Soil biota during forest rotation: Successional changes and implications for ecosystem performance

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1 INTRODUCTION

1.1 Background and objectives

Recent environmental concerns about global change and the need to reduce the carbon dioxide amount in the atmosphere have led to a renewal interest in the carbon cycle with a particular focus on the soil compartment as it represents a major reserve of carbon. Therefore, integrated research, which aimed to enhance understanding of the processes responsible of storage or release of carbon from soil ecosystems under different management, received attention from environmental agencies. In parallel advances in soil ecology have recently led to reconsider the role of soil organisms in ecosystem processes and in particular in biogeochemical cycles. It was thus opportune to devote energy in a PhD thesis focusing on the soil biota and the functioning of the forest soil ecosystems, with a particular focus on carbon trajectory and temporal dynamics.

After giving a brief overview of the state of forest ecosystem in Europe and its importance regarding environmental concerns, I will then introduce the different constituents of the forest soil ecosystem, which are further considered for investigation within this work.

1.2 Forest ecosystems and environmental concerns

With an area of about 154 million ha, forests currently cover 20 to 30% of Western Europe. Overexploitation by humans has strongly decreased the area originally covered by forests in the past, with the lowest amount of forest cover occurring during the 18th and 19th centuries (Communautés européennes 1994). Since the second half of the 19th century, however, policies of afforestation and increasing wood production led to a dramatic increase of forested areas in Europe by about 10% within only two decades (from 1960 to 1980). One major feature of these policies was to promote planting of large areas with productive coniferous tree species, which offer a greater industrial profitability. Thus, in several cases native deciduous species (e.g. beech) have been replaced by plantations of coniferous

species (e.g. Norway spruce). This has significantly modified the average composition of the western European temperate forest (Rousseau 1990, Communautés européennes 1994).

Although the area of forest plantation in Europe has increased little since achieving a maximum around 1990, forest ecosystems remain a very important component within the environment. This is especially true in the context of the Kyoto protocol that calls for a significant reduction of CO_2 emissions, but also allows for CO_2 sequestration in the biosphere. Approximately 14% of the global pool of carbon in forests is found in the temperate and boreal forests of central and northern Europe (145 Gt), and more than two-thirds of that carbon is located in the forest soils rather than in the trees (Dixon et al. 1994). This large pool of carbon is potentially very vulnerable to climate change and it has been suggested that the rise in temperature forecast for the next 50 years could lead to extensive decomposition and oxidation of this pool, with the result that forests that are now sinks may become sources of carbon. This is, however, a highly speculative suggestion, based on very little knowledge of the processes that actually determine carbon turnover in forest soils (Schulze et al. 2000). One of the major identified problems in assessing long-term evolution of soil carbon stocks in managed forests is the series of successional stages in which anabolic and catabolic processes are influenced not only by environmental variables but also by forest management itself.

Because alteration of the catabolic processing rate of soil organic matter will inevitably affect the balance between the gain and loss of carbon in soil (Schulze et al. 2000), the ecological understanding of such decomposition processes and their contribution to biogeochemical cycling is essential to environmental management purposes and questions of global change (Currie 1999). The scientific community has accepted the general model of controls on decomposition and mineralisation processes articulated by Swift et al. (1979), which describes the complex interaction between three main factors: Physico-chemical environment, substrate quality, and organisms. Nevertheless the mechanisms, functioning, strengths and drivers of these complex interactions are still poorly documented.

In this context, to provide an assessment of the potential carbon sequestration in European forest soils further investigations on **functioning of the belowground system** are clearly needed. In particular, a better characterisation of the

decomposer assemblage (structure and functions; see section 1.4) and **its temporal evolution** in relation to its **environment** (soil system; see section 1.3).

1.3 Soil system

Paul (1989) acknowledged the soil as the 'best overall reflection of ecosystem processes' due to its systemic internal organisation, i.e. its control and indication of numerous ecological processes at varying temporal scales. The soil is indeed an essential component of terrestrial ecosystems, encompassing mineral materials, plant roots, microbial and animal biomass, organic matter in various states of decay, as well as water and a gaseous atmosphere (Gobat et al. 2003). The uneven distribution of these components results in a great variety of conditions at all spatial scales; from the region to the individual soil micropore. Organisms living belowground are thus constrained by the varied nature of the soil habitat, especially in the topsoil horizons (i.e. humus layers) where they mainly live. The intermediate position between above- and below-ground systems confers to the humus a valuable potential as indicator of ecosystem state (Peltier et al. 2001, Ponge 2003). During this work I had the opportunity to investigate two forests on different soil types: a spruce forest on acid soil and a beech forest on a base-rich soil. Both soil types present humus forms with particular structural and functioning characteristics. Indeed, based on the association of organic matter with mineral matter, three main humus forms were defined in terrestrial and aerated habitat (Müller 1889, Ponge 2003):

a) **Mull** characterises a humus form with a rapid disappearance of leaf litter and a fast utilisation of nutrients (Ponge 2003) under the influence of burrowing animals (Staaf 1987) and/or white rots (Hintikka 1970). High activity of burrowing animals leads to the homogenisation of humified organic matter with mineral particles within macro-aggregates (Bernier 1998).

b) In **moder** humus, low diversity of organisms, especially burrowing species, induce a lower decomposition and homogenisation of litter. Within the therefore well-developed horizons comprised of organic matter, nutrients are released slower than in the mull and are kept inside plant debris, animal faeces and fungi. Moder humus

forms are predominant in coniferous and deciduous (oak and beech) forests with poor underlayer vegetation.

c) **Mor** humus originates from harsh climatic conditions, very poor parent rocks, and from the strong allelopathic properties of the associated vegetation. Animals and microbial communities are highly impoverished (very low abundance and diversity) inducing a very low humification rate, which results in the development of a thick holorganic layer.

The classification of humus form appears, therefore, to follow the biological activity of the soil system. Though humus morphology does not provide a complete overview of the decomposition system, which is needed to understand soil processes, it could provide useful information on the dynamic state of the soil decomposers (diversity and functioning). Therefore, combined accurate descriptions of humus structure (see Bernier and Ponge 1994) and soil biota should allow qualitative and quantitative analyses of the habitat structure and food resources available for soil organisms.

1.4 Decomposition process and decomposer system

As mentioned earlier, humification and mineralisation of soil organic matter are performed by decomposers located principally in the topsoil horizons. The performance of the soil ecosystem could be regarded as a function of the decomposition rate and merit then to be introduce to understand the relationship between processes taking place above- and belowground.

1.4.1 Decomposition process

Decomposition of any resources is the result of three processes: i) catabolism, i.e. chemical changes such as mineralisation of organic matter to inorganic forms (largely CO_2, H_2O, NH_4^+, NO_3^-, SO_4^-), and the synthesis of decomposer biomass and humus, ii) comminution, i.e. physical reduction in particle size and selective redistribution of litter, and iii) leaching, i.e. the abiotic transport of labile resources down the soil profile (Heal et al. 1997). Decomposition is the main link between the two largest terrestrial C pools, namely plant biomass (primary production) and soil organic matter (SOM) (Sollins et al. 1996). Principally, decomposition serves two key

ecological functions (sensu Likens 1992): the formation of soil organic matter (SOM) and the mineralisation of essential nutrients such as nitrogen and carbon. Released nutrients can then be absorbed in inorganic forms and converted to organic constituents within the cells.

From all the nutrients, nitrogen and carbon are the two main building blocks of cellular tissue. Nitrogen, the cornerstone of amino acids, is incorporated into such important biological components as chitin and mucopeptides, and is also an integral part of nucleic acids. Furthermore, plant growth in soils throughout the world is often restricted by the supply of available nitrogen. The flow of nitrogen in the soil (Fig. 1.1a) is intimately linked to the flow of carbon, as most transformations of nitrogen depend on the associated carbon supply (Paul 1976). The cycle of carbon and nitrogen into soil (Fig. 1.1b) critically depend on the performance of the decomposer system. However, in spite of the environmental concerns enumerated earlier, the significance of decomposers, especially the soil invertebrate fauna, on the carbon cycle is still a poorly understood area of research (Seastedt 2000).

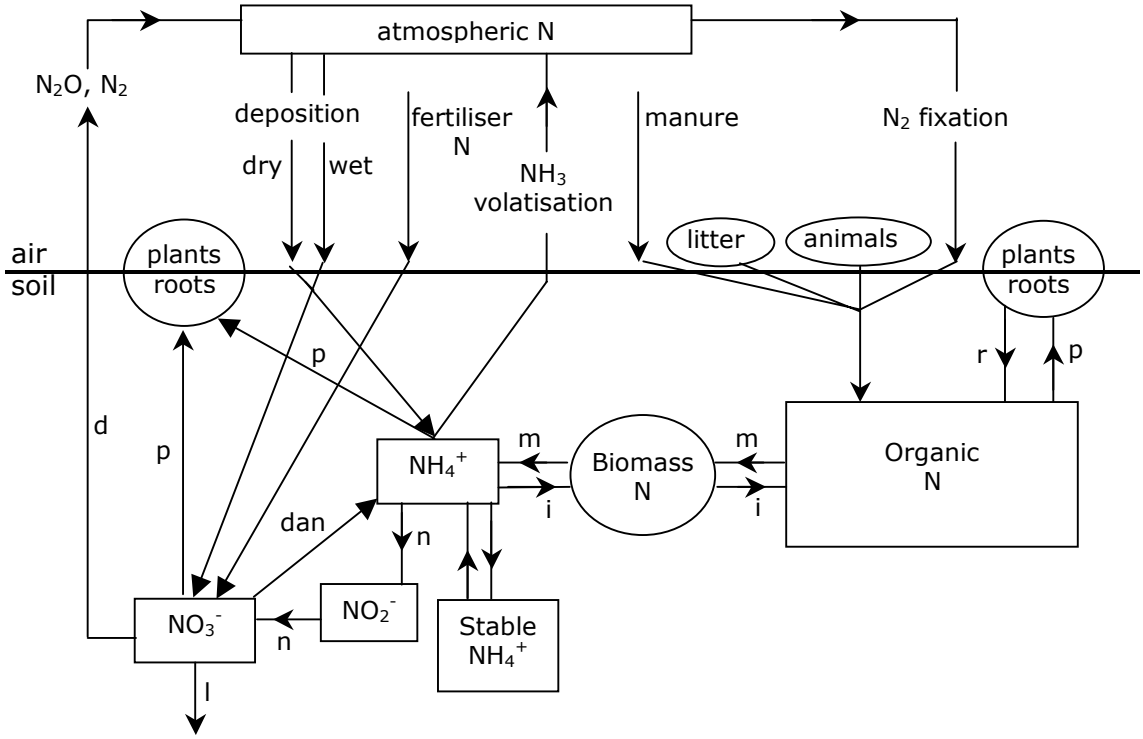


Fig. 1.1a: The soil nitrogen cycle. d: denitrification, dan: dissimilatory and assimilatory nitrate reduction to ammonium, i: immobilisation, m: mineralisation, n: nitrification and subsequent leaching (l), p: plant uptake, r: root exudation and turnover. (modified after Killham 1994)

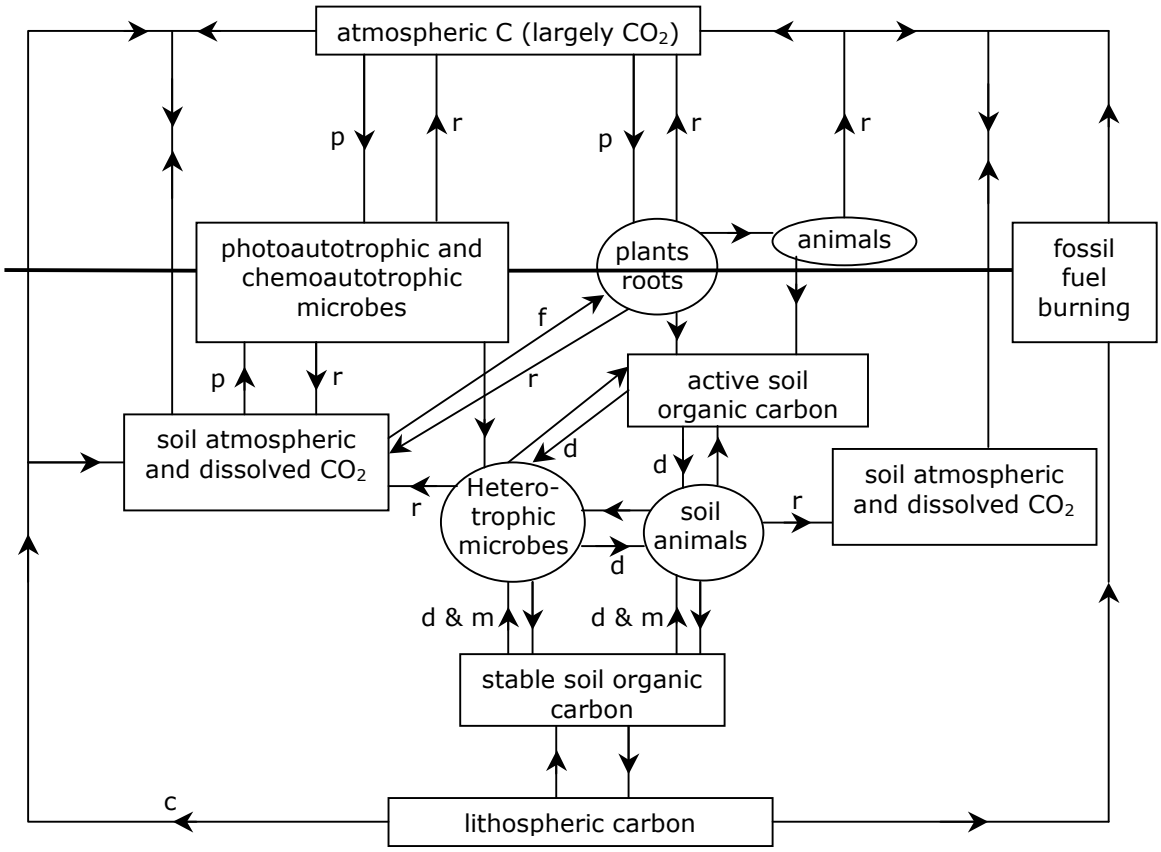


Fig. 1.1b: The soil carbon cycle. p: photosynthesis, r: respiration, f: fixation, d: decomposition, m: macromolecular synthesis, c: CO_2 from carbonates. (modified after Killham 1994)

1.4.2 Decomposer system

The description of the decomposer system was a first objective in this thesis, to be able, in a second step, to analyse its variability, functioning, and evolution in relation to environmental changes.

I mainly focused my diversity studies on a well-known arthropod group: namely Collembola. But as the decomposition of organic matter in soil involves the complex interaction of numerous microbial and animal taxa within the decomposer system, it was also necessary to gather information on the other major groups of the soil biota. Therefore I will provide a general description of the soil biota emphasizing its diversity and complexity.

It is, indeed, very difficult to effectively partition the functioning of the decomposer community in soil due to the reciprocal dependence of each organism on others. Nevertheless, size relationships play an important role in biological interactions in soil, primarily because the habitat is composed of different-sized pores

interconnected by necks of various sizes. Thus the soil biota is commonly subdivided into size classes: macrofauna measuring more than 2 mm in diameter; mesofauna measuring between 100 µm and 2 mm in diameter; and the microflora and microfauna measuring less than 200 µm in diameter (Swift et al. 1979).

- **The macrofauna compartment**

This class includes animals of relatively large size, distributed principally on the surface horizons of the soil. The numerous taxa included in this compartment can be clustered into different functional groups according to their feeding preferences: detritivores (e.g. dipterian larvae, Isopoda, Diplopoda, Lumbricidae and molluscs), predators (e.g. centipedes, ants, spiders), microphages (e.g. dipterian larvae) and also parasitoides (e.g. Hymenoptera, Diptera). The macrofauna can carry out initial physical comminution and dispersion of the litter to provide a greater surface area for microbial attack. In addition, residues passing through the gut of a soil animal will be partly decomposed by the gut microbes as well as microbially inoculated, leading to an accelerated decomposition in the soil.

- **The mesofauna compartment**

Collembola, mites and enchytraeids are the major taxa belonging to this group. These animals live in the pore system of the soil and most of them preferentially feed on fungi, but also ingest decomposed plant material and mineral particles. The impact of mesofauna on its environment is fairly similar to that of the previous compartment, but is also often masked by that of bigger-sized animals (i.e. animals belonging to the macrofauna). In humus profiles with abundant macrofauna (mull humus), the physical impact of mesofauna on decomposition and nutrient cycling will consequently be less apparent than in humus forms with abundant mesofauna but poor macrofauna (moder humus). Furthermore, mesofauna can enhance the growth of soil fungi by periodic or selective grazing, by dispersal of fungal inocula, and via the disruption of competing mycelial networks (Lussenhop 1992, Helling et al. 1998, Bolger et al. 2000). In this compartment several feeding groups are found, including detritivores and microphages (Oribatid mites, Uropodinae, Collembola, Enchytraeidae, dipteran larvae) as well as predators (Gamasid mites). Finally, it is interesting to notice that numerous dipterian larvae shift from the mesofauna to the macrofauna compartment during their growth.

- **The microfauna and microflora compartment**

The major taxa of the microfauna are protozoans and nematodes, which are relatively small aquatic animals (<200 µm) but extremely abundant (above 1.10^6 individuals per square meter). After the physical fragmentation and pulverisation of the vegetal material by the macro- and mesofauna, the microfauna play an important, if indirect, role with respect to the mode and the speed of the decomposition processes by regulating and stimulating the fungal and bacterial populations. Hence the microfauna contributes mainly to the maintenance of biological equilibrium in the soil. The microflora (archaea, bacteria and fungi) controls biochemical processes like enzymatic fragmentation of long polysaccharide molecules. It then completes the litter recycling process started by previous compartments, but with a much higher food utilization coefficient (2 to 5 times higher). In this third compartment, biochemical processes overtake physical processes due to microflora activity.

Although bacteria and fungi are present at each step of the decomposition process, there are clearly some general relationships between the size and function of the decomposer organisms in the soil as schematised in Fig. 1.2. However, when defined simply as mineralisation of carbon, 90% of the decomposition is carried out by microflora. But, the rate at which this processes operates is determined by the microfauna, while larger animals enhance the process in ‘hot spots’ such as the gut and excrements. This means that most soil animals are not directly involved in primary decomposition, but are rather consumers of primary decomposing soil microbes as well as other soil animals. Thus one of the major roles of the fauna appears to be the regulation of biotic components at the base of the food web (mostly the microorganisms), thereby mobilising nutrients for higher plants (Setälä et al. 1996).

Soil organisms interact on a multiplicity of spatial, temporal and organisational scales within a heterogeneous habitat (Lee 1994), resulting in countless interactions of the components of the soil’s biota. Trophic interactions are very important because they lead to energy and nutrient transfer within the food web. It is thus very valuable to assess the spatio-temporal organisation of the decomposer assemblage in the food web, which can help, for example, with predicting carbon and nitrogen transfer (Schroeter et al. 2003).

Structure of the decomposer assemblage can also be assessed from a functional point of view. The concept of functional groups composed of interchangeable, redundant species is appealing because it simplifies the study and management of ecological systems, which is particularly useful in community ecology and system ecology. Using the criterion of exploiting or processing a habitat resource in a similar manner, organisms can be grouped into a 'guild' (Root 1967) or 'functional group' (Cummins 1974). Root (1973) added 'mode of feeding' as a second criteria. Further criteria to distinguish 'functional groups' were added later by Moore et al. (1988), including 'reproductive rate', 'defence against predators' and 'distribution in the soil profile'. Species that are believed to play the same functional role in soil ecosystems are allocated into functional groups, types, guilds, or leagues (Faber 1991, Brussaard 1998). For example within the Collembola three functional groups were identified: epedaphic, hemiedaphic and euedaphic species (Gisin 1943). These differ in fundamental ecological properties such as reproduction, vertical distribution, and metabolic activity (Petersen 2002).

Predation, competition, and mutualistic relationships are essential interactions in regulating the micro food web and, subsequently, the decomposition process (Wardle and Yeates 1993, Wardle and Lavelle 1997). However, other biotic factors such as litter quality and quantity, in combination with a wide range of abiotic factors (i.e. climate and soil parameters) have also been considered important determinants of the decomposition process (Swift *et al.* 1979, Wright and Coleman 2002). Climatic variables such as temperature, moisture, and seasonality set limits to ecosystem productivity and determine to a large extent the composition of organism communities (e.g. Wolters 1991, Rusek 1998). Plant communities govern the quality and quantity of plant litter produced within an ecosystem, which in turns influences the quality of the soil. Soil characteristics (pH, texture, soil organic matter) combined with climate and vegetation exert a strong control over ecosystem processes such as nutrient cycling and litter decomposition, while also affecting soil organism abundance, species and trophic group composition, and organic matter turnover rates (Wright and Coleman 2002). These various determinants influence the soil system with different intensity. Anthropogenic activities and interventions are also a determining factor shaping the composition of soil faunal and microbial communities on a local and a global scale.

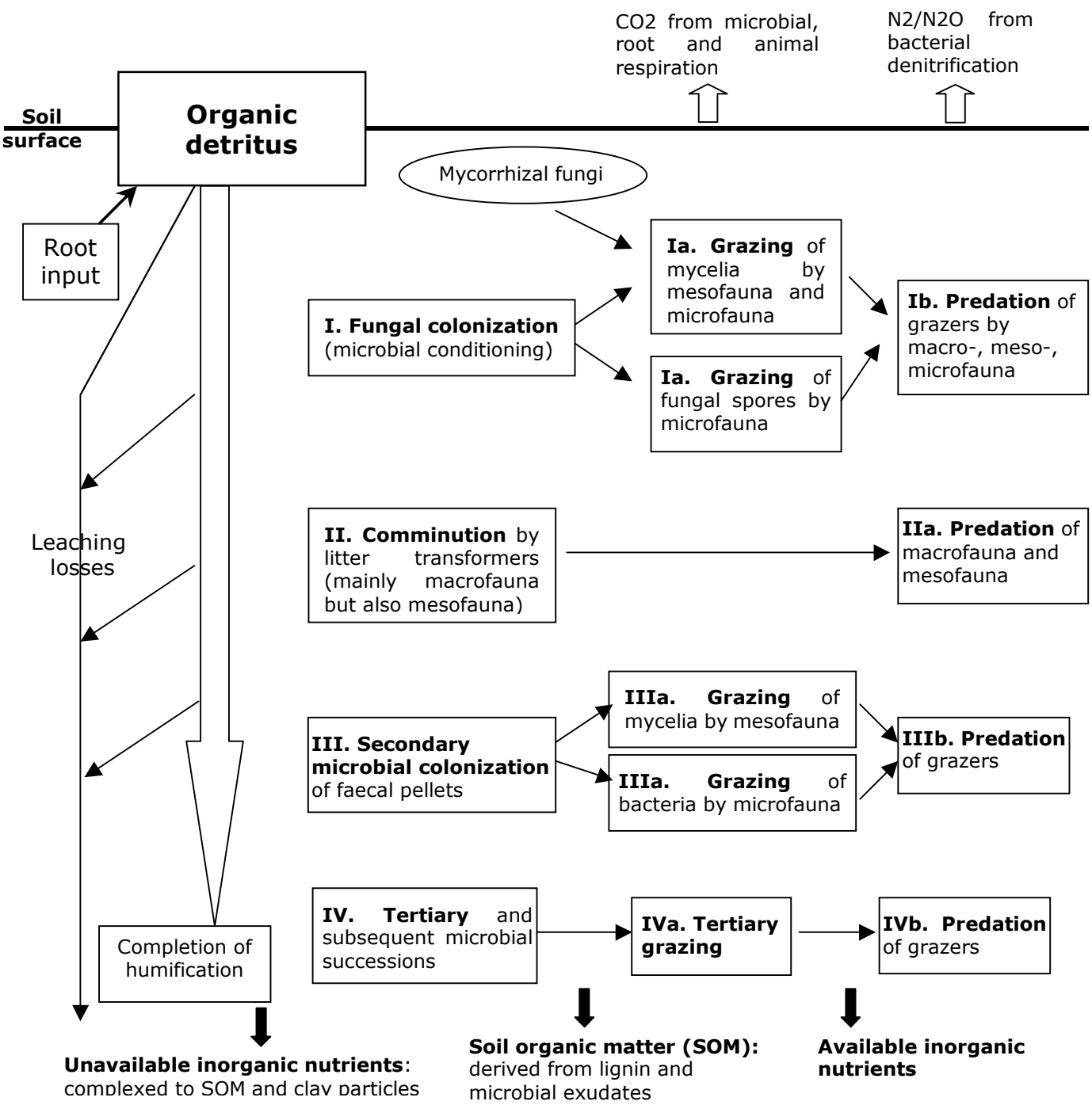


Fig. 1.2: Empirical scheme of decomposition in soils (compiled by Bignell in Brussaard et al. 1997)

1.5 Scope and outline of the thesis

The sustainability of forest resources depends on the continuation of essential ecological processes. These biological processes, affecting the C, nutrient, and hydrologic cycles, result from the activities of all forest organisms. Among the most important of these are invertebrates and micro-organisms inhabiting the soil and soil surface. With many thousands of named and unnamed species, they perform a vital role in decomposing litter by transforming dead organic material into a complex web of new substances, resulting in the food chains that characterise much of the edaphic environment (Marshall 1992). Soil organisms are essential to the productivity, high level of biodiversity, and homeostasis of undisturbed forests. Little is known about how the composition of the “non-crop” flora affects microorganisms, invertebrates and other fauna, nor how it influences the healthy functioning of forest ecosystems. Given the critical role of soil organisms in the forest, it is important to know how forestry practices and other types of environmental change affect them.

The possible responses of soil decomposers to long-term change occurring during forest rotation are also largely unknown, with even less being known regarding accompanying impacts on ecosystem performances (i.e. decomposition, mineralisation or stabilisation of organic matter). Clearly, a strong link exists between above- and below-ground systems, the connection of which subordinates performances of one system to the other. Evolution of the composition of the aboveground compartment during forest development and subsequent consequences on microclimatic parameters might disturb the balance of the ecosystem (Kratz 1991), leading to modifications of the structure and functioning of belowground organisms (Wolters et al. 2000). Consequently changes in the soil decomposer system might, in turn, influence plant growth and development, due to a feedback loop.

The aims of this study were therefore i) to investigate the influence of forest development on the habitat and structure of soil decomposer assemblage, and ii) to assess the consequences on ecosystem performances and nutrient cycling, especially on carbon trajectory.

