b, c) used these to extrapolate laboratory measurements of C and N mineralisation to the field. They are based on response functions for temperature and moisture determined in the laboratory (Seyferth 1998). We applied the same factors after adjusting them to the specific reference temperature. Consequently the corrected death rates take into account the site-specific mean monthly temperature as well as moisture.

The C:N-ratio of the organic layer (LFH layer) was calculated using data on the amount of L- and FH-layer and their C:N ratios from the CANIF data bank

(Persson et al. 2000a). The total C:N ratio of the substrate in a heterogeneous environment like the organic layer may differ from the C:N ratio of the material available to the primary consumers (Tezuka 1990, Hammel 1997). It is likely that primary consumers are to some extent adapted to the specific organic material they inhabit and that bacteria and fungi will consume fractions of the organic material with different C:N ratios. The organic material consumed by fungi was assumed to have the site-specific C:N ratios reduced by 20% and the material consumed by bacteria was assumed to have the site-specific C:N ratios reduced by 30%. This reflects the specific ability of fungi and bacteria to use recalcitrant substances (De Ruiter et al. 1993b, Dighton 1997) while the characteristic C:N ratios of the sites are still taken into account.

Impact of food web biomass structure on modelled rates

To test the importance of food web biomass structure for the estimated total mineralisation rates, the food web model was additionally run without site-specific adjustment of climate and resource quality. Equal climate (10°C, optimal moisture availability) and resource quality (C:N-ratio 22) was assumed for all sites in these model runs referred to as scenario "equal". Differences between sites in calculated mineralisation rates from scenario "equal" are due only to the site-specific food web structure.

Descriptive statistics

The food web model was run with the biomass input data from four separate sampling occasions per site, resulting in four sets of estimates for each site. Analyses of variance revealed no significant main effect of 'sampling time' on the biomass and C and N mineralisation rates of any functional group nor the total biomass and mineralisation of C and N (data were adequately transformed prior to analyses whenever necessary to improve normality). Therefore the four sets of estimates per site were treated as "replicate" estimates of the mineralisation rates to calculate mean values and standard deviations per site. However, since this is not a true, independent replication no further statistical analysis was performed. The standard deviations obtained by this approach represent general as well as temporal variations at each site.

Results

Modelling total C and N mineralisation

The total carbon and nitrogen mineralisation rates derived from the modelling approach did not simply follow the total food web biomasses (total mineralisation rates: Fig. 1, total biomasses: Table 3). The calculated rate of carbon mineralisation at N-SE (800 kg C ha^{-1} a^{-1}, Fig. 1A) was lower than the rates at FR and DE (2600 and 2800 kg C ha^{-1} a^{-1}). For S-SE an

Table 3. Biomasses of functional groups (%) and total food web (kg C ha^{-1}) at each site. Mean values of four sampling occasions, standard deviations are given in parentheses (see Table 1 for site abbreviations).

	N-SE		S-SE		DE		FR	
microflora								
Bacteria	5.1	(0.1)	6.9	(0.4)	4.1	(0.2)	11.4	(0.3)
Fungi	91	(1)	86	(5)	82	(4)	79	(2)
microfauna								
Testate amoebae								
panphytophagous	1.9	(1.2)	4.7	(3.7)	7.7	(4.0)	4.5	(2.6)
predaceous	0.4	(0.3)	1.4	(0.6)	2.2	(1.3)	1.1	(0.6)
Nematoda								
bacterivorous	0.16	(0.05)	0.04	(0.03)	0.06	(0.06)	0.07	(0.06)
fungivorous	0.04	(0.01)	0.02	(0.01)	0.02	(0.02)	0.02	(0.02)
omnivorous	0.02	(0.01)	0.02	(0.01)	0.05	(0.05)	0.02	(0.01)
predaceous	0.013	(0.004)	0.000	(0.000)	0.001	(0.001)	0.000	(0.000)
mesofauna								
Acari								
panphytophagous	0.3	(0.2)	0.5	(0.4)	0.8	(0.4)	0.4	(0.1)
predaceous	0.03	(0.01)	0.08	(0.04)	0.15	(0.10)	0.08	(0.01)
Collembola								
panphytophagous	0.5	(0.3)	0.4	(0.2)	1.6	(1.4)	1.3	(0.9)
predaceous	0.003	(0.004)	0.002	(0.002)	0.017	(0.002)	0.091	(0.047)
Enchytraeidae	0.1	(0.2)	0.4	(0.2)	1.9	(0.5)	1.8	(0.4)
total fauna	3.5	(2.3)	7.5	(5.2)	14.3	(7.7)	9.4	(4.8)
total food web	476	(105)	357	(122)	469	(197)	538	(195)

Table 4. Contributions of functional groups within the decomposer food web to N mineralisation (kg N ha^{-1} a^{-1}). Mean values of four sampling occasions are shown, standard deviations are given in parentheses (see Table 1 for site abbreviations).

	N-SE		S-SE		DE		FR	
microflora								
Bacteria	−11	(4)	−24	(9)	−14	(8)	−32	(20)
Fungi	2	(0)	13	(4)	46	(16)	30	(10)
microfauna								
Testate amoebae								
panphytophagous	9	(4)	34	(14)	65	(40)	57	(38)
predaceous	0.7	(0.5)	3.2	(1.0)	5.9	(3.3)	3.7	(2.4)
Nematoda								
bacterivorous	0.34	(0.07)	0.09	(0.02)	0.13	(0.13)	0.19	(0.16)
fungivorous	0.01	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
omnivorous	0.00	(0.00)	0.00	(0.00)	0.02	(0.02)	0.01	(0.01)
predaceous	0.01	(0.00)	0.00	(0.00)	0.00	(0.00)	0.00	(0.00)
mesofauna								
Acari								
panphytophagous	0.06	(0.03)	0.15	(0.10)	0.20	(0.07)	0.34	(0.15)
predaceous	0.03	(0.01)	0.10*	(0.02)	0.19	(0.05)	0.13	(0.03)
Collembola								
panphytophagous	0.17	(0.11)	0.18	(0.11)	0.68	(0.43)	0.74	(0.40)
predaceous	0.00	(0.00)	0.00	(0.00)	0.03	(0.01)	0.17	(0.11)
Enchytraeidae	0.04	(0.07)	0.12	(0.07)	0.76	(0.33)	1.52	(0.63)
total fauna	11	(5)	38	(16)	73	(44)	64	(42)
total food web	1	(1)	28	(9)	105	(50)	61	(31)

intermediate C mineralisation rate was estimated (1500 kg C ha^{-1} a^{-1}).

The pattern of calculated nitrogen mineralisation followed that of carbon (Fig. 1B, Table 4). N mineralisation was estimated to be almost zero at the boreal site N-SE. Nitrogen mineralisation was intermediate at S-SE and FR (28 and 61 kg N ha^{-1} a^{-1} respectively) and highest at DE (105 kg N ha^{-1} a^{-1}).

