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THE RELATIONSHIPS OF SOIL FAUNA TO LONG-TERM FOREST PRODUCTIVITY IN TEMPERATE AND BOREAL ECOSYSTEMS: PROCESSES AND RESEARCH STRATEGIES

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ABSTRACT

Forest management and use can affect soil fauna and alter the ecosystem characteristics and processes that they mediate. In this paper the distribution of soil fauna is described and the mechanisms through which they may regulate nutrient cycling and soil water dynamics are reviewed. Results from studies that evaluated the impact of forest management practices on soil fauna are summarized, and, finally, some future research directions are suggested.

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Although generalization is difficult, distribution patterns of soil fauna emerged across forest types, humus forms, and latitudinal gradients. Nutrient cycling is regulated by soil fauna through indirect means such as microbial grazing, predation on microbivores, modification of habitats and substrates through faeces production, transport of soil components across boundaries, and spread of microbial inoculum. Soil fauna have the potential to influence soil water dynamics by altering soil porosity and pore size distribution which can affect soil physical properties. Studies on the effects of harvesting, burning, and nitrogen fertilization on soil fauna have produced variable results suggesting that effects of forest disturbances will depend on site-specific pre-disturbance ecosystem processes and the nature of the disturbance.

A four-step strategy for research relating soil fauna to long-term productivity is proposed. Focus is placed on knowledge gaps identified in the review. Potential research topics include:

1. *collect descriptive information of forest soil fauna in North America where data are relatively sparse;*
2. *role of macrofauna in regulating fungal biomass and activity;*
3. *regulation of the balance between fungivores and bacterivores by soil fauna predators;*
4. *transport roles of micro- through macro-fauna that affect the proximities of substrates and microorganisms;*
5. *potential influences of fauna on soil water dynamics in forest ecosystems;*
6. *role of fauna in the special habitats of coarse woody debris and the rhizosphere;*
7. *links between soil fauna, the development of forest humus forms, and forest productivity;*
8. *the relationship between soil fauna faeces and forest productivity;*
9. *the potential for using the humus form as the link to facilitate scaling of results from process level studies up to the level of the forest stand, where measurements of forest productivity and management decisions are made;*
10. *an understanding of climate-induced synchronies between plant phenologies and activities of soil fauna that may help us understand and predict impacts of manipulations. These ideas should be applied to the longer-term "phenologies" of forest stand succession and timing silvicultural activities to minimize disruptions of desirable synchronies between above- and below-ground parts of forest ecosystems.*

For all investigations involving questions related to long-term productivity, interdisciplinary teams of researchers and managers should establish replicate sites for modal forest types and cooperate on baseline studies. Within this framework, an essential research goal should be to contribute an understanding of the relationship between soil biological agents and processes, the humus form, and forest productivity.

INTRODUCTION

Micro-, meso-, and macro-fauna (Figure 1) that spend all or portions of their life cycles in soils, including both organic and mineral horizons, participate in and affect a wide variety of processes in forest ecosystems (Figure 2, Table 1). Forest management and use can affect soil fauna and alter the ecosystem characteristics and processes which they mediate.

Table 1: Examples of major soil fauna in temperate or boreal coniferous forests.

Herbivores
- molluscs
- camel crickets
- Homoptera

Moss Feeders
- tingid bugs
- byrrhid beetles
- boreid scorpion flies

Seed Feeders
- lygaeid bugs
- carabid beetles
- tenebrionid beetles
- chalcidoid wasps

Root Feeders
- tylenchid nematodes
- symphylans
- ortheziid scales
- click beetles
- scarab beetles
- weevils

Primary Wood Channelers
- bupresid beetles
- cerambycid beetles
- scolytid weevils
- crane flies
- termites
- carpenter ants
- penknife oribatids
- isopods

Primary Comminutors
- millipedes
- click beetles
- crane flies

Bacterivores
- rhabditid nematodes
- tectamoebae
- ciliates
- slime moulds
- oribatids (part)

Microfungivores
- tylenchid nematodes
- nanorchestid mites
- tydaeid mites
- oribatid mites
- collembola
- ptiliid beetles

Mesofungivores
- protura
- pauropods
- campodeids
- thysanura
- psocoptera
- fungus beetles
- psychodid flies
- fungus flies
- fungus gnats
- drosophila
- earthworms
- enchytraeids

Micropredators
- mononchid nematodes
- gamasid mites
- siro
- pseudoscorpions
- skunk-spiders
- microphantid spiders
- predaceous springtails
- labidostommid mites
- geophilid centipedes
- staphylinid beetles
- pselaphid beetles
- parasitic wasps

Mesopredators
- phalangids
- glow worms
- parasitic wasps
- predaceous flies
- snakeflies
- lacewings
- rove beetles
- soldier beetles
- ground beetles
- lady beetles
- spiders

Macropredators
- snail beetles
- carabid beetles (part)
- trap-door spiders
- funnel web spiders
- wolf spiders
- lithobid centipedes
- ants
- salamanders
- shrews

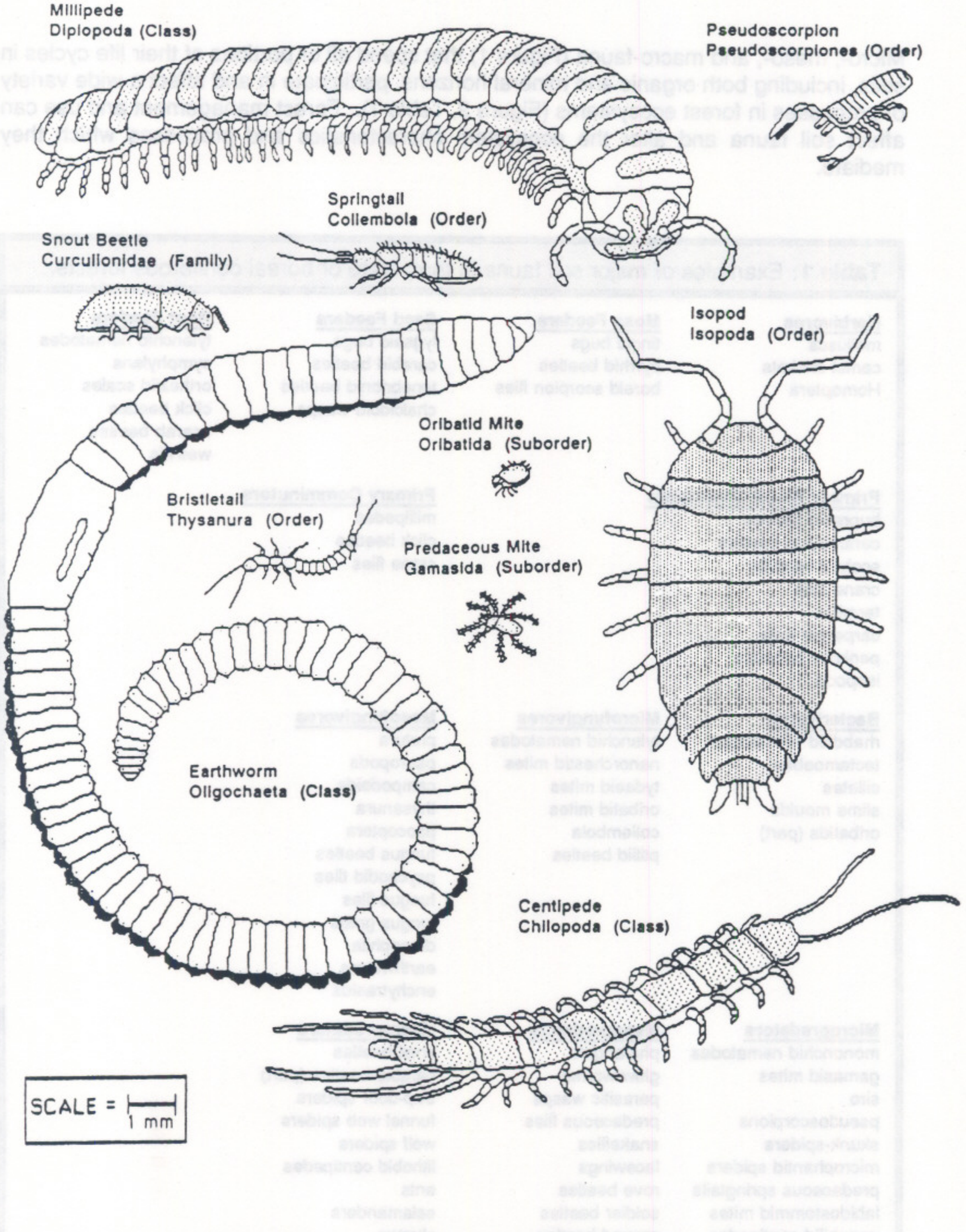

Figure 1: Examples of fauna found in the soil. (After H. Lutz and R. Chandler 1946, p. 95. Adapted by Sandi Shindler, Corvallis, Oregon).