Therefore three main hypotheses were formulated as starting point of this thesis:

Hypothesis 1: Soil decomposer assemblage and humus structure are strongly affected by successional changes of above ground system during forest rotation.
Hypothesis 2: The nature of the tree species (coniferous vs. deciduous) may strongly control or shape the effects observed on soil decomposer assemblage during forest monoculture rotation.
Hypothesis 3: Changes in decomposer assemblage may have a functional implication at the ecosystem-level and might subsequently affect ecosystem performances to a certain extent.

To test and answer those hypotheses, monitoring of soil ecosystem parameters (i.e. abiotic parameters, habitat structure, soil faunal and microbial communities) within two chronosequences and laboratory manipulations were carried out in four different studies. First, the Collembola and microbial communities were investigated in a managed spruce chronosequence (section 3.1). In a second step, still within the spruce chronosequence, the humus structure was assessed and linked to the functional structure of the soil fauna (Microarthropoda) and microflora (section 3.2). The belowground food web structure in a beech chronosequence was then studied, to allow a comparison with the spruce forest (section 3.3). Those three first studies were designed to answer the first two hypotheses and to give indications on the third hypothesis. The fourth study, a laboratory experiment was then designed to more specifically test the third hypothesis (section 3.4).

After a chapter providing a general description of the sites (section 2) where the investigations were performed, the results and discussion chapter (section 3) will be presented in a way that each study will be treated as an individual section with its own introduction, materials and methods, results and discussion parts. This for a better clarity of the work. Finally, major findings of the different studies will then be synthesized providing a general discussion (section 4) of the work followed by a conclusion chapter (section 5).

2 SITES

2.1 Chronosequence as ‘space for time’ substitution

To perform the field study two managed forest types were selected, namely a deciduous native tree species (*Fagus sylvatica*) and a coniferous tree species (*Picea abies*). Forest management practice in Europe consists primarily of monoculture forest rotation. The length of the cycle from plantation until felling depends mainly on the tree species. For coniferous tree species, for example, this does not exceed 100 years, while for deciduous species the rotation cycle could last for more than 150 years. Clearly, from a technical point of view studying forest development during the whole cycle is rather difficult if not impossible. However, to explore temporal changes in the soil ecosystem involved with forest development, it is nevertheless necessary to investigate the complete forestry cycle, i.e. to focus on important stages of development like regeneration, immature and mature stages. Therefore we decided to select chronosequences that offer the opportunity to simultaneously investigate forest sites of different age, enabling us to apply the ‘space for time’ substitution as a surrogate for long-term studies (cf. Pickett 1989). Despite some methodological shortcomings, this approach is often considered to be the only way of determining long-term changes in forest ecosystems (Trofymow 1998).

2.2 Spruce Chronosequence

Found in the ‘Tharandter Wald’, which is located 20 km to the South-West of Dresden (Germany) close to the city of Tharandt (50o 58' N; 13o 34' E), the spruce chronosequence was composed of four stands of different age-classes (Fig. 2.1): a regeneration stand (5y.o), two immature stands (25 and 45y.o) and a mature stand (95y.o). Those sites will be further abbreviated to 5 S, 25 S, 45 S, and 95 S, respectively. All sites were situated close to each other on a gently sloped area covering about 4 ha. They have all been regrown after clear-cutting of the previous forest generation at the age of approx. 90 years. The ground of the 5 S site was covered with tall grass and small spruce trees (25-40 cm of height). The 25 S and

45 S sites were dark and dense with hardly any grass cover. A patchy moss cover distinguished the 25 S site. The 95 S forest was relatively light due to the comparatively wide distance between trees and the ground vegetation is characterized by a patchy grass cover. The soils are loamy brown-earths developed on porphyr rocks. The surrounding area is covered by spruce forests (Picea abies (L.)) mixed with a small fraction of pine and deciduous trees. The climate is temperate continental with a mean annual temperature of +7.5°C and a mean annual precipitation of 820mm.

2.3 Beech Chronosequence

The beech study sites were located very close to each other in a forest close to Leinefelde (51 20'N, 10 22'E, Germany) at ca 445 m asl. Four secondary beech (*Fagus sylvatica*) monoculture forest sites were selected for investigation (Fig. 2.2). These form a chronosequence comprising of 30-, 62-, 111- and 153-year-old stands. It should be noted that in the oldest sites patches of young beech trees (ca 16 years old) have been allowed to grow in order to ensure natural regeneration. In the remainder of the text, these sites will be abbreviated to 30 S, 62 S, 111 S, and 153+16 S, respectively. Annual precipitation and mean air temperature for this area is 720mm and +7°C, respectively. The understorey vegetation was predominantly composed of grasses and herbaceous plants in the young sites, while woody species such as *Rubus* sp. dominate at the oldest stand. Moreover, the number of species present in the understorey increases with stand age (Gebauer, unpublished data). At all sites the soil type is cambisol developed on limestone rocks with a typical mull humus form presenting a litter layer (L) that declines strongly during the year.

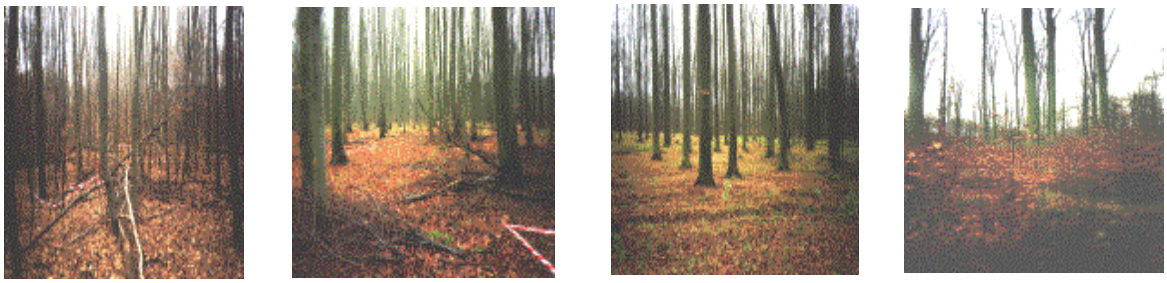
5 S 25 S 45 S 95 S

Fig. 2.1: Different stands of a spruce chronosequence in Tharandt (Germany).

A)

40 S 62 S 111 S 153+15 S

B)



40 S 62 S 111 S 153+15 S

Fig. 2.2 Four stands of a beech chronosequence in Leinefelde (Germany). A) in spring 2001; B) in Autumn 2001.

3 RESULTS AND DISCUSSION

3.1 Successional changes of Collembola and soil microbiota during forest rotation

3.1.1 Introduction

Successional changes in the structure of the decomposer community may significantly impact ecosystem processes during forest rotation. For example, alterations of the decomposition rate will inevitably affect the balance between the gain and loss of carbon (Schulze et al. 2000; Law et al. 2001). Studies aiming at understanding the processes associated with forestry cycles should thus include a thorough investigation of the dynamics of the decomposer community (Butterfield 1999; Horwood and Butt 2000; Johnston and Crossley 2002). However, many approaches to the functioning of forest ecosystems are still static (i.e. without taking into account the temporal scale) and ignore the biota below ground (Bengtsson et al. 2000). In a previous study the importance of Oribatid mites as a component of the buffering mechanisms of spruce forests against environmental changes was highlighted (Zaitsev et al. 2002). However Oribatids are slow-responding K-strategists (Walter and Proctor 1999), while Collembola, another mesofauna group, are generally assumed to follow an r-strategy (Petersen 2002) and rapidly respond to environmental changes (Butcher et al. 1971; Dunger 1975; Kaczmarek 1975; Hågvar 1982; Ponge 1983, 1993; Klironomos and Kendrick 1995). The ecological role of Collembola during forestry cycles might therefore be considerably different from that of Oribatida. Moreover Collembola have been shown to significantly influence decomposition processes (see Filser 2002). Most of these effects are indirect, i.e. act via alterations in microbial activities (Visser 1985; Moore 1988; Verhoef and Brussaard 1990) and by transporting fungal propagules (Seastedt 1984; Lussenhop 1992). In turn, the sapro-microphytophagous Collembola critically depend on food sources provided by the decomposer microflora (e.g., Schaefer 1995).

The starting point of the study was the question whether ecosystem changes during forest rotation are associated with parallel changes in microbial performances and collembolan community structure. Another question was: If these changes occur, do they provide any evidence for functional alterations of the decomposer system?

And finally, we wanted to test whether Collembola might be much better suited than Oribatida for indicating changes in the ecological role of the decomposer food web during forestry cycles.

3.1.2 Material and methods

The study was carried out at the Tharandt chronosequence (see 2.1) where the pH ranged from 3.6 at 25 S to 4.3 at 5 S. Collembola were sampled using a 5 cm diameter steel cylinder. Five cores were taken from the organic layer of each site in November 2000, April 2001 and September 2001. In addition, bulk samples of the comparable organic layer were collected for the determination of microbial parameters. Each sample was individually placed into plastic containers, transported to the laboratory in cool boxes and stored at 4°C before further treatment. Collembola were extracted from the core samples by means of the high-gradient-canister method using a modified Kempson-extractor (Wolters 1983). Identification to the species level followed Gisin (1960), Zimdars and Dunger (1994), Fjellberg (1998), and Pomorski (1998). According to Gisin (1943), all species maybe allocated to one of three different life forms: epedaphic, hemiedaphic and euedaphic species (see Appendix 3.1). These life forms differ in fundamental ecological properties (incl. reproduction, vertical distribution, and metabolic activity; cf. Petersen 2002) and can thus be considered as different functional groups.

The core samples were also used for determining dry mass, loss on ignition, bulk substrate density, and thickness of organic layer using standard methods (Alef & Nannipieri 1995). Soil microbial parameters were determined using material from the bulk samples. The C mineralisation rate (C_{min}) was measured as CO_2 evolution, determined gas chromatographically from 20 g aliquots of sieved fresh material incubated under conditions of 10°C and permanent darkness (Zaitsev et al. 2002). Microbial biomass (C_{mic}) was determined by means of the fumigation-extraction method (Vance et al. 1987; Bloem et al. 1997), with the C-content of the extracts being measured using a Continuous Flow System (Perstorp Analytical GmbH). The ergosterol content was determined by means of HPLC analysis as a measure of fungal biomass (Djajakirana et al. 1996). Due to the lack of a consistent conversion factor, ergosterol measurements were not converted to fungal biomass. Activity and functional diversity of bacteria were measured with BIOLOG GN microplates (BIOLOG Inc., Hayward, Calif.; Garland and Mills 1991) following the procedure described in

Dauber and Wolters (2000). BIOLOG measurable metabolic activity of the bacteria is given as average well color development (AWCD), functional diversity is given as substrate richness (S), i.e. the number of different substrates that are used by the microbial community (Zak et al. 1994).

Treatment of data and statistics

The C content of the organic material (C_{org}) was estimated from the loss on ignition applying the "Von Bemmelen" factor of 1.724 (Sutherland 1998). The amount of C stored in the organic layer (kg C_{org} m^{-2}) was calculated using the dry mass of the organic matter found in the core samples. The C release from the organic layer (metabolic potential in mg CO_2-C m^{-2} h^{-1}) was estimated by multiplying C_{min} by the amount of C stored in the organic layer. The metabolic quotient of the microflora (qC) was calculated by dividing C_{min} by C_{mic} (Anderson and Domsch 1990, 1993). In addition, the C availability to the microflora was assessed by dividing C_{mic} by C_{org} (Joergensen et al. 1995).

The dry weight (W) of each collembolan specimen (j) was calculated using the following regression equation:

$\log W_j = \log a + b * \log L_j$

with L_j denoting the average body length (mm) taken from the determination keys listed above. The parameters a and b were derived for each species from the literature (Tanaka 1970; Petersen 1975; Persson and Lohm 1977). Species for which no literature data were available received the same parameter values as species with a very similar body shape. The biomass of juveniles was estimated by assuming half of the body length of the respective adults. Two measures of collembolan species richness were calculated: total numbers of species found at each site (S_T) and mean number of species found at each site (S_M). The Shannon (H) and the Simpson (1-D) index were used as indicators of collembolan diversity (Magurran 1988). The dynamic of the collembolan community was estimated by calculating the species turnover rate (Mühlenberg 1993):

$$T = \frac{J + E}{S_I + S_{II}}$$

Where T is the turnover rate;

J the number of species not present at stage i but present at the subsequent stage j;

E the number of species present at stage i but not present at the subsequent stage j;

S_I the number of species at stage i; and

S_{II} the number of species at the subsequent stage j.

In addition, a single-link cluster analysis based on the Bray-Curtis index was calculated using BIODIVERSITY PRO Beta-version (The Natural History Museum, UK, 1996) to analyse faunistic similarity between sites (Magurran 1988).

The effect of the factor “stand age” on abiotic variables, microbial performance and Collembola communities’ parameters was tested by means of one-way ANOVAs (Sokal and Rohlf 1995). Since seasonal variations are beyond the scope of this study, the factor “sampling date” was used as a covariate. Data were log-transformed prior to analysis when necessary to ensure normal distribution and homogeneity of variance. Significant differences between means were tested at the 5%-level using the Tukey HSD test. Despite the fact that the factor stand age was not fully replicated it is justified to ascribe differences between plots as differences between stand ages, firstly because the vegetation at the sites is very typical for that of corresponding age classes, and secondly because we avoided differences caused by geographical or climatic variations by choosing sites that are situated very closely to each other. The relationship between microbial and collembolan parameters was tested by means of the General Regression Model (GRM). GRM applies the methods of the general linear model and allows including categorical as well as continuous predictor variables. We used microbial parameters as continuous predictors, “stand age” as categorical predictor and collembolan parameters as dependent variables. Statistical analyses were performed with the STATISTICA software package (version 6.0, StatSoft Inc., Tulsa, StatSoft 2001).

3.1.3 Results

The CO_2 release strongly increased after clear-cutting (5 S; F = 5.51; P<0.01, Fig. 3.1). It subsequently declined at intermediate stages of the forestry cycle, almost reaching the low level of CO_2 release measured at the oldest stand at 45 S already. The amount of C stored in the organic layer declined from 6.4 kg C m^{-2} before clear-cutting (95 S) to 4.0 kg C m^{-2} at 45 S (F = 10.9; P<0.001; Fig. III.1).

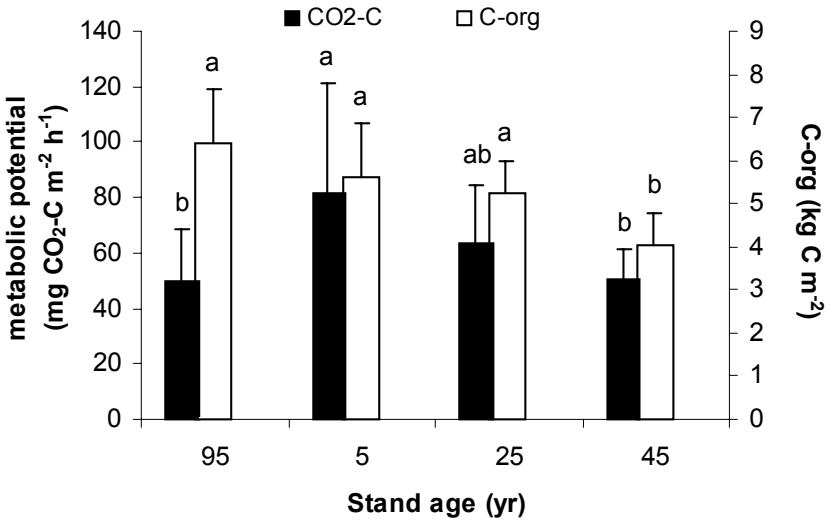


Fig. 3.1: C_{org} (kg m^{-2}) and CO_2 release (mgCO_2-C m^{-2} h^{-1}) of soils in four spruce forest stands (Tharandt, Germany) of different age. Means and standard deviations are given. Columns with different letters are significantly different from each other ($p < 0.05$, Tukey HSD).

No significant effect of the factor 'stand age' on the microbial biomass (C_{mic}) could be established (Tab. 3.1). The ergosterol content, in contrast, was increased 5 years after clear-cutting. This parameter reached a maximum at 25 S and was still high at 45 S (Tab. 3.1). While the BIOLOG measurable activity of bacteria (Average Well Colour Development) was also significantly increased at 5 S, it declined to very low values at intermediate stages of forest succession. Significant differences in the BIOLOG substrate richness parameter S between 5 S and 25 S indicate accompanying shifts in the functional structure of the bacterial community. The metabolic quotient (qC) was significantly increased at 5 S. The C availability (aC) gradually declined after clear-cutting (Tab. 3.1).

The total number of collembolan species sampled at all sites was 36 (see Appendix 3.1). The average abundance of Collembola ranged from 41500 ind. m^{-2} at 45 S to 87800 ind. m^{-2} at 5 S (Fig. 3.2). No significant effect of the factor 'stand age' on this parameter was found. Mean species richness (S_M) per site, in contrast, significantly changed with stand age ($F = 4.70$, $P<0.01$; Fig. 3.2). This largely reflects the depletion of the collembolan community at both 25 S and 45 S. Total species richness per site (S_T) closely paralleled S_M and varied between 17 at 45 S and 27 at 5 S (Appendix 3.1). The Simpson (1/D) and the Shannon (H) index of diversity ranged from 2.4 to 5.9 and from 1.5 to 2.1, respectively. Both indices had a minimum at 25 S. Evenness (E) varied between 0.51 and 0.71 and was also particularly low at 25 S.

Table 3.1: Means and standard deviations (in parenthesis) of soil microbial parameters in a chronosequence of four spruce forest stands (Tharandt, Germany). Means of the same parameter sharing identical letters are not significantly different (Tukey HSD test; p-level of significance: n.s = not significant; * = < 0.05; ** = < 0.01; *** = < 0.001).

Stand age (yr)	95	5	25	45	F-values	p-level	n
Microbial biomass (mg C_{mic} g^{-1}DW)	2.58^{A}	2.59^{A}	2.96^{A}	2.96^{A}	0.83	n.s	60
	(0.65)	(1.39)	(0.70)	(0.77)			
Metabolic quotient[a] (mg CO_2-C h^{-1} $g^{-1}C_{mic}$)	1.42^{B}	2.40^{A}	1.53^{B}	1.37^{B}	3.41	*	59
	(0.86)	(1.80)	(0.62)	(0.46)			
C-availability[a] (mgC_{mic} $g^{-1}C$-$_{org}$)	160.8^{A}	156.6^{AB}	121.3^{AB}	108.3^{B}	3.49	*	59
	(50.6)	(66.6)	(46.7)	(30.4)			
Ergosterol (µg g^{-1}DW)	43.8^{A}	52.0^{AB}	67.1^{B}	56.1^{AB}	3.30	*	60
	(9.14)	(40.8)	(23.0)	(11.3)			
AWCD[b] (Ext_{590nm} g^{-1}DW soil $48h^{-1}$)	18.1^{A}	26.0^{B}	4.5^{C}	9.8^{C}	23.2	***	56
	(9.7)	(8.6)	(5.9)	(8.6)			
Substrate richness[b] ($48h^{-1}$)	79.8^{AB}	86.2^{A}	65.9^{B}	79.5^{AB}	4.39	**	56
	(14.4)	(6.4)	(20.3)	(14.0)			

a: Calculated using data summarized in Zaitsev et al. (2002)
b: Average Well Colour Development, BIOLOG method

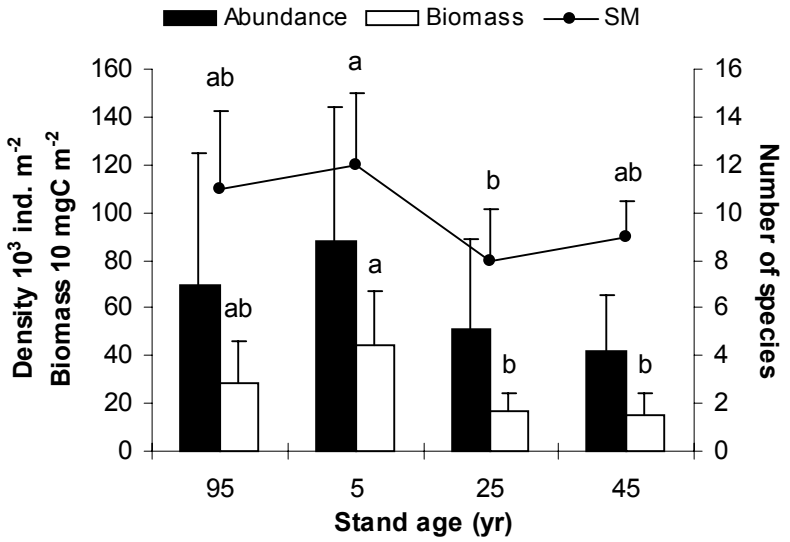


Fig. 3.2: Density, biomass and mean species richness (SM) of Collembola community at four spruce forest stands (Tharandt, Germany). Means and standard deviations are given. Different letters within a parameter denote significant differences ($p < 0.05$, Tukey HSD).

Accompanying changes in the dominance hierarchy are indicated by the fact that *Parisotoma notabilis* dominated at the oldest and at the youngest site, while *Xenyllodes armatus* dominated at the two intermediate sites (see Appendix 3.1). According to the Bray-Curtis index (data not shown), the level of community similarity between sites always remained above 50%. The cluster analysis did not reveal a major separation among groups of similarity.

Species turnover increased after clear-cutting (95 S to 5 S; Fig. 3.3). The change in total species richness was small, since the 7 species lost were replaced by 9 other species (see also the data summarized in the Appendix 3.1). Species turnover was particularly high from 5 S to 25 S and then returned to low levels (Fig. 3.3). Since species loss either strongly (25 S) or moderately (45 S) outweighed the gain of species, the community became impoverished.

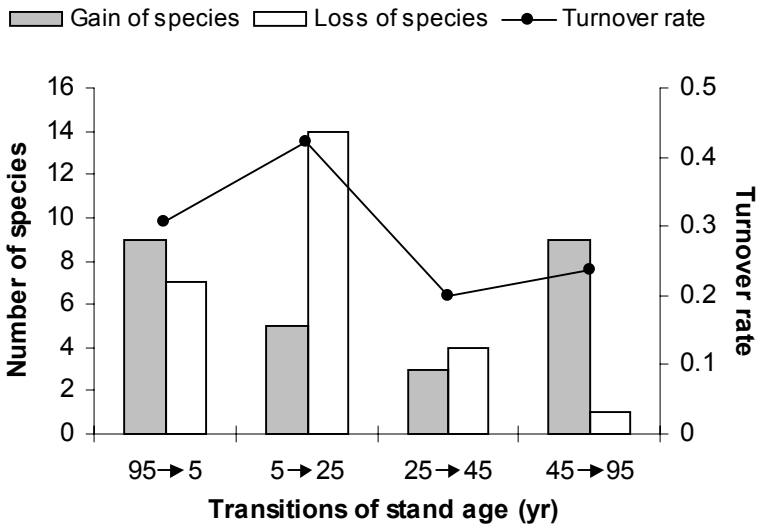


Fig. 3.3: Gain, loss, and turnover rate of soil-living Collembola species at each site of the spruce forest chronosequence (Tharandt, Germany).

A low level of loss and a high level of gain of species characterize the final period of forest development (45 S to 95 S). Species turnover led to significant shifts of functional groups (Fig. 3.4). The abundance of epedaphic and hemiedaphic species was high at 5 S and low at intermediate stages of forest development (epedaphic: $F = 9.95$, $P<0.001$; hemiedaphic: $F = 6.48$, $P<0.01$; Fig. 3.4). As a consequence, the relative contribution of euedaphic species to the collembolan community significantly increased at 25 S and 45 S ($F = 6.94$, $P<0.001$), though no effect of stand age on the absolute density of this group could be established.

Collembolan biomass was significantly higher at 5 S than at 25 S and 45 S (F = 4.10, *P*<0.05; Fig. 3.2).

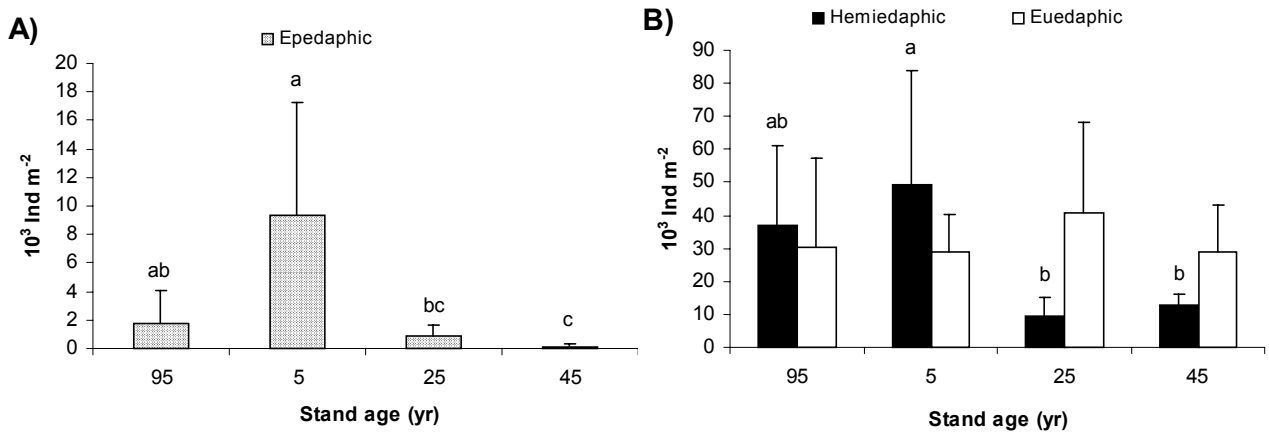


Fig. 3.4: Abundance of Collembolan functional groups (mean density and SD) in soils at four spruce forest stands (Tharandt, Germany). Columns with different letters are significantly different from each other (p < 0.01, Tukey HSD).
A): Epedaphic species
B): Hemi- and euedaphic species

The results of the GRM procedure are summarized in Table 3.2. The Biolog parameter AWCD was positively correlated to collembolan species richness, while the bacterial functional diversity (S) was adversely related to changes in collembolan density and biomass as well as to changes in the density of hemi- and euedaphic species. C_{mic} was positively correlated with epedaphic species, but as revealed by the significant interactions, C_{mic}*Stand age (SA), the positive correlation was only significant at 5 S and 95 S. C_{mic} was also positively correlated to the total density of Collembola at 5 S and 25 S as well as to the density of hemiedaphic species at 5 S, but it was negatively correlated with these two parameters at 95 S. And finally, the correlation between the ergosterol content and collembolan biomass was positive at 5 S but negative at all other sites.

Table 3.2: Results of the General Regression Models with microbial parameters as continuous predictors, stand age (SA) as categorical predictor and collembolan parameters as dependent variables. Only overall significant results are shown (Abd: abundance; sp.: species; S_M: mean species richness; EV: explained variance; *P*: level of significance; Trend: direction of effect: + = positive, - = negative, ns = no significant effect).