Comparison of modelled rates to rates based on incubations

The rates of total carbon and nitrogen mineralisation calculated by the food web model were compared to mineralisation rates derived from extrapolated laboratory incubation experiments for the same forest sites and soil layers conducted by Persson et al. (Fig. 1, Persson et al. 2000b, c). At the two Swedish sites N-SE and S-SE the food web model approach calculated total C mineralisation rates very similar to the extrapolated rates. At DE and FR calculated rates exceeded the extrapolated rates (Fig. 1A). The calculated N mineralisation rates were in good agreement with the extrapolated rates at all sites but FR, where the calculated exceeded this rate (Fig. 1B).

The decomposer food web: biomass and structure

Food web complexity, i.e. the number of trophic groups times connectance (Paine 1988), was very similar at all four sites. Merely the functional group of predaceous Nematoda was absent at FR and S-SE (Fig. 2). Many of the functional groups were omnivorous, which led to the obvious complexity of the web. Also the total biomass of the decomposer food web was relatively similar at the different sites, ranging from 360 to 540 kg C ha^{-1} (Table 3). In contrast, the food webs differed strongly from each other with respect to the pattern of functional group contributions to total food web biomass, in the following referred to as biomass structure. Such structural differences were found for all functional groups. Especially the contribution of predaceous microarthropods varied between sites over one order of magnitude (Table 3).

The biomass of fungi strongly dominated over that of bacteria at all sites. Fungi made up 79 to 91% of the total food web biomass, with their relative contribution being highest at N-SE, and lowest at FR (Table 3). Relative bacterial biomass was different between all sites with a maximum at FR (Table 3).

The overall faunal biomass ranged from 3.5% at N-SE to a maximum of 14.3% of the total food web at DE. Within the soil fauna the testate amoebae were the most important group (Table 3). Nematoda contributed little to total food web biomass. It was the only faunal group that showed maximum biomasses at N-SE, with the exception of omnivorous nematodes. The contributions of some functional groups to biomass correlated with the latitudinal gradient. Other groups seemed to follow the N depositional pattern (low at N-SE, intermediate at FR and S-SE, high at DE). For example the relative biomass of testate amoebae and Acari followed increasing N deposition, while increased biomass contributions of Enchytraeidae coincided with decreasing latitude.

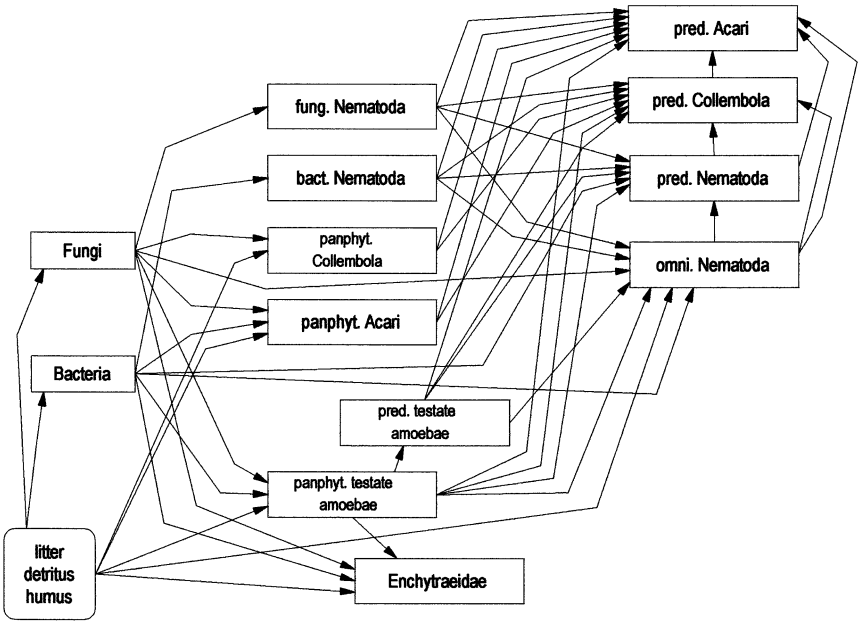

Fig. 2. Sketch of the decomposer food web (connectedness web). Feeding relationships are indicated by arrows pointing from prey to predator. The sketch applies to all sites, with the modification that the functional group of predaceous Nematoda was absent from the sites FR and S-SE. fung. = fungivorous; bact. = bacterivorous; panphyt. = panphytophagous; omni. = omnivorous; pred. = predaceous.

Impact of food web biomass structure

To test the importance of food web biomass structure for the estimated total mineralisation rates, the food web model was run without site-specific adjustments of environmental conditions. In this scenario, differences in calculated mineralisation rates between sites are due only to the site-specific food web structure (Table 5, scenario "equal"). The calculations from scenario "equal" are compared to those obtained after adequately adjusting the model to site-specific conditions (Table 5, scenario "site specific"). The estimates obtained with scenario "equal" are much higher than those of scenario "site specific", due to the lack of temperature and moisture constraints. However, a similar pattern of mineralisation rates in comparison of the sites is observed.

Table 5. Calculated N and C mineralisation rates (kg ha^{-1} a^{-1}) at the different sites for a scenario assuming equal climate and resource quality at all sites (scenario "equal") compared to the estimates obtained after adjusting the model to site specific conditions (scenario "site specific"). N mineralisation rates are rounded to the nearest ten, C mineralisation rates are rounded to the nearest hundred (see Table 1 for site abbreviations and section on methods for details).

	Scenario "equal"		Scenario "site specific"	
	Mineralisation (kg ha^{-1} a^{-1})			
	N	C	N	C
N-SE	80	2300	0	770
FR	190	5300	60	2600
S-SE	100	2600	30	1500
DE	200	5500	100	2800

Contribution of functional groups to C mineralisation

Fig. 3 shows the relative contribution of each functional group to total C mineralisation at each site. When comparing relative contributions the differences in overall mineralisation totals do not mingle principle differences within the functioning of the food webs.

The microflora was responsible for approximately 90% of the total C mineralisation (Fig. 3). There was a shift in the importance of fungi and bacteria to total C flux when comparing the boreal to the other sites. At the boreal site N-SE the ratio of bacterial to fungal respiration (%) was ca 30/70, while bacteria and fungi contributed similarly at the other sites (ca 50/40, Fig. 3). The 'metabolic activity' was calculated as unit carbon respired per unit carbon biomass using the absolute contributions to C mineralisation and the absolute biomass of the microflora groups. We found a trend towards increasing metabolic activity of microflora with increasing N deposition. Unit carbon respired per unit bacterial biomass ranged from 9 a^{-1} at the low N input site N-SE, over 19 a^{-1} (FR) and 27 a^{-1} (S-SE) at the intermediate N input sites, up to 61 a^{-1} at the high N input site DE. Regarding fungi the increase was not continuous and less pronounced, ranging from 1 a^{-1} at N-SE, over 2 a^{-1} at S-SE to 3 a^{-1} at FR and DE.

