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Soil Organisms and Litter Decomposition

Grizelle González

> *...The increasingly structured organization of contemporary science has left research students as the only large category of scientists who will habitually look at organisms. It seems important to re-open the windows on nature which, though not the source of hypotheses, is the source of experience on which intuitive faculties can operate.*—J.E. Satchell (1976)

Introduction

The processes associated with the physical breakdown of litter, the transfer of organic matter and nutrients to the soil, and the release of carbon dioxide to the atmosphere are all components of decomposition. Resource quality, decomposer organisms, and physicochemical conditions influence the decomposition of plant residues (Figure 16.1). Resource quality is defined by the chemical composition of the plant residues such as the C : N ratio, lignin, and polyphenol contents (Melillo et al., 1982; Palm and Sanchez, 1991; Tian et al., 1997). Physicochemical conditions include both climate and soil parent material, and help determine abiotic soil characteristics that in turn influence litter quality and, ultimately, the activity and composition of microbial and invertebrate communities (Wardle and Lavelle, 1997). Although decomposition is mainly the result of microbial activities, soil fauna are important in conditioning the litter and in stimulating microbial actions (Coleman and Crossley, 1996).

This trilateral model of the controls of plant litter decomposition *sensu* Swift et al. (1979) remains conceptually the most robust model of factors affecting decomposition. It is also the zeal of current experimental studies that try to tease apart the independent

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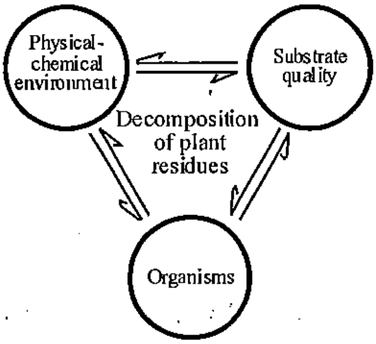

Figure 16.1. The regulation of decomposition by three interacting factors, the physico-chemical environment, and resource quality acting through decomposer organisms. Modified from Swift et al. (1979).

effects of these regulating factors. This is not an easy task, because the inference that soil organisms are an important regulating factor of ecosystem processes appears to the general scientific community as opaque (Seastedt, 2000) and intuitive. The function of soil arthropods may be considered opaque because the attributes of the fauna are in general terms captured into abiotic variables that are easier to measure (Seastedt, 2000) and incorporated to ecosystem models (e.g., CENTURY and GEM; González and Seastedt, 2001). Soil fauna effects on mineralization processes often seem intuitive because their importance is seldom properly quantified and put in the context of the other regulating factors. Most soil biologists encounter complex organismal interactions that vary among ecosystems and organism(s) of interest, as well as among the total or independent effects of the functionality, abundance, and diversity of the fauna. This tangle of interactions is imbedded within the organismal part of the simple and well-accepted three-factor model. Therefore, by no means should the effects of soil organisms be downplayed, but rather should be brought to light.

In this chapter, I discuss where the study of soil organisms currently stands in respect to theoretical setting presented in the literature by various models of plant litter decomposition and the contribution of soil microorganisms, soil fauna, and their interactions to decomposition and nutrient mineralization processes. At the end of the chapter, I present some concluding remarks to spark interest in the future directions of soil biology.

Modeling Decomposition

Several equations describing plant litter decomposition have been proposed in order to predict its rate (Heal et al., 1997). Working at continental and global scales, Meentemeyer (1978) found that the actual evapotranspiration (AET), which is a measure of the concurrent availability of energy and moisture to an ecosystem (a climatic variable), and lignin (a litter quality index) were good predictors of decomposition rates (Figure 16.2). Since then, most studies have concentrated on substrate quality, and climate effects on decomposition and have excluded explicit recognition of the decomposer flora and fauna in the process (González and Seastedt, 2001). However, two limitations can be found in this model: (1) AET is not an adequate predictor of mass loss rate in some biomes (e.g., subarctic and semiarid regions, Coûteaux et al., 1995), and (2) it assumes that the biota, the organisms responsible for the decomposition, are totally predicted by climate and substrate quality characteristics. In addition, the results from Meentemeyer (1978) indicate that the relative control of lignin on decomposition is not the same in different climates (Figure 16.2), suggesting the reduced control by lignin in cool climates is the result of reduced fragmentation ability by litter animals. Clearly, if the decomposer fauna are important in the decomposition process and major shifts occur in their composition that are not captured by the climatic and substrate quality effects, this model should fail. If the biota are linearly controlled by the physicochemical composition of the environment, this approach is justified. However, the global pattern observed in the composition and abundance of the decomposer fauna indicate that this is not the case.