	S_M			**Total density**			**Total biomass**		
	EV (%)	*P*	Trend	EV (%)	*P*	Trend	EV (%)	*P*	Trend
C_{mic} * SA				19.8	0.002	5S + 25S + 45S ns 95S -			
Ergosterol. * SA							30.9	0.0001	5S + 25S - 45S - 95S -
AWCD	9.0	0.0004	+						
S				16.6	0.0005	-	12.3	0.001	-

(Continuation of Table 3.2)

	Abd Epedaphic sp.			**Abd Hemiedaphic sp**			**Abd Euedaphic sp.**		
	EV (%)	*P*	Trend	EV (%)	*P*	Trend	EV (%)	*P*	Trend
C_{mic}	8.6	0.009	+						
Cmic * SA	37.3	6E-05	5S + 25S ns 45S ns 95S +	27.0	0.002	5S + 25S ns 45S ns 95S -			
S				12.1	0.006	-	14.7	0.005	-

3.1.4 Discussion

The study revealed significant changes of microbial performances and collembolan community structure during forest rotation. I cannot exclude the possibility that the results are partly biased by pseudoreplication, but I tried to minimize this effect by the design of the study (see Materials and methods). Oksanen (2001) has argued that concern about pseudoreplication in ecological studies (e.g. Hurlbert 1984) has lead to 'unwarranted stigmatisation of a reasonable way to test predictions referring to large-scale systems'. I am thus quite confident that the data allow me to ascribe differences between plots as differences between stand ages.

The high qC of the microflora at 5 S was accompanied by a stimulation of fungi, bacterial activity (BIOLOG), metabolic potential, and surface-oriented Collembola (ep- and hemiedaphic species). Though the suitability of qC as a universal bioindicator of ecosystem development has been questioned (Wardle and Ghani 1995), the high value at 5 S at least indicates an inefficient use of carbon at this early stage of forest succession (Anderson and Domsch 1990; Schipper et al. 2001). Fungal biomass increased even further at intermediate stages of forest development, but microbial activity as well as BIOLOG-measurable bacteria and surface-oriented Collembola declined. No significant impact of the factor 'stand age' on C_{mic} or total collembolan abundance could be established. This contrasts to the findings of some other authors who found significant changes in C_{mic} (Pietikainen and Fritze 1995) and collembolan abundance (Huhta 1976) after clear-cutting of coniferous forests. This apparent contradiction may partly be explained by the low sensitivity of coarse parameters such as total biomass or abundance (e.g. Wardle 1998; Wright and Coleman 2002). However, the significant impact of stand age on the correlation between collembolan density and C_{mic} revealed by the GRM procedure shows that the combination of different biotic parameters allows a much deeper insight into temporal changes of the decomposer community than any of these coarse parameters alone.

Density as well as species richness and composition of the collembolan community at 95 S are in the range reported for other mature spruce forests in temperate regions (Rusek 2001). Clear-cutting accelerated the species turnover-rate without inducing a rapid change in species richness. The abundance of ep- and hemiedaphic species was high at this early stage of forest development. This also explains the parallel increase of collembolan biomass, since the body size of

springtails is systematically related to their life form (epedaphic > hemiedaphic > euedaphic; cf. Petersen 2002). The fact that some epedaphic species invaded the clear-cut area proves the high dispersal ability of those species stressed by various authors (Greenslade and Majer 1993; Ojala and Huhta 2001). Several collembolan species tend to climb up trees (Wolters 1983). It is thus not clear whether the increase of other species is due to population growth or rather reflects the fact that more individuals are forced to remain in the litter layer after the removal of trees. Regardless of the underlying mechanisms, however, high abundance of ep- and hemiedaphic species a few years after clear-cutting may have considerable functional implications. Surface-dwelling species have been shown to significantly enhance decomposition rates by facilitating the microbial use of organic matter (Takeda 1988; Faber et al. 1992; Hasegawa and Takeda 1995). I thus hypothesize that the high metabolic activity of the microflora at 5 S can partly be attributed to the various direct and indirect effects of the soil fauna on microbial performances (Visser 1985; Faber et al. 1992).

The decline of aC with stand age indicates a gradual accumulation of secondary compounds and recalcitrant materials in the organic layer during re-establishment of the forest (cf. Sollins et al. 1996). High ergosterol contents and low AWCD values indicate that fungi are much better adapted for degrading recalcitrant organic matter than bacteria (Wolters et al. 2000). In addition, the functional diversity of the microflora decreased. Similar to the changes reported by Setälä and Marshall (1994), the collembolan community became impoverished and community structure considerably changed. The results of the GRM procedure indicate a shift from specific associations between Collembola and microbiota to a more diffuse pattern without any correlations between microbial biomass and the density of individual functional groups. I do not have a straightforward explanation for the inverse relationship between Collembolan biomass and ergosterol content at all sites other than 5 S. Most probably, Collembola responded to qualitative rather than to quantitative changes of the fungal community, because Collembola are able to sensitively discriminate between different fungi (McMillan 1976; Hedlund et al. 1995). For example, Collembola positively respond to darkly pigmented fungi that are much more common in the litter layer of forests than in deeper horizons (Klironomos and Kendrick 1995). In addition, Collembola might have interfered with fungivorous oribatids, which markedly increased at 25 S and 45 S (Zaitsev et al. 2002).

In conclusion, it has been showed that collembolan communities of spruce forests need a very long time to fully recover from clear-cutting (Setälä and Marshall 1994). An interesting question for future research would be whether this also applies to forestry practices that are not based on the management of monospecific stands with only one age class. The consistently high community similarity of Collembola also confirms that at least some components of the microarthropod assemblages inhabiting forest soils are remarkably resistant to changes in environmental conditions (cf. Zaitsev et al. 2002). Moreover, the hypothesis that Collembola are much more sensitive than Oribatida is supported by the fast response at the level of functional groups (Petersen 2002; Zaitsev et al. 2002). While the increase of easily dispersed species at the earliest stage of forest rotation is coherent with conventional theories on secondary succession (e.g. Morin 1999), the diversity decline at intermediate stages of forest succession is more conflicting. However, 'bottom-up' control of community diversity by changes in the resource base seems to be the rule in terrestrial ecosystems (Polis and Strong 1996). I thus hypothesize that the impoverishment of the collembolan community at 25 S and 45 S is partly due to the loss of suitable food sources associated with the accumulation of recalcitrant soil organic matter. As for herbivorous arthropods (cf. Southwood et al. 1979), the considerable decline in microhabitat diversity may also be important. Other investigations on successional changes of the soil fauna demonstrated either a decrease of diversity with time (Decaens et al. 1998; Nowak 2001) or a non-directional change (Paquin and Coderre 1997; Horwood and Butt 2000). The shift from a soil community that is characterized by a very active decomposer microflora and a high abundance of surface oriented Collembola to a community that is dominated by a microflora with low metabolic activity, reduction in the functional diversity of bacteria and an impoverished collembolan community with a high share of euedaphic species nevertheless provides ample evidence of substantial functional implications. One important implication could be a less effective decomposer community leading to a less effective tree nutrition. Moreover, stand age-independent correlations between BIOLOG measurable bacterial parameters and Collembola point to the overarching impact of the composition of microbial communities on microarthropods. This aspect has been widely neglected in soil ecology and deserves much more attention in future studies on the factors determining the structure and performance of the soil food web.

Appendix 3.1: Species list, functional groups (Fg), dominance structure [%] and species richness of Collembola at four spruce forest stands (Tharandt, Germany) (Ep: epedaphic, He: hemiedaphic, Eu: euedaphic).

	Fg	95	5	25	45
Folsomia quadrioculata (TULLBERG 1871)	He	10.4	22.0	13.4	19.1
Isotomiella minor (SCHÄFFER 1896)	Eu	10.8	11.4	3.6	10.7
Parisotoma notabilis (SCHÄFFER 1896)	He	38.5	29.6	0.5	10.1
Tetracanthella arctica (CASSAGNAU 1959)	He	0.1	-	3.0	-
Sminthurinus aureus (LUBBOCK 1862)	He	-	0.7	-	-
Sminthurinus signatus (KRAUSBAUER 1898)	He	3.7	0.6	0.9	0.6
Megalothorax minimus (WILLEM 1900)	Eu	2.3	4.2	2.0	0.5
Sphaeridia pumilis (KRAUSBAUER 1898)	Eu	0.9	0.2	-	-
Dicyrtomina minuta (FABRICIUS 1783)	Ep	-	0.5	-	-
Dicyrtoma fusca (LUCAS 1842)	Ep	-	0.7	0.1	-
Allacma fusca (LINNE 1758)	Ep	-	-	0.4	0.2
Allacma gallica (CARL 1899)	Ep	-	0.1	-	-
Sminthurus sp.	Ep	-	0.1	-	-
Mesaphorura sensibilis (RUSEK 1973)	Eu	-	0.1	-	-
Mesaphorura macrochaeta (RUSEK 1976)	Eu	1.0	0.3	-	0.8
Mesaphorura yosii (RUSEK 1971)	Eu	1.2	1.4	1.5	0.7
Mesaphorura tenuisensillata (RUSEK 1974)	Eu	0.3	0.5	5.5	3.8
Protaphorura fimata (GISIN 1952)	Eu	-	0.1	-	-
Protaphorura armata (TULLBERG 1869)	Eu	4.8	5.7	2.3	11.0
Protaphorura pseudovanderdrifti (GISIN 1957)	Eu	1.6	7.5	-	6.0
Protaphorura tricampata (GISIN 1956)	Eu	0.2	-	-	0.9
Protaphorura juv.	Eu	0.2	-	0.4	-
Paratullbergia callipygos (BÖRNER 1907)	Eu	1.7	0.2	0.5	0.8
Micranurida pygmaea (BÖRNER 1901)	He	0.4	-	-	-
Micranurida granulata (AGRELL 1943)	He	-	0.3	-	-
Neanura muscorum (TEMPLETON 1935)	He	0.1	0.3	-	-
Willemia anophthalma (BÖRNER 1901)	Eu	1.3	1.3	1.9	1.7
Xenyllodes armatus (AXELSON 1903)	Eu	17.5	0.1	62.2	32.3
Ceratophysella denticulata (BAGNALL 1941)	He	0.1	2.8	-	-
Pseudachorutes parvulus (BÖRNER 1901)	He	-	-	0.1	-
Orchesella bifasciata(NICOLET 1841)	Ep	0.2	-	-	-
Pseudosinella mauli (STOMP 1972)	He	0.1	-	0.6	0.5
Lepidocyrtus lanuginosus (GMELIN 1788)	Ep	1.9	8.7	1.3	0.1
Lepidocyrtus curvicollis (BOURLET 1839)	Ep	-	0.2	-	-
Pogonognathellus flavescens (TULLBERG 1871)	Ep	0.2	0.3	-	-
Tomocerus baudoti (DENIS 1932)	Ep	0.3	-	-	-
Total species richness		25	27	18	17
Number of epedaphic species		4	7	3	2
Number of hemiedaphic species		8	7	6	4
Number of euedaphic species		13	13	9	11

3.2 Humus structure dynamics during a spruce forest rotation: Quantitative changes and relationship to soil biota.

3.2.1 Introduction

Soil carbon pools play an important role as both a source and sink during global environmental change (King et al. 1997, see 1.2). Scientific interest in the transformation of soil organic matter has thus strongly increased (Lal 2004; Wolters 2000). The humus compartment is the crossroad between above and belowground systems (Perry et al. 1989; Wardle et al. 1997; Ponsard et al. 2000; Ponge, 2003). It is the hot spot of litter transformation and soil biological activity, but also provides physical support to primary producers and soil decomposers (Wolters et al. 2000, see 1.3). By studying the morphological structure of this compartment it is thus possible to get a direct insight into both performances of soil biota and growth conditions of plants. Research is still in its early stages, however, because the wealth of descriptive studies on different humus fractions has not been paralleled by a similar increase in our understanding of the underlying processes (Heal et al. 1997). It is thus very promising that the potential for using humus analysis as a tool for getting insight into ecosystem functioning (Bernier and Ponge 1994; Peltier et al. 2001) has strongly increased, since it evolved from a merely descriptive method (Kubiëna 1938) to a very versatile and up-to-date analytical approach (Topoliantz et al. 2000; Gillet and Ponge 2002; Davidson et al. 2004).

Here I focus on changes in the humus structure during a spruce sylvogenetic cycle. Temporal dynamics of forest ecosystems have been widely neglected in soil ecology (Bengtsson et al. 2000). This is a major shortcoming, because alterations in the composition of edaphic communities appear to be major drivers of numerous processes taking place in forests (Pietikainen and Fritze 1995; Paquin and Coderre 1997; Schipper et al. 2001; Wright and Coleman 2002; Johnston and Crossley 2002). This has been confirmed by investigations on Collembola and Oribatida that were carried out at the same spruce forest chronosequence used for this study (see 3.1 and Zaitsev et al. 2002). The dual nature of the humus layer might help to better understand the results gained by these organism oriented approaches by deepening the insight into the dynamic habitat conditions of soil biota and their modification by biotic activities I addressed the following questions:

- What are the humus components characterising different successional stages of a spruce forest rotation?
- Are shifts in humus composition and structure paralleled by systematic changes of the soil community?

To answer the second question we included data on microbiota and microarthropods from section 3.1.3 and from Zaitsev et al. (2002) into the analyses. Despite the many papers on the modification of particular soil features by invertebrate activities (Marinissen and Bok 1988; Ziegler and Zech 1992; Dawod and Fitzpatrick 1993; Ciarkowska and Niemyska-Lukaszuk 2002; Vetter at al. 2004), the relationship of faunal effects to changes of the soil environment has rarely been investigated (Bardgett and Cook 1998).

3.2.2 Material and methods

Sampling

At the spruce chronosequence (see 2.1), five (25 S, 45 S, 95 S) or four (5 S) replicate samples were taken at the sites in October 2001 according to the method of Bernier and Ponge (1994). Blocks of 25cm^2 surface area and 9cm depth that included the whole organic layer (cf. Zaitsev et al. 2002) were prepared directly in the field with a sharp knife. Each block was then separated into different horizons: OL, OF, OH and A (Brêthes et al. 1995). Thick horizons (more than 1.5cm) were subdivided into several layers. Each layer was separately fixed in 95% ethanol in the field then transferred to the laboratory. A total of 111 humus samples were available.

Humus Analysis

All layers were carefully spread out in a Petri dish filled with 95% ethanol. The different solid humus components were identified under a dissecting microscope (x40) and their relative volume was quantified using the point-count method (Jongerius 1963; Bal 1970; Rozé 1989). To do so, a transparent film with a 300-point grid was placed above each of the humus samples and all components falling below grid nodes were identified. Results are expressed as percentages of the volume ratio of each solid element. A total of 62 humus components were identified.

Data treatment and statistics

Data were analysed by principal components analyses (PCA) using samples and humus components as active variables. Horizons (OL, OF, OH, and A) and stand age (5-, 25-, 45-, 95-years) were coded as 0 or 1 and served as passive variables for interpreting the graph without affecting the ordination. Data were standardized prior to ordination (Ponge 1999). In a second step a reduced matrix of humus components confined to the OL and OF layers was PCA ordinated. A k-means clustering algorithm was applied on the ordination scores to group humus components of similar response patterns (cf. Hartigan and Wong 1979). The clusters centres and boundaries were moved to minimize variability within clusters and maximize variability among clusters. The quality of the clustering structure was assessed by the overall average silhouette coefficient, i.e. a measure of the strength of each object's membership to its cluster (Kaufman and Rousseeuw 1990). The effect of the factor “stand age” on these groups was analysed by means of one-way ANOVAs (Sokal and Rohlf 1995). Significant differences between means were tested at the 5% level using the Unequal N HSD test.

The availability of data from complementing studies (section 3.1 and Zaitsev et al. 2002) allowed me to analyse relationships between soil biota and groups of humus components. This was done by means of the General Regression Model technique using soil biotic data (collembolan life forms, oribatid feeding groups, microbial parameters; original data are in Appendix 3.2), as dependent variables and functional groups of humus components as continuous predictors. All analyses were performed with the STATISTICA software package (version 6.0, StatSoft Inc., Tulsa, StatSoft 2001).

3.2.3 Results

A PCA carried out using the humus data from all horizons (111 samples, 62 humus components; data not shown) revealed that only coordinates of the OL and OF layers allowed for discriminating between sites, while OH and A layers were very close to the origin. This suggests a very stable composition of the deeper humus layers during the almost 100 years of the forestry cycle. It also indicates, however, that OH and A layers are not suited for evaluating the contribution of the various humus components to different stages of forest conversion. Thus, a second PCA

confined to the cumulative results for the OL and OF layers was performed (19 samples, 47 humus components; Fig. 3.5).

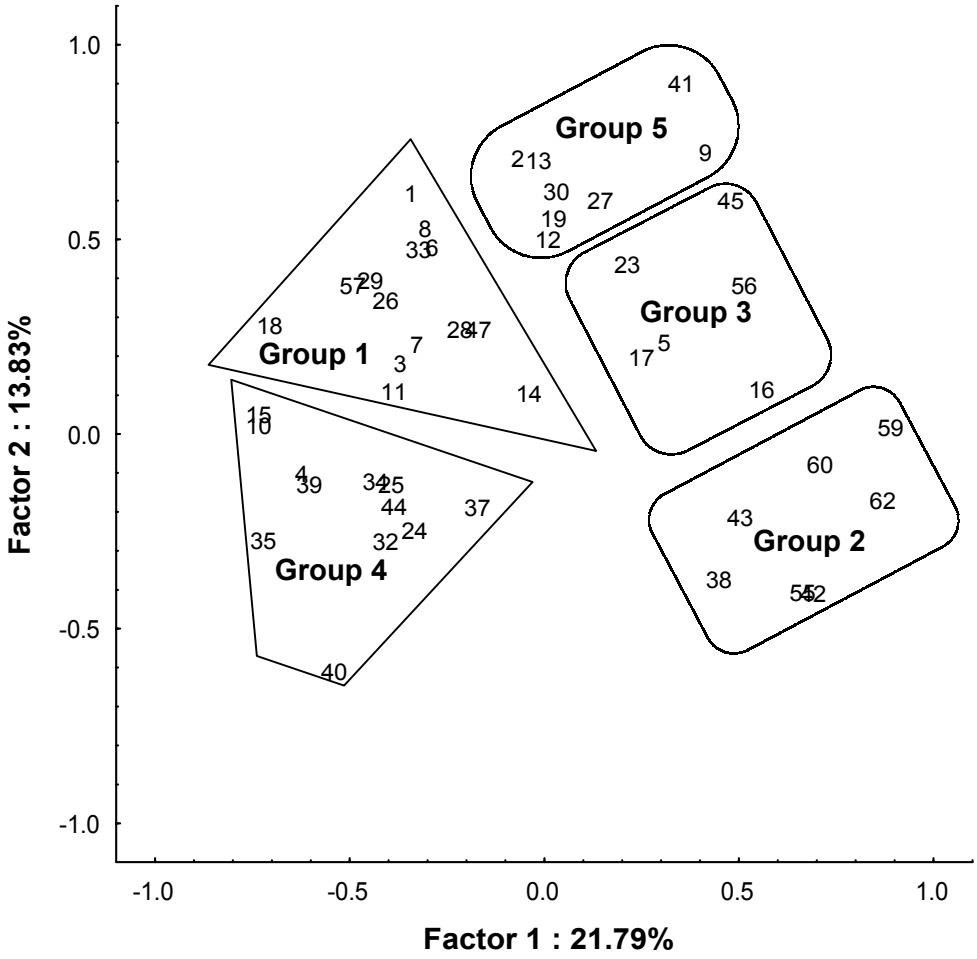


Fig. 3.5: PCA ordination of the 47categories of humus components found in the OL and OF horizons in a chronosequence of four spruce stands showing the five groups identified by k-means clustering procedure. For explanations of codes see Appendix 3.1.

Grouping of the scores of the first two axes of this analysis using k-means clustering revealed five groups. The relative contribution of the different humus components to each of these groups is summarized in Appendix 3.3. Groups received associative names based on the dominating humus components (excluding components with a relative contribution < 5%). Group 1 is dominated by debris of herbaceous plants (> 85%) and is thus referred to as ‘herbaceous litter’. Most components of group 2 relate to freshly fallen and slightly decomposed spruce litter (> 80%, group name: ‘recent spruce litter’). Fragmented components of spruce litter characterize group 3 (> 80%, group name: ‘fragmented spruce litter’) and strongly degraded spruce litter components characterize group 4 (> 80%, group name: ‘decomposed spruce litter’).

Finally, group 5 mainly is a mix of faecal and fungal components (> 75%, group name: ‘faeces and fungi’).

Each of the five groups was significantly affected by the factor ‘stand age’ (Table 3.3). The share of ‘herbaceous litter’ (group 1) was significantly higher at 5 S than at all other sites, though it slightly increased again at 95 S (Fig. 3.6).

Table 3.3: Summary of ANOVA results (F, *p*-levels) on the effect of “Stand age” on groups of humus components in the OL+OF horizons as identified by k-means procedure. *p*-level: level of significance: *** < 0.001.

		Stand age	
	n	**F**	***p*-level**
Herbaceous litter (Group 1)	19	48.6	***
Recent spruce litter (Group 2)	19	10.5	***
Fragmented spruce litter (Group 3)	19	26.6	***
Decomposed spruce litter (Group 4)	19	22.9	***
Faeces and fungi (Group 5)	19	48.6	***

Significant differences between values of ‘recent spruce litter’ (group 2) reflect that the share of this group was particularly low at 5 S and particularly high at 45 S, with the two other sites having intermediate values. Though the contribution of ‘fragmented spruce litter’ (group 3) was low at all sites (< 10%), it was significantly higher at 5 S and 95 S than at 25 S and 45 S. The share of ‘decomposed spruce litter’ (group 4) significantly declined after the clear-cut (from 95 S to 5 S) and remained low at intermediate stages. ‘Faeces and fungi’ (group 5) contributed significantly more to the humus components of intermediate stages than to that of 5 S and 95 S and were even significantly higher at 25 S than and 45 S. A comparison of the individual stages shows that ‘herbaceous litter’ dominated at 5 S, while ‘recent spruce litter’ and ‘faeces and fungi’ dominated at 25 S and 45 S. The mature stand (95 S) is characterized by a shift from ‘recent spruce litter’ to ‘decomposed spruce litter’ and an emerging part of ‘herbaceous litter’ (Fig. 3.6).

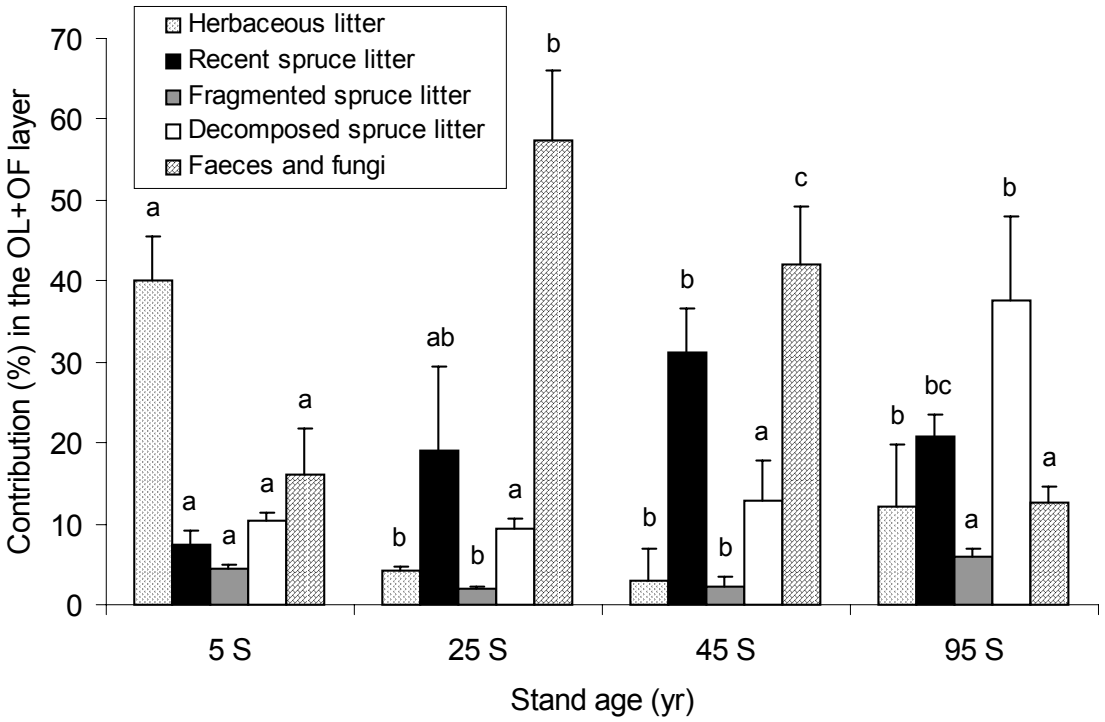


Fig. 3.6: Contribution of each identified group of components to the humus composition in the OL+OF layer at each site of our spruce chronosequence. Columns of the same functional group with identical letters are not significantly different ($p < 0.05$, Tukey unequal N HSD).

Results of the GRM relating the five groups of humus components to functional groups of soil biota are summarized in Table 3.4. Most significant results were found for 'faeces and fungi', with fungivorous oribatids (both browsers and grazers), microbial biomass as well as the ergosterol content being positively correlated and hemiedaphic Collembola being negatively correlated to this humus group. Moreover, 'herbaceous litter' was positively correlated to epedaphic Collembola and 'fragmented spruce litter' to omnivorous oribatid mites. No significant correlation of 'recent spruce litter' and 'decomposed spruce litter' to any of the soil biotic variables could be established.

Table 3.4: Results of the General Regression Models with humus components groups as continuous predictors and functional groups of fauna and microbial parameters as dependent variables. Only significant results are shown. (P: level of significance: *<0.05, **<0.01, ***<0.001; Trend: direction of correlation: + = positive, - = negative).