The total fauna contributed from 7% (51 kg C ha^{-1} a^{-1}) to 13% (391 kg C ha^{-1} a^{-1}) to C mineralisation, with testate amoebae being the dominating group. Their relative contribution to C mineralisation ranged from 6% (44 kg C ha^{-1} a^{-1}) at N-SE up to 11% (342 kg C ha^{-1} a^{-1}) at DE (Fig. 3). This paralleled the trend of increasing bacterial activity with a maximum

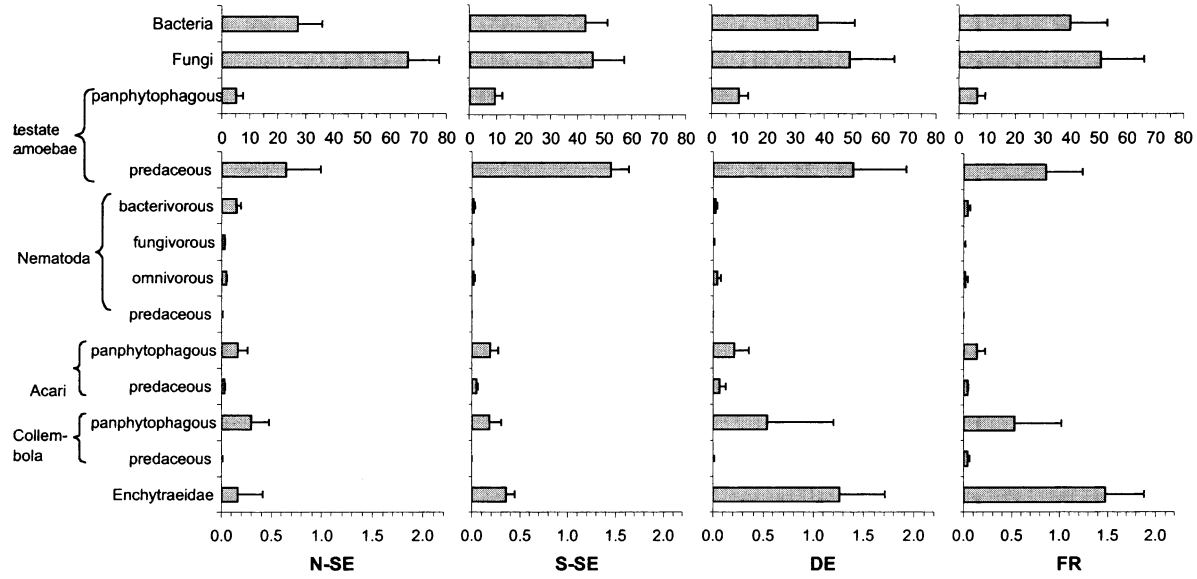

Fig. 3. Relative contributions of the functional groups to C mineralisation (%) at the sites. Whiskers on bars represent standard deviation (see Table 1 for site abbreviations).

relative C mineralisation at the high N input site DE. At S-SE and DE the predaceous testate amoebae species contributed more to carbon flux than at the other sites.

The second important group of microfauna, the Nematoda added little to overall carbon mineralisation (0.1–0.2% or 1–2% kg C ha^{-1} a^{-1}). In contrast to testate amoebae, the impact of Nematoda functional groups reached a maximum at the low N input site N-SE. The contribution of Acari, in contrast, resembles that of bacteria and testate amoebae in following the pattern of N deposition. It reached a maximum of 0.3% (6 kg C ha^{-1} a^{-1}) at DE and varied around 0.2% (1–4 kg C ha^{-1} a^{-1}) at the other sites.

The collembolan contribution to C mineralisation did not coincide with the N depositional pattern but rather with the latitudinal gradient. Collembola mineralised between 0.2–0.3% (2–3 kg C ha^{-1} a^{-1}) at the two northern sites and up to 0.5–0.6% (10–11 kg C ha^{-1} a^{-1}) at the two southern sites. Similarly, the contribution of Enchytraeidae followed the latitudinal decrease. This group became increasingly important from north to south. Their contribution ranged from 0.2% (1 kg C ha^{-1} a^{-1}) at N-SE and 0.4% (5 kg C ha^{-1} a^{-1}) at S-SE to up to 1.3–1.5% (32–35 kg C ha^{-1} a^{-1}) at the two southern sites (Fig. 3).

Contribution of functional groups to N mineralisation

The model calculated negative contributions to N mineralisation by the bacteria at all sites. This indicates N immobilisation. Therefore, only absolute estimates are given in Table 4.

The total amount of nitrogen mineralised by fauna ranged from 11 kg N ha^{-1} a^{-1} at N-SE to 73 kg N ha^{-1} a^{-1} at DE (Table 4). Panphytophagous testate amoebae made the largest contribution to N mobilization at all sites, followed by fungi, and predaceous testate amoebae. These three groups had a pattern along the transect that followed the latitudinal gradient: the maximum was at DE, followed by FR, less at S-SE and a minimum at N-SE. In contrast, Nematoda contributed most at N-SE. The mesofauna (Microarthropoda and Enchytraeidae) played a minor role for the N flux at N-SE and their contribution generally increased from north to south.

The fauna is of greater importance for N than for C mineralisation. At all sites except DE fungi alone could not have counterbalanced bacterial N immobilisation. In fact, relative to bacterial immobilisation the contribution of decomposer fauna is essential at the boreal site N-SE, where fungi counterbalanced only about one fifth of bacterial N immobilisation.

Discussion

Evaluation of model estimates

The food web model approach delivered values very similar to the extrapolated rates derived from incubations (Persson et al. 2000b, c) in most cases. However, deviations were considerable in two cases of total carbon mineralisation and in one case for total nitrogen

mineralisation. It is hard to draw conclusion about the causes of these differences. They might be due to the model formulations, the assumptions underlying the equations, and the uncertainties with respect to particular values of the input parameters (De Ruiter et al. 1993a). Especially the specific death rates of the microflora as well as the C:N ratios of the microbial substrate are difficult to establish and may have a great impact on the outcome of the model (see e.g. sensitivity analyses carried out by De Ruiter et al. 1993a). It is however also possible that the discrepancy between modelling results and extrapolations are due to shortcomings of the latter approach. This is supported by the fact that estimates of C mineralisation delivered by alternative techniques lay in between the two estimates discussed here (^{14}C technique Harrison et al. 2000 and NUCOM model simulation by van Oene et al. 2000). Indeed there is no flawless method for estimating mineralisation rates of the decomposer system. A considerable part of the variation within all approaches is due to deviating estimates of the total C pool of the forest soils, site variability and differences in sampling frequency (e.g. Persson et al. collected soil cores at a single sampling time while the food web model runs with estimates from 4 sampling times). Deviations from preliminary food web model results reported earlier (Wolters et al. 2000) result partly from an attempt to standardize C pool estimates within the CANIF project.