The abundance of various soil fauna changes with latitude (Figure 16.3; Swift et al., 1979). The soil microfauna are relatively more abundant in the temperate regions than in the tropics, whereas soil macrofauna are more common in tropical regions than in temperate zones (González and Seastedt, 2000). In addition, the hierarchy of the determinants of decomposition might not be the same across latitudinal gradients (e.g., Heneghan et al., 1999; González and Seastedt, 2001; González et al., 2001). The relative importance of the three regulating factors varies in a predictable way within and between sites (Heal et al., 1997). Lavelle et al. (1993) suggested that the hierarchy of the determinants of decomposition is different in temperate and tropical ecosystems (Figure 16.4). In tropical ecosystems, climatic determinants are likely to be less important than the biological regulation by soil macrofauna (Figure 16.4). Strong seasonal differences in climate are most likely the dominant control of plant litter decomposition in temperate areas. Coleman and Crossley (1996) stated that fauna are potentially more important in tropical areas, for example, "breakdown and decomposition are viewed as the result of biota acting on substrate quality within the constraints of climate" (p. 111).

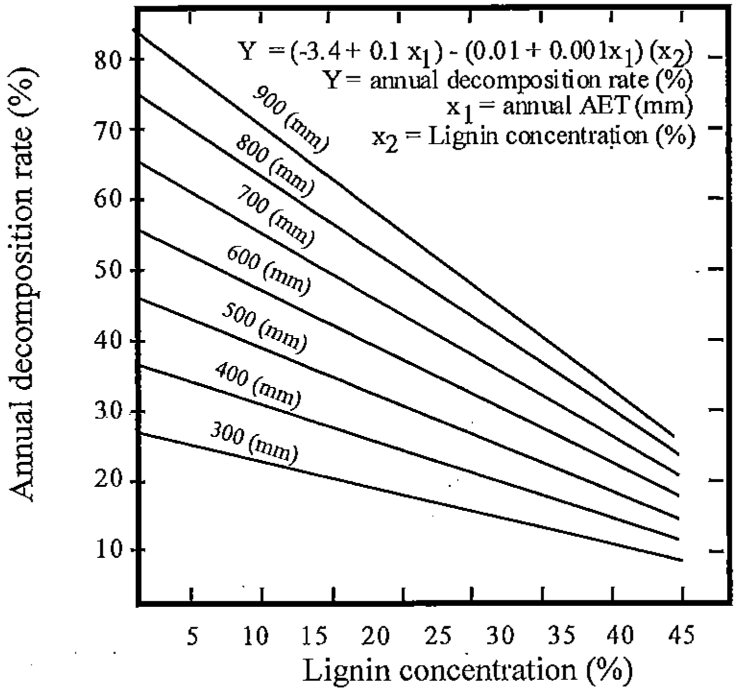

Figure 16.2. Generalized model of the changes in the slope and intercept of the relationship between initial lignin concentration (%) and annual weight loss (%) with climatic actual evapotranspiration. From Meentemeyer (1978).