	Herbaceous litter		Fragmented Spruce litter		Faeces and Fungi	
	P	Trend	P	Trend	P	Trend
Epedaphic Collembola	***	+				
Hemiedaphic Collembola					*	-
Fungivorous Oribatida					***	+
Omnivorous Oribatida			*	+		
Microbial biomass					**	+
Fungal biomass					**	+

3.2.4 Discussion

This study has for the first time come up with evidence for a quantitative relationship between major stages of the forest development, humus dynamics and soil community composition. The combination of PCA techniques with k-means clustering allowed to clearly identify meaningful humus groups dominating the uppermost layers of a spruce forest chronosequence: herbaceous litter, recent spruce litter, fragmented spruce litter, decomposed spruce litter as well as faeces and fungi. The contribution of these groups to the organic layer changed dramatically during forest rotation. In particular, the changes associated with the shift from the early stage to intermediate stages of the chronosequence confirm the dual nature of the humus layer as an important crossing point between above and belowground systems (Wardle et al. 1997; Ponsard et al. 2000). Moreover, it was shown that humus dynamics are significantly correlated to alterations in the structure of the soil community. Thus, all questions posed in the introduction of this study have to be answered positively. The fact that these changes were confined to OL and OF layers suggests a long-lasting stability of the lower strata of the organic layer. It points to the role of the deeper organic horizons as an important decomposer refuge allowing a delayed response of soil biota to vegetational changes and disturbance (e.g. Ruf 2000). I cannot exclude, however, that the apparent invariance of the lowermost layers is partly caused by a methodological bias that is related to the difficulty of

classifying humus components that are strongly transformed (Bernier and Ponge 1994).

The beginning of the forestry cycle is characterized by the addition of large amounts of herbaceous components to the uppermost horizons of the organic layer. Several authors report about the flourishing of ground vegetation after clear-cut (Butterfield 1999; Thomas et al. 1999; Frey et al. 2003; Okland et al. 2003). Similar situations occur in canopy gaps (Collins and Pickett 1988; DeGrandpré and Bergeron 1997; Taskinen et al. 2003). Gartner and Cardon (2004) emphasize the important role of less-recalcitrant material in stimulating decomposers activity. Thus, the stimulation of the decomposition process a few years after clear-cut reported by various authors (Schulze et al. 2000; Law et al. 2001) could partly be explained by the priming effect of herbaceous litter. Increasing amounts of herbaceous components in the organic layer of the mature stand suggest that the rapid response of the decomposer community to the dramatic change induced by clear-cutting is facilitated by a considerable time of pre-adaptation to the collapse of the forest ecosystem (Fons and Klinka 1998; Ruf 2000).

A major shift in the state of the ecosystem occurs at intermediate stages of the forestry cycle, when canopy closure leads to increasing inputs of comparatively fresh spruce litter. Herbaceous litter declines, since the understory vegetation is out competed by the drastic reduction of the light regime (Thomas et al. 1999; Legare et al. 2001; Hunt et al. 2003). Though the resource quality of fresh spruce litter is poor (Harrison 1971; Breznak and Brune 1994), the amount of invertebrate excrements considerably increases. Accumulation of faeces particles not only reflects the stimulation of consumer activity with forest growth, but also points to a delay of decomposition processes that is typical to moder soils (cf Ponge 2003). However, initiation of further steps of the decomposer cascade is indicated by increasing amounts of hyphae. This confirms that fungi are well adapted for degrading recalcitrant organic matter in acid environments (Gobat et al. 2003). The joint increase of invertebrate faeces and fungal components at 25 S and 45 S thus points to an important feed-back loop among different groups of soil biota postulated by several authors, with invertebrate consumers opening up new surfaces for microbial colonization and fungal preconditioning of litter increasing the accessibility of the organic resource for primary decomposers (Anderson and Ineson 1983; Heal et al.

1997). The accumulation of decomposed and fragmented spruce litter at 95 S shows a continuation of this process during forest maturation.

The GRM approach chosen in this study has proven to be a very promising tool for directly relating humus dynamics to decomposer community structure (cf. Wolters 2001). First, the positive correlation between 'herbaceous litter' and epedaphic Collembola points to the positive response of surface dwelling microarthropods to the high quality food sources provided by the ground vegetation (Wolters 1987; Petersen 2002). Than, the close correlation between microbial parameters (total and fungal biomass) and 'feces and fungi' supports the contention of the decomposer loop outlined above. Associated changes of the resource base obviously stimulate fungivorous oribatids (O'Connell and Bolger 1998; Behan-Pelletier 1999). The negative response of hemiedaphic Collembola suggests, however, that the effect of increasing food availability may be offset by changes in the spatial configuration of the microhabitat. For example, declining habitable space or spatial configuration modifying microclimatic conditions (Hansen 2000; Maraun et al. 2001; Eaton et al. 2004). Moreover, a certain degree of niche differentiation between fungivorous and omnivorous oribatids is indicated by the weak positive correlation between the latter group and fragmented spruce litter. And finally, the absence of a significant correlation between euedaphic Collembola and any group of humus components highlights the insensitivity of deep dwelling taxa to changes taking place in the uppermost parts of the organic layer. Euedaphic species can efficiently use the buffering capacity of deep organic layers due to both high nutritional plasticity (Ponge 2000) and a low metabolic activity (Petersen 2002).

In conclusion, this study provides a concise framework for the factors characterizing organic matter transformation during spruce forest rotation. Boundary conditions are set by the shift from coniferous litter dominating at intermediate and later stages to herbaceous litter dominating at early stages. Increased metabolic activity associated with the priming of decomposition processes by high-quality litter leads to a rapid decline of strongly decomposed spruce litter after clear-cut. However, the response of the soil community is far less dramatic than expected for two reasons: (i) opening of the canopy at mature stands allows the decomposers to adopt to changes in resource input considerable time before the collapse of the forest actually occurs, and (ii) the long-term stability of deep organic layers provides a decomposer refuge that allows a rapid response to both adverse and favourable

conditions taking place in the OL- and OF-layers. Within this framework, the autocatalytic process of primary consumers stimulating fungal decomposition and vice versa leads to an accumulation of faecal pellets at intermediate stages of forest succession. Higher levels of the decomposer food web respond differentially, with some microarthropod groups profiting from increased food availability and other suffering from the decline in habitable space. Litter fragmentation nevertheless continues – even after clear-cut – and accumulation of particles of litter at the oldest and at the youngest stand initiates the downward transport of organic matter into deeper layers of the humus profile.

Appendix 3.2: Original biotic data used for the General Regression Model in combination with micromorphological data at the Tharandt spruce chronosequence. Ep: epedaphic; Hemi: Hemiedaphic; Eu: euedaphic.

	Collembola life forms (ind. m^{-2})			**Oribatida feeding groups (ind. m^{-2})**				**Microbial parameters**		
Stand age (yr)	Ep	Hemi	Eu	Fungi. browsers	Fungi. grazers	Herbi-fungi	Omni	Microbial biomass (mgC gDW^{-1})	Fungal biomass (µg gDW^{-1})	Respiration (µg CO_2-C gDW^{-1} h^{-1})
5	6621	16552	15279	4420	5610	14450	2040	2.54	50.57	7.48
5	23173	104151	39980	5610	12410	8330	3570		46.16	4.15
5	4074	43545	39470	4930	5610	12920	2720	2.35	57.91	3.65
5	4584	57550	30812	5780	6290	6290	15300	2.45	53.68	5.37
25	1019	4584	83524	14110	79050	28900	680	3.12	50.47	4.53
25	255	5348	15533	19890	71400	12410	510	2.87	70.00	4.12
25	764	15533	25465	9860	35020	4250	850	3.38	79.15	6.30
25	2037	6112	52712	10540	52530	9690	680	2.69	77.91	3.71
25	509	15788	27247	11730	125800	5610	0	2.73	57.92	3.30
45	509	15279	51693	11560	14280	1700	3570	3.11	58.05	3.30
45	0	11459	21136	20060	17680	1700	340	2.96	60.12	4.43
45	255	6875	14515	11220	28050	3570	11730	3.50	61.21	4.54
45	0	15788	24191	6290	41480	18020	170	2.79	58.28	3.46
45	0	13496	32340	12580	30430	4930	1870	2.44	43.21	3.47
95	1273	66282	73338	6970	7650	10710	9690	2.25	43.16	3.49
95	1019	57805	16552	11220	22780	9690	6800	2.41	42.98	3.57
95	1019	28011	40489	9010	34340	8670	18870	2.15	35.54	4.21
95	0	22918	10950	3910	7310	1360	510	2.72	56.20	2.78
95	5673	9931	11204	3910	21760	1530	9180	3.07	41.21	1.99

Appendix 3.3: List and codes of humus components found in the OL and OF horizons in four spruce stands. Components are classified into five groups regarding their PCA coordinates analysed by K-means clustering procedure. Rel. cont.: Relative contribution. In parenthesis are components with a relatice contribution lower than 5%.

Code	Categories	Rel. cont. to the group (%)
	Group 1: Herbaceous litter	
60	Herbaceous plant component	31.9
38	Herbaceous components compacted in pellet	26.6
62	Fragmented herbaceous plant component	14.1
59	Fragmented herbaceous root	13.4
43	Millipede faeces	8.9
(55	Undetermined plant fragment)	
(42	Holorganic enchys faeces)	
	Group 2: Recent spruce litter	
57	Unidentifiable spruce component	21.5
11	Slightly broken grey spruce needle	17.2
3	Orange entire spruce needle + white mycelium	14.6
14	Spruce bark	7.3
26	Hemorganic aggregate	6.6
1	Bleached entire spruce needle	6.1
8	Brown entire spruce needle + black mycelium	6.0
7	Brown entire spruce needle + white mycelium	5.0
(18	Central cylinder of spruce needle)	
(6	Brown entire spruce needle)	
(33	Fine hemorganic particle)	
(47	Collembola faeces)	
(29	Fine mineral particle)	
(28	Mineral-dominant aggregate)	
	Group 3: Fragmented spruce litter	
23	Fragmented spruce root	34.9
5	Fragmented orange spruce needle	31.8
45	Fragments compacted by earthworms	14.7
16	Fragmented spruce twig	10.9
56	Undetermined fragmented leaf	5.1
(17	Spruce cone scale)	
	Group 4: Decomposed spruce litter	
9	Brown spruce needle particle	19.6
27	Organo-dominant aggregate	18.0
30	Organo-dominant mass	13.3
13	Decomposed spruce male flower scale	12.9
41	Mineral dominant enchys faeces	12.3
19	Spruce cone scale particle	10.9
12	Spruce male flower scale	8.4
(2	Fragmented bleached spruce needle)	
	Group 5: Faeces and fungi	
40	Hemorganic enchys faeces	26.7
39	Organo-dominant faecal mass	13.1
34	White mycelium	12.4
4	Black mycelium	8.9
44	Oribatid faeces	7.5
15	Spruce twig	6.0
32	Hemorganic mass	5.9
35	Brown mycelium	5.8
10	Grey entire spruce needle	5.5
24	Mosses part	5.4
(37	Mycorrhizas)	
(25	Fragmented mosses part)	

3.3 How do soil fauna and soil microbiota respond to beech forest growth?

3.3.1 Introduction

Understanding the temporal dynamic of the soil carbon pool during forestry rotation is crucial for predicting future impacts of global environmental changes on the C storage capacity of terrestrial ecosystems (Schulze et al. 2000, Law et al. 2001, Johnston and Crossley 2002). Considering the role of biota in the mineralisation, transformation and stabilisation of soil organic matter (see 1.4), the performance of the belowground community is key in this respect (Swift et al. 1979, Anderson et al. 1981,Coleman and Crossley 1996, Setälä et al. 1998, Berg et al. 2001, Bradford et al. 2002). However, the response of soil biota to dynamic changes of forest ecosystems is a widely neglected field of research (see 3.1, Paquin and Coderre 1997).

Here, in order to test whether changes in belowground system associated to spruce forest rotation are transposable to a completely different forest ecosystem, I will present the results of a study on the soil biota of a beech forest chronosequence on calcareous soils (Leinefelde, Germany). Chronosequence sites are windows through which several decades or centuries of reality can be observed at the same time (Oksanen 2001). Despite some methodological pitfalls, the “space for time” surrogate remains one of the best way to evaluate long-term environmental changes (cf. Pickett 1989, Trofymow and Porter 1998). I addressed the following questions: Does the developmental stage of a deciduous forest affect the soil fauna and microbial communities? If yes, do all biota respond similar and what is the incidence on the structure of the decomposer assemblage? And finally, how do potential differences in the response patterns relate to ecosystem processes?

3.3.2 Material and Methods

Sampling

The study was conducted at the Leinefelde chronosequence (see 2.2). Microfauna (Nematoda) and mesofauna (Collembola, Oribatida, Gamasinae, and Enchytraeidae) were sampled using steel cylinders (5cm in diameter). Five cores per group were taken in November 2000 and September 2001 at each site and were separated into L and A (first 5cm) horizons. Macroarthropods (Araneidae, Chilopoda,

Diplopoda, Isopoda) were sampled in May and September 2001 following the same scheme but using a bigger steel cylinder (22cm in diameter). At the macroarthropod sampling, Lumbricidae were extracted from the forest floor by the formalin method (Raw 1959). Two watering were performed at 15min intervals, using 37% formalin diluted in tap water to a concentration of 4%. Earthworm individuals captured were immediately preserved in 70% alcohol. Bulk samples of comparable size and depth were collected from the L and A horizons at each sampling occasion for the determination of abiotic and microbial parameters. All samples were separately placed into plastic containers, transported to the laboratory in cool boxes, and stored at 4°C before further treatment.

Micro- and macroarthropod groups were extracted from the core samples by means of the high-gradient-canister method using a modified Kempson-extractor (Wolters 1983). Enchytraeids were extracted following the O'Connor's wet-funnel-technique (O'Connor 1955) and nematodes were extracted using a modified Cobb technique (Van Bezooijen 1999). Abiotic and microbial parameters were determined separately for the two layers (L and A) using aliquots from the bulk samples. Abiotic parameters (i.e. thickness of the organic layer, loss on ignition, bulk density, water content and pH_{H2O}) were determined with standard methods (Alef and Nannipieri 1995). The C content of the organic material (Corg) was estimated from the loss on ignition applying the "Von Bemmelen" factor of 1.724 (Sutherland 1998). The C mineralization rate (Cmin) was measured as CO_2 evolution. It was determined gas chromatographically from aliquots of sieved fresh material (L: 20g, A: 40g) that were incubated under conditions of 10°C and permanent darkness (Zaitsev et al. 2002). Microbial biomass (Cmic) was determined by means of the fumigation-extraction method (Vance et al. 1987, Bloem et al 1997). The C-content of the extracts was measured with a Continuous Flow System (Perstorp Analytical GmbH). The ergosterol content was determined using HPLC analysis. This parameter served as a measure of fungal biomass (Djajakirana et al 1996).

Data treatment and statistics

Cmin, Cmic, ergosterol, and Corg are expressed on a square meter basis, using bulk density, depth of each layer and surface of the sampling plots as conversion factors. Values for the biological parameters and Corg were bulked for the two layers. Due to the lack of a consistent conversion factor, ergosterol

measurements were not converted into fungal biomass values. Instead, the ergosterol – to – Cmic ratio (Ergo/Cmic) was calculated to estimate the relative contribution of fungi to the microbial biomass. The calculation of biomass of mesofauna is based on density-to-dry weight ratios established for a comparative site at Leinefelde forest. Biomass of Nematoda, Lumbricidae, Isopoda, and Diplopoda are based on formula given in (Scheu 1990, Pflug 2001) while biomass of Araneidae and Chilopoda are based on own measurements by means of an electronic balance.

The effect of the factor “stand age” on abiotic variables, microbial parameters and biomasses of soil faunal groups and trophic groups was tested by means of one-way ANOVAs (Sokal and Rohlf 1995). Since seasonal variations are beyond the scope of this study, the factor “sampling date” was used as covariate. When necessary, data were transformed prior to analysis to ensure normal distribution and homogeneity of variance. Significant differences between means were tested at the 5%-level using the Tukey HSD test. Biomass data of the animal taxa were analysed by principal components analysis (PCA). Sites, abiotic (pH and Corg), and microbial parameters (Cmin, Cmic, and ergosterol) were used as passive variables to help interpreting the graph. The relationship of faunal groups (dependent variables) to other groups, abiotic factors (pH, Corg, water content), and microbial parameters (independent variables) was analysed with the GRM technique (see chapter 3.1). All statistical analyses were performed using the STATISTICA software package (version 6.0, StatSoft Inc., Tulsa, StatSoft 2001).

3.3.3 Results

The thickness of the organic layer and the amount of soil organic carbon were not affected by the factor “stand age” (Table 3.5). The pH was considerably higher in the organic layer than in the mineral soil. It gradually decreased in both layers after clear-cut and was still significantly lower at 111 B than at 153+16 B. The water content of the L layer increased during the first three stages of forest growth and then slightly decreased again at 153+16 B. This parameter was relatively stable in the A layer during the first three stages of forest growth, but significantly increased at 153+16 B.

Table 3.5: Means and standard deviations (in parenthesis) of selected environmental parameters measured in a chronosequence of four beech forest stands (Leinefelde, Germany). Means of the same parameter sharing identical letters are not significantly different (Tukey HSD test; p-level of significance: n.s = not significant; * = < 0.05; ** = < 0.01). WC: water content; DW: dry weight; Corg: organic carbon.

	F-values	p-level	30 B	62 B	111 B	153+16 B
Thickness L layer (cm)	0.86	n.s	1.71^{A}	1.48^{A}	1.77^{A}	1.77^{A}
			(0.76)	(0.67)	(0.66)	(0.5)
Corg (g m^{-2})	0.24	n.s	3149^{A}	3078^{A}	2857^{A}	2905^{A}
			(412)	(594)	(1159)	(1410)
pH H_2O L layer	4.84	*	6.4^{AB}	6.2^{AB}	5.8^{B}	6.8^{A}
			(0.3)	(0.2)	(0.5)	(0.5)
pH H_2O A layer	3.42	*	5.6^{AB}	5.3^{AB}	5.0^{B}	6.1^{A}
			(0.2)	(0.1)	(0.4)	(0.8)
WC L layer (%DW)	3.96	*	112.4^{B}	124.8^{AB}	151.3^{A}	133.7^{AB}
			(43.7)	(24.2)	(30.1)	(48.1)
WC A layer (%DW)	6.03	**	40.1^{B}	48.2^{B}	42.1^{B}	62.0^{A}
			(7.5)	(6.4)	(9.6)	(8.8)

Despite considerable changes in average values, no effect of stand age on microbial biomass and respiration could be established (Table 3.6). A marked increase of the fungal contribution to total microbial biomass (ergosterol content, Ergo/Cmic ratio) nevertheless indicates a significant shift in the composition of the microflora at 62 B.

No effect of stand age on the biomass of the micro- and mesofauna could be established (Table 3.6). With the exception of Lumbricidae, in contrast, the biomass of the macrofauna significantly changed during forest rotation. The biomass of Diplopoda at 62 B significantly exceeded that at 111 B, with the biomass at other two sites being intermediate. A similar pattern was observed for Isopoda, but the average biomass was significantly lower at 30 B than at 62 B. The biomass of the two predatory macroarthropod groups was markedly increased at 111 B. This was significant for Chilopoda in comparison to all other sites and significant for Araneidae in comparison to 62 B and 153+16 B.

Table 3.6: Means and standard deviations (in parenthesis) of microbial parameters and biomass of selected micro-, meso-, and macrofaunal groups at four beech forest stands (Leinefelde, Germany). Means of the same parameter sharing identical letters are not significantly different (Tukey HSD test; p-level of significance: n.s = not significant; * = < 0.05; ** = < 0.01; *** = <0.001).

	F-values	p-level	30 B	62 B	111 B	153+16 B
Microbial parameters						
Cmin (mgC m^{-2} h^{-1})	0.57	n.s	102.6^{A} (47.8)	100.3^{A} (61.4)	81.1^{A} (46.1)	91.2^{A} (55.5)
Cmic (gC m^{-2})	0.63	n.s	47.2^{A} (11.1)	39.7^{A} (12.5)	37.6^{A} (25.2)	43.0^{A} (27.7)
Ergosterol (g m^{-2})	3.70	**	0.84^{AB} (0.45)	1.03^{A} (0.24)	0.59^{B} (0.29)	0.83^{AB} (0.44)
Ergo/Cmic (*100)	5.87	**	1.78^{B} (0.85)	2.77^{A} (0.87)	1.66^{B} (0.50)	2.06^{AB} (0.83)
Microfauna						
Nematoda	0.26	n.s.	79.4^{A} (46.7)	86.4^{A} (74.9)	89.5^{A} (71.5)	66.2^{A} (56.1)
Mesofauna						
Enchytraeidae	0.33	n.s.	144.6^{A} (140.4)	164.5^{A} (134.3)	189.0^{A} (196.2)	179.7^{A} (149.9)
Collembola	2.26	n.s.	72.0^{A} (55.4)	112.8^{A} (68.0)	155.2^{A} (111.2)	95.5^{A} (34.9)
Oribatida	1.47	n.s.	96.5^{A} (51.0)	84.8^{A} (60.5)	93.3^{A} (49.9)	135.8^{A} (72.3)
Gamasina	0.36	n.s.	77.7^{A} (41.9)	63.3^{A} (34.1)	74.7^{A} (38.2)	65.5^{A} (31.3)
Macrofauna						
Diplopoda	3.63	*	290.5^{AB} (320.3)	675.9^{A} (563.6)	140.1^{B} (154.9)	249.6^{AB} (392.1)
Isopoda	5.03	**	21.5^{B} (16.5)	114.9^{A} (103.2)	42.3^{B} (19.6)	50.6^{AB} (50.6)
Lumbricidae	0.02	n.s.	2103.4^{A} (4408)	2041.0^{A} (3646)	2285.7^{A} (2775)	1920.4^{A} (2183.4)
Chilopoda	7.54	***	135.6^{B} (98.2)	169.3^{B} (131.3)	386.1^{A} (221.7)	227.3^{B} (171.2)
Araneidae	3.95	*	41.8^{AB} (79.5)	33.4^{B} (33.8)	131.5^{A} (120.5)	30.5^{B} (32.1)

The first and the second axis of the PCA together explained more than 45% of the total variance (Fig. 3.7). The distribution of data points underpins the close association of the two saprophagous macroarthropod groups (Isopoda, Diplopoda) with 62 B and the close association of the two predaceous macroarthropod groups (Chilopoda, Araneidae) with 111 B. Most notably, predatory groups tend to be associated with their main prey (i.e. chilopods with Nematoda and Enchytraeidae,

Gamasid mites with Oribatida and Collembola). Lumbricidae are positioned quite apart from the other groups. Finally, Corg, Cmin and Ergosterol seem to affect the structure of the soil food web.

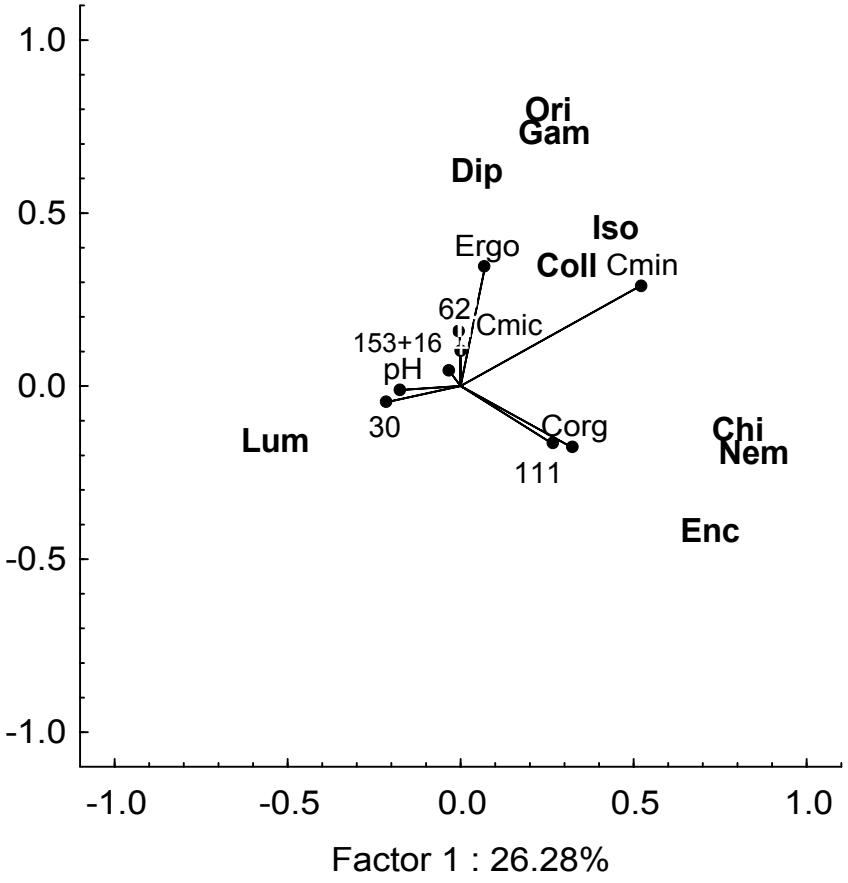


Fig. 3.7: Ordination (PCA) of the biomass of different soil fauna groups (in bold) found at four sites of a beech chronosequence. Abiotic variables and microbial parameters were used as passive variables. Ara: Araneidae, Chi: Chilopoda, Col: Collembola, Dip: Diplopoda, Enc: Enchytraeidae, Gam: Gamasida, Iso: Isopoda, Lum: Lumbricidae, Nem: Nematoda, Orib: Oribatida, pH: pH H_20, Corg: amount of organic Carbon, Cmic: microbial biomass, Ergo: ergosterol content, Cmin: metabolic potential, 30: 30-year-old stand, 62: 62-year-old stand, 111: 111-year-old stand, 153+16: 153+16-year-old stand.

Results of the GRM confirm and clarify the PCA results (Table 3.7). Strong positive correlations were found between predators and their prey. In addition, nematods were negatively correlated to the microbial biomass and positively to the amount of organic carbon. Diplopods were positively correlated to the ergosterol content. And finally, lumbricids were negatively correlated to the C mineralization rate.

Table 3.7: Results of the General Regression Models with biomass of faunal groups as dependent variables and different parameters as categorical predictor. Only significant results are shown. (P: level of significance: *<0.05, **<0.01, ***<0.001; Trend: direction of correlation: + = positive, - = negative).

	Predators[1]		Prey[2]		Ergosterol		Cmin		Cmic		Corg	
	P	Trend	P	Trend	P	Trend	P	Trend	P	Trend	P	Trend
Nematoda	***	+							**	-	***	+
Enchytraeidae	**	+										
Diplopoda					*	+						
Lumbricidae							**	-				
Chilopods			***	+								

[1]Biomass of the predators is the cumulative biomass of Gamasid mites, chilopods, and spiders.
[2]Biomass of prey is the cumulative biomass of mesofauna, excluding gamasid mites, and microfauna.

3.3.4 Discussion

The main results of the study are: (i) resource availability (litter layer, soil organic mater), biomass of the two dominant decomposer groups (microflora, earthworms) as well as the biomass of mesofauna and microfauna remain quite stable during forest succession, (ii) the marked increase of primary decomposers at 62 B (fungi, saprophagous macroinvertebrates) followed by an increase of macropredators at 111 B nevertheless indicate substantial changes of some components of the edaphic community during forest succession, and (iii) constant values of soil respiration suggest that the overall performance of the soil food web does not change during forest succession. Thus, the decomposer system of beech forests on calcareous soils seems to be very resistant against the strong environmental perturbations associated with the forestry cycle (cf. Ulrich 1987). This finding contrasts to the results of complementing studies carried out in spruce forests on acid soils (see 3.1.3). I cannot exclude that some of our results are biased by the "space-for-time-substitution" approach chosen for this study. However, as discussed in section 3.1.4, this approach is the only way of determining long-term changes in forest ecosystems (Trofymow and Porter 1998).