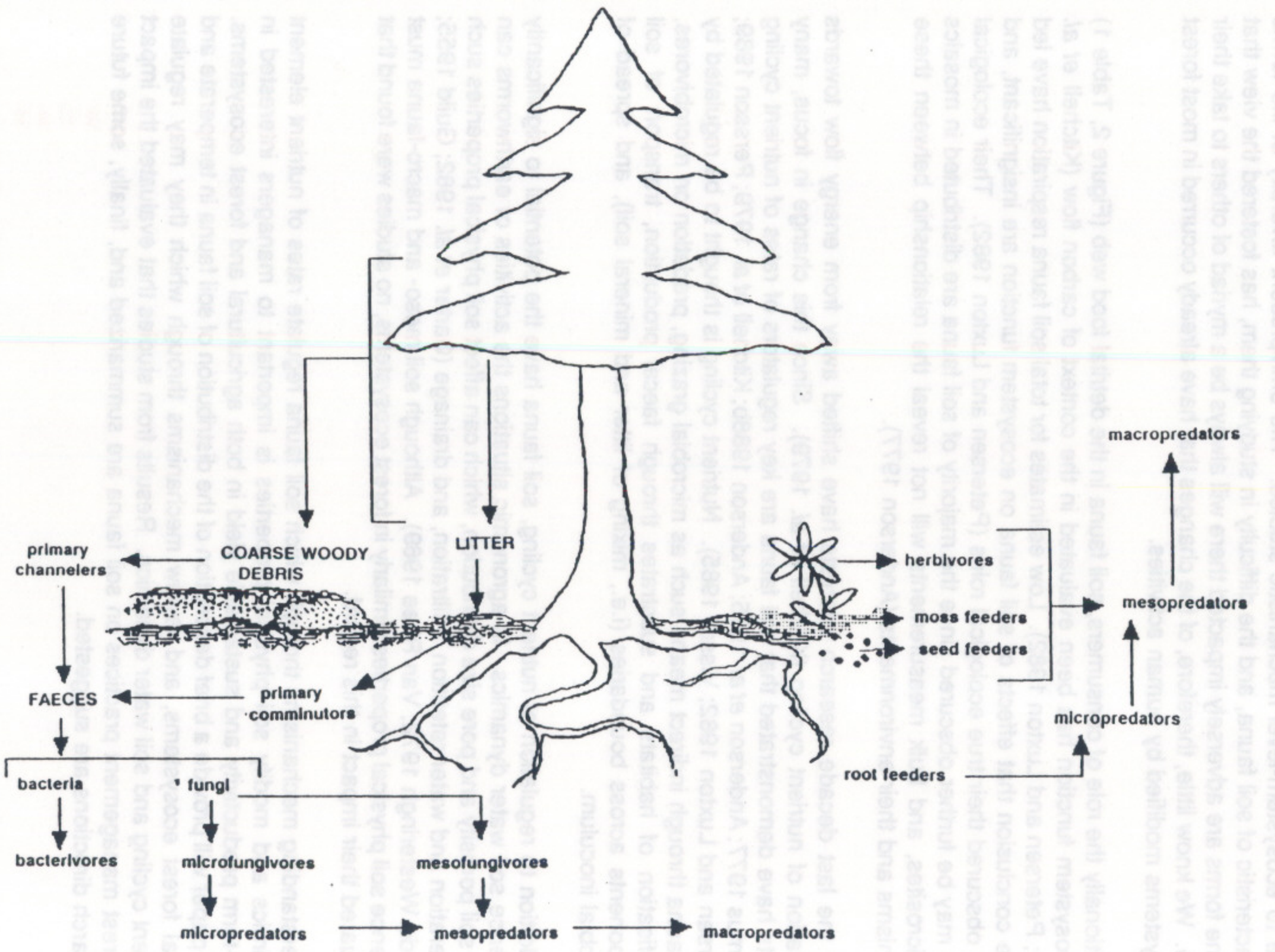

Figure 2: Schematic of relationships between plants, coarse woody debris, litter, and functional groups of soil fauna in a coniferous forest ecosystem. (Refer to Table 1 for examples of soil fauna within functional groups).

The importance of soil fauna in ecosystem processes is widely accepted in Europe. However, this field has received less attention in North America, particularly in forest ecosystems. The paucity of individuals with soil fauna taxonomic skills, particularly in North America, makes it difficult for soil zoology to progress far beyond the descriptive phase to ecosystem-level mechanistic studies. The omnipresent diversity of life forms characteristic of soil fauna, and the difficulty in studying them, has fostered the view that if some forms are adversely impacted there will always be a myriad of others to take their place. We know little, therefore, of the changes that have already occurred in most forest ecosystems modified by human activities.

Traditionally the role of consumers, soil fauna in the detrital food web (Figure 2, Table 1) in ecosystem function has been evaluated in the context of carbon flow (Kitchell *et al.* 1979; Petersen and Luxton 1982). Low estimates for total soil fauna respiration have led to the conclusion that effects of soil fauna on ecosystem function are insignificant, and have obscured their true ecological roles (Petersen and Luxton 1982). Their ecological roles may be further obscured since the majority of soil fauna are distributed in mosaics of microsites, and bulk measurements will not reveal the relationship between these organisms and their environments (Anderson 1977).

Over the last decade research interests have shifted away from energy flow towards regulation of nutrient cycling (Kitchell *et al.* 1979). Since this change in focus, many results have demonstrated that soil fauna are key regulators of rates of nutrient cycling (Ausmus 1977; Anderson *et al.* 1985; Anderson 1988b; Kitchell *et al.* 1979; Persson 1989; Petersen and Luxton 1982; Visser 1985). Nutrient cycling is thought to be regulated by soil fauna through indirect means such as microbial grazing, predation on microbivores, modification of habitats and substrates through faecal production, transport of soil components across boundaries (i.e., mixing of litter and mineral soil), and spread of microbial inoculum.

In addition to regulation of nutrient cycling, soil fauna have the potential to significantly influence soil water dynamics. In agronomic situations the activities of earthworms can alter soil porosity and pore size distribution, which can affect soil physical properties such as aeration and water retention, infiltration, and drainage (Carter *et al.* 1982; Guild 1955; Van de Westeringh 1972; Van Rhee 1969). Although soil meso- and macro-fauna must influence soil physical properties similarly in forest ecosystems, no studies were found that evaluated their impact in this regard.

Understanding mechanisms through which soil fauna regulate rates of nutrient element dynamics and modify soil physical properties is important to managers interested in long-term productivity and sustainable yield in both agricultural and forest ecosystems. This paper will provide a brief description of the distribution of soil fauna in temperate and boreal forest ecosystems, and review mechanisms through which they may regulate nutrient cycling and soil water dynamics. Results from studies that evaluated the impact of forest management practices on soil fauna are summarized and, finally, some future research directions are suggested.

DISTRIBUTION OF SOIL FAUNA IN TEMPERATE AND BOREAL FOREST ECOSYSTEMS

Before discussing the mechanisms through which soil fauna affect ecosystem processes, a brief description of their distribution in temperate and boreal forest ecosystems is necessary. Additional information is available in a variety of textbooks and review papers (Burges and Raw 1967; Dindal 1990; Fitter *et al.* 1985; Petersen and Luxton 1982; Richards 1987; Wallwork 1976). Behan-Pelletier *et al.* (1985) provided a list of major reference texts for soil fauna in general, grouped by major taxa. Recently Moldenke *et al.* (1990a) developed a computer-based resource that permits the novice to key out soil fauna to various taxonomic levels. Once an identification is made the user is provided with basic ecological information and a list of pertinent references.

Petersen and Luxton (1982) reviewed a large number of studies (published and unpublished) in which soil fauna numbers and biomass were estimated. Their synthesis of estimates for soil fauna biomass in coniferous and deciduous temperate forest ecosystems is shown in Table 2. Most of these biomass measurements were from studies where samples were taken from soil horizons dominated by organic matter. These would include Oi and Oe (L and F horizons often referred to as the "forest floor"), Oa (H), and Ah horizons. Sometimes forest soils were described according to the type of humus form present; mull, moder, or mor (Hoover and Lunt 1952; Klinka *et al.* 1981; Müller 1878).

Recently forest ecologists have identified the rhizosphere (mycorrhizosphere) and coarse woody debris as ecosystem components deserving special attention. These are discussed in a special section on unique habitat types. All other discussion on the distribution of soil fauna and their influence on processes related to long-term productivity, is based primarily on research on fauna inhabiting the "forest floor" and mineral soil.

Petersen and Luxton (1982) discussed difficulties in evaluating soil fauna population data which are highly variable within ecosystem types that are defined by crude climatological and vegetational characteristics. The difficulty in relating species assemblage to vegetation type or the physico-chemical characteristics of the habitat may be related to a failure to define, and the difficulty in measuring, environmental variables on a scale meaningful to soil animals (Anderson 1977). Three patterns emerged from the data Petersen and Luxton (1982) evaluated relevant to coniferous and temperate forests, namely forest type, humus form, and latitude.

Table 2: Typical soil fauna biomass (mg d wt /m^2) estimate in temperate forest ecosystems (summarized from Petersen and Luxton 1982). [Petersen and Luxton (1982) grouped all coniferous ecosystems regardless of whether temperate or boreal].

Major Groups of Soil Fauna		**Biomass*** **(mg(dry) wt/m^2)** **Coniferous**	**Deciduous** **(mor)**	**Deciduous** **(mor and mull)**	**Deciduous** **(mull)**
Microfauna (< 200 µm)	Nematoda (nematodes)	120		330	
Mesofauna (200 µm - 1 cm)	Enchytraeida (enchytraeids, potworms)	480		430	
	Collembola (springtails)	80	(130)		110
	Acari (total) (mites)	**500**	**(900)**		(300)
	Cryptostigmata (oribatid)	**450**	**(700)**		180
	Mesostigmata (gamasid)	(80)		40	
	Prostigmata	(30)		(10)	
Macrofauna (> 1 cm)	Large Oligochaetes (earthworms)	450	200		**5300**
	Diplopoda (millipedes)	50		**420**	
	Diptera larvae (fly larvae)	260		330	
	Chilopoda (centipedes)	70		130	
	Carabidae & Staphylinidae (predaceous beetles)	120		90	
	Araneae (spiders)	50		40	
	Gastropoda (slugs, snails)	(20)		**270**	
	Formicoidea (ants)	*(10)*		*(10)*	
	Isoptera (termites)	0		0	
TOTAL:	From summing columns	2210	3280		**7760**
	† After correction	2400	3500		**8000**

* Estimates in brackets are tentative based on less than five studies; estimates in bold are high relative to other ecosystems; and estimates in italics are low relative to other ecosystems. Other ecosystems evaluated include tundra, temperate grassland, tropical grassland, and tropical forest.

† Corrected estimates for total soil fauna biomass represent an attempt by Peterson and Luxton (1982) to account for groups, in particular the Protozoa, for which no biomass estimates were available.