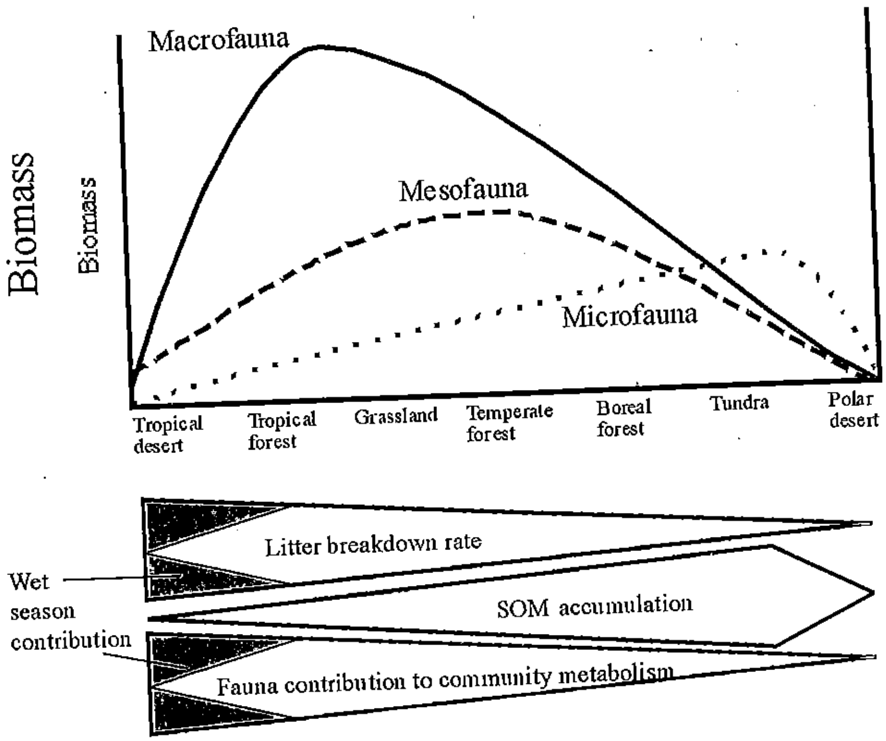

Figure 16.3. Hypothetical patterns of latitudinal variation in the contribution of the macro-, meso-, and microfauna to total soil fauna biomass. The effects on litter breakdown rates of changes in the relative importance of the three fauna size groups are represented as a gradient, together with the fauna contribution to soil community metabolism. The favorability of the soil environment for microbial decomposition is represented by the cline of soil organic matter (SOM) accumulation from the poles to the equator; SOM accumulation is promoted by low temperatures and waterlogging where microbial activity is impeded. From Swift et al. (1979).

The relative control of climate and substrate quality on decomposition processes across latitudinal gradients has been pondered in the literature. Coûteaux et al. (1995) suggested that (1) climate is the dominant factor in areas subject to unfavorable (dry and cold) weather conditions, whereas (2) litter quality is the dominant factor under favorable (wet and warm) conditions. Berg et al. (1998) suggested that if climate and site conditions are constant, then the chemical composition and physical structure of the organic matter regulate decomposition rates. Both the Coûteaux et al. (1995) and Berg et al. (1998) interpretations of the controls of decomposition are concordant with the Meentemeyer (1978) model, because both identify the same causal mechanisms for decay (González and Seastedt, 2001).

If modeling efforts of decomposition rates pragmatically assume that the biota are completely constrained by the physicochemical environment and substrate quality characteristics then they will be limited particularly when applied to lower hierarchical levels (from global to local scales). For example, González and Seastedt (2001) found the lowest density of soil fauna in a tropical dry forest, a site with an intermediate value of AET, when compared to a tropical wet and subalpine forests. Whitford et al. (1981) and Schaefer et al. (1985) showed that termites are capable of improving the microclimate and fragmentation of the litter in arid ecosystems via incorporation of the material into the soils, resulting in faster decomposition rates than those predicted from the previous models. The loss of this group, together with the general decline in abundance of macroinvertebrate decomposers,

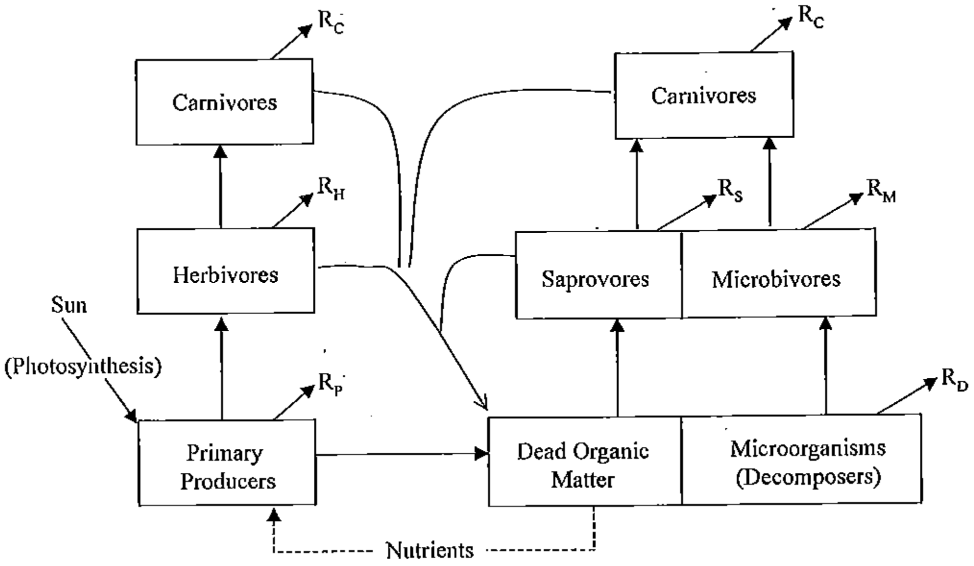

Figure 16.5. The intervention of animals in ecosystems. From MacLean (1974).