The similarity of edaphic biota between the oldest and the youngest stand suggests that the soil food web either re-establishes quite rapidly after clear-cutting or recovers rapidly after strong disturbances. This is consistent with the results of (Kalisz and Powell 2000) for forests of the Appalachian Mountains. It confirms that disturbance due to timber harvesting has little effect on soil faunal temporal variability (Bengtsson et al. 1997). Considering the major impact of lumbricids on soil structure and organic matter dynamics (Lavelle et al. 1993, Lavelle et al. 1994), the constantly high biomass of earthworms might be key in this respect. Several authors emphasized the impact of earthworms on the microarthropods assemblages (Marinissen and Bok 1988, Loranger et al. 1998). The PCA results seem to confirm the conclusion of an antagonism between Lumbricidae and other soil fauna groups (Maraun et al. 1999, McLean and Parkinson 2000). I thus hypothesize that perturbation by earthworms mask impacts of forest development on other soil biota by exerting a constant stress upon the micro- and mesofauna. In a similar vein, the stability of the microflora may also be a consequence of the dominance of earthworms.

Several changes nevertheless occurred at the level of macroarthropods and fungi. In contrast to common theory, the lowest fungal biomass was found at the stand with the lowest pH (Killham 1994, Gobat et al. 2003). This suggests that the joint increase of fungi and saprophagous macroarthropods at 62 B is rather due to changing substrate conditions than to a shift in the abiotic environment (cf. 3.1). The results of the GRM confirm this conclusion. Similarly, PCA and GRM results suggest that the high biomass of macrocarnivores (spiders and chilopods) at 111 B is due to increased prey availability at this site (cf. Scheu et al. 2003). This is consistent with contention of soil carnivores being controlled by bottom-up forces (Ekschmitt et al. 1997, Chen and Wise 1999, Ponsard et al. 2000). The correlation of nematodes to several environmental factors, namely biomass of their predators, microbial biomass and the amount of organic carbon, indicates the sensitivity of this group to soil conditions. Considering the broad range of nematode feeding groups Yeates et al. 1993), however, these correlations may only reflect the specific response of certain components of the nematode assemblages that were strong enough to alter the total biomass. However, the fact that none of the changes caused by forest rotation altered functional parameters such as C mineralization points to the strong buffering capacity of the soil food web (cf. Vetter et al. 2004). The much higher stability of soil

communities inhabiting deciduous forests on base-rich soils as compared to those of spruce forests on acid soils (see 3.1.3, Zaitsev et al. 2002) confirms that forest management aiming at conserving soil organic matter pools must adapt to regional differences in soil and substrate conditions (cf. Wolters and Schaefer 1994).

3.4 Response of soil biota to manipulation of collembolan biomass

3.4.1 Introduction

In addition to climate, vegetation, and soil parameters (e.g. texture, organic matter, pH), the soil food web is an essential factor determining the rate of breakdown and release of nutrient minerals from forest litter (Seastedt 1984, Lussenhop 1992, Cortet et al. 2003). Given that nutrient limitation controls plant productivity and species composition in most terrestrial ecosystems, the effects of soil decomposers can significantly alter ecosystem processes (Seastedt 1984, Verhoef and Brussaard 1990, Setälä and Huhta 1991, De Deyn et al. 2003). But surprisingly little is known about the relation between soil decomposers assemblage and soil functioning. In particular, the consequences of temporal variations in the structure of soil food webs upon ecosystem performances (Hoover and Crossley 1995). Predation, competition, and mutualistic relationships are known as fundamental factors regulating the functioning of the food web (Wardle and Yeates 1993, Wardle and Lavelle 1997) but understanding and quantifying those relationships remains an important issue in soil ecology.

Collembola, a dominant soil faunal group in European forest soils, influence decomposition and mineralisation of soil organic matter via direct effects through fragmentation of litter and production of nutrient-rich excreta (Berg et al. 2001, Filser 2002) but also and mostly via indirect effects especially through interactions with microflora (Klironomos and Kendrick 1995, Bakonyi et al. 2002). Therefore, to clarify how structural changes in the soil food web affect its functioning and subsequently ecosystem performance, we carried out a microcosm experiment on the influence of different collembolan biomass on faunal groups, microorganisms, and ecosystem function. The questions we would like to address are:

- Do and how soil food web structure will react to the strong changes in biomass of one of its component?
- And will this subsequently affect the soil ecosystem performance?

3.4.2 Material and methods

The experiment was conducted in microcosms (7.5cm diameter and 11cm height) using soil (L and A horizons) and living organisms from a 62-year-old beech

stand (pH H_2O = 6.2) located close to Leinefelde (51 20'N, 10 22'E, Germany) (see 2.2).

Experimental Set-Up

Three different treatments were established corresponding to three biomass of Collembola reflecting approximately half time, once, and twice the ambient collembolan biomass from the site (Table 3.8). Further in the text those three treatments will be abbreviated to Low, Ambient and High, respectively. In parallel to the addition of Collembola (collembolan species are given in Appendix 3.4) in each microcosm, other groups of the decomposer food web were introduced (i.e. Microflora, Nematoda, Oribatida, Gamasid mites, Enchytraeidae, Chilopoda, and Diplopoda) with a biomass representative of the biomass encountered at the beech site where the soil was excavated (Table 3.8).

Part of the collected litter and topsoil was defaunated by repeated deep-freezing (-28°C) and thawing (Schlatte et al. 1998, Chauvat and Ponge 2002) to be used as substrate in the microcosms (approximately 140g DW soil per microcosm). From the remaining part of the collected soil humus, microflora and invertebrates were extracted in order to set the different treatments. Extraction of arthropods (Collembola, Acari, diplopods, and chilopods) was performed by means of a modified Kempson-extractor (high-gradient-canister method, MacFadyen 1953, Wolters 1983). Extraction of Enchytraeidae was done following the O'Connor's wet-funnel-technique (O'Connor 1955), and finally extraction of nematodes was performed using Cobb´s method modified according to Van Bezooijen (1999).

Microflora was re-inoculated prior to any other groups, by adding "soil extract". This inoculum was produced by stirring a sample combining the L and A layers in distilled water and afterwards filtrating the suspension through a cloth with a 5µm mesh size (see Hågvar 1988). Microflora re-inoculation was followed, one week later, by addition of the different faunal groups including the three different collembolan biomass into the microcosms (see Table 3.8). Each treatment (Low, Ambient and High) comprised six replicates, incubated in December 2002 and kept in the dark under constant climatic conditions (temperature: 10°C; water content: 60% DW), for a period of ten weeks. At the end of the incubation period, arthropods were extracted in a modified Kempson-extractor (see above).

Treatment of data and statistics

Biomass calculation of Acari (Oribatida and gamasid), enchytraeids and nematods was derived from their abundance, using specific conversion factors (Pflug 2001 and citations therein). The dry weight (W) of each collembolan specimen (j) was calculated using the following regression equation:

$\log W_j = \log a + b * \log L_j$

with L_j denoting the average body length (mm) taken from the determination keys listed above. The parameters a and b were derived for each species from the literature (Tanaka 1970; Petersen 1975; Persson and Lohm 1977). Species for which no literature data were available received the same parameter values as species with a very similar body shape. The biomass of juveniles was estimated by assuming half of the body length of the respective adults. Biomass of Chilopoda and Diplopoda is based on density-to-dry weight ratios established for the 62-year-old site at Leinefelde forest (see 3.3.3). The biomass of the fauna was transformed from µg DW per individual to µg C per individual based on values given in Berg (1997).

Microbial biomass (Cmic) was determined at the end of the experiment using the fumigation-extraction-method (Brookes *et al.* 1985, Vance *et al.* 1987, Bloem *et al.* 1997). The C-content of the extracts was measured with a Continuous Flow System (Perstorp Analytical GmbH). During the incubation period, the CO_2-evolution (as a measure of decomposition rate) was monitored three times a week by automatic gas chromatography (Shimadzu GC-14 B). Water content and pH_{H2O} were measured using standard methods (Alef and Nannipieri 1995).

Data on soil faunal biomass and species richness were analysed by two-ways ANOVAs, with the factor “treatment” and “time” using microcosms as replicates. One-way ANOVAs were used to assess the impact of the factor “treatment” on microbial parameters (Cmic and Cmin) at the end of the experiment. When necessary data were transformed prior to analysis in order to ensure additivity of variances. Comparisons among means following ANOVA were achieved a posteriori by the Tukey HSD test. Finally, significant correlations between parameters were achieved using Pearson’s correlation coefficient. All statistical analyses were performed with the STATISTICA software package (version 6.0, Statsoft, Tulsa, Statsoft 2001).

3.4.3 Results

Results of the two-ways ANOVAS are summarized in Table 3.8.

Table 3.8: Mean biomass and standard deviations (in parenthesis) of the faunal groups [µgC gDW^{-1}] and species richness (SR) of Collembola, in the three treatments: Low (L), Ambient (A) and High (H), at the start (initial) and at the end (final) of the experiment. Within parameter rows, mean values sharing the same letter are not significantly different at p = 0.05 (Tukey HSD test). Results of the 2-ways Anovas (F and p) with the factors: treatment (T) (Low, Ambient, High), and time (t) (initial, final) are given; p-level: n.s: not significant, *<0.05, **<0.01 ***<0.001.

	T		**t**		**T x t**		**Initial**			**Final**		
	F	p	F	p	F	p	L	A	H	L	A	H
Nematoda	3.42	n.s	-	-	-	-	2.30^{A} (0.06)	2.22^{A} (0.069	2.24^{A} (0.05)	-	-	-
Oribatida	0.19	n.s	12.1	**	0.45	n.s	3.02^{A} (0.08)	2.91^{A} (0.10)	2.93^{A} (0.07)	3.56^{A} (1.12)	3.90^{A} (0.89)	4.02^{A} (1.16)
Gamasid	5.14	*	3.9	n.s	5.91	**	2.16^{B} (0.06)	2.08^{B} (0.05)	2.10^{B} (0.05)	1.80^{B} (0.77)	2.35^{AB} (0.93)	3.32^{A} (0.68)
Enchytraeidae	0.97	n.s	11.4	**	0.78	n.s	3.21^{A} (0.09)	3.09^{AB} (0.08)	3.11^{AB} (0.07)	2.52^{AB} (1.45)	2.47^{AB} (0.78)	1.77^{B} (0.99)
Collembola												
Biomass	50.9	***	60.8	***	9.48	***	2.20^{CD} (0.24)	3.89^{B} (0.30)	5.89^{A} (0.27)	1.75^{D} (0.54)	2.13^{CD} (0.82)	3.21^{BC} (1.09)
SR	2.71	n.s	255	***	2.45	n.s	10^{A}	10^{A}	10^{A}	3.83^{C} (0.41)	5.00^{BC} (1.55)	5.50^{B} (0.84)
Diplopoda	0.14	n.s	12.3	**	0.23	n.s	40.5^{A} (1.15)	39.1^{A} (1.09)	39.4^{A} (0.9)	20.3^{A} (22.3)	26.2^{A} (20.3)	19.4^{A} (21.2)
Chilopoda	10.2	***	12.5	**	15.2	***	15.2^{BC} (0.43)	14.6^{C} (0.41)	14.8^{C} (0.33)	13.5^{C} (2.44)	17.1^{AB} (1.46)	18.6^{A} (1.21)

Collembola biomass and species richness

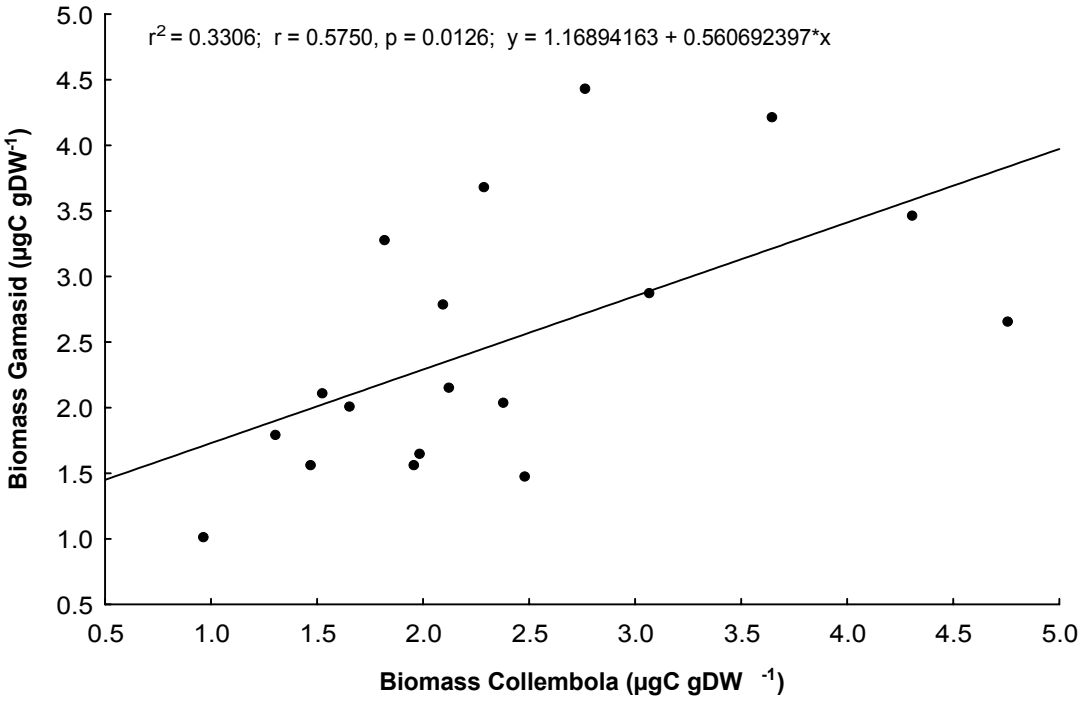
The collembolan biomass was affected by both factors “treatment” and “time” as well as by their interaction. In opposite, species richness was only affected by the factor “time” (Table 3.8). In general, whatever the treatment, we observed a general decrease of Collembolan biomass and species richness in the course of the experiment. Only the collembolan biomass in the Low treatment did not significantly decreased even if a loss of about 26% compared to the start of the experiment was monitored. The biomass reduction was found to be significantly and positively correlated to the biomass at the beginning of the experiment (R^2 = 0.67; p < 0.001). The higher the collembolan biomass in the beginning the higher the loss during the

experiment. However, at the end of the experiment differences of collembolan biomass between the three treatments were still significant, even if it was only between the High and the Low treatment. Reduction of collembolan species richness seemed also more important in the Low treatment (loss of about 62%) compared to the other treatments (loss of 50% or less) (Table 3.8).

Others invertebrates biomass

Biomass of saprophagous and microphytophagous taxa (i.e. Enchytraeidae, Oribatida and Diplopoda) were only significantly affected by the factor “time” with either a global increase (Oribatida) or a decrease (Enchytraeidae and Diplopoda) (Table 3.8). In opposite, biomass of predatory groups were significantly affected by at least the factor “treatment” and by the interaction “treatment x time”. First, biomass of chilopods significantly increased with time in both Ambient and High treatments leading in final conditions to a significantly higher biomass in High treatment compared to the Low one. The same pattern was observed for Gamasid mites with significantly higher biomass values in High treatment compared to Low treatment. Furthermore, at the final condition, biomass of each of the two predatory groups (chilopods, gamasid mites) was significantly and positively correlated to the collembolan biomass (Fig. 3.8).

A)



B)

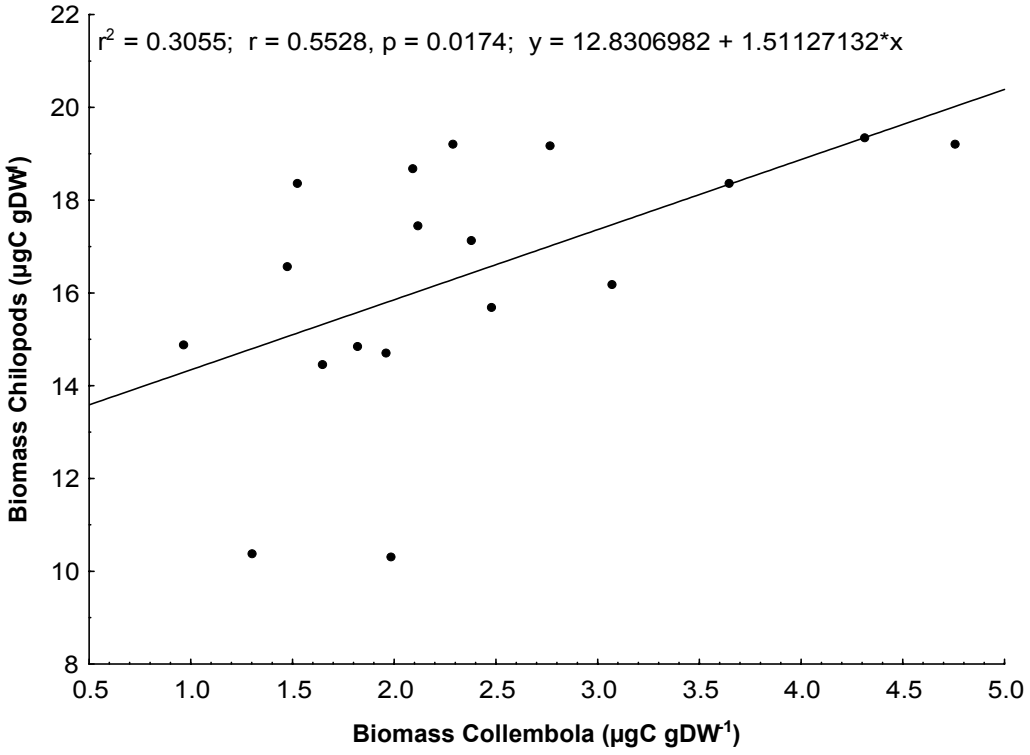


Fig. 3.8: Correlations between biomass of Collembola and A) biomass of Gamasid mites and B) biomass of Chilopods, at the end of the experiment.

Microbial biomass and ecosystem performance

Cmic, only monitored at the end of the experiment, was significantly influenced by the factor "treatment" ($F = 7.69$; $p < 0.01$). Values in the Ambient treatment were significantly higher than those in the High treatment, the Low treatment having an intermediate position (Fig. 3.9A). Cmin showed the same pattern with a significantly higher mean value in the Ambient treatment ($F = 7.41$; $p < 0.01$; Fig 3.9B). Finally, a significant positive correlation was found between both parameters ($R^2 = 0.59$; $p < 0.001$) as well as a negative correlation between collembolan biomass and Cmin ($R^2 = 0.29$; $p < 0.05$).

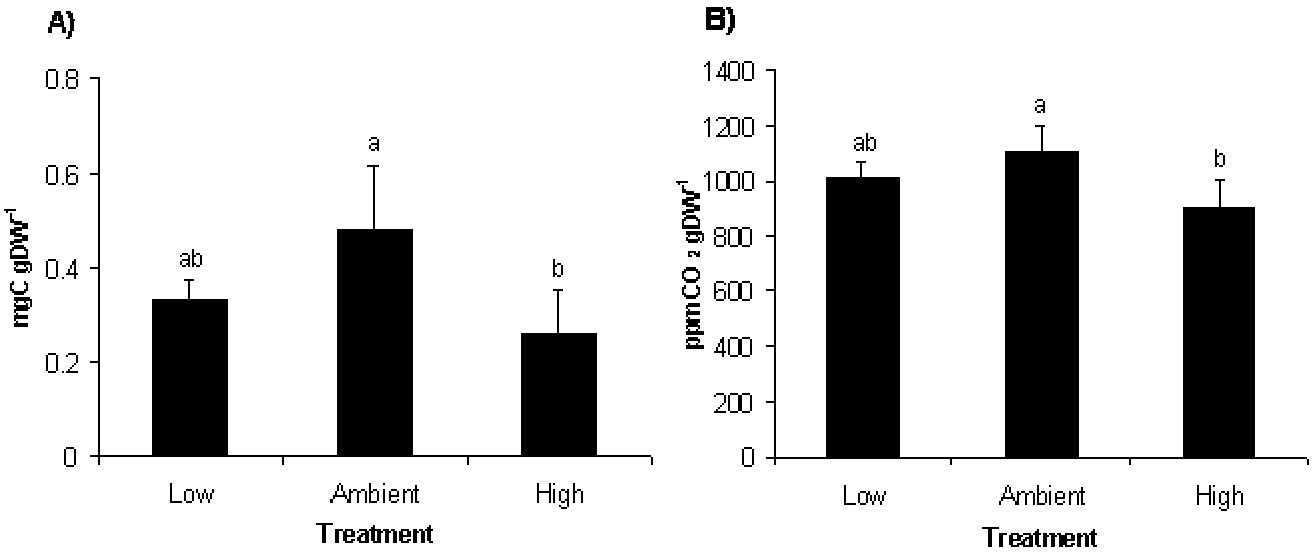


Fig. 3.9: A) Microbial biomass (Cmic) in the different treatments (Low, Ambient, and High) at the end of the experiment. Columns with different letters are significantly different from each other (Tukey HSD test, $p < 0.05$). B) Cumulative CO_2 release (Cmin) in the different treatments (Low, Ambient, and High) at the end of the experiment. Columns with different letters are significantly different from each other (Tukey HSD test, $p < 0.05$).

3.4.4 Discussion

Results of our study revealed the importance of biotic interactions as driver of food web structure and functioning. Within a complex food web, manipulating the biomass of a single group strongly impacted the whole food web structure affecting both lower and higher trophic levels, resulting subsequently in changes of the ecosystem functioning. Furthermore, different group-specific reactions were recorded according to the levels of collembolan biomass. In consequence, both hypotheses formulated earlier could be answered positively.

Incubating during ten weeks different biomass of Collembola in microcosms within a defined food web structure resulted in an overall decrease of collembolan biomass whatever the treatment. The decrease was found to be proportional to the biomass introduced. Moreover, at the end of the experiment biomass of Collembola and predators were significantly correlated. While it is often suggested that micro-phytophages as Collembola are food controlled in detritivore communities (see III.1, Polis and strong 1996, Laakso and Setälä 1999), our data would rather attribute the collembolan decrease to the predation pressure. In fact, many predaceous mite species and chilopods are generalist predators and attack any arthropod or worm they encounter (Christiansen 1964, Karg 1971, Laakso et al. 1995, Huhta et al. 1998), thus the increase biomass of Collembola naturally increase the prey availability, then, logically, the probability of a predator first to meet a prey and second that this prey would be a Collembola. This could have resulted in a predation pressure proportional to the biomass of Collembola introduced. However, no other results corroborated this hypothesis and strong evidence of endogenous regulation of collembolan density was already demonstrated experimentally (Ferguson and Joly 2002). We would rather suggest a complex interaction of density-dependent mechanisms (e.g. competition for food, limitation space) and top-down control (predation) influencing the collembolan community. The decrease of collembolan species richness seems a logical consequence of biomass decrease.

Higher trophic levels appeared, hence, to be highly sensitive to variations in collembolan biomass. Indeed, the biomass of predaceous groups (chilopods and Gamasid mites) was found to be a direct function of the food supply. Their biomass increased in function of the collembolan biomass, and generally of their potential preys. It confirms the bottom-up control of predators reported in several studies (Ekschmitt et al. 1997, Chen and Wise 1999, Ponsard et al. 2000).

In contrast, saprophage (Diplopoda) or microphytophage (Enchytraeidae and Oribatida) groups rather seemed indifferent to the biomass-level of Collembola during the course of the experiment. The overall slight decrease in biomass of diplopods and enchytraeid worms during the experiment most likely resulted of experimental manipulations (perturbations) or conditions as limited space generating food competition for example. In opposite, the slight increase of Oribatid mites highlights the particular strong resilience of this group against perturbations.

Increasing the collembolan biomass led to a reduction of soil respiration, a measure of microbial activity, confirming that the effects of invertebrate grazing on microbial activity are density dependent (Anderson et al. 1981, Hedlund and Sjögren-Öhrn 2000, Cortet et al. 2003, Cole et al. 2004). In parallel, the same grazing impact was observed on microbial biomass. Moreover, further indication of a relation between microbial biomass and activity was found, it is thus hypothesized that the decrease of microbial activity in due in our study to a decrease of its biomass.

To conclude this experiment provides evidence that the functioning of the food web and ecosystem is highly sensitive to variations of the biomass of a group from an intermediate level. However, manipulation of biomass led at the end of the experiment to different level of species richness between the treatments. While the relation between species richness and ecosystem functioning is still in debate, recent findings (Laakso and Setälä 1999, Cragg and Bardgett 2001, Cole et al. 2004) supported the notion that the trophic position of species is likely to be more important than the number of species per se for maintaining critical ecosystem processes. This is supported by our data as no relation was found between species richness and Cmin or Cmic. Primary production seemed to be predominantly controlled by organisms at low trophic positions in the decomposer food web. However, without time series analysis it is particularly difficult to detect cascading effect from the predator to the microbial biomass or activity.

Biotic relationships appeared then to be essential drivers of food web functioning and further investigations are needed in order to integrate such parameters into models, which aimed at predicting the turnover of carbon or nitrogen based on food web performances.

Appendix 3.4: Collembolan species used in the experiment set-up.

Collembolan Species
Folsomia quadrioculata (Tullberg 1871)
Isotomiella minor (Schäffer 1896)
Parisotoma notabilis (Schäffer 1896)
Lepidocyrtus lanuginosus (Gmelin 1788)
Tomocerus minor (Lubbock 1862)
Protaphorura sp.
Isotoma violacea (Tullberg 1876)
Pseudosinella alba (Packard 1873)
Sminthurinus aureus (Lubbock 1862)
Neanura muscorum (Templeton 1835)

4 GENERAL DISCUSSION

The main focus of this study was to investigate changes taking place in the soil system (biota and structure) during forest rotation in relation to ecosystem performances. Particular emphasis was given to the possible connections occurring between the different functional entities of the decomposer assemblage during forestry cycles. After an objective critic of the methods used for this thesis, the general results of the different chapters will be synthesized and discussed in light of recent advances in soil ecology research.