Food web structure and total mineralisation rates

Although the measured total food web biomasses at the different sites were similar, the estimated total C and N mineralisation rates of the decomposer food webs in the organic layer were different. This pattern of total mineralisation rates could be a consequence of three factors: (i) direct climatic and other environmental effects on the process rates of the organisms, (ii) differences in resource quality, and (iii) different biomass structures of the food webs. The influence and interdependency of the former two groups of factors is beyond controversy. But what is the importance of the differences in the biomass structure to determine total mineralisation of C and N at the sites? To test this, the food webs were modelled again without taking climatic differences and specific resource quality into account. While the absolute estimates changed drastically, the pattern of mineralisation in comparison of the different sites remained. Hence, the food web structure accounted considerably for the differences in mineralisation rates between the sites. This corroborates the hypothesis that the structure and not only the total biomass of the decomposer food web determines C and N fluxes (Moore et al. 1993, Setälä et al. 1996, 1998, Berg et al. 2001).

Environmental conditions and total mineralisation rates

In addition to analysing the functioning of the food webs in general, our study allows a comparison of forest sites that are subject to different environmental conditions. The sites lie on a latitudinal gradient. However, resulting climatic differences are partly counteracted by increasing altitude towards south, so that the three southern sites are exposed to relatively similar climatic conditions (mild temperatures, high moisture level, Table 1). The sites receive different amounts of atmospheric nitrogen deposition, ranging from very low inputs at the boreal site N-SE, over intermediate loads of nitrogen at FR and S-SE to the highest load at DE. Obviously our case study was not designed to pin down the exact effect of these factors on the decomposer food web and its function. It rather sought to find patterns that, apart from small-scale variations, are likely to be caused by the large-scale factors involved.

At the low N input boreal site N-SE mineralisation rates were low and the bacteria-to-fungi-ratio of C mineralisation (%) was estimated to be around 30/70. These findings corroborate results of Taylor et al. (2000) who compared the ectomycorrhizal community of three of the studied sites (namely N-SE, FR, DE). These authors found highest species richness, highest diversity and highest abundance of mycorrhizal root tips at the northern-most site N-SE. The role of fungi is known to be pivotal for boreal forest ecosystems (Näsholm et al. 1998, Lindahl et al. 2002). Their ability to translocate carbon and nutrients and their capacity to utilise organic nutrients are a competitive advantage especially under conditions of low N supply (Leake and Read 1997). In contrast, the sites that received intermediate and high loads of atmospheric nitrogen can be characterised as being bacterial-based with rather fast turnover rates. Bacteria and fungi contributed similarly to C mineralisation at these sites (bacteria-to-fungi-ratio ca 50/40). A ratio very similar to that was found in a long-term study of a Scots pine stand in central Sweden (i.e. 55/45, Jädraås, Persson et al. 1980).

We thus identify a fungal-based food web at N-SE in contrast to three bacterial-based food webs at the more southern sites with higher nitrogen input. Fungal based food webs are typically a result of extreme moisture fluctuations and have a greater tendency of nutrient immobilisation and slower turnover of nutrients, while bacterial based food webs indicate a more stable moisture level and fast nutrient cycling (Parmelee 1995). Besides the climatic conditions, nitrogen deposition may have contributed to the differences between the food webs. Along the transect we observed a highly increased metabolic activity of bacteria that coincided with increasing N deposition. Tietema (1998) has suggested that during nitrogen saturation, soil microbial communities move from being fungal, and probably

mycorrhizal, dominated to being bacterial dominated. Further evidence for the fact that the observed difference in food web structure is related to the availability of nitrogen is provided by a study carried out in a number of boreal systems (Pennanen et al. 1999). It was found that increasing fertility decreased the relative abundance of fungi while total microbial biomass, as in our study, remained unchanged.

N availability may be directly stimulating for bacteria if degradable C is available as an energy source to successfully exploit the available nitrogen (Paul and Clark 1989, Mikola and Setälä 1998, Currie 1999). Triggering the bacteria to enter growth phase may then have a stimulating, strong bottom-up effect on the primary predators, the testate amoebae. Increased grazing by Protozoa would further enhance bacterial turnover and finally, enhance mineralisation.

This mechanism could explain why N mineralisation is especially high at DE, even though the three southern sites are exposed to rather similar climates. DE receives the highest load of N input from the atmosphere and probably experiences increased energy supply due to the bioavailability of C originating from the vegetation. The nitrophilous dense understory vegetation is likely to supply easily degradable root exudates. Similarly, the trees may increase C allocation to the decomposer system due to enhanced N nutrition (Bauer et al. 2000, Scarascia-Mugnozza et al. 2000). In contrast, the low N mineralisation rates at S-SE may be explained by the poor nutrient status of the trees (Bauer et al. 2000), the youth of the tree stand and the lacking contribution of Enchytraeidae to N mineralisation. The poor nutrient status despite high N deposition at S-SE might be linked to the youth and past land use of the stand, which acknowledges the need to consider site history (Aber et al. 1998, Watson and Mills 1998).

N immobilisation and faunal grazing

Our estimates of N mineralisation suggest that nitrogen within coniferous forests is immobilised by the bacteria and released by the fauna grazing upon them at all sites. Bacterial immobilisation of N was also found in the organic layers of a pine forest (Berg et al. 2001). In contrast, bacteria are reported to contribute substantially to N mineralisation in agricultural and grassland soils (Hunt et al. 1987, De Ruiter et al. 1993a). This indicates a principle difference between forest and agricultural decomposer systems reflecting the adaptation of the decomposer system to relatively stable conditions and recalcitrant substrate in the forest and to heavily disturbed high input systems in agricultural soils.

Because the resources of secondary consumers are relatively nitrogen rich, compared to detritus, the soil fauna was of more importance for N than for C mineralisation, a fact that has been emphasised in various studies (Anderson et al. 1981, Hunt et al. 1987, Persson 1989, Andrén et al. 1990, Setälä et al. 1990). The pronounced positive effect of protozoan grazing on N mineralisation has also been demonstrated in microcosm studies (Clarholm 1985, Vreeken-Buijs et al. 1997) and the positive influence of decomposer fauna on N mineralisation in general is well established (De Ruiter et al. 1993b, Ekelund and Ronn 1994, Beare et al. 1995). The contribution of the fauna to N cycling is particularly important at the boreal site.

The role of decomposer fauna

The fauna contributed 7–13% to total C mineralisation with a minimum at N-SE and a maximum at DE. These estimates are considerably higher than others reported from studies in coniferous forest soils (i.e. 1–5% as reviewed by Persson 1989). This is most probably due to the fact that we have quantified the testate amoebae using a direct counting method instead of a culturing technique. Testate amoebae constitute the dominant protozoan group in coniferous forest soils (Schönborn 1992b). Culturing techniques like the most probable number (MPN) method that have been used in previous studies are unsuitable for this group of protozoa (Foissner 1987, Aescht and Foissner 1992, Ekelund and Ronn 1994). Among the fauna, testate amoebae made by far the largest contributions to mineralisation. Their contribution to the C flux ranged from 6 to 11% (44 to 342 kg C ha^{-1} a^{-1}). The absolute values were similar to values previously reported for other forest sites (Lousier and Parkinson 1984, Meisterfeld 1986, Schönborn 1992a). The contribution of testate amoebae increased with increasing N input. This was suggested to be an indirect effect of the N input enhancing bacterial turnover, and therefore increasing food availability to the bacterivores (see discussion in the above section Environmental conditions and total mineralisation rates).