Forest Type

Coniferous forest types had amongst the lowest (1-7 g d wt /m^2) and deciduous temperate forest types amongst the highest (4-30 g d wt /m^2) total soil fauna biomass when compared with all other types of ecosystems evaluated (Table 2). Typically the presence of a high proportion of macrofauna in the population is the reason for high total soil fauna biomass, and accounts for the higher values for deciduous compared with coniferous forests. Within coniferous and deciduous forest types the larger biomass estimates are associated with presence of significant biomass of earthworms (coniferous - Southern Finnish site; deciduous - French hornbeam site) or millipedes (coniferous - *Pseudotsuga* of the Pacific Northwest, USA), while the lower estimates are associated with the dominance of the smaller Enchytraeida and Acari (coniferous - boreal taiga; deciduous - German beech).

Humus Form

Differences in total soil fauna biomass and composition were often related to humus form. Mull soils are typical in temperate deciduous forests and are characterized by high total soil fauna biomass, with endogeous and epi-anecique earthworms constituting more than 50% of the total biomass. (Endogeous and epi-anecique are names given to ecological classes of earthworms that are active in mineral soil and may feed on surface litter.) The activities of these earthworms result in mixing of organic and inorganic soil components. Mull-like and moder soils have been recognized in some temperate coniferous forests, but the earthworm biomass in these soils is not dominated by epi-anecique or endogeous types. Consequently, mineral and organic soil components are not mixed to the same degree as in the true mull soils. Mor soils typically have low total soil fauna biomass with equal contribution of several taxa but dominated by Acari and Enchytraeida. They are typical of taiga, boreal, and northern coniferous forests, and also occur in coniferous forests of the central and southern temperate regions and in some deciduous forests (beech, oak).

Latitude

Distribution of total soil fauna biomass exhibits a pattern related to latitudinal sequence, which is interrelated with climate, vegetation, and humus form. Soil fauna biomass is similar in both the tundra and the boreal taiga forest zones and increases to highest levels in the temperate deciduous forests and grasslands. High levels exist in Mediterranean and subtropical zones, whereas indications are that soil fauna biomass values are low in the tropics. Macrofauna dominate in deciduous forests through to the tropics, while mesofauna increase in dominance from the deciduous forests north to the tundra.

Petersen and Luxton (1982) suggest that Enchytraeida, Collembola, and Dipteran larvae dominate extreme and adverse environments because of their high reproductive capacity and ability to recover quickly after mortality from adverse environmental conditions, whereas earthworms and cryptostigmatid mites are found in more stable, protected environments.

ROLES OF SOIL FAUNA IN LONG-TERM PRODUCTIVITY

Regulation of Nutrient Cycling

The mechanisms through which soil fauna can regulate decomposition and the cycling of nutrients can be direct or indirect. The weight of evidence in the literature supports the view that direct contributions of most soil fauna are limited (Edwards 1974; Reichle 1977). It is generally accepted that values for carbon utilization efficiency (ingested carbon converted to biomass) of soil fauna are low relative to bacteria or fungi (40-60%), ranging from 2% for earthworms and enchytraeids to 20-28% for collembola and mites (Burges and Raw 1967; Luxton 1981; Paul and Clark 1989; Petersen and Luxton 1982; Richards 1987). This means that the majority of carbon in soil organic matter ingested by soil fauna is lost as respiration or egested as faeces. Further support for the view that most soil fauna do not directly decompose detritus is found in studies that tested soil fauna for the presence of a wide array of gut enzymes. Few demonstrated that soil fauna possess the suite of enzymes necessary to break down soil organic matter originating from plant detritus (Nielsen 1962; Petersen and Luxton 1982). Some specialized fauna such as termites, molluscs, and fungus-feeding ants are exceptions; they have unique symbiotic gut flora that enable them to assimilate carbon from substrates that are typically difficult to degrade (Coulson and Lund 1973; Crowson 1981; Kaufman *et al.* 1986; Martin 1987; Nielsen 1962). Despite the lack of evidence that soil fauna directly decompose soil organic matter, researchers have repeatedly demonstrated that they influence the mobilization and immobilization of mineral nutrients (Anderson *et al.* 1983; Anderson 1988a; Ingham *et al.* 1989; Krivolutsky and Pokovzhevsky 1977; Malone and Reichle 1973; Persson 1989). Explanation of this phenomenon has been sought in the indirect influences of soil fauna on decomposition and nutrient cycling processes. These indirect mechanisms of regulation may include grazing, predation, faecal substrates, and translocation.

Grazing

When soil fauna feed on microorganisms in search of carbon for energy, net mineralization of nitrogen can result because the carbon-to-nitrogen ratio of soil fauna is similar to that for microbes (McGill *et al.* 1981). In addition to releasing nutrients immobilized in microbial biomass, grazing by soil fauna can stimulate microbial activity if grazing intensity is low, but can reduce microbial activity when grazing intensity is high and resources are over-utilized (Hanlon and Anderson 1980). Microcosm studies have demonstrated that mycophagy by some collembola can affect success of competition between different species of fungi (Newell 1984; Parkinson *et al.* 1977) and influence the direction and rate of mineralization and immobilization of mineral nutrients (Ineson *et al.* 1982; Parkinson *et al.* 1979).

Detailed discussions about the relationships between grazers and microorganisms and their potential role in nutrient cycling have been discussed by Coleman *et al.* (1983) and McGill *et al.* (1981). These reviews concentrated on results from studies using micro- and meso-fauna. Attention has focused on studying the smaller fauna in relation to microbivory, probably because their size in relation to mats of mycelia and bacterial colonies makes it easy to visualize them as "grazers". Many large meso- and macrofauna have mouthparts large enough to ingest litter, leading to emphasis on their role in comminution of litter, and obscuring their function in modifying microbial communities.

Yet, evidence exists that macro-fauna preferentially feed on and assimilate microbial biomass, and, like the "grazers", can directly influence the make-up and activity of microbial populations (Cooke and Luxton 1980; Kukor and Martin 1987; Shaw and Pawluk 1986b).

Mycophagy (feeding on fungi) may be more important than bacterial feeding to macrofauna, as well as mesofauna, particularly in temperate and boreal forest ecosystems where fungal biomass typically is much greater than bacterial biomass (Ingham *et al.* 1989; Kimmins 1987). Surveys of digestive enzymes of detritivores suggest greater ability to utilize fungal *versus* plant polysaccharides and that values for approximate digestibility were low for detritus-fed animals (6-35%) but high (42-97%) when the animals were fed only on the fungal component of the detritus (Kukor and Martin 1987). Spiers *et al.* (1986) showed the intestine of the earthworm *Arctiostrotus* spp. was completely filled with mycelia, suggesting a fungivorous role for this inadequately studied indigenous earthworm of the Pacific Northwest. Evidence exists for the dietary importance of fungi to the earthworm *Lumbricus terrestris* (Cooke and Luxton 1980; Niklas and Kennel, 1981) and that its fungivory may lead to modifications in the overall microbial population and decomposition rates (Shaw and Pawluk 1986b). Ausmus (1977) suggested that preferential feeding on fungi by channel-forming soil macro-invertebrates may result in a temporary shift in microbial populations that favour bacteria so that net mineralization proceeds. Thus, fungivores directly regulate the amount of nutrients in fungal biomass and may indirectly regulate the competitive success of bacteria (Seastedt 1984).

Predation

Few studies exist relating predation to nutrient cycling, even though it may play a role by altering the balance of fungivores to bacterivores, and regulating the total standing crop of microbivores. Coleman *et al.* (1983) cite two studies in which mites predatory on bacterial-feeding nematodes increased CO_2 evolution and increased the recycling of nitrogen and phosphorus compounds. Walter (1988) provided evidence for nutritional dependence of some mites on nematode predation which were previously thought to be bacterial or fungal feeders.

Faecal Substrates

The activity of modifying substrates by converting leaf litter to faeces may be a major role for arthropods in forest soils (Crossley 1977). Conversion of litter into faeces significantly modifies the geometry and chemistry of substrates and their availability to microbial attack. These faeces become substrates for other decomposers, and form the habitat which enables or limits their colonization success. Together the fauna and the substrate interact to form a characteristic structure of the forest soil which is known as the humus form.

As early as 1878 Müller recognized the important links between the role of soil fauna in the genesis of different humus forms and between humus form and forest productivity. After collating the current state of knowledge on European soils, Kubiena (1955) described 30 well-defined humus forms. In all the humus forms, the special influence of animal activity was visible or most characteristic (Plate 1). Several humus forms in forest ecosystems may be almost entirely composed of soil faunal faecal material (Babel 1975; Bal 1982; Rusek 1986).

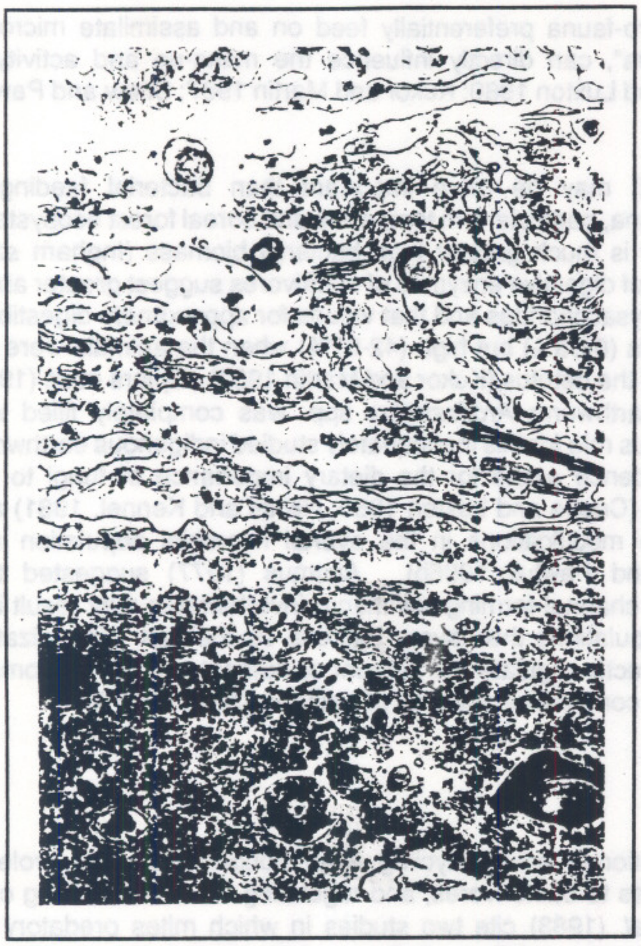

Plate 1:

32-µm thick section of a humus form from under a deciduous forest (in central Alberta, Canada) which developed under the strong influence of soil fauna. 2x magnification. Image courtesy of Dr S. Pawluk and Michael Abley, Department of Soil Science, University of Alberta, Canada.