4.1 Comments on the methodological approach

Chronosequence approach

To study successional changes in the soil system during forest rotation, a chronosequence approach using the 'space for time' substitution concept (cf. Pickett 1989) was applied. Two chronosequences, differing from each other by many factors, such as tree species (spruce vs. beech) or soil type (mull vs. moder), were selected for investigations (see section 2). This required pseudoreplicated studies to be performed. Previously, this would have been seen as a major drawback creating bias (e.g. Hurlbert 1984), but recently, and as already discussed in section 3.1.4, this issue was positively reconsidered by Oksanen (2001).

Microcosm experiment

Analysing the performance of soil ecosystems in the laboratory, as it was done in section 3.4, is generally problematic (Pflug 2001) due to artificial conditions and restricted space. An important limitation of microcosm experiments is that no inputs and outputs of nutrients and fauna take place (Carpenter 1996). Furthermore, complex interrelationships between abiotic and biotic factors emphasise the difficulty of applying laboratory data obtained at constant climatic conditions to the field (Laakso et al. 1995). Nevertheless, the use of microcosms is widely recognized and widespread: for example, Teuben and Verhoef (1992) found the same trends when comparing field data with microcosm and mesocosm measurements. In the literature, the vast majority of microcosm experiments regarding the relationship between fauna

and ecosystem processes have often dealt with only a single-species or an assemblage comprising a few species, and therefore not really representative of a real soil food web (Verhoef and de Goede 1985, Mebes and Filser 1998, Kaneko et al. 1998, Liiri et al. 2002). Such major reduction of the decomposer food web may have a strong effect on the population dynamics of the species involved (Vreeken-Buijs and Brussaard 1996). Therefore, retaining almost the whole faunal composition as it was done in section 3.4.2, theoretically represents the natural situation more accurately.

Bacterial activity – Biolog method

To analyse both the functional diversity and the activity of the bacterial community, the Biolog method was employed (see section 3.1.2). This method, although well acknowledged, faces several drawbacks. The main criticism is that it quantifies the metabolic activity of only a limited group of so-called 'cultivable' bacteria and is consequently very selective (Biolog 1993; Bossio and Scow 1995). Recent advances in the field of molecular biology have led to a rise of enthusiastic hopes in their application in soil ecology. In fact, molecular biology methods can be used to analyse diversity in DNA extracted directly from soil, and thus can examine diversity across the whole microbial community (Giller et al. 1997). Use of molecular methods to characterise soil bacterial community will inevitably serve to gain further insights in all topics related to biodiversity and conservation.

4.2 Major findings of the different studies

The hypotheses formulated at the beginning of this work have all been confirmed. The results from the sections 3.1 to 3.3 clearly demonstrated the influence of forestry cycles on soil biota communities and topsoil structure. A direct comparison between both investigated forests is a far more complicated task considering the numbers of parameters (climatic, geographic, history, etc…) differing between the forests (see sections 2.1, 2.2, 3.1.2, and 3.3.2). Nevertheless, two major phases during forest rotation can be identified. Firstly, the transition from a mature to regeneration stand, which implies a sudden and strong perturbation, i.e. a clear-cut with removal of trunks followed by plantation of new trees. Secondly, the growth of the forest from the regeneration stand to the mature stand that, compared to clear-cut, operates as a long-term process (in our case, over a century). In general, and

regardless from the chronosequence investigated, both phases showed specific effects on soil biota and soil structure (sections 3.1.3, 3.3.3, Bernier and Ponge 1994, Setälä and Marshall 1994, Marshall et al. 1998, Butterfield 1999, Kalisz and Powell 2000).

A major finding is the indication of a certain degree of ecosystem integrity maintained during the whole cycle (Fig. 3.3 and Tab. 3.6). This is important for maintaining site productivity for sustainable timber production, as with a more stable soil biota community, plant available nutrients (e.g. N, P, K) released would become more stabilized, and the physical conditions of the soil would become more suitable for root growth and plant water uptake. However, the recovery of the soil fauna community from disturbances caused by clear-cutting and tree removal takes a rather long time (Fig. 3.2 to 3.4, Butterfield 1999, Bird et al. 2000, Zaitsev et al. 2002).

The large panel of reactions of soil fauna to ecosystem changes monitored in the beech forest chronosequence (see Tab. 3.6), raises the question of the value of soil fauna as bioindicator of ecosystem perturbations or of environmental conditions. Soil ecologists tend to select a particular taxonomic group and analyse its relationship with different soil parameters, hoping that the selected group might turn out to serve as a ‘surrogate for larger communities’ (Markert et al. 2003). As shown in the results section 3.1.3 and 3.3.3, considering different taxonomic groups led to observation of different reactions at different levels (e.g. species diversity to functional) in response to environmental changes. In other words, during forestry cycles, what is true for a particular group does not necessarily provide an accurate indication for the vast majority of other groups. This is understandable with regard to the important biodiversity, and thus to the high diversity of life strategies encountered in the soil (section 1.4, Wolters 2001, Gobat et al. 2003). However, according to Markert et al. (2003), a bioindicator is an organism, a part of an organism or a community of organisms, which contains information on the quality of the environment. Lumbricids, for example, are good indicators to show the reactions of soil fauna to forest soil-liming (Makeschin 1991, Geissen et al. 1998, Kautz and Topp 1998).

During this work, even if part of the Collembolan assemblage was clearly related to changes encountered at above- or below-ground system during spruce forest rotation as shown in sections 3.1 and 3.2, further studies are needed to depict good indication traits. Furthermore, the suitability of soil fauna (and Collembola in

particular) as bioindicators must be questioned with respect to feasibility given the time and manpower input necessary to gather sufficient data to draw clear relationships (see Geissen and Kampichler 2004). In addition, the usefulness of a bioindicator depends on the strength of the relationship between the causative environmental factor and the ecological endpoint (e.g. species composition; Van Straalen and Verhoef 1997).

It is therefore essential to know the complete physiology, ecology and behaviour of a bioindicator. In this respect soil zoology is far beyond other disciplines such as hydrobiology (Gobat et al. 2003). In particular, most of our knowledge in the assessment and understanding of biotic and abiotic interactions, and their consequences on community structure, is still anecdotic. This has been identified as a major shortcoming in soil ecological research as the knowledge of mechanisms prevailing in biotic interactions is a prerequisite for a sound prediction of the fate of most ecosystems in an increasingly changing world (Seastedt 2000).

In this thesis, particular emphasis was given in highlighting strong interactions between different actors of the decomposition process. In the field, positive correlations between collembolan biomass and ergosterol content (Tab. 3.2) suggest a close association between the spatio-temporal variability of large collembolan species and the patchy distribution of fungi. This support the idea that Collembola species may prefer to feed on specific fungi (McMillan, 1976, Chen et al. 1995, Thimm and Larink 1995). Moreover, for the first time evidence was given for quantitative relationships between forest development stages, humus dynamic, and soil community composition (section 3.2). In the beech chronosequence (section 3.3) correspondence analysis revealed clear biotic interactions modelling the soil fauna assemblage both spatially and temporally (Fig. 3.7). Experimentally (section 3.4), finally, changes in collembolan communities significantly affected other trophic levels (i.e. primary decomposers and predators; Tab. 3.8), confirming regulation mechanisms taking place in the soil food web (Ponsard et al. 2000, Cortet et al. 2003, Cole et al. 2004). Highlighting such biotic or abiotic relationships was necessary to assess, before drawing conclusions on their functional implications at the ecosystem level processes later on.

Changes taking place in the aboveground system may have strong consequences on the belowground system and vice versa (Wolters et al. 2000). Ponge (1999) described interactions between soil organisms and their environment in

terms of positive or negative feedback loops taking place in the build-up or steady state of soil ecosystems, respectively. This would suggest that during spruce forest development, self-reinforcing processes drive the ecosystem through different successional changes characterised by specific performances. Development of spruce from the regeneration to the immature stage, for example, lead to detrimental effects on soil structure (3.2) and decomposer performance, resulting in decrease of decomposition rate (Fig. 3.1). This implied a lower nutrient availability for plants and stabilization of soil organic matter.

On the other hand, no dramatic changes in ecosystem performance (soil respiration rate) were recorded during the beech forest rotation investigated (Tab. 3.6). This contrasts to the general agreement that beech monoculture rotation management suppressed the expression of early-successional functional groups of plant species in young phases with the potential to alter the ecosystem functioning in the long term (see Aubert at al. 2004). However, Teuben and Roelofsma (1990) concluded that respiration measurements alone are not enough to explain decomposer activity during the decomposition process. Nevertheless, it seemed that in this particular case study, soil decomposer system was more stable under native beech trees than under introduced spruce trees (sections 3.1.3 and 3.3.3). Role of “ecosystem engineer” as earthworms might be key in this respect as underlined in section 3.3.4

In fact, there is ample evidence that the replacement of deciduous forests by monoculture coniferous stands has considerable environmental trade-offs, including soil acidification, high wind throw susceptibility, frequent pest outbreaks, and low value for nature conservation (e.g. Nihlgrad, 1971; Ulrich et al., 1976; Ulrich, 1994; Kazda and Pichler, 1998). Therefore, the idea of re-establishing mixed forests that are better adapted to site conditions has attracted increasing attention of forest owners and governmental institutions over the last decades (Cannel et al., 1992; Kazda and Pichler, 1998). It is argued that the conversion process succeeds in reducing the environmental risks associated with pure spruce stands (Saetre et al., 1999). Available data on soil biota and ecosystem processes in such managed forests are still rare but tend to prove that the lasting effect of coniferous litter on the resource quality has an important ‘memory effect’ on the decomposers assemblage (cf. Wallwork, 1976, Salamon et al. 2004). Soil system is rather conservative (Ruf 2000) and its evolution, with accompanying forest conversion, is not quick, even if

quantitative or qualitative changes of resources in the topsoil horizons could be comparatively fast (section 3.2.3).

To conclude, this work provides consistent results on associated successional changes in the belowground system occurring during forest rotation. Further potential consequences on ecosystem functioning were also assessed and the need to take into account not only the landscape forest cover, but also the type of forest, its developmental stage, its status (managed or not) and the soil system in its unity when monitoring and for example modelling potential soil sinks or sources of carbon was underlined. Indeed, all of these parameters influence the balance between stored and released carbon.

However, many questions are still open and especially on symmetrical relationships between soil organisms and their proximate or remote environment. This is particularly important if we want to measure the degree of organization of the soil ecosystem, and thus be able to predict its capability to face the chaotic influence of mankind, global changes and other disturbing influences.

5 CONCLUSIONS

In regard to the mains objectives and aims of this thesis, the major conclusions that can be drawn are:

- There are important modifications of the soil decomposer assemblage during forest rotation, emphasizing the strong link between above- and below-ground system.
- Studying the humus structure and the evolution of its morphology during forestry cycle allow a good understanding of the associated changes occurring at the soil biota level. In this respect, food resources and habitat structure appeared to be consistent driving factors of mesofauna and microbiota.
- The stability of deeper horizons of the humus layer confers to the soil a strong buffering capacity, which allows a certain unity in the decomposer assemblage to be maintained under strong environmental changes.
- The hypothesis that the nature of the tree species may strongly control the effects observed on soil decomposer assemblage during forest monoculture rotation was corroborated. Group specific reactions were observed in each chronosequence, both on taxonomical and functional level.
- Changes in the decomposer system, however, do not have systematically strong repercussions on ecosystem performance. Indeed, even if modifications of the decomposer assemblage between the different beech forest stages were found, no subsequent consequences on ecosystem performance were recorded. It is suggested that the role of “ecosystem engineer” as earthworms is key in this respect.
- This thesis provides, nevertheless, ample evidences (in the field or in a microcosm experiment) for substantial ecosystem-level implications of changes in the soil food web and thus corroborated the third hypothesis.
- Finally, forest management aiming at conserving soil organic matter pools must then adapt to regional differences in soil and substrate conditions.

6 SUMMARY

The sustainability of forest resources depends on the continuation of essential ecological processes. These biological processes, affecting the C, nutrient, and hydrologic cycles, result from the activities of all forest organisms. Among the most important of these are invertebrates and microorganisms inhabiting the soil and soil surface. They perform a vital role in decomposing litter by transforming dead organic material into a complex web of new substances, resulting in the food chains that characterise much of the edaphic environment.

The possible responses of soil decomposers to long-term change occurring during forest rotation are largely unknown, with even less being known regarding accompanying impacts on ecosystem performances (i.e. decomposition, mineralisation or stabilisation of organic matter). Evolution of the composition of the above-ground compartment during forest development and subsequent consequences on microclimatic parameters might disturb the balance of the ecosystem, leading to modifications of the structure and functioning of below-ground organisms. Consequently changes in the soil decomposer system might, in turn, influence plant growth and development, due to a feedback loop.

The aims of this study were therefore i) to investigate the influence of forest development on the habitat and structure of soil decomposer assemblage, and ii) to assess the consequences on ecosystem performances and nutrient cycling, especially on carbon trajectory.

Monitoring of soil ecosystem parameters (i.e. abiotic parameters, habitat structure, soil fauna and microbial communities) within two chronosequences and laboratory manipulations were carried out to test and answer the following hypotheses:

- Soil decomposer assemblage and humus structure are strongly affected by successional changes of above ground system during forest rotation.
- The nature of the tree species (coniferous vs. deciduous) may strongly control or shape the effects observed on soil decomposer assemblage during forest monoculture rotation.

- Changes in decomposer assemblage may have a functional implication at the ecosystem-level and might subsequently affect ecosystem performances to a certain extent.

Sites and Methods:

Two forest chronosequences in Germany were selected as study sites: a spruce forest on acid soil at Tharandt and a beech forest on base-rich soil in Leinefelde. Both chronosequences were composed of four stands of different age-classes: 5, 25, 45, 95 and 30, 62, 111, 153+16 years for the spruce and the beech forest, respectively.

At each chronosequence, the structure of the soil faunal and microfloral communities, as well as environmental parameters were assessed by common methods. Furthermore in the spruce chronosequence, description of the humus micromorphology was performed in order to evaluate the habitat and resources modifications during spruce forest growth.

Collembola and microbiota during spruce forest rotation:

CO_2 release significantly increased after clear-cutting and the amount of C stored in the organic layer subsequently declined. The early phase of forest rotation was characterized by a very active decomposer microflora, stimulation of both fungi and bacteria as well as by a high abundance of surface-oriented Collembola. In addition, collembolan species turnover was accelerated. While the biomass of fungi further increased at intermediate stages of forest rotation, the metabolic activity of the microflora was low, the functional diversity of bacteria declined and the collembolan community became impoverished. Euedaphic species dominated during this stage of forest development. These changes can be explained by both reduction in microhabitat diversity and depletion of food sources associated with an accumulation of recalcitrant soil organic matter. Results of the General Regression Model procedure indicate a shift from specific associations between collembolan functional groups and microbiota at the early stage of forest rotation to a more diffuse pattern at intermediate stages.

Though the hypothesis that Collembola are relatively responsive to changes in environmental conditions is confirmed, consistently high community similarity suggests a remarkable persistence of some components of microarthropod

assemblages. This study provides evidence for substantial ecosystem-level implications of changes in the soil food web during forest rotation. Moreover, correlations between bacterial parameters and Collembola point to the overarching impact of differences in the composition of the microbial community on microarthropods.

Humus micromorphology and soil organisms in a spruce chronosequence:

The relationship between changes in the humus structure and functional groups of soil biota in the spruce chronosequence was investigated. Due to the very stable composition of the deeper humus layers, it was only possible to discriminate between sites on the basis of the OL and OF layers. A PCA confined to these two layers followed by a k-means clustering analysis revealed five functional groups of humus components named after their major constituents: herbaceous litter, recent spruce litter, fragmented spruce litter, decomposed spruce litter, and faeces and fungi. Each group was significantly affected by the factor ‘Stand age’.

Boundary conditions of organic matter transformation are set by the shift from coniferous litter dominating at intermediate and later stages to herbaceous litter dominating at early stages. A rapid decline of decomposed spruce litter after clear-cut suggests increased metabolic activity associated with the priming of decomposition processes by high-quality litter. It is hypothesized that the moderate response of the soil community to these changes can be explained by two reasons: (i) opening of the canopy at mature stands allows adaptation to changes in resource input a considerable time before the collapse of the forest actually occurs, and (ii) deep organic layers provide a decomposer refuge.

The accumulation of faecal pellets at intermediate stages of forest succession reflects the autocatalytic process of primary consumers stimulating fungal decomposition and vice versa. Some microarthropod groups seem to profit from increased food availability, while other suffer from the decline in habitable space. High amounts of litter particles at the oldest and at the youngest stand initiate the downward transport of organic matter into deeper layers of the humus profile.

Decomposer system during beech forest rotation:

Resource availability (litter layer, soil organic mater), biomass of the two dominant decomposer groups (microflora, earthworms) as well as the biomass of mesofauna and microfauna remain quite stable during beech forest succession. Nevertheless, the marked increase of primary decomposers at the 62-year-old stand (fungi, saprophagous macroinvertebrates) followed by an increase of macropredators at the 111-year-old stand, indicate substantial changes of some components of the edaphic community during forest development. However, constant values of soil respiration suggest that the overall performance of the soil food web does not change during forest succession. Thus, the decomposer system of beech forests on calcareous soils seems to be very resistant, compared to the spruce forest on acid soil, against the strong environmental perturbations associated with the forestry cycle. It is suggested that earthworms activities might have masked impacts of forest development on other soil biota and led to an amazing stability of decomposer assemblages during beech forest rotation.

Food web structure and ecosystem functioning:

In a microcosm experiment, three different treatments corresponding to three different biomass of Collembola were established. In the microcosms, in parallel to Collembola, individuals from major groups of the soil decomposers (Microflora, microfauna, mesofauna, and macrofauna) were also introduced achieving therefore a complex food web.

At the end of the experiment, predators (Chilopoda and Gamasid mites) appeared to be highly sensitive to variations in collembolan biomass. Indeed, the biomass of predaceous groups was found to be a direct positive function of the food supply, confirming the bottom-up control of predators reported in several other studies. In contrast, saprophage (Diplopoda) or microphytophage (Enchytraeidae and Oribatida) groups rather seemed indifferent to the biomass-level of Collembola. Increasing collembolan biomass led to a reduction of microbial biomass and of soil respiration, a measure of microbial activity, suggesting that the effects of invertebrate grazing on microbial activity are density dependent.

The results clearly revealed the importance of biotic interactions as driver of food web structure and functioning. They also supported the notion that the trophic

position of species is likely to be more important than the number of species per se for maintaining critical ecosystem processes.

General discussion and conclusion:

The hypotheses formulated at the beginning of this work have all been confirmed. Results from the sections 3.1 to 3.3 clearly demonstrated the influence of forestry cycles on soil biota communities and topsoil structure. A direct comparison between both investigated forests is a far more complicated task considering the numbers of parameters (climatic, geographic, history, etc…) differing between the forests. Nevertheless, two major phases during forest rotation can be identified. Firstly, the transition from a mature to regeneration stand, which implies a sudden and strong perturbation, i.e. a clear-cut with removal of trunks followed by plantation of new trees. Secondly, the growth of the forest from the regeneration stand to the mature stand that, compared to clear-cut, operates as a long-term process (in our case, over a century). In general, and regardless from the chronosequence investigated, both phases showed specific effects on soil biota and soil structure. However, all changes in the decomposer food web did not lead to modifications of the ecosystem performance. In the beech chronosequence on calcareous soil, biomass stability of “ecosystem engineer” as earthworms are suggested to be responsible for stability of meso- and microbiota leading subsequently to constancy of ecosystem processes.

A major finding is the indication of a certain degree of ecosystem integrity maintained during the whole cycle. This is important for maintaining site productivity for sustainable timber production, as with a more stable soil biota community, plant available nutrients (e.g. N, P, K) released would become more stabilized, and the physical conditions of the soil would become more suitable for root growth and plant water uptake. However, the recovery of the soil fauna community from disturbances caused by clear-cutting and tree removal takes a rather long time.

The large panel of reactions of soil fauna to ecosystem changes monitored in the beech forest chronosequence (section 3.3), raises the question of the value of soil fauna as bioindicator of ecosystem perturbations or of environmental conditions.

To conclude, this work provides ample evidence (in the field or in a microcosm experiment) for substantial ecosystem-level implications of changes in the soil food web and thus corroborated the third hypothesis. Finally, forest management aiming at

conserving soil organic matter pools must then adapt to regional differences in soil and substrate conditions. It is also of a particular importance when monitoring or modelling potential soil sinks or sources of carbon.

However, many questions are still open and especially on symmetrical relationships between soil organisms and their proximate or remote environment. This is particularly important if we want to measure the degree of organization of the soil ecosystem, and thus be able to predict its capability to face the chaotic influence of mankind, global changes and other disturbing influences.

7 AUSFÜRHLICHE ZUSAMMENFASSUNG

Einleitung/Zielsetzungen:

Die Nachhaltigkeit von Waldressourcen ist abhängig von der Dauer von essentiellen ökologischen Prozessen. Diese biologischen Prozesse, die die Kohlenstoff-, Nährstoff- und hydrologischen Kreisläufe betreffen, sind auf die Aktivitäten aller Waldorganismen zurückzuführen. Zu den wichtigsten Gruppen zählen hierbei die Invertebraten und die Mikroorganismen im Boden und auf der Bodenoberfläche. Mit vielen Tausend bekannten und unbekannten Arten spielen sie durch die Umwandlung von totem organischem Material zu neuen Substanzen eine wichtige Rolle im Streuabbau. Daraus ergeben sich charakteristische Nahrungsketten für die edaphische Umwelt. Bodenorganismen sind essentiell für die Produktivität sowie den hohen Grad an Biodiversität und das Gleichgewicht von ungestörten Wäldern. Es ist nur wenig bekannt wie die Zusammensetzung der Vegetation die Mikroorganismen, die Invertebraten und die restliche Fauna so wie das einwandfreie Funktionieren eines Waldökosystems beeinflusst. In Anbetracht der bedeutenden Rolle der Bodenorganismen im Wald wird die Notwendigkeit einer genauen Kenntnis ihrer Reaktion auf Forstarbeiten und andere Umweltänderungen deutlich.

Die möglichen Reaktionen von Destruenten auf Langzeitänderungen, die durch Waldumwandlungen hervorgerufen werden, sind ebenso weitgehend unbekannt wie die begleitenden Einflüsse auf die Ökosystemleistungen (z.B. Dekomposition, Mineralisation und Stabilisierung von organischem Material). Sicherlich besteht eine starke Vernetzung zwischen über- und unterirdischen Systemen. Dabei beeinflussen sich die Systeme gegenseitig in ihrer Leistung. Die Veränderung der Zusammensetzung des überirdischen Systems während der Waldentwicklung und die daraus folgenden Konsequenzen für die mikroklimatischen Parameter können die Balance des Ökosystems stören. Dieses führt zu einer Modifikation der Struktur und Funktion der unterirdischen Organismen. Radikale Änderungen im Destruentensystem können andererseits in einem Rückkopplungsmechanismus das Pflanzenwachstum und die Pflanzenentwicklung beeinflussen.

Ziel der vorliegenden Untersuchung war es (i) den Einfluss der Forstentwicklung auf das Habitat und die Struktur der Destruentengemeinschaft zu untersuchen und (ii) die Folgen auf die Ökosystemfunktionen und Nährstoffkreisläufe, insbesondere der Kohlenstoffumsetzung, abzuschätzen. In zwei Chronosequenzen sowie in ergänzenden Laborversuchen wurden verschiedene Bodenökosystemparameter betrachtet (z.B. abiotische Parameter, Habitatstruktur, Bodenfauna und mikrobielle Gemeinschaften), um folgende Hypothesen zu testen:

Die Desturentengemeinschaft und die Humusstruktur werden stark von den sukzessiven Änderungen im überirdischen System während der Waldumwandlung beeinflusst.

Die Waldform (Nadelwald vs. Laubwald) kann die beobachteten Effekte auf die Destruentengemeinschaft während der Umwandlung der Waldmonokultur stark kontrollieren oder beeinflussen.

Änderungen in der Destruentengemeinschaft können eine funktionelle Auswirkung auf der Stufe des Waldökosystems haben und in einem bestimmten Umfang die Ökosystemleistungen beeinflussen.

Untersuchungsflächen und Methoden:

Als Untersuchungsflächen wurden zwei Waldchronosequenzen mit einem Anbau in Monokulturen in Deutschland ausgewählt. Dabei wurde ein Fichtenwald auf saurem Boden in Tharandt einem Buchenwald auf basenreichen Boden in Leinefelde gegenübergestellt. Beide Chronosequenzen setzen sich aus vier verschiedenen Altersklassen zusammen: 5, 25, 45, 95 und 30, 62, 111, 153+16 Jahre für den Fichten- beziehungsweise den Buchenwald.

Für jede Chronosequenz wurde die Zusammensetzung der Bodenfauna und der Mikrofloragemeinschaften sowie die Umweltparameter mit den üblichen Methoden bestimmt. Außerdem wurde in der Fichtenchronosequenz die Humusmikromorphologie bestimmt, um die Habitat- und die Ressourcenveränderungen während des Fichtenforstwachstums abzuschätzen.

Collembola und Mikrobiota während der Fichtenwaldumwandlung:

Untersuchungen, die dynamische Prozesse in Waldökosystemen berücksichtigen, sind erstaunlicherweise selten. In der ersten Untersuchung wurde daher die sukzessive Änderungen in der Struktur der Collembolengemeinschaft und

der mikrobiellen Leistung während der Waldumwandlung analysiert. Die Untersuchung wurde in einer Fichtenchronosequenz in Tharandt durchgeführt.

Die CO_2-Freisetzung stieg signifikant nach dem Kahlschlag an. In Folge dessen sank der Gehalt von gebundenen C in der organischen Schicht. Die frühe Phase des Waldumbaus war durch eine sehr aktive Destruentenmikroflora, eine Steigerung Pilz- und bakteriellen Biomasse sowie einer hohen Abundanz oberflächenorientierter Collembolen charakterisiert. Zusätzlich war der Wechsel der Artenzusammensetzung der Collembolengemeinschaften beschleunigt. In den Zwischenstufen des Waldumbaus nahm die Biomasse der Pilze weiter zu. Die metabolische Aktivität der Mikroflora war in dieser Stufe gering. Darüber hinaus sank die funktionelle Diversität der Bakterien und die Collembolengemeinschaft verarmte. In dieser Phase der Waldentwicklung dominierten euedaphische Collembolenarten. Diese Veränderungen sind sowohl durch die Verringerung der Mikrohabitatdiversität bedingt, als auch durch die Auszehrung der Nahrungsressourcen verbunden mit einer Anreicherung abbauresistenter organischer Bodensubstanz.