Regarding the structure of the decomposer fauna of the fungal based food web at the boreal site N-SE the food web is shifted in favour of Nematoda and to the disadvantage of testate amoebae in comparison to the other three sites. Nevertheless the contribution of testate amoebae to mineralisation remained higher than that of Nematoda. This shift in the importance of Nematoda could be due to competitive release, a higher ability to deal with low temperatures and/or released predaceous pressure on Nematoda by other fauna.

The contribution of Microarthropoda to total biomass and total C mineralisation increased with decreasing latitude. This can be attributed to both the climatic sensitivity of this group (e.g. limited feeding capabilities during ice formation) and the less adverse conditions towards south (Lavelle et al. 1995, Seastedt 2000). The mean biomass calculated over the four

sampling occasion may be an underestimation, due to the effect of bulking samples at the first sampling occasion. Bulking can detrimentally affect soil microarthropods, which is the reason that fauna was extracted from untreated soil cores at the following three sampling occasions.

Enchytraeidae were the second important faunal group for C mineralisation at the two southern sites, while their contribution at the boreal site N-SE was estimated to be of minor importance. Several microcosm studies, in contrast, suggest that Enchytraeidae are a keystone group in boreal forest soils (Huhta et al. 1998, Laakso and Setälä 1999). This apparent discrepancy can probably be explained by the fact that Enchytraeidae gain importance through indirect rather than through direct effects (Anderson 1995). Such indirect influences become obvious in the overall mineralisation rates measured in microcosms but remain largely unconsidered in our modelling approach. On the other hand microcosm studies may overestimate the effect of Enchytraeidae due to artificial conditions favouring the growth of semi-aquatic animals, which may lead to Enchytraeid densities far exceeding those in the field (Sulkava et al. 1996). In a microcosm experiment where Enchytraeidae were kept at field density levels their presence had no measurable effect on soil respiration (Hedlund and Augustsson 1995). The whole argument largely springs from the difficulty to define the term 'keystone group' since our estimates for the contribution of Enchytraeidae to C mineralisation are in good agreement with findings from field investigations (Huhta and Koskenniemi 1975, Huhta 1976, Berg 2001). For example Huhta and Koskenniemi (1975) found the C mineralisation by Enchytraeidae to be ca 3.3 kg C ha^{-1} a^{-1} at a boreal site comparable to N-SE (our result: 1.4 kg C ha^{-1} a^{-1}) and ca 8.7 kg C ha^{-1} a^{-1} at a eutrophic spruce site comparable to S-SE (our result: 5.2 kg C ha^{-1} a^{-1}).

Our estimates of the contributions of predaceous faunal groups to mineralisation support the view that the functional importance of soil fauna is inversely related to the trophic position of the group (Laakso and Setälä 1999). However, this conclusion must be tested more thoroughly in subsequent studies, since a number of potentially important predaceous taxa such as Diptera larvae, spiders, staphylinid and carabid beetles and centipedes had to be neglected in our study due to time constraints.

Conclusions

Besides some discrepancies between modelled and extrapolated mineralisation rates, the food web model was a useful tool in estimating the contribution of functional groups to C and N fluxes and in relating the structure of the decomposer community to variations in soil C and N fluxes. We found that a combination of climatic and nutritional factors results in two basic types of decomposer food webs in forests: (1) fungal based food webs with slow turnover rates of C and N favoured by climatic extremes and low N availability and (2) bacterial food webs with fast turnover rates of C and N favoured by more stable moisture levels and higher N availability. The bioavailability of degradable C sources is suggested to be a limiting factor for microbial activity and overall mineralisation rates. In this respect above- and belowground interactions e.g. transfers of labile C sources from the vegetation to the decomposer system, deserve further attention. Grazing by testate amoebae (Protozoa) was an important direct contributor to overall fluxes and indirectly stimulated bacterial turnover. Faunal groups, i.e. testate amoebae, nematodes, microarthropods and enchytraeids, were essential to counteract bacterial N immobilisation.

With respect to global change, the effect of atmospheric nitrogen deposition is studied less often than climatic influences on ecosystems. Our study stresses the importance of considering the combined effects of climate and nutrient inputs to ecosystems and the subsequent changes in the structure and functioning of the systems. From a global perspective increased N deposition may result in an increase of the carbon sink of forests in the Northern Hemisphere through increased primary production (Kundzewicz and Parry 2001). It is, however, recognised that the considerable uncertainty in this projection results to a large extent from our limited understanding of the soil and the decomposition processes (Dufresne et al. 2002). It would therefore be interesting to reconsider the terrestrial C sink of the Northern Hemisphere by taking the decomposer system into account. If decomposition, and therefore carbon loss, is stimulated as a consequence of structural and/or nutritional changes, for example resulting from continuous industrial N emission, the storage capacity of northern forests could be altered.

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References

Aber, J., McDowell, W., Nadelhoffer, K. et al. 1998. Nitrogen saturation in temperate forest ecosystems. – BioScience 48: 921–934.