Although soil micromorphologists have established that faecal production is a major activity in the genesis of humus forms, far less is understood about how faeces are related to ecosystem productivity. Most mechanistic studies on the faeces of soil fauna have been done using macrofauna such as earthworms, millipedes, and isopods, which produce faeces large enough to manipulate and study. In some studies contents of the faeces of micro- and meso-arthropods have been described (Anderson and Healy 1972; Bal 1982).

Early results from faecal studies indicated that microbial numbers and decomposition rates were higher in faeces compared with control materials (Day 1950; Lunt and Jacobson 1944; Parle 1963). The most common explanation for these results was that comminution of litter by fauna increased the surface area of substrates available to bacteria and fungi, and that faeces provided a favourable physico-chemical environment for microbial activity. Attention was focused on these kinds of results since "more" is frequently interpreted as "better", and the results were successfully rationalized. Yet other studies have shown that microbial numbers were lower (Atlavintye and Pociene 1973; Dawson 1947) and carbon-to-nitrogen ratios higher (Syers *et al.* 1979; Watanabe 1975) in faeces compared to control soil. Recently, progress has been made in understanding these apparently contrary results by considering age of faeces and the biological potential and physical nature of the system under consideration (Czerwinski *et al.* 1974; Shaw and Pawluk 1986b). Recent microcosm studies have indicated that the flush of microbial activity in faeces is transitory (Hanlon 1981a,b) and that the faeces of the isopod and millipede studied tended not to decompose because fungi were restricted to the surface of the aggregate (Anderson 1988a).

Faeces of many macrofauna tend to be excreted as a diarrhetic liquid in series of droplets (Bal 1982; Romell 1935; Shaw and Pawluk 1986a). This makes them physically and functionally different from the faeces of most microfauna (especially the faeces of oribatid mites which are enclosed by a thick peritrophic membrane) which are excreted in a pelletized form (Bal 1982; Rusek 1986). Faeces of microfauna and mesofauna tend to persist in systems where macrofauna are absent (Bal 1982; Kevan 1962) and are so stable they can survive passage through the gut of an earthworm (Harding and Stuttard 1974). Microbiological studies have demonstrated that macrofauna faeces do not decompose rapidly, but micromorphological investigations have shown that they are relatively unstable in the field. The faeces tend to physically degrade because of the washing and leaching action of water or be biologically altered as a result of coprophagy (faeces feeding) (Bal 1970; Bal 1982).

Coprophagy is not uncommon in the animal world (Dindal 1986). In soil systems micromorphologists have shown that collembola ingest faeces of earthworms and that enchytraeids ingest faeces of microarthropods (Rusek 1986). Coprophagy is a common means of inoculum transfer between ruminants (Stanier *et al.* 1970). Evidence suggests soil fauna may have special relationships with microbes which significantly influence the composition of the microbial community in a manner similar to ruminants (Shaw and Pawluk 1986b; Kaufman *et al.* 1986; Lawson *et al.* 1984).

The balance between microfaunal, mesofaunal, and macrofaunal faeces, and their relative stabilities may be an important mechanism contributing to the regulation of nutrient cycling. Webb (1977) postulated that the balance of large to small arthropod activity (this can be extended to include other fauna) constitutes a regulatory mechanism controlling rates of litter decomposition, where comminution produces two opposite effects on particle size (Kitchell *et al.* 1979). Decomposer biomass is supported in relation to the surface area of the faeces or litter conglomerates, not to the surface area of the constituent particles (Kitchell *et al.* 1979). Webb (1977) hypothesized that micropellets tend to persist because of the strong interparticulate bonding between the micro-sized particles contained within them. The long-term effect is maintenance of a surface area, much larger than that provided by the unaltered litter, which favours microbial decomposition. Constituent particles of macrofauna faeces tend to be larger than for micropellets and are held together by weak forces. The integrity of these faeces is maintained as long as litter (Kitchell *et al.* 1979) and the overall, long-term effect is one of reducing surface area relative to the original litter. The balance between microfaeces and macrofaeces can be influenced by the number and activity of microfauna, mesofauna, and macrofauna, the degree of coprophagy that occurs, and the degree to which faeces resist physical and microbiological degradation.

Translocation

The mobility and behaviour of soil animals can effect rapid redistribution of substrates, nutrients, and other biota across ecosystem boundaries (Kitchell *et al.* 1979). Indeed this could be the most important role soil mesofauna and macrofauna play: facilitating microbial inoculation of substrates and moving soil constituents across subsystem boundaries. Movement of soil fauna may occur in response to climatic gradients (moisture/temperature) or to escape, reproductive, social, or feeding behaviour.

In forest soil ecosystems, subsystems with boundaries can be defined on one scale as horizons (L, F, H, A, B), the rhizosphere, and coarse woody debris. At this scale, transport is dominated by the relatively mobile large mesofauna and macrofauna. Within these soil subsystems, another conceptual set of subsystems and boundaries, such as aggregates and pores, exists at a smaller scale for microorganisms. To microbes, which are ultimately responsible for most chemical transformations of litter, distances of millimeters to centimeters are often insurmountable. At this scale, transport is dominated by soil microfauna and mesofauna.

Movement can result in transport of soil inorganic and organic matter by carriage of food, deposition of faeces (Anderson 1988a), and construction of permanent dwellings (ant and termite nests, channel systems of some earthworms and wood-boring insects). Other biota will be transported on the body surface of larger organisms, or microbiota as spores and cysts within their guts (Bamforth 1988; Krantz 1989).

At this micro-scale, microfauna and mesofauna play the critical roles of spreading microbial inoculum and moving substrates to where they can be accessed by microorganisms. For the most part, movement is restricted to within forest soil subsystems (within horizons, logs, etc.). At the forest soil scale, large mesofauna and macrofauna serve the same functions described at the micro-scale, but they cross soil subsystem boundaries frequently. Macrofauna can extend the regions that microfauna explore when they are transported on the bodies of macrofauna (Krantz 1989) and when macrofauna tunnels and channels provide habitats and passageways for microarthropods (Moldenke *et al.* 1990b; Rusek 1986).

The following ecological classification system used by Bouché (1977) to classify earthworms is useful to describe transport effects at the forest soil scale, and can be extended to include other macrofauna (Anderson 1988a).

1. epigeic (active primarily in the L, F, H)
2. endogeic (active primarily in the mineral soil)
3. anecique (actively transport soil constituent between organic and inorganic horizons).

In transport processes epigeic macrofauna primarily play the role of microbial inoculation and fragmentation of detritus into particulates which can be washed down the soil profile (Anderson 1988a). Anecique earthworms in a temperate hardwood forest were able to draw almost an entire year's worth of litterfall into their tunnels to an average depth of 11 cm (Nielson and Hole 1964). Unlike the epigeic fauna, the effect on nutrient and water transport by endogeic and anecique invertebrates can be strongly influenced by the chemical and physical nature of the mineral soil, which is their habitat (Shaw and Pawluk 1986a). These fauna figure prominently in the genesis of mull humus forms by bringing organic matter from the soil surface into intimate contact with clay minerals. The degree to which intermediate products resulting from the decomposition of the buried and/or ingested litter are stabilized in faecal aggregates can depend on the proportion of clays present and their mineralogy (Shaw and Pawluk 1986a,b). In some forest ecosystems endogeic or anecique earthworms are not found, but other soil fauna such as millipedes, fly larvae, enchytraieds, and isopods may fill the same ecological niche, since they are known to ingest mineral soil (Rusek 1986).

Regulation of Soil Water Dynamics

In agricultural ecosystems it has been repeatedly demonstrated that soil macrofauna, especially earthworms, can significantly alter porosity and pore size distribution which can affect soil physical properties such as aeration and water retention, infiltration, and drainage (Carter *et al.* 1982; Guild 1955; Van de Westeringh 1972; Van Rhee 1969). The earthworm, *Lumbricus terrestris*, constructs permanent, vertical channels lined with faeces, which act as conduits that enhance drainage of free water. The faeces of these earthworms are often preferentially enriched in colloidal materials and usually have a high water retention capacity. Similar effects by termites (Wood 1988) and ants (Wicken *et al.* 1976) have been reported. These soil fauna construct permanent structures (channel systems throughout underground and aboveground nests) which may have long-term effects on soil hydrology over time scales of forest succession or forest stand rotation.

No studies were found where the influence of soil microfauna and mesofauna on soil hydrology were examined. It is known that microchannels are produced by phthiracaroid mites (Moldenke *et al.* 1990b), some collembola and enchytraeids (Rusek 1986). Although channels and voids formed by these small mesofauna and microfauna will not influence infiltration rates and transport of free water, they could be important in controlling rates of capillary flow of water, and nutrients within that water, at scales relevant to microbes and plant roots.

UNIQUE HABITAT TYPES

So far we have considered soil fauna that utilize soils, including organic horizons (forest floor), as habitats. Recently researchers have drawn attention to the special contributions the rhizospheres (Fogel 1988; Vogt *et al.* 1986) and coarse woody debris (Ausmus 1977; Harmon *et al.* 1986; Swift 1977) may make to forest ecosystem processes. A dearth of studies are available relating soil fauna to these special habitats.

Coarse Woody Debris

Entomologists and wood scientists have long recognized roles of insects in degrading wood (Coulson and Lund 1973). Since insects are known to reduce the quality of wood destined for human use, silvicultural systems have been developed to encourage the removal of coarse woody debris. Now, in the Pacific Northwest of the United States, considerable attention is focused on the possible ecological benefits of coarse woody debris in forests (Harmon *et al.* 1986). In terrestrial systems coarse woody debris acts as habitats for autotrophs and heterotrophs, may be a long-term source of energy and nutrients, and in some systems may play critical roles in water retention (Ausmus 1977; Harmon *et al.* 1986). Forest management practices clearly alter the masses, distributions, and compositions (in time and space) of coarse woody debris in forest ecosystems. Gains for long-term ecosystem stability and productivity may result from retaining coarse woody debris in intensively managed forests, but ecosystems in which coarse woody debris is critical have not yet been identified.