Die statistische Analyse mit Hilfe eines General Regression Model (GRM) zeigt einen Wechsel von spezifischen Zusammenhängen zwischen den funktionellen Gruppen der Collembolen und der Mikrobiota in der frühen Phase des Waldumbaus zu einer eher diffusen Verteilung in den Zwischenstadien. Obwohl unumstritten ist, dass Collembolen sensibel auf Umweltveränderungen reagieren, lässt die beständige hohe Ähnlichkeit der Gemeinschaften in den verschiedenen Stadien eine beachtliche Persistenz von Teilen der Mikroarthropodengemeinschaft vermuten. Diese Studie verdeutlicht die umfangreichen ökosystemaren Auswirkungen des Waldumbaus auf das Bodennahrungsnetz. Außerdem deuten Korrelationen zwischen bakteriellen Parametern und Collembolen auf einen starken Einfluss von Unterschieden im Aufbau der mikrobiellen Gemeinschaft auf Mikroarthropoden hin.

Humusmikromorpholgie und Bodenorganismen in einer Fichtenchronosequenz:

In der zweiten Untersuchung wurde die Beziehung zwischen Änderungen in der Humusstruktur und funktionellen Gruppen von Bodenbiota in einer Fichtenchronosequenz betrachtet. Aufgrund der sehr stabilen Zusammensetzung der tieferen Humusschichten konnten die Untersuchungsflächen lediglich anhand der OL und OF-Schicht unterschieden werden. Eine auf diese beiden Schichten beschränkte

PCA mit nachfolgender K-gemittelten Clusteranalyse zeigte fünf funktionelle Gruppen von Humuskomponenten, die nach ihren Hauptbestandteilen benannt sind: krautige Streu, frische Fichtenstreu, fragmentierte Fichtenstreu, zersetzte Fichtenstreu und Fäzes und Pilze. Jede Gruppe wurde signifikant durch den Faktor “Standortalter” beeinflusst. Die gemeinsame Analyse mit zusätzlichen Daten aus ergänzenden Studien zur Fichtenchronosequenz in Tharandt ermöglichten es mir, die Beziehungen zwischen der Bodenbiota und verschiedenen Gruppen von Humusbestandteilen mit Hilfe eines GRM zu analysieren.

Der Wechsel von Nadellaub in den intermediären und späten Stadien zu krautiger Streu in jungen Stadien prägt die Umwandlung der organischen Substanz. Der rasche Rückgang der zersetzten Fichtenstreu nach dem Kahlschlag führt zu einer erhöhten metabolische Aktivität verbunden mit dem Beginn des Zersetzungsprozesses von qualitativ hochwertiger Streu. Es wird angenommen, dass die geringe Reaktion der Bodengemeinschaft auf diese Veränderungen durch zwei Gründe erklärt werden kann: (i) Die Öffnung der Baumkrone in erntereifen Beständen ermöglicht die Anpassung an Änderungen des Ressourceneintrags deutlich vor dem Zusammenbrechen des Waldbestands (ii) und tiefere organische Schichten bieten den Destruenten ein Refugium. Die Akkumulation von Fäzespellets im mittleren Stadium der Waldsukzession zeigt den autokatalytischen Prozess der Primärkonsumenten, die die pilzliche Zersetzung stimulieren und umgekehrt selbst stimuliert werden. Einige Mikroarthropodengruppen scheinen von der steigenden Nahrungsverfügbarkeit zu profitieren, während andere unter der Abnahme des Lebensraumes leiden. Große Mengen von Streupartikeln am ältesten und am jüngsten Standort lösen einen abwärtsgerichteten Transport von organischem Material in tiefere Schichten des Humusprofils aus.

Das Destruentensystem während der Buchenwaldumwandlung:

Um zu testen, ob sich die zeitliche Dynamik in verschiedenen Waldökosystemen unterschiedlich auf die Struktur und Leistungen der Bodenbiota auswirkt, wurde in einer dritten Studie eine Buchenwaldchronosequenz in Leinefelde während der Umwandlung eines Laubwaldes untersucht. Hierzu wurde die Biomasse von Hauptgruppen der Mikroflora, Mikro-, Meso- und Makrofauna aufgenommen.

Die Ressourcenverfügbarkeit (Streuschicht, organische Bodensubstanz), die Biomasse der zwei dominanten Destruentengruppen (Mikroflora, Regenwürmer)

sowie die Biomasse von Mikro- und Mesofauna blieben während der Waldsukzession stabil. Nichtsdestotrotz zeigt der deutliche Anstieg an Primärdestruenten an dem 62-jährigen Standort (Pilze, saprophage Makroinvertebraten), gefolgt von einem Anstieg an Makropredatoren am 111-jährigen Standort, beträchtliche Veränderungen einiger Komponenten der Bodengemeinschaft während der Waldentwicklung. Die konstanten Werte der Bodenatmung suggerieren dennoch, dass sich die durchschnittliche Leistung des Bodennahrungsnetzes während der Waldsukzession nicht verändert. Das Destruentensystem von Buchenwäldern auf kalkhaltigen Böden scheint daher sehr resistent gegen die starken Umweltstörungen, die mit dem Waldumbau verbunden sind, zu sein. Es wird angenommen, dass die Regenwurmaktivität möglicherweise den Einfluss der Waldentwicklung auf andere Bodenlebewesen kaschiert und zu einer überraschenden Stabilität der Zersetzergruppen während der Waldumwandlung geführt hat.

Nahrungsnetzstruktur und Ökosystemfunktion:

Neben Klima, Vegetation und abiotischen Bodenparametern ist das Bodennahrungsnetz ein bedeutender Faktor, der die Zersetzungsrate der Waldstreu und die Freisetzung von Nährstoffen daraus bestimmt. Leider ist bisher nur wenig über die Beziehungen zwischen den Destruentengruppen und der Funktion des Bodens bekannt. Besonders die Folgen der zeitlichen Veränderung in der Struktur der Bodennahrungsnetze auf die Ökosystemleistung sind noch wenig erforscht. Predation, Kompetition und mutualistische Beziehungen sind als die fundamentalen Faktoren bekannt, die die Funktion des Nahrungsnetzes regulieren, aber das Verständnis und die Quantifizierung dieser Beziehungen bleiben nach wie vor ein wichtiger Ansatz in der Bodenökologie.

In einem Mikrokosmosexperiment wurden drei verschiedene Ansätze, drei verschiedenen Collembolenbiomassen entsprechend, unter konstanten Bedingungen im Labor für zehn Wochen etabliert. Parallel zu den Collembolen wurden in den Mikrokosmen Individuen der Hauptgruppen der Destruenten (Mikroflora, Mikrofauna, Mesofauna und Makrofauna) eingesetzt, um ein komplexes Nahrungsnetz zu erhalten. Am Ende des Experimentes, schienen die Predatoren (Chilopoda und Gamasida) höchst sensitiv auf die Variation in der Biomasse der Collembolen zu reagieren. In der Tat konnte die Biomasse der räuberischen Gruppen als eine direkte

Funktion des Nahrungsangebots ausgedrückt werden, was die bottom-up Kontrolle der Räuber bestätigt, wie sie in einigen anderen Studien gefunden wurde.

Im Gegensatz dazu schienen sich saprophage (Diplopoda) oder mikrophage (Enchytraeidae und Oribatida) Gruppen unabhängig von dem Biomasselevel der Collembolen zu verhalten. Die ansteigende Collembolenbiomasse führte zu einer Reduktion der mikrobiellen Biomasse und der Bodenatmung als Maß der mikrobiellen Aktivität. Dies suggeriert einen dichte-abhängigen Effekt des Abweidens auf die mikrobielle Aktivität.

Die Ergebnisse lassen deutlich die Bedeutung der biotischen Interaktionen für die Nahrungsnetzstruktur und -funktion erkennen. Sie unterstützen außerdem die Auffassung, dass die trophische Stellung von Arten für den Erhalt kritischer Ökosystemprozesse wichtiger ist als die Anzahl an Arten per se. Letztlich sind weitere Untersuchungen der biotischen Interaktionen notwendig, um solche Parameter in Modelle zu integrieren, die zum Beispiel gezielt den Umsatz von Kohlenstoff basierend auf der Nahrungsnetzleistung vorhersagen.

Allgemeine Diskussion und Schlussfolgerungen:

Die zu Beginn dieser Arbeit formulierten Hypothesen konnten alle bestätigt werden. Die Ergebnisse der Kapitel 3.1 bis 3.3 zeigen deutlich den Einfluss der Waldumwandlungsmaßnahmen auf die Bodenlebewelt und die Humusstruktur. Ein direkter Vergleich der Buchenwald und Fichtenchronosequenz ist weitaus komplizierter, da sie über die in der Analyse betrachteten Parameter hinaus noch in solchen wie z.B. Klima, Geographie oder Nutzungsgeschichte voneinander unterscheiden. Nichtsdestotrotz konnten zwei übergeordnete Phasen während der Waldumwandlung identifiziert werden: Erstens der Übergang von einem reifen zu einem regenerierenden Bestand, der auch plötzliche und starke Störungen enthalten kann, wie sie z.B. durch Abholzungen mit verbleibenden Baumstämmen gefolgt von Pflanzungen neuer Bäume auftreten. Zweitens das Wachstum des Waldes von dem regenerierenden zu einem reifen Bestand, der – verglichen mit den Abholzungen – als langfristiger Prozess (in unserem Fall über ein Jahrhundert) anzusehen ist. Allgemein und unabhängig von dem untersuchten Zeitabschnitt zeigten beide Phasen spezifische Effekte auf die Bodenbiota und ihre Struktur.

Ein wichtiges Ergebnis dieser Arbeit ist die Identifizierung eines bestimmten Grades an Ökosystem-Integrität, die während des gesamten Waldumbauzyklus

erhalten bleibt. Dies ist wichtig, um die Produktivität eines Standortes für die nachhaltige Holzproduktion zu erhalten, da mit einer stabileren Destruentengemeinschaft die abgegebenen und Pflanzen-verfügbaren Nährstoffe (z.B. N, P, K) stabilisierter und die physikalischen Bedingungen des Erdbodens geeigneter für ein Wurzelwachstum und für die pflanzliche Wasseraufnahme werden. Jedoch nimmt die Erholung der tierischen Bodenbiota nach Störungen wie Abholzungen und Baumentfernungen eine lange Zeit in Anspruch.

Das breite Reaktionsspektrum der Boden-Fauna auf Ökosystem-Veränderungen, welches in der Buchenwaldchronosequenz beobachtet wurde, wirft die Frage auf, welchen Wert die Boden-Fauna als Bioindikator für Ökosystem-Störungen oder für wechselnde Umweltbedingungen hat. Auch wenn Teile der untersuchten Collembolengemeinschaft einen deutlichen Zusammenhang zwischen den aufgetretenen über- und unterirdischen Veränderungen während der Fichtenwaldumwandlung zeigten, sollten weitere Studien durchgeführt werden, um geeignete Indikationsmerkmale zu bestimmen. Eine Art ist nur dann als Bioindikator geeignet, wenn ihre Physiologie, Ökologie und ihr Verhalten bekannt ist. In dieser Hinsicht steht die Bodenzoologie weit hinter anderen Disziplinen wie z.B. der Hydrobiologie. Das bisherige Wissen über die biotischen und abiotischen Wechselwirkungen sowie ihrer Konsequenzen für die Gemeinschaftsstruktur ist noch lange nicht ausreichend. Dies wurde als ein großer Mangel der bodenökologischen Forschung herausgestellt, da ein Wissen der vorherrschenden Mechanismen in biotischen Interaktionen eine Voraussetzung für eine fundierte Vorhersage der Veränderungen der meisten Ökosysteme in einer ständig wechselnden Welt ist. In dieser Arbeit wurde ein Schwerpunkt auf die starken Wechselwirkungen zwischen den verschiedenen Akteuren des Dekompositionsprozesses sowohl unter Feld- als auch unter den kontrollierten Laborbedingungen gelegt.

Zusammenfassend stellt diese Arbeit fundierte Ergebnisse zusammenhängender sukzessiver Änderungen des unterirdischen Systems dar, die während des Waldumwandlung auftreten. Weitere potentielle Konsequenzen auf ein funktionierendes Ökosystem wurden ebenso untersucht. Dabei wurde die Notwendigkeit erkannt, nicht nur den reinen Waldanteil in einer Landschaft, sondern auch die Waldart, das Entwicklungsstadium, den Status (z.B. bearbeitet oder nicht) sowie das Bodensystem in seiner Einheit zu betrachten, wenn z.B. potentielle Boden-Kohlenstoffquellen oder Boden-Kohlenstoff-Verbraucher modelliert werden sollen.

Tatsächlich beeinflussen alle diese Parameter die Balance zwischen dem gebundenen sowie dem abgegebenen Kohlenstoff.

Es sind jedoch noch viele Fragen unbeantwortet geblieben, besonders die symmetrischen Beziehungen zwischen Bodenbiota und ihrer Umwelt. Dies ist insbesondere dann von Bedeutung, wenn der Organisationsgrad des Boden-Ökosystems gemessen werden soll, um damit in der Lage zu sein, die Fähigkeit des Bodens vorhersagen zu können, mit dem chaotischen Einfluss des Menschen durch globale Veränderungen sowie andere störenden Einflüssen umzugehen.

8 REFERENCES

Alef K, Nannipieri P (1995) Methods in Applied Soil Microbiology and Biochemistry. Academic Press. London

Anderson JM, Ineson P (1983) Interactions between soil arthropods and microorganisms in carbon, nitrogen and mineral element fluxes from decomposing leaf litter. In: Lee JA, macNeill S, Morison IH (eds) Nitrogen as an ecological factor. Blackwell, Oxford, pp 413-432

Anderson RV, Coleman DC, Cole CV (1981) Effects of saprotrophic grazing on wet mineralization. Ecol Bull 33:201-216

Anderson TH, Domsch KH (1990) Application of ecophysiological quotients (qCO2 and qD) on microbial biomasses from soils of different cropping histories. Soil Biol Biochem 22:251-256

Anderson TH, Domsch KH (1993) The metabolic quotient for CO2 (qCO2) as a specific activity parameter to assess the effect of environmental conditions such as pH on the microbial biomass of forest soils. Soil Biol Biochem 25:393-395

Aubert M, Bureau F, Alard D, Bardat J (2004) Effect of tree mixture on the humic epipedon and vegetation diversity in managed beech forests (Normandy, France). Can J For Res 34:233-248

Augusto L, Ranger J, Binkley D, Rothe A (2002) Impact of several common tree species of European temperate forests on soil fertility. Ann For Sci 59:233-253

Bal L (1970) Morphological investigation in two moder-humus profiles and the role of the soil fauna in their genesis. Geoderma 4:5-36

Bardgett RD, Cook R (1998) Functional aspects of soil animal diversity in agricultural grasslands. Appl Soil Ecol 10:263-276

Behan-Pelletier VM (1999) Oribatid mite biodiversity in agroecosystems: role for bioindication. Agr Ecosyst Environ 74:411-423

Bengtsson J, Nilsson GS, Franc A, Menozzi P (2000). Biodiversity, disturbances, ecosystem function and management of European forests. For Ecol Manage 132:39-50

Bengtsson J, Persson T, Lundkvist H (1997) Long-term effects of logging residue addition and removal on macroarthropods and enchytraeids. J Appl Ecol 34:1014-1022

Berg MP (1997) Decomposition, nutrient flow and food web dynamics in a stratified pine forest soil. In Department of Ecology and Ecotoxicology, Section Soil Ecology, Vrije Universiteit (thesis), Amsterdam

Berg MP, de Ruiter PC, Didden W, Janssen R, Schouten T, Verhoef H (2001) Community food web, decomposition, and nitrogen mineralisation in a stratified Scots pine forest soil. Oikos 94:130-142

Bernier N, Ponge JF (1994) Humus form dynamics during the sylvogenetic cycle in a mountain spruce forest. Soil Biol Biochem 26:183-220

Bernier N (1998) Earthworm feeding activity and development of the humus profile. Biol Fertil Soils 26:215-223

Binkley D, Giardina C (1998) Why do tree species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry 42:89-106

Bird S, Coulson RN, Crossley DA (2000) Impacts of silvicultural practices on soil and litter arthropod diversity in a Texas pine plantation. For Ecol Manag 131:65-80

Biolog (1993) instructions for Use of Biolog GP and GN microplates. Biolog Inc.

Bloem J, Veninga M Sheperd J (1997) Vollautomatische Messung von Bodenbakterien mit Hilfe der konfokalen Laser-Scanningmikroskopie und der Bildanalyse. Mitt Wissenschaft Tech 11:143-148

Bolger, TM, Heneghan LJ, Neville P (2000) Invertebrates and nutrient cycling in coniferous forest ecosystems: Spatial heterogeneity and conditionality. In Coleman DC, Hendrix

PF (eds) Invertebrates as Webmasters in Ecosystems. CAB International, New York, pp 255-269
Bossio DA, Scow KM (1995) Impact of carbon and flooding on the metabolic diversity of microbial communities in soils. Appl Environ Microbiol 61:4043-4050
Bradford MA, Jones TH, Bardgett RD, Black HIJ, Boag B, Bonkowski M, Cook R, Eggers T, Gange AC, Grayston SJ, Kandeler E, McCaig AE, Newington J, Prosser JI, Setälä H, Staddon PL, Tordoff GM, Tscherko D, Lawton JH (2002) Impacts of soil fauna community composition on model grassland ecosystems. Science 298:615-618
Brêthes A, Brun JJ, Jabiol B, Ponge JF, Toutain F (1995) Classification of forest humus forms: a French proposal. Annales des Sciences Forestières 52:535-546
Breznak JA, Brune A (1994) Role of microorganisms in the digestion of lignocellulose by termites. Annu Rev Entomol 39:453-487
Brookes PC, Landman A, Pruden G, Jenkinson DS (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
Brussaard L (1998) Soil fauna, guilds, functional groups and ecosystem processes. Appl Soil Ecol 9:123-135
Brussaard L, Behan-Pelletier V, Bignell DE, Brown VK, Didden W, Folgarait P, Fragoso C, Wall D, Gupta VVSR, Hattori T, Hawksworth DL, Klopatek C, Lavelle P, Malloch DW, Rusek J, Söderström B, Tiedje JM, Virginia RA (1997) Biodiversity and ecosystem functioning in soil. Ambio 26:563-570
Butcher JW, Snider R, Snider RJ (1971) Bioecology of edaphic Collembola and Acarina. Ann Rev Ent 16:249-288
Butterfield J (1999) Changes in decomposition rates and Collembola densities during the forestry cycle in conifer plantations. J App Ecol 36:92-100
Cannell MGR, Malcolm DC, Robertson PA (1992) The ecology of mixed-species stands of trees. Oxford, Blackwell Scientific.
Carpenter S (1996) Microcosm experiments have limited relevance for community ecosystem ecology. Ecology 77:677-680
Chauvat M, Ponge JF (2002) Colonization of heavy metal-polluted soils by Collembola: preliminary experiments in compartmented boxes. Appl Soil Ecol 21:91-106
Chen B, Snider RJ, Snider RM (1995) Food preference and effects of food type on the life history of some soil Collembola. Pedobiologia 39:496-505.
Chen BR, Wise DH (1999) Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. Ecology 80:761-772
Christiansen K (1964) Bionomics of Collembola. Annu Rev Entomol 9:147-178
Ciarkowska K, Niemyska-Lukaszuk J (2002) Microstructure of humus horizons of gypsic soils from the Niecka Nidzianska area (South Poland). Geoderma 106:319-329
Cole L, Dromph KM, Boaglio V, Bardgett RD (2004) Effect of density and species richness of soil mesofauna on nutrient mineralisation and plant growth. Boil Fertil Soils 39:337-343
Coleman DC, Crossley DA (1996) Fundamentals of soil ecology, Academic Press, San Diego, USA
Collins BS, Pickett STA (1988) Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest. J Ecol 76:437-450
Communautés Européennes – Parlement européen (1994) L'Europe et la forêt, Office des publications officielles des communautés européennes, Luxembourg, pp 1528
Cortet J, Joffre R, Elmholt S, Krogh PH (2003) Increasing species and trophic diversity of mesofauna affects fungal biomass, mesofauna community structure and organic matter decomposition processes. Biol Fertil Soils 37:302-312
Cragg RG, Bardgett RD (2001) How changes in soil fauna diversity and composition within a trophic group influence decomposition processes. Soil Biol Biochem 33:2073-2081
Cummins KW (1974) Structure and function of stream ecosystems. BioScience 24:631-641
Currie WS (1999) The responsive C and N biogeochemistry of the temperate forest floor. Trends Ecol Evol 14:316-320

Dauber J, Wolters V (2000) Microbial activity and functional diversity in the mounds of three different ant species. Soil Biol Biochem 32:93-99

Davidson DA, Bruneau PMC, Grieve IC, Wilson CA (2004) Micromorphological assessment of the effect of liming on faunal excrement in an upland grassland soil. Appl Soil Ecol 26:169-177

Dawod V, FitzPatrick EA (1993) Some population sizes and effects of the Enchytraeidae (Oligocheta) on soil structure in a selection of Scottish soils. Geoderma 56:173-178

Decaëns T, Dutoit T, Alard D, Lavelle P (1998) Factors influencing soil macrofaunal communities in post-pastoral successions of western France. Appl Soil Ecol 9:361-367

DeGrandpré L, Bergeron Y (1997) Diversity and stability of understorey communities following disturbance in the southern boreal forest. J Ecol 85:777-784

Dixon RK, Brown S, Houghton RA, Solomon AM, Trexler MC, Wisniewski J (1994) Carbon pools and flux of global forest ecosystems. Science 263:185-190

Djajakirana G, Joergensen RG, Meyer B (1996) Ergosterol and microbial biomass relationship in soil. Biol Fertil Soils 22:299-304

Dunger W (1975) On the delimitation of soil microarthropod coenoses in time and space. In: Vanek J (ed) Progress in Soil Zoology, Proceedings of the 5th International Colloquium on Soil Zoology. Prague, Czechoslovakia, 17/IX-22/IX 1973. Academia, Prague pp 43-49

Eaton RJ, Barbercheck M, Buford M, Smith W (2004) Effects of organic matter removal, soil compaction, and vegetation control on Collembolan populations. Pedobiologia 48:121-128

Ekschmitt K, Weber M, Wolters V (1997) Spiders, Carabids and Staphylinids - the Ecological Potential of Predatory Macroarthropods. In: Benckiser G (ed) Fauna in Soil Ecosystems. Marcel Dekker Inc., New York, pp 307-362

Faber JH, Teuben A, Berg MP, Doelman P (1992) Microbial biomass and activity in pine litter in the presence of Tomocerus minor (Insecta, Collembola). Biol Fertil Soils 12:233-40

Filser J (2002) The role of Collembola in carbon and nitrogen cycling in soil. Pedobiologia 46:234-245

Fisher RA, Corbet AS, Williams CB (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. J Anim Ecol 12:42-58

Fjellberg A (1998) The Collembola of Fennoscandia and Denmark. Part I: Poduromorpha. Fauna entomologica scandinavica 35. E J Brill, Leiden Boston Köln

Fons J, Klinka K (1998) Temporal variations of forest floor properties in the Coastal Western Hemlock zone of southern British Columbia. Can J For Res 28:582-590

Frey BR, Lieffers VJ, Munson AD, Blenis PV (2003) The influence of partial harvesting and forest floor disturbance on nutrient availability and understory vegetation in boreal mixedwoods. Can J For Res 33:1180-1188

Garland JL, Mills AL (1991) Classification and Characterization of Heterotrophic Microbial Communities on the Basis of Patterns of Community-Level Sole-Carbon-Source Utilization. Appl Environ Microbiol 57:2351-2359

Gartner TB, Cardon ZG (2004) Decomposition dynamics in mixed-species leaf litter. Oikos 104:230-246

Geissen V, Rüdinger C, Schöning A, Brümmer GW (1998) Microbial biomass and earthworm populations in relation to soil chemical parameters in an oak-beech forest soil. Verh Ges Ökol 28:249-258

Geissen, V, Kampichler, C (2004) Limits to the bioindication potential of Collembola in environmental impact analysis: a case study of forest soil-liming and fertilization. Biol Fertil Soils 39:383-390

Giller KE, Beare MH, Lavelle P, Izac AMN, Swift MJ (1997) Agricultural intensification, soil biodiversity and agroecosystem function. Appl. Soil Ecol. 6:3-16

Gillet S, Ponge JF (2002) Humus forms and metal pollution in soil. Eur J Soil Sci 53:529-539

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

Gisin H (1960) Collembolenfauna Europas. Museum d'histoire naturelle, Genève
Gobat JM, Aragno M, Matthey W (2003) Le sol vivant, 2nd edition, Presses polytechniques et universitaires romandes, Lausanne
Greenslade P, Majer JD (1993) Recolonization by Collembola of rehabilitated bauxite mines in Western Australia. Aust J Ecol 18:385-394
Hågvar S (1982) Collembola in Norwegian coniferous forest soils. I. Relations to plant communities and soil fertility. Pedobiologia 24:255-296
Hågvar S (1988) Decomposition studies in an easily-constructed microcosm: Effects of microarthropods and varying soil pH. Pedobiologia 31:293-303
Hansen RA (2000) Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. Ecology 81:1120-1132
Harrison AF (1971) The inhibitory effect of oak leaf litter tannins on the growth of fungi, in relation to litter decomposition. Soil Biol Biochem 3:167-172
Hartigan JA, Wong MA (1979) A k-means clustering algorithm. Appl Stat 28:100-108
Hasegawa M, Takeda H (1995) Changes in feeding attributes of 4 collembolan populations during the decomposition process of pine needles. Pedobiologia 39:155-169
Heal OW, Anderson JM, Swift MJ (1997) Plant litter quality and decomposition: An historical overview. In: Cadisch G, Giller KE (eds) Driven by Nature - Plant Litter Quality and Decomposition. CAB International, Wallingford, pp 3-30
Hedlund K, Bengtsson G, Rundgren S (1995) Fungal odour discrimination in two sympatric species of fungivorous collembolans. Funct Ecol 9:869-875
Hedlund K, Sjögren-Öhrn M (2000) Tritrophic interactions in a soil community enhance decomposition rates. Oikos 88:585-591
Helling B, Pfeiff G, Larink O (1998) A comparison of feeding activity of collembolan and enchytraeid in laboratory studies using bait-lamina test. Appl Soil Ecol 7:207-212
Hintikka V (1970) Studies on white-rot humus formed by higher fungi in forest soils. Comminucationes Instituti Forestalis Fenniae 69:1-68
Hoover CM, Crossley DA (1995) Leaf litter decomposition and microarthropod abundance along an altitudinal gradient. In Collins HP, Robertson GP, Klug MJ (eds) The significance and regulation of soil biodiversity. Kluwer Academic Publishers, the Netherlands, pp. 287-292
Horwood JA, Butt KR (2000) Changes within oribatid mite communities associated with Scots pine regeneration. Web Ecol. 1:76-81
Huhta V (1976) Effects of clear-cutting on numbers, biomass and community respiration of soil invertebrates. Ann Zool Fenn 13:63-80
Huhta V, Sulkava P, Viberg K (1998) Interactions between enchytraeid (*Cognettia sphagnetorum*), microarthropod and nematode populations in forest soil at different moistures. Appl Soil Ecol 9:53-58
Hunt SL, Gordon AM, Morris DM, Marek GT (2003) Understory vegetation in northern Ontario jack pine and black spruce plantations: 20-year successional changes. Can J For Res 33:1791-1803
Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. Ecol Monogr 54:187-211
Joergensen RG, Anderson TH, Wolters V (1995) Carbon and nitrogen relationships in the microbial biomass of soils in beech (*Fagus sylvatica* L.) forests. Biol Fertil Soils 19:141-147
Johnston JM, Crossley DA (2002) Forest ecosystem recovery in the southeast US: soil ecology as an essential component of ecosystem management. For Ecol Manage 155:187-203
Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69: 373-386
Jongerius A (1963) Optic-volumetric measurements on some humus forms. In: Doeksen J, Van der Drift J (eds) Soil Organisms. North-Holland, Amsterdam, pp 137-148
Kaczmarek M (1975) An analysis of Collembola communities in different pine forest environments. Ekol Polska 23:265-293

Kalisz PJ, Powell JE (2000) Invertebrate macrofauna in soils under old growth and minimally disturbed second growth forests of the Appalachian mountains of Kentucky. Am Midl Nat 144:297-307

Kaneko N, McLean MA, Parkinson D (1998) Do mites and Collembola affect pine litter fungal biomass and microbial respiration? Appl Soil Ecol 9:209-213

Karg W (1971) Acari (Acarina), Milben Unterordnung Parasitiformes (Anactinochaeta). Die freilebenden Gamasina (Gamasides), Raubmilben. In Dahl F (ed) Die Tierwelt Deutschlands und der angrenzenden Meeresteile. Vol. 59, pp. 1-475.