Aescht, E. and Foissner, W. 1992. Enumerating soil testate amoebae by direct counting. Soc. Protozool. B-6.1–B-6.4.
Anderson, J. M. 1995. Soil organisms as engineers: microsite modulation of macroscale processes. – In: Jones, C. G. and Lawton, J. H. (eds), Linking species and ecosystems. Chapman and Hall, pp. 94–106.
Anderson, R. V., Coleman, D. C. and Cole, C. V. 1981. Effects of saprophytic grazing on net mineralization. – In: Clark, F. E. and Rosswall, T. (eds), Terrestrial nitrogen cycles. Ecol. Bull. pp. 201–206.
Andrássy, I. 1956. Die Rauminhalts- und Gewichtsbestimmung der Fadenwürmer (Nematoden). – Acta Zool. Hung. Acad. Sci. 2: 1–15.
Andrén, O., Lindberg, T. and Boström, U. 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. Munksgaard, pp. 85–125.
Bauer, G., Persson, H., Persson, T. et al. 2000. Linking plant nutrition and ecosystem processes. – In: Schulze, E.-D. (ed.), Carbon and nitrogen cycling in forest ecosystems. Springer, pp. 63–98.
Beare, M. H., Coleman, D. C., Crossley Jr, D. A. et al. 1995. A hierarchical approach to evaluating the significance of the soil biodiversity to biogeochemical cycling. – Plant Soil 170: 5–22.
Beck, L. and Woas, S. 1991. Die Oribatiden-Arten (Acari) eines südwestdeutschen Buchenwaldes I. – Carolinea 49: 37–82.
Berg, M., De Ruiter, P. C., Didden, W. et al. 2001. Community food web, decomposition and nitrogen mineralisation in a stratified Scots pine forest soil. – Oikos 94: 130–142.
Berg, J., Woas, S. and Beck, L. 1990. Zur Taxonomie der Phthiracarus-Arten (Acari, Oribatei) eines südwestdeutschen Buchenwaldes. – Andrias 7: 61–90.
Berg, M. 1997. Decomposition, nutrient flow and food web dynamics in a stratified pine forest soil. – PhD-thesis, Vrije Universiteit, Amsterdam, The Netherlands.
Berg, M., De Ruiter, P., Didden, W. et al. 2001. Community food web, decomposition and nitrogen mineralisation in a stratified Scots pine forest soil. – Oikos 94: 130–142.
Bloem, J., Veninga, M. and Shepherd, J. 1997. Vollautomatische Messung von Bodenbakterien mit Hilfe der konfokalen Laser-Scanningmikroskopie und der Bildanalyse. – Mitteilungen für Wissenschaft und Technik XI 143–148.
Bongers, T. 1994. De Nematoden van Nederland – Een identificatietabel voor de in nederland aangetroffen zoetwater – en bodembewonende nematoden. – Uitgeverij Pirola, Schoorl, Utrecht, The Netherlands.
Bonnet, L. 1964. Le peuplement thécamoebien des sols. – Rev. Écol. Biol. Sol. 1: 123–408.
Brookes, P. C., Landman, A., Pruden, G. and Jenkinson, D. S. 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct method for measuring microbial biomass nitrogen in soil. – Soil Biol. Biochem. 17: 837–842.
Clarholm, M. 1985. Interactions of bacteria, protozoa and plants leading to mineralization of soil nitrogen. – Soil Biol. Biochem. 17: 181–187.
Coûteaux, M.-M. 1976. Dynamisme de l'quilibre des thécamoebiens dans quelques sols climacique. – Imprimerie Nationale.
Currie, W. S. 1999. The responsive C and N biogeochemistry of the temperate forest floor. – Trends Ecol. Evol. 14: 316–320.
De Ruiter, P. C., Moore, J. C., Zwart, K. B. et al. 1993a. Simulation of nitrogen mineralization in the below-ground food webs of two winter wheat fields. – J. Appl. Ecol. 30: 95–106.
De Ruiter, P. C., van Veen, J. A., Moore, J. C. et al. 1993b. Calculation of nitrogen mineralization in soil food webs. – Plant Soil 157: 263–273.
De Ruiter, P. C., Neutel, A.-M. and Moore, J. C. 1994. Modelling food webs and nutrient cycling in agro-ecosystems. – Trends Ecol. Evol. 9: 378–383.
Dighton, J. 1997. Nutrient cycling by saprophytic fungi in terrestrial habitats. – In: Wicklow, D. T. and Söderström, B. E. (eds), Environmental and microbial relationships. Springer, pp. 271–279.
Djajakirana, G., Joergensen, R. G. and Meyer, B. 1996. Ergosterol and microbial biomass relationship in soil. – Biol. Fertility Soils 22: 299–304.
Dufresne, J.-L., Fairhead, L., Le Treut, H. et al. 2002. On the magnitude of positive feedback between future climate change and the carbon cycle. – Geophys. Res. Lett. 29: 43/1–43/4.
Dunger, W. and Fiedler, H. J. 1989. Methoden der Bodenbiologie. – Gustav Fischer.
Ekelund, F. and Ronn, R. 1994. Notes on protozoa in agricultural soil with emphasis on heterotrophic flagellates and naked amoebae and their ecology. – Fems. Microbiol. Rev. 15: 321–353.
Ekschmitt, K., Bakonyi, G., Bongers, M. et al. 1999. Effects of the nematofauna on microbial energy and matter transformation rates in European grassland soils. – Plant Soil 212: 45–61.
Fjellberg, A. 1980. Identification keys to Norwegian Collembola. – Norsk Entomologisk Förening.
Fjellberg, A. 1998. The Collembola of Fennoscandia and Denmark. Part I. Poduromorpha. – Brill Academic Publishers.
Foissner, W. 1987. Soil protozoa: fundamental problems, ecological significance, adaptations in ciliates and testaceans, bioindicators, and guide to the literature. – Progr. Protistol. 2: 69–212.
Foissner, W. 1994. Soil protozoa as bioindicators in ecosystems under human influence. – In: Darbyshire, J. F. (ed.), Soil Protozoa. CAB International, Wallingford, pp. 147–193.
Galloway, J. N. 2001. Acidification of the world: natural and anthropogenic. – Water Air Soil Pollution 130: 17–24.
Giljarov, M. S. and Krivolutsky, D. A. 1975. Bestimmungsbuch der bodenbewohnenden Milben – Sarctoptiformes (russian). – Akad. Nauka SSSR, Moscow.
Gisin, H. 1960. Collembolenfauna Europas. – Museum d'Histoire Naturelle, Genève.
Górny, M. and Grüm, L. 1993. Methods in soil zoology. – Polish Scientific Publishers.
Hammel, K. E. 1997. Fungal degradation of lignin. – CAB International.
Harrison, A. F., Harkness, D. D., Rowland, A. P. et al. 2000. Annual carbon and nitrogen fluxes in soils along the European forest transect, determined using ^{14}C-bomb. – In: Schulze, E.-D. (ed.), Carbon and nitrogen cycling in forest ecosystems. Springer, pp. 237–256.
Heal, O. W. 1965. Observations on testate amoebae (Protozoa: Rhizopoda) from Signy Island, South Orkney Islands. – Brit. Antarct. Surv. Bull. 6: 43–47.
Heal, O. W. 1967. Quantitative feeding studies on soil amoeba. – In: Graff, O. and Satchell, J. E. (eds), Progress in soil biology. North Holland Publ. Co, pp. 120–125.
Hedlund, K. and Augustsson, A. 1995. Effects of Enchytraeid grazing on fungal growth and respiration. – Soil Biol. Biochem. 27: 905–909.
Huhta, V. 1976. Effects of clear-cutting on numbers, biomass and community respiration of soil invertebrates. – Ann. Zool. Fenn. 13: 63–80.
Huhta, V. and Koskenniemi, A. 1975. Numbers, biomass and community respiration of soil invertebrates in spruce forests at two latitudes in Finland. – Ann. Zool. Fenn. 12: 164–182.
Huhta, V., Persson, T. and Setälä, H. 1998. Functional implications of soil fauna diversity in boreal forests. – Appl. Soil Ecol. 10: 277–288.