Harmon *et al.* (1986) consider any woody component greater than 2.5 cm in diameter originating from standing dead trees or downed boles or large branches as coarse woody debris. Throughout temperate and boreal forests inputs range from 0.12-14.9 t/ha/yr and mass from 1-269 t/ha. Successional stage and forest type significantly affect the mass of coarse woody debris. Less mass accumulates in deciduous and certain low-productivity coniferous forests than most coniferous forests (Harmon *et al.* 1986).

A wide variety of bark- and wood-boring beetles, their larvae, and termites, contribute to the decomposition process by physically altering the wood of standing dead and downed trees, and through interactions with microorganisms (Kåårik 1974). Some wood-decomposing insects passively inoculate wood with microorganisms while others have a nutritional or physiological dependence on bacteria or fungi (obligate endosymbionts in some termites and beetles) (Crowson 1981; Martin 1987).

Although the bark- and wood-boring beetles are characteristic of the initial stages of insect attack on wood, their actions set off a long chain of successional events involving a wide variety of fauna and microorganisms whose interaction leads to the decomposition of wood and cycling of nutrients. During succession preferences shift from host plant specificity to habitat specificity, so that by the end of succession the decay stage is more important than the original tree species (Howden and Vogt 1951). In the initial stages of coniferous log decomposition (first 2 years after felling logs) soil fauna other than beetles, but commensal within their galleries, were involved in the decomposition process (Moldenke *et al.* 1990b). The most abundant invertebrates in Scolytidae burrows were microbial-feeding nematodes, while commensal arthropods included gamasid, acarid and oribatid mites, and springtails. Vast numbers of microchannelizing oribatid mites were associated with termite channels. Once ambrosia beetles abandoned their burrows, the burrows became filled with fungi and yeast which fly larvae (particularly *Drosophila*) fed upon.

Invertebrates and microorganisms inhabiting wood can interact to regulate rates of nutrient release (Ausmus 1977; Swift 1977) in temperate deciduous forests. Swift (1977) proposed that the interplay of the timing of branch fall with the state of decomposition of the branch when it fell, determines whether decomposition of the wood on the forest floor will be dominated by fungi alone, or a fungal/faunal association. Decomposition of branches dominated by fungi was characterized by net immobilization and accumulation of nitrogen and calcium through concentration, import of nutrients from the surrounding environment, and possibly nitrogen fixation. Soil fauna (non-wood boring types) became involved only after 90% of the branch weight was lost. Decomposition of branches involving faunal activity was associated with nutrient loss, which was attributed to export by fauna moving out of the decomposing wood and high leaching losses after wood was comminuted. Ausmus (1977) described similar interactions occurring in log decomposition but with a significant difference. Soil arthropods were considered integral to all phases of decomposition, acting as agents that caused temporal shifts between periods of fungal- or bacterial-dominated decomposition. The branches studied by Swift (1977) constitute much smaller units of wood with significantly shorter half lives than logs (Harmon *et al.* 1986). The short half life and small size of branches may be the reason that decomposition was dominated by one path (fungal and immobilization of nutrients) or the other (faunal/fungal and release of nutrients). With logs, sufficient time and space may permit development of a subsystem characterized by faunal/microbial interactions separated in space and time, which results in pulsed release and immobilization of nutrients.

As well as the potential of coarse woody debris to act as long-term nutrient stores for forest ecosystems, it is also important to soil-inhabiting fauna because it provides alternate habitats when environmental conditions in normal habitats are adverse. Slugs, snails, isopods, centipedes, and earthworms migrate to wood during warm weather and live in the litter during the more favourable cool periods (Lloyd 1963). The carabid beetle *Feronia oblongopunctata* hibernates and aestivates in logs, but is normally a litter-inhabiting species (Penney 1967). Eggs and instars of the millipede *Cylindroiulus punctatus* are found under logs while the adults are found in the litter (Banerjee 1967). Thus, removal of coarse woody debris could directly affect life cycles and habitat of litter and mineral soil inhabiting fauna and their participation in nutrient cycling processes.

Since few studies have focused on ecological roles of soil fauna inhabiting wood, their contribution to total soil fauna population structure and biomass may have been underestimated. For example, the termite *Zootermopsis angusticollis* (Hagen) is common throughout the Pacific Northwest (Harmon *et al.* 1986) and was observed to be important to initial stages of log decomposition (Moldenke *et al.* 1990b). Yet, termites were considered to be a negligible component of soil fauna biomass in temperate forest ecosystems (Petersen and Luxton 1982). Spiers *et al.* (1986) described the ecology of the indigenous earthworm *Arctiostrotus* spp. on Vancouver Island on the west coast of Canada. These earthworms were found in a variety of forest types characterized by the presence of acid podzolic soils. Earthworms were found in decomposing logs of *Tsuga heterophylla*, *Abies amabilis*, and *Alnus rubra* often at heights of 1-2 m above the ground surface and in densities up to 220/m^2. Yet textbooks about earthworms have stated that earthworms do not exist in this ecological niche in coniferous systems with acid soil horizons (Edwards and Lofty 1977). Few ecological studies exist for other soil fauna, such as slugs, snails, and millipedes, known to occur in coniferous forest ecosystems. Indications are that they may play major roles in nutrient cycling via wood decomposition (Fog 1979 a,b).

Rhizosphere (Mycorrhizosphere)

Vogt *et al.* (1986) discussed the importance of fine root mass and turnover in nutrient cycling of a wide variety of forest ecosystems. They concluded that, with the exception of cold temperate broad-leaved deciduous forests, 18-58% more N was added to the soil through root turnover than by litterfall. In warm temperate zones evergreen forests averaged 5000 kg/ha more root mass than deciduous forests. In cold temperate forests estimates of mean residence time of organic matter based on "litter" have been high, but Vogt *et al.* (1986) showed how these estimates could be reduced 19-77% by including root inputs. Their analyses suggest that turnover of fine roots makes significant contributions to nutrient cycling of some temperate forest ecosystems. Despite this evidence only a dearth of studies exist on the role of soil fauna in the regulation of fine root turnover (Fogel 1988).

Jacot (1936) observed that dead roots of trees were finally decomposed by saprophagous mites and that a relationship existed between mite size and root diameter. Fine roots were decomposed by oribatid larvae and nymphs while large roots were inhabited by adult mites and other saprophagous animals. This mode of decomposition left a network of passages replacing the old root system which provide an ideal environment for new root growth since they are enriched in plant nutrients in the form of faeces.

Since ectomycorrhizae dominate coniferous forest ecosystems they create a "mycorrhizosphere" rather than the traditional concept of the rhizosphere (Fogel 1988). In the mycorrhizosphere additions to soil organic matter are from exudates and sloughed cells largely of a fungal origin, rather than the soluble mucigels characteristic of the non-mycorrhizal rhizospheres. Consequently one might expect relationships between decomposers and mycorrhizospheres to be substantially different from those with rhizospheres. Fogel (1988) indicated that virtually no literature exists regarding the relation of macrofauna to forest plant roots and provided some evidence for microfaunal associations with ectomycorrhizae. For example, some mites have been shown to regularly associate with the ectomycorrhizae of loblolly pine and one species of collembola was shown to exhibit a preference for feeding on ectomycorrhizae over saprophytic fungi (Shaw 1985 in Fogel 1988). The presence of soil fauna can promote (Warnock *et al.* 1982) or reduce (Sutherland and Fortin 1968) success in mycorrhizal establishment. These conflicting results probably reflect the density-dependent nature of mycorrhizal establishment and soil fauna, interacting with conditions for plant growth. For example, unrestricted feeding by the nematode *Aphelenchoides* on ectomycorrhizae of *Pinus ponderosa* resulted in death only when the seedlings were moisture stressed.

Although soil fauna may influence the success, and facilitate the spread of mycorrhizal inoculum, ectomycorrhizal mats, in turn, can provide special habitats for soil fauna. Cromack *et al.* (1988) compared ectomycorrhizal mats of the basidiomycete *Hysterangium setchellii* to non-mat soil in a 50-75 year-old Douglas-fir stand. They found numbers and biomass of soil microarthropods and nematodes were higher in the mat *versus* the non-mat soils, which they attributed to greater microbial biomass in the mat soil serving as a food source for the soil fauna.

IMPACTS OF MANAGEMENT

Silvicultural practices have the potential to affect soil fauna directly or indirectly. Direct effects are largely immediate and include effects on fauna growth, metabolism, other body processes, and behaviour. Indirect effects are often delayed and include effects on amounts and distributions of, and competition for, suitable food and space as well as effects on predators, parasites, pathogens, symbionts, and commensals. Forest manipulations alter habitats for soil fauna by affecting the composition and amounts of organic matter, temperatures of forest floors and mineral soils, and water relations. These same changes affect litter-decomposing bacteria and fungi which are primary food sources for many soil fauna.

A variety of scientists working in Canada, the United States, Finland, and Sweden have studied the effects of harvesting, burning, and fertilizer and lime application on soil fauna (Blair and Crossley 1988; Hill *et al.* 1975; Huhta *et al.* 1969; Lundkvist 1983). The following discussion summarizes results from their studies and reviews.

Harvesting

Harvesting trees changes a number of physical, chemical, and biological factors in the soil. Harvesting may result in increases in soil pH, nitrification rates, and the amplitude of soil moisture and temperature fluctuations. Depending on the ecosystem, clear-cut harvesting may cause increases, decreases, or no long-lasting effects on faunal populations.