Kaufman L, Rousseeuw PJ (1990) Finding Groups in Data. An Introduction to Cluster Analysis. John Wiley & Sons, New York

Kautz G, Topp W (1998) Nachhaltige waldbauliche Massnahmen zur Verbesserung der Bodenqualität. Forstwiss Centralbl 117:23-43

Kazda M, Pichler M (1998) Priority assessment for conversion of Norway spruce forests through introduction of broadleaf species. For Ecol Manag 102:245-258

Killham K (1994) Soil ecology, Cambridge University Press, United kingdom

King AW, Post WM, Wullschleger SD (1997) The potential response of terrestrial carbon storage to changes in climate and atmospheric CO2. Climatic Change 35:199-227

Klironomos JN, Kendrick B (1995) Relationships among microarthropods, fungi, and their environment. Plant Soil 170:183-197

Kratz W (1991) Cycling of nutrients and pollutants during litter decomposition in pine forest in the Grünewald, Berlin. In Nakagoshi N, Golley FB (eds) Coniferous Forest Ecology from an International Perspective. Academic Publishing, The Hague, The Netherlands, pp 151-160

Kubiëna WL (1938) Micropedology. Collegiate Press, Ames

Laakso J, Salminen J, Setälä H (1995) Effects of abiotic conditions and microarthropod predation on the structure and function of soil animal communities. Acta Zool Fennica 196:162-167.

Laakso J, Setälä H (1999) Sensitivity of primary production to changes in the architecture of belowground food webs. Oikos 87:57-64

Lal R (2004) Soil carbon sequestration impacts on global climate change and food security. Science 304:1623-1627

Lavelle P, Bignell D, Lepage M, Wolters V, Roger P, Ineson P, Heal OW, Dhillion S (1997) Soil function in a changing world: the role of invertebrate ecosystem engineers. Eur J Soil Biol 33:159-193

Lavelle P, Blanchart E, Martin A, Spain A, Toutain F, Barois I, Schaefer R (1993) A hierarchical model for decomposition in terrestrial ecosystems : applications to soils of the humid tropics. Biotropica 25:30-150

Lavelle P, Dangerfield M, Fragoso C, Eschenbrenner V, Lopez-Hernandez D, Pashanasi B, Brussaard L (1994) The relationship between soil macrofauna and tropical soil fertility. In: Swift MJ, Woomer PL (eds) Tropical soil Biology and Fertility. John Wiley-Sayce, New York, pp 137-169

Law BE, Thornton PE, Irvine J, Anthoni PM, van Tuyl S (2001) Carbon storage and fluxes in ponderosa pine forests at different developmental stages. Glob Change Biol 7:755-777

Lee KE (1994) The biodiversity of soil organisms. Appl Soil Ecol 1:251-254

Legare S, Bergeron Y, Leduc A, Pare D (2001) Comparison of the understory vegetation in boreal forest types of southwest Quebec. Can J Bot 79:1019-1027

Liiri M, Setälä H, Haimi J, Pennanen T, Fritze H (2002) Soil processes are not influenced by the functional complexity of soil decomposer food webs under disturbance. Soil Biol Biochem 34:1009-1020

Likens GE (1992) The ecosystem approach: Its use and abuse. In Kinne O (ed) Excellence in Ecology, book 3. Ecology Institute, Oldendorf/Luhe, pp 1-166

Loranger G, Ponge JF, Blanchart E, Lavelle P (1998) Impact of earthworms on the diversity of microarthropods in a vertisol (Martinique). Biol Fertil Soils 27:21-26

Lussenhop J (1992) Mechanisms of microarthropod-microbial interactions in the soil. Adv Ecol Res 23:1-33

MacFadyen A (1953). Notes on Methods for the Extraction of Small Soil Arthropods. J. Anim. Ecol., 22, 65-78.

MacMillan JH (1976) Laboratory observations on the food preferences of *Onychiurus armatus* (TULLB.) GISIN (Collembola, Family Onychiuridae). Rev Écol Biol Sol 13:353-364

Magurran AE (1988) Ecological Diversity and its Measurement. Princeton University Press

Makeschin F (1991) Auswirkungen von saurer Beregnung und Kalkung auf die Regenwurmfauna (Lumbricidae: Oligochaeta) im Fichtenaltbestand Höglwald. In Kreutzer K, Göttlein A (eds) Ökosystemforschung Höglwald. Forstwiss Forsch 39:117-127

Maraun M, Alphei J, Beste P, Bonkowski M, Buryn R, Migge S, Peter M, Schaefer M, Scheu S (2001) Indirect effects of carbon and nutrient amendments on the soil meso- and microfauna of a beechwood. Biol Fertil Soils 34:222-229

Maraun M, Alphei J, Bonkowski M, Buryn R, Migge S, Peter M, Schaefer M, Scheu S (1999) Middens of the earthworm *Lumbricus terrestris* (Lumbricidae): microhabitats for micro- and mesofauna in forest soil. Pedobiologia 43:276-287

Marinissen JCY, Bok J (1988) Earthworm-amended soil structure: its influence on Collembola populations in grassland. Pedobiologia 32:243-252

Markert BA, Breure AM, Zechmeister HG (2003) Definitions, strategies and principles for bioindication/biomonitoring of the environment. In: Markert BA, Breure AM, Zechmeister HG (eds) Bioindicators and biomonitors. Elsevier, Amsterdam, pp 3-39

Marshall VG (1992) sustainable forestry and soil fauna diversity. In Fenger MA, Miller EH, Johnson JA, Williams EJR (eds) Our living legacy: symposium on biological diversity. Royal British Columbia Museum, Victoria, pp 239-248

Marshall VG, Setälä H, Trofymow, JA (1998) Collembolan succession and stump decomposition in Douglas-fir Northwest science 72:84-85

McLean MA, Parkinson D (2000) Introduction of the epigeic earthworm *Dendrobaena octaedra* changes the oribatid community and microarthropod abundances in a pine forest floor: a mesocosm study. Appl Soil Ecol 7:125-136

Mebes KH, Filser J (1998) Does the species composition of Collembola affect nitrogen turnover. Appl Soil Ecol 9:241-247

Mikola J, Setälä H (1998) No evidence of trophic cascades in experimental microbial-based soil food web. Ecology 79:153-164

Moore JC (1988) The influence of microarthropods on symbiotic and non-symbiotic mutualism in detrital-based below-ground food webs. Agr Ecosyst Environ 24:147-159

Moore JC, Walter DE, Hunt HW (1988) Arthropod regulation of micro- and mesobiota in below-ground detrital food webs. Ann. Rev. Entomol. 33:419-439

Morin PJ (1999) Community Ecology. Oxford, England, Blackwell Science Inc.

Mühlenberg M (1993) Freilandökologie. Wiesbaden, UTB

Müller PE (1889) Recherches sur les formes naturelles de l'humus et leur influence sur la végétation et le sol. Annales de la Science Agronomique Française et Etrangère 6:85-423.

Nihlgard B (1971) Pedological influence of spruce planted on former beech forest soils in Scania, South Sweden. Oikos. 22, 302-314

Nowak E (2001) Enchytraeid communities in successional habitats (from meadow to forest). Pedobiologia 45:497-508

O'Connor FB (1955) Extraction of enchytraeid worms from a coniferous forest soil. Nature 175:815-816

O'Connell T, Bolger T (1998) Intraspecific aggregation 'probability niches' and the diversity of soil microarthropod assemblages. Appl Soil Ecol 9:63-67

Ojala R, Huhta V (2001) Dispersal of microarthropods in forest soil. Pedobiologia 45:443-450

Okland T, Rydgren K, Okland RH, Storaunet KO, Rolstad J (2003) Variation in environmental conditions, understorey species number, abundance and composition among natural and managed *Picea abies* forest stands. For Ecol Manag 177:17-37

Oksanen L (2001) Logic of experiments in ecology: is pseudoreplication a pseudoissue? Oikos 94:27-38

Paquin P, Coderre D (1997) Changes in soil macroarthropod communities in relation to forest maturation through three successional stages in the Canadian boreal forest. Oecologia 112:104-111

Paul EA (1976) Carbon, Nitrogen, Phosphorus, Sulfur and Selenium Cycles. In Nrigu JO (ed) Proc. 2nd Int. Symp Environ Biogeochem

Paul EA (1989) Soils as components and controllers of ecosystem processes. In Grubb PJ, Whittacker JB (eds) Toward a more exact ecology. Blackwell Scientific Publications, Oxford, pp 353-374

Peltier A, Ponge JF, Jordana R, Arino A (2001) Humus forms in Mediterranean scrublands with Aleppo pine. Soil Sci Soc Am J 65:884-896

Perry DA, Amaranthus MP, Borchers JG, Borchers SL, Brainerd RE (1989) Bootstrapping in ecosystems. Bioscience 39:230-237

Persson T, Lohm U (1977) Energetical significance of the annelids and arthropods in a Swedish grassland soil. Ecological Bulletin 23

Petersen H (1975) Estimation of dry weight, fresh weight, and calorific content of various Collembolan species. Pedobiologia 15:222-243

Petersen H (2002) General aspects of collembolan ecology at the turn of the millenium. Pedobiologia 46:246-260

Pflug A (2001) Determinants of soil community structure and function in European coniferous forests with particular emphasis on Collembola. Justus-Liebig-University of Giessen, Ph D Dissertation

Pickett STA (1989) Space-for-time substitution as an alternative to long-term studies. In: Likens GE (ed) Long-term studies in ecology. Springer Verlag, New York, pp. 110-135

Pietikainen J, Fritze H (1995) Clear-cutting and prescribed burning in coniferous forest – comparison of effects on soil fungal and total microbial biomass, respiration activity and nitrification. Soil Biol Biochem 27:101-109

Polis GA, Strong DR (1996) Food web complexity and community dynamics. Am Nat 147:813-846

Pomorski RJ (1998) Onychiurinae of Poland (Collembola: Onychiuridae). Genus-International Journal of Invertebrate Taxonomy (Supplement)

Ponge JF (1983) Les collemboles, indicateurs du type d'humus en milieu forestier. Résultats obtenus au sud de Paris. Acta Oecol Gen 4:359-374

Ponge JF (1993) Biocenoses of Collembola in atlantic temperate grass-woodland ecosystems. Pedobiologia 37:223-244

Ponge JF (1999) Horizons and Humus forms in beech forests of the belgian Ardennes. Soil Sci Soc Am J 63:1888-1903

Ponge JF (2000) Vertical distribution of Collembola (Hexapoda) and their food resources in organic horizons of beech forests. Biol Fertil Soils 32:508-522

Ponge JF (2003) Humus forms in terrestrial ecosystems: a framework to biodiversity. Soil Biol Biochem 35:935-945

Ponsard S, Arditi R, Jost C (2000) Assessing top-down and bottom-up control in a litter-based macroinvertebrate food chain. Oikos 89:524-540

Raw F (1959) Estimating earthworm populations by using formalin. Nature 184:1161-1662

Root RB (1967) The niche exploitation pattern of the blue-gray gnatcatcher. Ecol Monogr 37:317-350

Root RB (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecol Mon 43:95-124

Rousseau P. (1990) L'évolution de forêts françaises métropolitaines d'après les statistiques forestières. Rev. For. Fr. 47:56-65

Rozé F (1989) Mise au point d'une méthode d'échantillonnage par points pour l'interprétation de lames minces : application à la comparaison de deux humus de landes après incendie. Rev Ecol Biol Sol 26:189-196

Ruf A (2000) The long-term memory of soils: soil microarthropods in forest sites with different land use history. In Rusek J (ed) XIII International Colloquium on Soil Zoology, Abstract. Ceske Budejovice, Czech Republic, p 190

Rusek J (1998) Biodiversity of Collembola and their functional role in the ecosystem. Biodiv Conserv 7:1207-1219

Rusek J (2001) Microhabitats of Collembola (Insecta: Entognatha) in beech and spruce forest and their influence on biodiversity. Eur. J. Soil Biol. 37:237-244

Saetre P, Brandberg PO, Lundkvist H, Bengtsson J (1999) Soil organisms and carbon, nitrogen and phosphorus mineralisation in norway spruce and mixed norway spruce – birch stands. Biol Fertil Soils. 28:382-388

Salamon JA, Gärtner S, Zaitsev A, Pflug A, Wolters V Soil macrofauna response to forest conversion. Forestry (in press)

Schaefer M (1995) Interspecific interactions in the soil community. Acta Zool Fenn 196:101-106

Scheu S (1990) Die saprophage Makrofauna (Diplopoda, Isopoda und Lumbricidae) in lebensräumen auf Kalkgestein: Sukzession und Stoffumsatz. Berichte des Forschungszentrums Waldökosysteme Göttingen A57:1-302

Scheu S, Albers D, Alphei J, Buryn R, Klages U, Migge S, Platner C, Salamon JA (2003) The soil fauna community in pure and mixed stands of beech and spruce of different age: trophic structure and structuring forces. Oikos 101:225-238

Schipper LA, Degens BP, Sparling GP, Duncan LC (2001) Changes in microbial heterotrophic diversity along five plant successional sequences. Soil Biol Biochem 33:2093-2103

Schlatte G, Kampichler C, Kandeler E (1998) Do soil microarthropods influence microbial biomass and activity in spruce forest litter. Pedobiologia 42:205-214

Schroeter D, Wolters V, de Ruiter PC (2003) C and N mineralisation in the decomposer food webs of a European forest transect. Oikos 102:294-308

Schulze ED, Wirth C, Heimann M (2000) Managing forests after Kyoto. Science 289:2058-2059

Seastedt TR (1984) The role of microarthropods in decomposition and mineralization processes. Ann Rev Ent 29:25-46

Seastedt TR (2000) Soil fauna and Controls of Carbon dynamics: Comparisons of Rangelands and forests across latitudinal gradients. In: Coleman DC, Hendrix PF (eds) Invertebrates as webmasters in Ecosystems. CAB International, New York, pp 293-312

Setälä H, Laakso J, Mikola J, Huhta V (1998) Functional diversity of decomposer organisms in relation to primary production. Appl Soil Ecol 9:25-31

Setälä H, Marshall VG (1994) Stumps as a habitat for Collembola during succession from clear-cuts to old-growth Douglas-fir forests. Pedobiologia 38:307-326

Setälä H, Marshall VG, Trofymow JA (1996) Influence of body size of soil fauna on litter decomposition and 15N uptake by poplar in a pot trial. Soil Biol Biochem 28:1661-1675.

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

Sokal RR, Rohlf FJ (1995) Biometry. The Principles and Practice of Statistics in Biological Research. 3rd ed. Freeman, New York

Sollins P, Homann P, Caldwell BA (1996) Stabilization and destabilization of soil organic matter: Mechanisms and controls. Geoderma 74:65-105

Southwood TRE, Brown VK, Reader PM (1979) The relationship of plant and insect diversities in succession. Biol J Linn Soc Lond 12: 327-348

Staaf H (1987) Foliage turnover and earthworm populations in three beech forests of contrasting soil and vegetation types. Oecologia 72:58-64

Sutherland RA (1998) Loss-on-ignition estimates of organic matter and relationships to organic carbon in fluvial bed sediments. Hydrobiologia 389:153-167

Swift MJ, Heal OW, Anderson JM (1979) Decomposition in terrestrial ecosystems. Studies in Ecology, Blackwell Scientific Publications, Oxford

Takeda H (1988) A 5 year study of pine needle litter decomposition in relation to mass loss and faunal abundance. Pedobiologia 32:221-226

Tanaka M (1970) Ecological studies on communities of soil Collembola in Mt. Sobo, southwest Japan. Jap J Ecol 20:102-110

Taskinen O, Ilvesniemi H, Kuuluvainen T, Leinonen K (2003) Response of fine roots to an experimental gap in an boreal Picea abies forest. Plant Soil 255:503-512

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

Teuben A, Verhoef H (1992) Direct contribution by soil arthropods to nutrient availability through body and faecal nutrient content. Boil Fertil Soils 14:71-75

Thimm T, Larink O (1995) Grazing preferences of some Collembola for endomycorrizhal fungi. Biol Fertil Soils 19:266-268

Thomas SC, Halpern CB, Falk DA, Liguori DA, Austin KA (1999) Plant diversity in managed forests: Understory responses to thinning and fertilization. Ecol Appl 9:864-879

Topoliantz S, Ponge JF, Viaux P (2000) Earthworm and enchytraeid activity under different arable farming systems, as exemplified by biogenic structures. Plant Soil 225:39-51

Trofymow JA, Porter, GL (1998) Introduction to the coastal forest chronosequence project. In: Trofymow JA, MacKinnon A (eds) Proceedings of a workshop on Structure, Process, and Diversity in Successional Forests of Coastal British Columbia, Victoria, British Columbia. Northwest Science vol 72. Washington State University Press pp 4-8

Ulrich B (1987) Stability, elasticity, and resilience of terrestrial ecosystems with respect to matter balance. In: Schulze ED, Zwölfer H (eds) Potentials and Limitations of Ecosystem Analysis. Springer-Verlag, Berlin, pp 50-67

Ulrich B (1994) Nutrient and acid-base budget of Central European forest ecosystems. In: Godbold D L and Hüttermann A (eds) Effects of acid rain on forest processes. New York, J. Wiley, pp. 1-50

Ulrich B, Mayer R, Khanna PK, Seekamp G, Fassbender HW (1976) Input, output und interner Umsatz von chemischen Elementen bei einem Buchen- und einem Fichtenbestand. Verh Ges Ökol 17-28

Van Bezooijen J (1999) Methoden en technieken voor nematologie, Vakgroep Nematologie, Wageningen

Van Straalen NM, Verhoef HA (1997) The development of a bioindicator system for soil acidity based on arthropod pH preferences. J Appl Ecol 34:217-232

Vance ED, Brookes PC, Jenkinson DS (1987) An extraction method for measuring soil microbial biomass C. Soil Biol Biochem 19:703-707

Verhoef HA, de Goede RGM (1985) Effects of collembolan grazing on nitrogen dynamics in a coniferous forest. In Fitter A, Atkinson D, Read D, Usher M (eds) Ecological interactions in soil: Plants, microbes and animals. Blackwell, Oxford, pp 367-376

Verhoef HA, Brussaard L (1990) Decomposition and nitrogen mineralization in natural and agroecosystems: the contribution of soil animals. Biogeochemistry 11:175-211

Vetter S, Fox O, Ekschmitt K, Wolters V (2004) Limitations of faunal effects on soil carbon flow: density dependence, biotic regulation and mutual inhibition. Soil Biol Biochem 36:387-397

Visser S (1985) Role of the soil invertebrates in determining the composition of soil microbial communities. In: Fitter AH, Atkinson D (eds) Biological Interactions in Soil. Blackwell Scientific Publishers, Oxford, pp. 297-317

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

Wallwork JA (1976) The distribution and diversity of soil fauna. Academic Press, London

Walter DE, Proctor HC (1999) Mites: Ecology, Evolution and Behaviour. University of NSW Press. Sydney and CABI. Wallingford

Wardle DA (1998) Controls of temporal variability of the soil microbial biomass: A global-scale synthesis. Soil Biol Biochem 30:1627-1637

Wardle DA, Yeates GW (1993) The dual importance of competition and predation as regulatory forces in terrestrial ecosystems: Evidence from decomposer food webs. Oecologia 93:303-306

Wardle DA, Ghani A (1995) A critique of the microbial metabolic quotient (qCO2)) as a bioindicator of disturbance and ecosystem development. Soil Biol Biochem 27:1601-1610

Wardle DA, Lavelle P (1997) Linkages between soil biota, plant litter quality and decomposition. In Cadisch G, Giller KE (eds) Driven by Nature - Plant Litter Quality and Decomposition. London, pp. 107-124

Wardle DA, Zackrisson O, Hömberg G, Gallet C (1997) The influence of island area on ecosystem properties. Science 277:1296-1299

Wolters V (1983) Ökologische Untersuchungen an Collembola eines Buchenwaldes auf Kalk. Pedobiologia 25:73-85

Wolters V (1987) Die Bedeutung der Krauterschicht für die Springschwänze eines Buchenwaldes. Mitteilung der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie 5:41-42

Wolters V (1991) Soil invertebrates - Effects on nutrient turnover and soil structure - A review. Z Pflanzenernähr Bodenk 154:389-402

Wolters V (2000) Invertebrate control of soil organic matter stability. Biol Fertil Soils 31:1-19

Wolters V (2001) Biodiversity of soil animals and its function. Eur J Soil Biol 37:221-227

Wolters V, Schaefer M (1994) Effects of acid deposition on soil organisms and decomposition processes. In: Godbold D, Hüttermann A (eds) Effects of Acid Rain on Forest Processes. John Wiley & Sons, New York, pp 83-127

Wolters V, Silver WL, Bignell DE, Coleman DC, Lavelle P, van der Putten WH, de Ruiter PC, Rusek J, Wall DH, Wardle DA, Brussaard L, Dangerfield JM, Brown VK, Giller KE, Hooper DU, Sala O, Tiedje JM, van Veen JA (2000) Effects of global changes on above- and below-ground biodiversity in terrestrial ecosystems: Implications for ecosystem functioning. BioScience 50:1089-1098

Wright CJ, Coleman DC (2002) Responses of soil microbial biomass, nematode trophic groups, N-mineralization, and litter decomposition to disturbance events in the southern Appalachians. Soil Biol Biochem 34:13-25

Yeates GW, Bongers T, de Goede RGM, Freckman DW, Georgieva SS (1993) Feeding habits in soil nematode families and genera – an outline for soil ecologists. J Nematol 25:315-331

Zaitsev AS, Chauvat M, Pflug A, Wolters V (2002) Oribatid mite diversity and community dynamics in a spruce chronosequence in Germany. Soil Biol Biochem 34:1919-1927

Zak JC, Willig MR, Moorhead DL, Wildman HG (1994) Functional diversity of microbial communities: A quantitative approach. Soil Biol Biochem 26:1101-1108

Ziegler F, Zech W (1992) Formation of water stable aggregates through the action of earthworms: implication from laboratory experiments. Pedobiologia 36:91-96

Zimdars B, Dunger W (1994) Synopses on Palearctic Collembola, Part 1. Tullbergiinae Bagnall 1935. Abh. Ber. Naturkundemus, Görlitz 68:1-71

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LIST OF PUBLICATIONS

Articles

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- **M Chauvat**, AS Zaytsev, E Gabriel, V Wolters How do soil fauna and soil microbiota respond to beech forest growth? *Submitted to Eur J Soil Biol*.
- **M Chauvat,** JF Ponge, V Wolters Humus structure dynamics during a spruce forest rotation: Quantitative changes and relationship to soil biota. *Submitted to Soil Biol Biochem*.
- **M Chauvat**, AS Zaitsev, V Wolters (2003) Successional changes in Collembola and soil microbiota during forest rotation. *Oecologia 137:269-276*.
- **M Chauvat**, JF Ponge (2002) Colonization of heavy metal-polluted soils by Collembola : preliminary experiments in compartmented boxes. *Appl Soil Ecol 21:91-106*.
- L Caner, B Zeller, E Dambrine, JF Ponge, **M Chauvat**, C Llanque (2004) Origin of the nitrogen assimilated by soil fauna living in decomposing beech litter. *Soil Biol Biochem 36, 1861-1872*.
- AS Zaitsev, **M Chauvat**, A Pflug, V Wolters (2002) Oribatid mite diversity and community dynamics in a spruce chronosequence. *Soil Biol Biochem 34, 1919-1927*.

Proceedings:

- **M Chauvat**., AS Zaytsev, E Gabriel, V Wolters (2004) Temporal changes of decomposer assemblages structure and functioning during beech forest growth. XIVth International Colloquium on Soil Zoology and Ecology, *France, Rouen 30 Aug. – 3 Sept. 2004. Abstract book p84.*
- **M Chauvat**, AS Zaitsev, V Wolters (2003) Dynamic association between Collembola and soil microbiota during forest development. GfÖ meeting, *Allemagne, Halle 8-13 Sept. 2003. Verh Ges Öko 33, p407.*
- **M Chauvat**, AS Zaitsev, E Gabriel, A Pflug, V Wolters (2002) Soil Faunal Diversity in Successional Forest ecosystems. 2nd CarboEurope Meeting, *Hungary, Budapest, 4/5-8 March 2002.*
- **M Chauvat**, AS Zaitsev, A Pflug, V Wolters (2001) Structural changes of soil fauna biodiversity and forest succession. *Verh. Ges. Öko. 31, p162*.
- V Wolters, **M Chauvat**, E Gabriel, AS Zaitsev, J Salamon (2003) Spatial and temporal dynamics of detrital food webs in European Forests: Determinants of diversity and C-stock. 3rd CarboEurope Meeting, *Portugal, Lisbon, 17/19-21 March 2003.*
- A Pflug**, M Chauvat**, AS Zaitsev, V Wolters (2001) Soil Biota and Forest Succession: Functional Implications of Structural Changes. Global Change Open Science Conference, *Pays-bas, Amsterdam, 10-13 July 2001. Stockholm, IGBP, p.105*.

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