Hunt, H. W., Coleman, D. C., Ingham, E. R. et al. 1987. The detrital food web in a shortgrass prairie. – Biol. Fertility Soils 3: 57–68.
Jordana, R., Arbea, J. I., Simón, C. and Luciáñez, M. J. 1997. Collembola-Poduromorpha. – Museo Nacional de Ciencias Naturales.
Kempson, D., Lloyd, M. and Ghelardi, R. 1963. A new extractor for woodland litter. – Pedobiologia 3: 1–21.
Kundzewicz, Z. W. and Parry, M. L. 2001. Europe. – In: McCarthy, J. J., Canziani, O. F., Leary, N. A. et al. (eds), Climate change 2001 – Impacts, adaptation, and vulnerability. Contribution of working group II to the 3rd Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge Univ. Press, pp. 641–692.
Laakso, J. and Setälä, H. 1999. Sensitivity of primary production to changes in the architecture of belowground food webs. – Oikos 87: 57–64.
Laminger, H. 1980. Bodenprotozoologie. – Mikrobios 1: 1–142.
Laminger, H., Geisler-Moroder, K., Stess, A. et al. 1980. Populationsdynamik terrestrischer Protozoen (Testacea, Rhizopoda) in zentralalpinen Lagen Tirols. I. Untersuchungen subalpiner Böden im Raum Obergurgl (Tirol/Österreich). – Arch. Protistenk. 123: 280–323.
Lavelle, P., Lattaud, C., Trigo, D. and Barois, I. 1995. Mutualism and biodiversity in soils. – Plant Soil 170: 23–33.
Leake, J. R. and Read, D. J. 1997. Mycorrhizal fungi in terrestrial habitats. – In: Wicklow, D. T. and Söderström, B. E. (eds), Environmental and microbial relationships. Springer, pp. 281–301.
Lindahl, B., Taylor, A. F. S. and Finlay, R. D. 2002. Defining nutritional constraints on carbon cycling – towards a less ''phytocentric'' perspective. – Plant Soil 242: 123–135.
Lousier, J. D. 1985. Population dynamics and production studies of species of Centropyxidae (Testacea, Rhizopoda) in an aspen woodland soil. – Arch. Protistenk. 130: 165–178.
Lousier, J. D. and Parkinson, D. 1984. Annual population dynamics and production ecology of Testacea (Protozoa, Rhizopoda) in an aspen woodland soil. – Soil Biol. Biochem. 16: 103–114.
Luxton, M. 1972. Studies on the oribatid mites of a Danish beech wood Soil – I. Nutritional Biology. – Pedobiologia 12: 434–463.
Macfadyen, A. 1953. Notes on methods for the extraction of small soil arthropods. – J. Anim. Ecol. 22: 65–78.
Meisterfeld, R. 1986. The importance of protozoa in a beech forest ecosystem. – Adv. in Protozool. Res. (Symp. Biol. Hung.) 33: 291–299.
Meisterfeld, R. 1987. Die Bedeutung der Protozoen im Kohlenstoffhaushalt eines Kalkbuchenwaldes (Zur Funktion der Fauna in einem Mullbuchenwald III). – Verhandlungen der Gesellschaft für Ökologie XVII: 221–227.
Mikola, J. and Setälä, H. 1998. Productivity and trophic-level biomasses in a microbial-based soil food web. – Oikos 82: 158–168.
Moore, J. C. 1994. Impact of agricultural practices on soil food-web structure – theory and application. – Agric. Ecosyst. Environ. 51: 239–247.
Moore, J. C., Walter, D. E. and Hunt, H. W. 1988. Arthropod regulation of micro- and mesobiota in belowground food webs. – Annu. Rev. Entomol. 33: 419–439.
Moore, J. C., De Ruiter, P. C. and Hunt, W. H. 1993. Influence of productivity on the stability of real and model ecosystems. – Science 261: 906–908.
Nadelhoffer, K. J., Emmett, B. A., Gundersen, P. et al. 1999. Nitrogen deposition makes minor contribution to carbon sequestration in temperate forests. – Nature 398: 145–148.
Näsholm, T., Ekblad, A., Nordin, A. et al. 1998. Boreal forest plants take up organic nitrogen. – Nature 392: 914–916.
O'Connor, F. B. 1955. Extraction of Enchytraeid worms from a coniferous forest soil. – Nature 175: 815–816.
O'Neill, R. V. 1969. Indirect estimation of energy fluxes in animal food webs. – J. Theoret. Biol. 22: 284–290.
Paine, R. T. 1988. Food webs: road maps of interactions or grist for theoretical development? – Ecology 69: 1648–1654.
Palissa, A. 1964. Insekten – Teil I: Apterygota. – In: Brohmer, P., Ehrmann, P. and Ulmer, G. (eds), Die Tierwelt Mitteleuropas. Quelle & Meyer, p. 299.
Parmelee, R. W. 1995. Soil fauna: linking different levels of the ecological hierarchy. – In: Jones, C. G. and Lawton, J. (eds), Linking species and ecosystems. Chapman and Hall, pp. 107–116.
Paul, E. A. and Clark, F. E. 1989. Soil microbiology and biochemistry. – Academic Press.
Pennanen, T., Liski, J., Bååth, E. et al. 1999. Structure of the microbial communities in coniferous forest soils in relation to site fertility and stand development stage. – Microbiol. Ecol. 38: 168–179.
Persson, T. 1983. Influence of soil animals on nitrogen mineralisation in a northern Scots pine forest. – In: Lebrun, P., André, H. M., De Medts, A., Grégorie-Wibo, C. and Wauthy, G. (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. – In: Clarholm, M. and Bergström, L. (eds), Ecology of arable land. Kluwer Academic Publishers, pp. 185–189.
Persson, T. and Lohm, U. 1977. Energetical significance of the Annelids and Arthropods in a Swedish grassland soil. – Ecol. Bull. 23: 218.
Persson, T., Bååth, E. and Clarholm, M. 1980. Trophic structure, biomass dynamics and carbon metabolism of soil organisms in a scots pine forest. – In: Persson, T. (ed.), Structure and function of northern coniferous forests – an ecosystem study. Swedish Nat. Sci. Res. Council (NFR), pp. 419–459.
Persson, T., van Oene, H., Harrison, A. F. et al. 2000a. Experimental sites in the NIPHYS/CANIF project. – In: Schulze, E.-D. (ed.), Carbon and nitrogen cycling in forest ecosystems. Springer, pp. 14–46.
Persson, T., Karlsson, P. S., Seyferth, U. et al. 2000b. Carbon mineralisation in European forest soils. – In: Schulze, E.-D. (ed.), Carbon and nitrogen cycling in forest ecosystems. Springer, pp. 257–275.
Persson, T., Rudebeck, A., Jussy, J. H. et al. 2000c. Soil nitrogen turnover-mineralisation, nitrification and denitrification in European forest soils. – In: Schulze, E.-D. (ed.), Carbon and nitrogen cycling in forest ecosystems. Springer, pp. 297–331.
Petersen, H. 1975. Estimation of dry weight, fresh weight, and calorific content of various Collembolan species. – Pedobiologia 15: 222–243.
Petersen, H. and Luxton, M. 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. – Oikos 39: 286–388.
Pomorski, R. J. 1998. Onychiurinae of Poland (Collembola: Onychiuridae). – Genus suppl 9.
Scarascia-Mugnozza, G., Bauer, G. A., Persson, H. et al. 2000. Tree biomass, growth and nutrient pools. – In: Schulze, E.-D. (ed.), Carbon and nitrogen cycling in forest ecosystems. Springer, pp. 49–62.
Schönborn, W. 1975. Ermittlung der Jahresproduktion von Boden-Protozoen. I. Euglyphidae (Rhizopoda, Testacea). – Pedobiologia 15: 415–424.
Schönborn, W. 1977. Production studies on Protozoa. – Oecologia 27: 171–184.
Schönborn, W. 1978. Untersuchungen zur Produktion der Boden-Testaceen. – Pedobiologia 18: 373–377.
Schönborn, W. 1981. Populationsdynamik und Produktion der Testaceen (Protozoa: Rhizopoda) in der Saale. – Zool. Jb. Syst. 108: 301–313.
Schönborn, W. 1982. Estimation of annual production of Testacea (Protozoa) in mull and moder (II). – Pedobiologia 23: 383–393.