Huhta *et al.* (1969) compared cut and uncut Norway spruce stands in Finland and found that enchytraeids and collembola populations increased, reaching a peak 4 years after cutting. Seven to 8 years after clear-cutting the collembola population decreased, approaching that of the control stand. Over the same period of time the enchytraeid population dropped, but not as far as for the collembola, to twice that of control stand. Both oribatid mites and other mites decreased to approximately 50% of the population density of the control forest 2-4 years after cutting. Eight years after clear-cutting the oribatid mites remained at the same level while the population of the other mites rose back to the level of the control stand. The authors suggested that the relatively short-term increase in the enchytraeid and collembolan populations was caused by a response to the increased food supply from the felling residues, while the more long-lasting negative effect on the oribatid mite population was caused by decreased availability of certain fungal spores and hyphae resulting from the interruption in litterfall.

Blair and Crossley (1988) reported work from an 8-year series of studies on a xeric mixed hardwood forest in North Carolina, USA, that had been clearcut and compared with an adjacent uncut watershed. After 8 years, microarthropod densities in litter were lower in the clearcut and differences existed in relative abundance of microarthropod groups, especially some predators and fungivores. These differences were associated with reduced rates of litter decomposition in the clearcut, which apparently resulted from increased temperature extremes in litter and more frequent wetting and drying cycles. The authors cautioned that no cause-effect relationships were established between reduced fauna and reduced litter decomposition. They contrasted their sites with those at Hubbard Brook in New Hampshire, USA, where cutting resulted in increased litter decomposition, and concluded that effects of forest disturbances would likely depend on pre-disturbance ecosystem processes and site specific effects, as well as on the nature of the disturbance.

Results from an investigation in a Scots pine forest in Sweden on the effects of clear-cutting with whole-tree and conventional (stem-only), harvesting showed that a number of soil organism groups were affected not only by the clear-cutting as such, but by the removal of felling residues (Figure 3). The total biomass of fungi did not change in either of the harvested treatments as compared with that of an uncut control forest (Bååth 1980). However, although it could not be detected with the method used for estimations, there probably was a shift from mycorrhizal fungi to decomposer fungi (Bååth 1980). The bacterial population on the other hand increased (Lundgren 1982). The bacterial increase was followed by an increase in bacterial feeding nematodes (Sohlenius 1982) that peaked in the first year after clear-cutting. Conventional harvest resulted in higher bacterial and nematode populations than did whole-tree harvesting. After the peaks in the first year after harvesting, the populations were back to the level of the control again in year 2. The amount of extractable inorganic nitrogen increased 3-fold from the first to third year after clear-cutting.

The most dramatic effect was found in the enchytraeid population that increased more than six times in the stem-only harvested and more than four times in the whole-tree harvested treatment, during the first 2 years after clear-cutting (Lundkvist 1983). The increase may be a response to increased food availability through root litter additions made soon after harvest, and later on from the input of organic matter from the felling slash. Three years after clear-cutting, the dense enchytraeid population crashed to the level of the population in the control. In connection with this population crash an increased rate of parasite infestation was observed in the worm population. Since there still seemed to be a lot of felling residues left by this time, the population was likely no longer regulated by food availability but by predation by parasites. After clear-cutting, the dominating species of enchytraeid *Cognettia sphagnetorum*, that normally reproduces through fragmentation, occurred for the first time at the site as a sexually mature specimen.

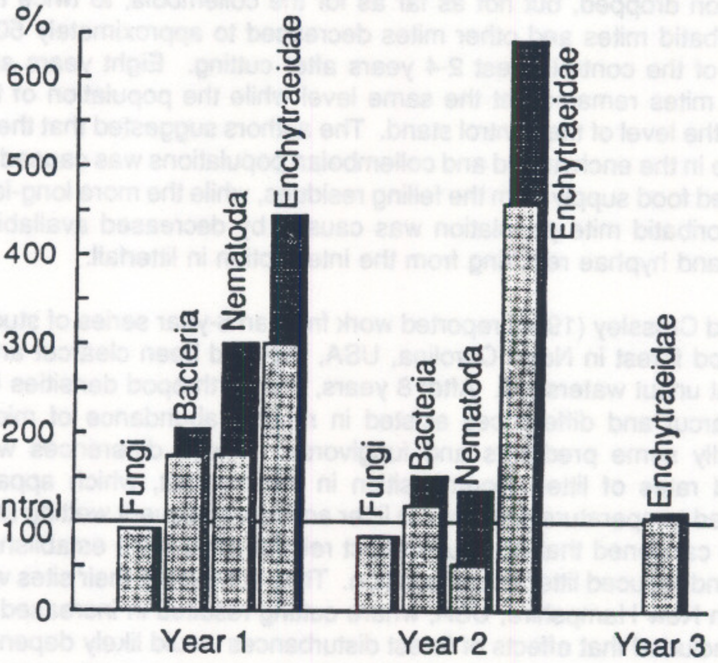

Figure 3: *Soil organisms in the early phase after clear-cutting and whole-tree harvesting of a 120-year-old Scots pine stand in central Sweden. The organism populations in a conventionally harvested treatment (dark shaded bars) and in a whole-tree harvested treatment (light shaded bars) are shown in relation to the organism population in a still growing control stand in the same forest. The organism populations in the growing control stand are set to 100%. (Adapted from Bååth 1980; Lundgren 1982; Lundkvist 1983; and Sohlenius 1982).*

Researchers working in a mixed conifer-hardwood forest in Ontario, Canada, also found that both conventional and whole-tree harvests had major effects on microarthropod populations, with declines of 56% to 68% in 2 years after harvests (Bird and Chatarpaul 1986). While species composition was unaffected, there were shifts in dominance of certain groups. Oribatids, prostigmatids, and collembola were more abundant after conventional harvest than in whole-tree sites. High and variable soil surface temperatures, surface drying, and litter inputs were thought to have caused the changes.

Burning

Springett (1976) and Majer (1984) in Australia have reported highly variable responses of soil fauna to burning, including immediate or delayed density reduction, temporary post-fire absence, long-term (4-year) population reduction, density stimulation, and no apparent effect. From 1-4 years after burning, litter decomposition was "disrupted", with little of the fragmentation found in *Eucalyptus marginata* litter with normal fauna populations (Majer 1984).

In their review, Hill *et al.* (1975) reported similar variability in the effects of intense wildfires, annual or otherwise frequent prescribed burns, and longer-interval low- to modest-intensity burns. Intense heat and complete and/or frequent removal of litter will eliminate or severely deplete populations of most soil fauna. Light and infrequent burns, especially with refugia in unburned patches or adjacent forests, may have relatively brief and modest effects. The composition of the post-fire forest may influence the quantity and quality of litter and alter habitats of soil fauna.

Fertilization

Fertilizer applications to forests may have a variety of effects related to soil fauna (Hill *et al.* 1975; Marshall 1977). These include direct effects on fauna by altering their chemical environments and indirect effects by influencing growth and composition of vegetation which in turn influences litter quality as well as site hydrology and microclimate.

Nitrogen Fertilization

Nitrogen fertilizers are commonly used to increase forest production. They affect the physical soil environment by increasing the osmotic pressure of the soil solution and by changing soil pH. Nitrogen fertilizers also influence the food supply for the soil fauna through changes in abundance and composition of the soil microorganism community, and in the long run through influencing growth and composition of vegetation and consequently litter input and soil organic matter.

Enchytraeids that sometimes contribute up to one-third of total faunal biomass in many Scandinavian coniferous forest soils appear to be particularly sensitive to nitrogen fertilization. Several authors have reported decreased enchytraeid abundance after modest as well as after high doses (+200 kg N/ha) (Abrahamsen and Thompson 1979; Huhta *et al.* 1969; Huhta *et al.* 1986). Enchytraeids are soft-bodied animals sensitive to changes in soil moisture conditions. Lohm *et al.* (1976) suggested a shock effect caused by increased osmotic potential in the soil solution as one likely explanation for the short-term decrease in enchytraeid numbers after fertilization in their experiments. Heungens (1984) demonstrated this "salt-effect" in pine litter. Some years after fertilization the population might recover and even increase, as shown by Huhta *et al.* (1969) (Figure 4), in a study of soil fauna in a Scots pine forest in Finland.

Other researchers have found that the type of nitrogen fertilizer may dictate the nature of nematode response. In Finland, bacterial-feeding nematodes initially increased after fertilization of Norway spruce and Scots pine forests with urea (Huhta *et al.* 1986). However, in an earlier experiment the same researchers found that 150 kg/ha ammonium nitrate decreased the abundance of bacterial-feeding nematodes (Huhta *et al.* 1983). A similar result came from research in a Swedish Scots pine stand that showed a decrease in the abundance of bacterial-feeding nematodes after 7 years of repeated ammonium nitrate fertilization (Sohlenius and Wasilewska 1984).

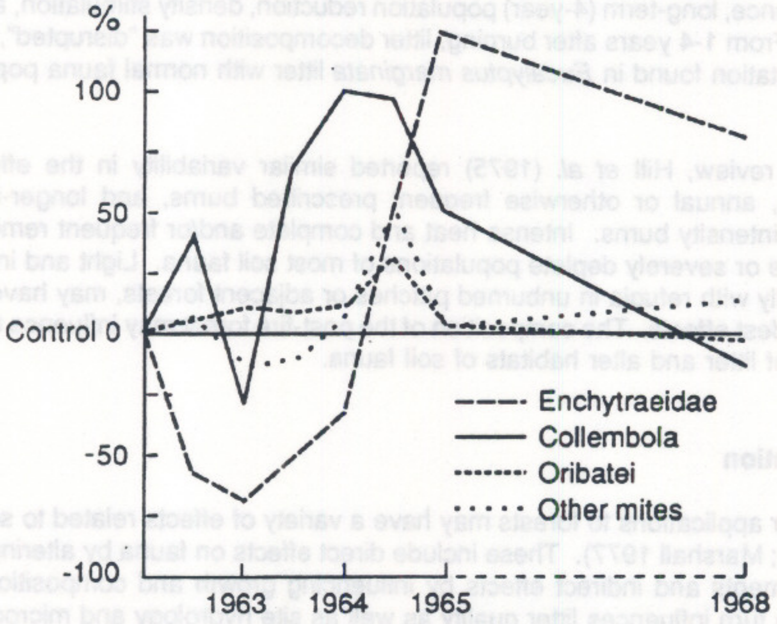

Figure 4: *Course of development of population sizes of soil animal groups after nitrogen fertilization (90 kg N/ha) in a Finnish Scots pine stand. The organism populations in the fertilized treatment are given in relation to the organism populations in the control treatment which is set to zero. (After Huhta* et al. *1969).*

Moderate doses of fertilizers seem to have little short-term effect on mites or collembolans, while higher doses or repeated fertilization could cause decreased abundances (Huhta *et al.* 1986; Lohm *et al.* 1976). On the other hand, positive effects on collembola and to some extent on mites some years after fertilization have been observed (Huhta *et al.* 1969, Figure 4).