compounds (Yang and Insam, 1991), because microbes colonize and chemically break down the organic matter via utilization of enzymatic activities that release nutrients from complex organic compounds and the mineral fractions of the soil (Sharma et al., 1995; Schinner, 1996). The microorganisms ultimately make nutrients available for plant growth. Singh et al. (1989) showed a decline in microbial biomass and nutrient pools during a wet period coupled with rapid plant growth and an increase of nutrients in the microbial biomass during the dry period. Most of the aboveground net primary production of terrestrial ecosystems is returned to the soil system, and the recycling of those plant materials drives elaborate belowground food webs, where the chemical form of the nutrient elements become modified (Coleman and Crossley, 1996; Wardle and Lavelle, 1997). The microbial biomass reflects the status of accumulation and conservation of nutrients in the soil (e.g., Singh et al., 1989).

The microorganisms associated with the decomposition of organic material are extremely diverse. Fungi, bacteria, actinomycetes, and algae are soil microorganisms that have different functional capabilities. For example, soil enzymes are mostly of bacterial and fungal origin (Schinner, 1996). It has been shown that actinomycetes can comprise up to 70% of the microflora in the gut content and the casts of earthworms (e.g., Contreras, 1980). The decomposition of plant remains is facilitated by actinomycetes, because many groups synthesize cellulase and lignin-degrading enzymes (McCarthy, 1987; Crawford, 1988, as cited in Willington and Tóth, 1994). Actinomycetes are also known sources of antibiotics that could have important implications in the determination of the composition of soil microbial communities (Krištůfek et al., 1993). Microalgae contribute to the fertility of the soils as they fix nitrogen and produce organic matter production via photosynthesis. The functional role and the metabolic activities of the different components of the microbial communities are associated with the rates of decomposition, nutrient mineralization processes and soil fertility (Swift, 1976). Additionally, differences in the functionality of the microorganisms result in varying interactions with the soil fauna, the resource quality, and the physicochemical environment (Sharma et al., 1995).

Much is known about the factors that control total microbial biomass in the soil, but less information is available on (1) the relative proportions of functional groups to the total microbial biomass and (2) how their relative abundance affects nutrient mineralization process. We need to understand population dynamics of microorganisms and overcome methodological constraints in order to characterize specific functions of microorganisms (Colores et al., 1996). In this sense, physiological and kinetic approaches are the most commonly used methods for estimating the biomass of specific metabolic functional groups. The substrate-induced respiration (SIR) technique relies on the respiratory response of an active population of microbes that is stimulated by the addition of a particular carbon substrate over a given period of time (Anderson and Domsch, 1978). This induced respiration is converted to biomass using a coefficient that is related to the efficiency of the mineralization process (Carter et al., 1999) that varies from soil to soil. Therefore, the SIR method might be inappropriate for comparative studies of the same functional group in different soils if a constant conversion coefficient is used. The substrate-induced growth response (SIGR) method uses growth kinetics instead of conversion factors to obtain the biomass and maximum growth rate of microorganisms. These characteristics are a reflection of metabolic activity and are independent of soil type (e.g., Schmidt, 1992; Colores et al., 1996; Lipson et al., 1999). SIGR models used to describe the growth of the microbial populations must take into account all the physiological changes induced in the microbial biomass after the substrate amendment (Panikov and Sizoka, 1996).