Schönborn, W. 1986. Population dynamics and production biology of testate Amoeba (Rhizopoda, Testacea) in raw humus of two coniferous forest soils. – Arch. Protistenk. 132: 325–342.
Schönborn, W. 1992a. Comparative studies on the production biology of Protozoan communities in freshwater and soil ecosystems. – Arch. Protistenk. 141: 187–214.
Schönborn, W. 1992b. The role of Protozoan communities in freshwater and soil ecosystems. – Acta Protozool. 31: 11–18.
Schulze, E.-D. (ed.) 2000. Carbon and nitrogen cycling in forest ecosystems. – Springer.
Seastedt, T. R. 2000. Soil fauna and control of carbon dynamics: comparison of rangelands and forests across latitudinal gradients. – In: Coleman, D. C. and Hendrix, P. F. (eds), Invertebrates as webmasters in ecosystems. CAB International, pp. 293–312.
Sellnick, M. 1928. Formenkreis: Hormilben, Oribatei. – In: Brohmer, P., Ehrmann, P. and Ulmer, G. (eds), Die Tierwelt Mitteleuropas. Quelle & Meyer, pp. 1–42.
Setälä, H., Martikainen, E., Tyynismaa, M. and Huhta, V. 1990. Effects of soil fauna on leaching of nitrogen and phosphorus from experimental systems simulating coniferous forest floor. – Biol. Fertility Soils 10: 170–177.
Setälä, H., Marshall, V. G. and Trofymow, J. A. 1996. Influence of body size of soil fauna on litter decomposition and N-15 uptake by poplar in a pot trial. – Soil Biol. Biochem. 28: 1661–1675.
Setälä, H., Laakso, J., Mikola, J. and Huhta, V. 1998. Functional diversity of decomposer organisms in relation to primary production. – Appl. Soil Ecol. 9: 25–31.
Seyferth, U. 1998. Effects of soil temperature and moisture on carbon and nitrogen mineralisation in coniferous forests. – Lic. thesis. Univ. of Agricultural Science, Uppsala, Sweden.
s'Jakobs, J. J. and van Bezooijen, J. 1984. A manual for practical work in nematology. – Nematology Dept, Wageningen, The Netherlands.
Sulkava, P., Huhta, V. and Laakso, J. 1996. Impact of soil faunal structure on decomposition and N-mineralisation in relation to temperature and moisture in forest soil. – Pedobiologia 40: 505–513.
Tanaka, M. 1970. Ecological studies on communities of soil Collembola in Mt. Sobo, southwest Japan. – Jap. J. Ecol. 20: 102–110.
Taylor, A. F. S., Martin, F. and Read, D. J. 2000. Fungal diversity in ectomycorrhizal communities of Norway spruce (*Picea abies* [L.] Karst.) and beech (*Fagus sylvatica* L.) along north-south transects in Europe. – In: Schulze, E.-D. (ed.), Carbon and nitrogen cycling in forest ecosystems. Springer, pp. 343–365.
Tezuka, Y. 1990. Bacterial regeneration of ammonium and phosphate as affected by carbon:nitrogen:phosphorus ratio of organic substrates. – Microbiol. Ecol. 19: 227–238.
Tietema, A. 1998. Microbial carbon and nitrogen dynamics in coniferous forest floor material collected along a European nitrogen deposition gradient. – For. Ecol. Manage. 101: 29–36.
van Oene, H., Berendse, F., Persson, T. et al. 2000. Model analysis of carbon and nitrogen cycling in *Picea* and *Fagus* forests. – In: Schulze, E.-D. (ed.), Carbon and nitrogen cycling in forest ecosystems. Springer, pp. 419–467.
Vance, E. D., Brookes, P. C. and Jenkinson, D. S. 1987. An extraction method for measuring soil microbial biomass C. – Soil Biol. Biochem. 19: 703–707.
Volz, P. 1951. Untersuchungen über die Mikrofauna des Waldbodens. – Zool. Jb. Syst. 79: 514–566.
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 belowground food web; microcosm experiment and simulation of interactions. – Pedobiologia 41: 481–493.
Walter, D. E. and Proctor, H. C. 1999. Mites: ecology, evolution and behaviour. – CABI Publishing.
Wanner, M. 1991. Zur Ökologie von Thekamöben (Protozoa: Rhizopoda) in süddeutschen. – Wäldern.-Arch. Protistenk. 140: 237–288.
Watson, C. J. and Mills, C. L. 1998. Gross nitrogen transformations in grassland soils as affected by previous management intensity. – Soil Biol. Biochem. 30: 743–753.
Willmann, C. 1931. Moosmilben oder Oribatiden (Oribatei). – In: Dahl, F. (ed.), Die Tierwelt Deutschlands. V. G. Fischer, pp. 79–200.
Wolters, V. 1983. Oekologische Untersuchungen an Collembolen eines Buchenwaldes auf Kalk. – Pedobiologia 25: 73–85.
Wolters, V., Pflug, A., Taylor, A. R. and Schroeter, D. 2000. Diversity and role of the decomposer food web. – In: Schulze, E.-D. (ed.), Carbon and nitrogen cycling in forest ecosystems. Springer, pp. 366–381.
Wunderle, I., Beck, L. and Woas, S. 1990. Zur Taxonomie und Ökologie der Oribatulidae und Scheloribatulidae (Acari Oribatei) in. Südwestdeutschland. – Andrias 7: 15–60.
Yeates, G. W., Bongers, T., de Goede, R. G. M. et al. 1993. Feeding habits in soil nematode families and genera – an outline for soil ecologists. – J. Nematol. 25: 315–331.
Zimdars, B. and Dunger, W. 1994. Synopses on Parlaearctic Collembola, Part 1. Tullbergiinae Bagnall, 1935. – Abh. Ber. Naturkundemus 68: 1–71.