Liming

The history of liming forests goes back to the middle of the 19th century (Messmer 1959). This practice was common and strongly supported in Germany during the first half of the 20th century. In northern Europe the interest in forest liming on a large scale occurred in connection with concerns about acid deposition and depletion of base cations in many Scandinavian soils. In many places in the southern part of Scandinavia the pool of base cations has decreased to half of what it was 30 years ago (Falkengren-Grerup *et al.* 1987). Liming is likely to become a common practice used to counteract the effects of acid deposition. Application of plant nutrients like Mg, K, Mn, B, or wood ash, in conjunction with liming, may also become common in areas where N-deposition is suspected to cause nutrient imbalance.

The effects of lime on earthworms and enchytraeids was investigated in a Swedish field experiment with different doses of dolomitic lime in a 40-year-old stand of Norway spruce (Persson 1988). The earthworms increased drastically after liming with 1.6 tonnes/ha (Figure 5), while the dominating enchytraeids species, *Cognettia sphagnetorum*, decreased (Figure 6). The negative impact on enchytraeids from liming has been demonstrated in previous studies (Abrahamsen 1983; Bååth *et al.* 1980). Persson (1988) attributes the decrease in enchytraeids to direct effects from the liming rather than to competition between earthworms and enchytraeids.

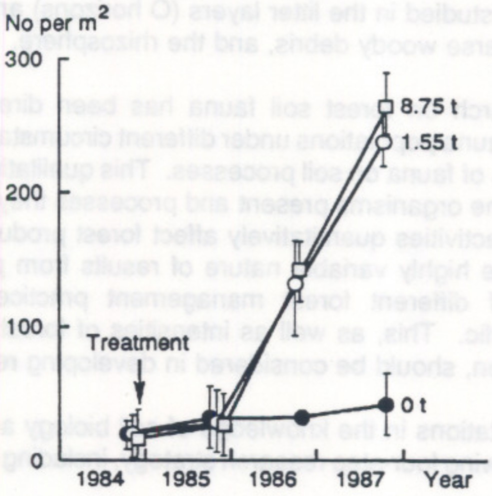

Figure 5: *Earthworms (no./m^2) after treatment with 0, 1.6, and 8.8 tonnes/ha of dolomitic lime in a 40-year-old Norway spruce stand in south-west Sweden. Arrow denotes time of treatment. (After Persson 1988).*

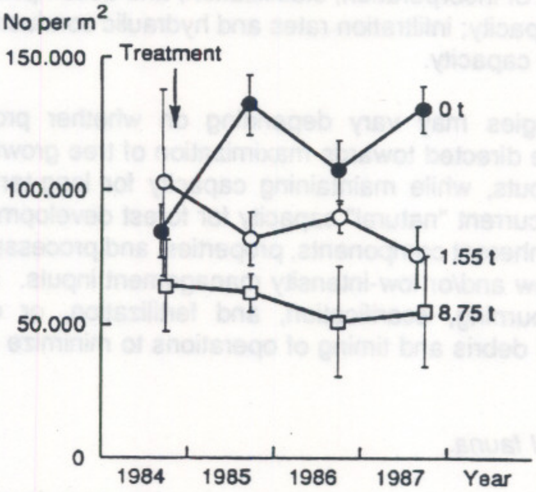

Figure 6: Cogettia sphagnetorum *(Enchytraeidae) (no./m^2) after treatment with 0, 1.6, and 8.8 tonnes/ha of dolomitic lime in a 40-year-old Norway spruce stand in south-west Sweden. Arrow denotes time of treatment. (After Persson 1988).*

FOCI FOR RESEARCH – PRIORITIES AND POTENTIAL APPROACHES

To this point we have discussed soil fauna and some management activities in relation to nutrient and water dynamics in temperate and boreal forest ecosystems. Some of these interactions are likely to influence potential long-term productivity of forests under intensive management regimes. Nutrient element dynamics may be regulated by soil fauna mainly through indirect means such as microbial grazing, predation, production of faecal substrates, or translocation of materials. In forest ecosystems, these processes have been most studied in the litter layers (O horizons) and to a lesser extent in mineral soil horizons, coarse woody debris, and the rhizosphere.

Most field research on forest soil fauna has been directed towards description and mapping of soil fauna populations under different circumstances. Microcosm studies have described effects of fauna on soil processes. This qualitative information provides us with some notion of the organisms present and processes they are involved in, but we do not know how their activities quantitatively affect forest production and long-term forest site productivity. The highly variable nature of results from process-level studies and field investigations of different forest management practices suggests that effects are ecosystem-specific. This, as well as intensities of forest manipulations at each site or within each region, should be considered in developing research strategies.

The general limitations in the knowledge of soil biology and forest productivity led us to suggest the following four-step research strategy, including considerations for each system of interest.

1. *Identify key ecosystem characteristics and processes likely to limit long-term productivity in managed systems.*

Ecosystem characteristics and processes that might be considered include nutrient availability; rates of incorporation, stabilization, and decomposition of organic matter; soil water-holding capacity; infiltration rates and hydraulic conductivity; soil structure; and soil cation exchange capacity.

Research strategies may vary depending on whether proposed systems of forest management are directed towards maximization of tree growth with many and intensive management inputs, while maintaining capacity for long-term productivity, or towards maintaining the current "natural" capacity for forest development by protecting (avoiding disturbance of) inherent components, properties, and processes controlling forest growth, and assuming few and/or low-intensity management inputs. For example, management might include burning, scarification, and fertilization, or could involve only gentle manipulations of debris and timing of operations to minimize ecosystem disturbance.

2. *Inventory soil fauna.*

The inventory must be conducted at a scale of taxonomic resolution meaningful at the functional level. For example, the total number of millipedes may be meaningful since most have the same function, but total "Coleoptera" or "Oligochaetes" is meaningless because of the wide variety of functions performed by organisms within these taxonomic groups.

Although a considerable amount of information on the population ecology of soil fauna has accumulated in the European literature, this is not true for North America. The lack of attention given the soil fauna inhabiting woody debris in many forest ecosystems makes their contribution to total soil fauna population structure and biomass difficult to gauge. The severity of information shortage is evident – recent studies have included descriptions of only the elementary ecology of newly discovered species (Spiers *et al.* 1986). Production of reliable soil fauna inventories for North American forest ecosystems is critical to furthering research into the relationship between soil fauna and long-term productivity. For some North American systems implementation of strategies 3 and 4 below will be seriously impaired until inventories are available.

In order to facilitate this step in a timely fashion, Moldenke *et al.* (1990a) have initiated a computer-based taxonomic key for soil fauna (COMTESA), which is intended ultimately to encompass all soil fauna in North America. Because of the dearth of taxonomic expertise in North America, the success of this undertaking hinges on multi-national participation from taxonomic experts.

3. *Focus on meaningful combinations of (1) ecosystem characteristics and processes likely to limit long-term productivity in managed systems, and (2) soil fauna present in the system under consideration.*

The following are brief examples of what we can conclude from our review of the literature for selected forest regions. Stated or implied unknowns or uncertainties indicate research needs.

For boreal forest ecosystems litter quality and rates of decomposition seem most limiting to availability of plant nutrients; and enchytraeidae, oribatid mites, collembola, and primitive dipteran larvae appear to be important soil fauna. Severe loss of forest floor mass resulting from extreme scarification and/or whole-tree harvesting simultaneously removes potentially crucial element supplies and threatens integrity of soil fauna populations involved in decomposition.

Generalizations are difficult for temperate coniferous forests. For example, Hill *et al.* (1975) noted variability of conditions and management practices in forests of Southeastern USA including: physiography ranging from coastal plains to mountains, soils from skeletal to aquic, and land-use histories from continuous forest to "worn out" and severely eroded cotton fields. In the latter, concern for long-term productivity must include maintenance of organic matter and organically bound nutrients, particularly phosphorus, which may be in limited supply because of incorporation in stable, secondary minerals. In this connection, interactions of soil fauna with mycorrhizal roots may be a fruitful area. In the Pacific Northwest, USA, and in coastal British Columbia, Canada, forest growth is most often limited by availability of moisture and nitrogen (Gessel *et al.* 1973; Spittlehous and Black 1981). Therefore, controls on formation and maintenance of soil structure, and nitrogen mineralization-immobilization relationships need to be identified and understood. Large mesofauna to macrofauna including the millipedes and indigenous species of earthworms may well be critical agents. Investigations into the potential role of microfauna to mesofauna in fine-root turnover may also prove fruitful for coniferous forests of the Pacific Northwest.

For temperate deciduous forests the works of Crossley and associates (e.g., Blair and Crossley 1988), mostly in the North Carolina mountains, indicate the temperature-, moisture-, and substrate quality- sensitivities of soil fauna. Severe burning, total changes of plant species (converting hardwoods to pine), or other intensive management alters normal processes of organic matter and nutrient recycling. Macrofauna, such as millipedes and native and/or introduced species of earthworms, probably play important roles in organic matter turnover and nutrient cycling. Studies involving these fauna should pay special attention to their varying ecological niches (epigeous, endogeous, anecique) and roles in transport processes, soil structure, and humus form development, as well as interactions with microorganisms. This approach has been emphasized in the works of Anderson and colleagues (Anderson 1988a; Anderson *et al.* 1983) and Shaw and Pawluk (1986a,b).

4. *Determine in qualitative and quantitative terms the impact of soil fauna activities, as identified above, on forest productivity.*

Research, predominantly in the form of microcosm studies, has led to some understanding of the qualitative means, or mechanisms, through which soil fauna can influence ecosystem processes important to long-term productivity of forest ecosystems. The following examples illustrate where there still exist many gaps in our knowledge.

Several microcosm studies have demonstrated that microfauna and mesofauna can affect the direction and rates of mineralization/immobilization of mineral nutrients. Potentially, a similar role may exist for soil macrofauna such as earthworms, millipedes, insect larvae, and enchytraeids, but this has not been adequately investigated. More common are the studies on the detritivore role for macrofauna and their function in fragmentation of litter. The prevalence of such studies should not obscure the potentially more significant roles of macrofauna as mycophages, and regulators of fungal biomass and activity.

There has been little research on effects of soil fauna predators, yet they may play an important role determining the balance between fungivores and bacterivores, which can feed back on microbial grazing effects on mineralization/immobilization of mineral nutrients.

Soil animals can effect rapid redistribution of substrates, nutrients, and other biota across ecosystem boundaries. Transport in soil across horizon boundaries is dominated by large mesofauna and macrofauna whereas transport within horizons is dominated by small mesofauna and microfauna. Translocation of substrates and microorganisms by soil fauna could be crucial determinants in rates of organic matter turnover and mineralization/ immobilization of nutrients. Yet, little attention has been focused on the transport role of soil fauna. A need to understand the transport role of soil fauna provides impetus to support research on their fundamental ecology, since movement of soil fauna occurs in response to climatic gradients, or escape, reproductive, social, or feeding behaviour.

The importance of soil macrofaunal influences on soil water dynamics in agricultural ecosystems has been demonstrated frequently. Similar effects may be important in forest ecosystems, but have not been investigated. Microchannels formed by soil microfauna and mesofauna may have an important influence on capillary water and solute movement at scales important to microbes and roots, but no research exists to support this potential effect.

Few studies have focused on the contributions of soil fauna in the specialized habitats of coarse woody debris and the rhizosphere in forest ecosystems. Soil fauna may play an important role in regulation of fine-root turnover. Management of woody residues could directly affect the life cycles and habitat of litter and mineral soil inhabiting fauna and their participation in nutrient cycling processes. This may be particularly true for macrofauna such as earthworms, termites, ants, slugs, snails, and millipedes which have largely been ignored.

As far back as 1878 Müller recognized the important link between the forest humus form and forest productivity. Since then micromorphologists have established that, especially in forest ecosystems, production of faeces by soil fauna is an important aspect of humus form development. Despite these links, far less is known about any relationships between forest productivity and distribution, type, and abundance of faunal faeces. The balance between the quantity and quality of different faeces types may be one determinant of rates of organic matter turnover and nutrient cycling. This balance can be influenced by the numbers and activities of microfauna, mesofauna, and macrofauna, the degree of coprophagy between them, and the degree to which faeces resist physical and microbial degradation. All of these processes deserve special attention in research relating soil fauna to long-term productivity.

The humus form is an ideal integrator of the forest ecosystem over long periods of time, reflecting all the soil forming factors (climate, landscape, organisms, relief, parent material, time, and management). Research investigating the qualitative, or mechanistic, means through which soil fauna affect ecosystem processes which can be directly related to a specific humus form may be critical to forest management and long-term productivity. Because the humus form can be readily identified in the field it provides the link between basic process level soil fauna research and quantitative measures of forest productivity necessarily made on a much larger scale. Scaling up is possible once process level research conducted in the field or in laboratory microcosms is correlated with a specific humus form. Then a suite of humus forms can be linked to a specific biogeoclimatic land unit with an associated productivity.

The following provides an example of how this approach might work in a coastal forest of British Columbia, where the question of interest is the effect of soil fauna on nitrogen mineralization which may be related to forest productivity. Microcosm studies could be conducted, and the contribution of soil fauna to nitrogen mineralization evaluated using the approach of Anderson *et al.* (1985) with their ANREG model. Samples should be taken from replicate plots within the same biogeoclimatic land classification unit (Pojar *et al.* 1987) and the humus form classified according to the system developed by the British Columbia Forest Service (Klinka *et al.* 1981). An estimate of the proportion of different humus forms in the Biogeoclimatic Zone can be used to weight results from the ANREG model to scale them up to the same level (plots representing a Biogeoclimatic Zone) at which measures of forest productivity are made. Using this approach on a variety of sites within the same zone subjected to different management practices, or of different site indices, may lead to an understanding of the effect of soil fauna on nitrogen mineralization in relation to forest productivity. This approach could be extended to other ecosystems taking advantage of existing site classification systems such as the "Cajander" site-type system of Finland or the Swedish site classification system described by Lundmark (1988).

In addition to dealing with the problems of spatial variability and scaling, attention must also focus on temporal variations. Recently, researchers in agriculture have emphasized the need to develop management systems that maintain or enhance the synchrony between plant phenology and nutrient cycling (Anderson 1988b; McGill and Myers 1987). McGill and Myers (1987) used an index of the relative rate of soil biological activity and relative crop yield to compare plant-soil synchronization over a range of climatic zones. A close correspondence of plant and soil biotic processes characterized a cool temperate climatic zone (Alberta, Canada) whereas summer-grown grain sorghum was poorly synchronized with soil biotic processes in a subtropical system (Queensland, Australia). In the subtropical system crop nitrogen requirements peaked between February and April while supply of nitrogen in the soil would be expected to peak between October and January (McGill and Myers 1987). In this system, management practices could be modified to reduce losses of nitrogen and improve timing of nitrogen release with crop demand.

A similar approach to research and management may be useful in forest ecosystems. In forest ecosystems the period in which the synchrony between plant and soil biotic processes should be studied and enhanced is not just one growing season, but the entire rotation. During this period significant changes to the forest ecosystem can occur, which are described in terms of forest succession. Typically ecologists describe stages of forest succession in terms of vegetative communities. Far less attention is paid to the attendant soil genesis, which is frequently determined by successional changes in the soil fauna community. Thus, in forest ecosystems, the synchrony that must be understood to maintain and enhance long-term productivity is the synchrony between succession of forest plants and succession of soil fauna communities, which in turn modify soil physical properties and regulate rates of nutrient mobilization/immobilization.

Establishment of certain groups of soil animals depends on successional stages (Rusek 1978). Silvicultural systems that focus only on establishment and efficient growth of trees may degrade ecosystem synchrony by placing the plant community ahead of the soil biological community in the successional sequence. Thus, silvicultural systems that intend to maintain or enhance long-term productivity should consider the ecosystem as a whole, managing each stage of succession so that plant succession is matched with the appropriate stage of soil biota succession. If the management objective is to accelerate succession and growth rates of trees to shorten rotation age, then management practices should be modified to ensure that succession of soil biota is also accelerated to accommodate the synchrony between plant processes and soil biotic processes. This would be particularly important in the management of sites where synchrony may be damaged through logging practices (very sensitive site types); or for sites where synchrony has a high potential for manipulation to enhance long-term productivity.

CONCLUSION

An attempt was made in this paper to outline, for temperate and boreal forest ecosystems, the current state of knowledge regarding the distribution of soil fauna, the mechanisms through which they may affect processes important to long-term productivity, examples of the effects of management on soil fauna and associated processes, and finally to emphasize where gaps exist in our knowledge and to suggest some research strategies. The review is by no means comprehensive and concentrated on results from systems (boreal and temperate) for which information is available across the breadth of topics considered.

Although descriptive information on soil fauna populations is available for many forest ecosystems in Europe, in North America data are relatively sparse. In order for research directed at discerning the roles of soil fauna in long-term productivity of North American forests to proceed, this critical step of developing an understanding of their population ecology and biology must be addressed.

Several gaps in our knowledge of the roles of soil fauna in processes potentially important to long-term productivity were identified. These include the potentially significant role for macrofauna such as earthworms, millipedes, insect larvae, and enchytraeids in regulating fungal biomass and activity, regulation of the balance between fungivores and bacterivores by soil fauna predators, and the transport roles of microfauna through macrofauna that affect the proximities of substrates and microorganisms. More research is needed on potential influences of fauna on soil water dynamics in forest ecosystems, or on the role of fauna in the specialized habitats of coarse woody debris and the rhizosphere.

Important links exist between soil fauna and the development of forest humus forms, and between humus forms and forest productivity. Yet, far less is known about the relationship between soil fauna faeces and forest productivity. The balance between the quantity and quality of different faeces types may be one determinant of rates of organic matter turnover and nutrient cycling. This balance can be influenced by the numbers and activities of microfauna, mesofauna, and macrofauna, the degree of coprophagy between them, and the degree to which faeces resist physical and microbial degradation.

A challenge today is to integrate results from the experimental scale necessarily employed in laboratory studies, with the patchiness of forest soils and the temporal scales of forest rotations. The humus form may be the critical link to facilitate scaling of results from process-level studies up to the level of the forest stand, where measurements of forest productivity and management decisions are made. Anderson (1988b) and McGill and Myers (1987) emphasized the need in agricultural ecosystems to develop management systems that maintain or enhance the synchrony between plant phenology and nutrient cycling. A similar approach to research and management may be useful in forest ecosystems where the synchrony between plant and soil biotic processes should be studied over not just one growing season, but rather the entire rotation. Understanding climate-induced synchronies between plant phenologies and activities of soil fauna may help us understand and predict impacts of manipulations. These ideas should be applied to the longer-term "phenologies" of forest stand succession and to considerations for timing silvicultural activities to minimize disruptions of desirable synchronies between aboveground and belowground parts of forest ecosystems.

For all investigations involving questions related to long-term productivity, interdisciplinary teams of researchers and managers should establish replicate sites for modal forest types and cooperate on baseline studies. Within this framework, one of several research goals should be to contribute to an understanding of the relationship between soil biological agents and processes, the humus form, and forest productivity. Examples of programmes which have provided, or continue to provide, integrated research environments appropriate to the above research strategies include the Long Term Ecological Research Sites located across the United States (Brenneman 1989), the Regional Forest Nutrition Research Project – Washington, USA (Peterson *et al.* 1984), the Canadian Forest Service Shawnigan Lake Project (Brix 1983), and SWECON (Lohm 1980).

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