The SIR method has been used with selective inhibitors that allow for the separation of prokaryotic and eukaryotic contributions to the total respiratory response (Beare et al., 1990). This technique identifies the metabolically active component of the microbial community as related to the fungal and bacterial contributions. The bacterial : fungal ratio has been associated with different stages of the decomposition process and the quality of the decomposing substrate. For example, bacterial biomass dominates sites where there are decomposing residues of low carbon : nitrogen ratio and base-rich, high pH soils (Parkinson and McLean, 1998). Fungal biomass is often associated with the slow metabolism of recalcitrant organic residues with high lignin or polyphenol contents (Doube and Brown, 1998). The SIR has been evaluated mostly in temperate forest or agricultural soils (e.g., Anderson and Domsch, 1975, 1978; West and Sparling, 1986), in agricultural soils of different water contents (West and Sparling, 1986; Wardle and Parkinson, 1990), and in decaying plant residues (e.g., Beare et al., 1990; Neely et al., 1991). It has not been used extensively in tropical soils, because its suitability needs to be cautiously assessed. Both Yang and Insam (1991) and Feigl et al. (1995) tested the SIR protocol in tropical soils and showed that microbial C was underestimated when the standard conversion factor was applied (*sensu* Sparling et al., 1990). Lodge (1996) argued for a high incidence of streptomycin resistance in soils from a tropical rain forest in Puerto Rico. Antibiotic resistance may indicate exposure due to resource competition in the microbial community. A high antibiotic incidence might be related to a high abundance of soil macrofauna, for example, earthworms that support actinomycete dominance in their gut flora and surrounding soil (e.g., Contreras, 1980; Krištůfek et al., 1993), but whether there is a pattern of antibiotic resistance in different forest types is unknown. Limited information is available on the roles played by inhibitory microorganisms in soil ecology due to failures to detect antibiotics in the soil (Goodfellow and Williams, 1983; Krištůfek et al., 1993).

Soil Fauna

There are two courses by which soil fauna can affect plant litter decomposition and the rates of mineralization and humification of soil organic matter: directly, by physically modifying the substrate and soil environments, and indirectly, through interactions with the microbial community (Figure 16.6; e.g., Seastedt, 1984; Brown, 1995; Lavelle et al., 1997). The discussion in this section focuses on the direct effects by which soil fauna affect plant litter decomposition and nutrient mineralization processes. The indirect effects of soil fauna on decomposition are evaluated in the upcoming soil fauna–microbial interaction section of this chapter.

Soil fauna modify the soil environment by mixing organic and mineral particles, and changing the water infiltration and aeration regimens. Tillering by soil fauna directly alters soil physical, chemical, and biological properties. The effects of the substrate modification by the soil fauna to the decomposition process are diverse. The breakdown of litter increases the surface area for microbial use and leaching of nutrients. Soil fauna can also augment the nutrient pool in soil solution by adding nitrogenous compounds present in their excreta and dead tissue (González and Zou, 1999). However, it has been argued that

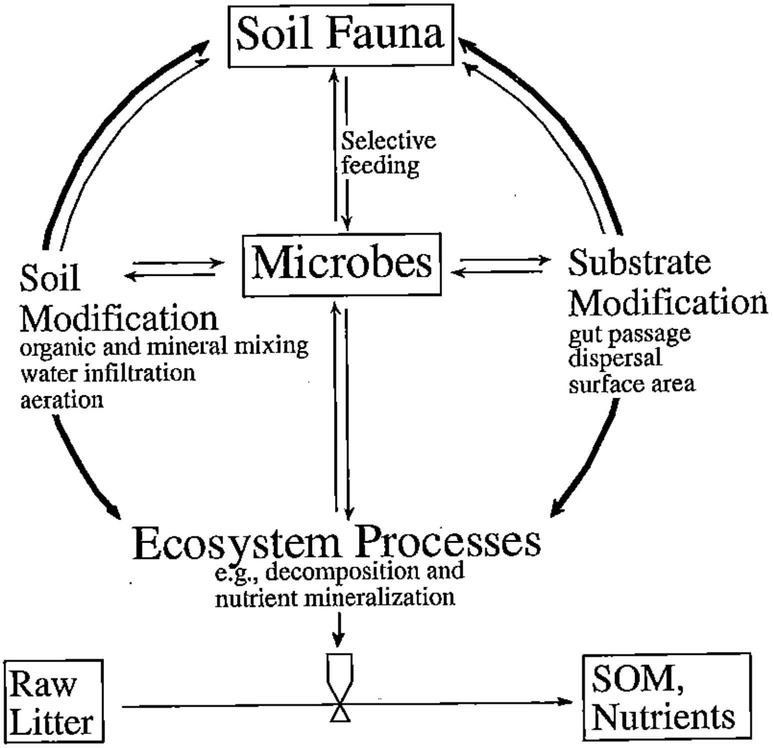

Figure 16.6. Conceptual model indicating direct and indirect paths by which soil fauna affect ecosystem processes (e.g., decomposition and mineralization) and the interaction with microorganisms. Modified from González et al. (2001).

arthropod feces might reduce the surface : volume ratio of organic materials, increasing their persistence in the soil and nutrient unavailability to plants (Webb, 1977).

The quantification of soil fauna effects is feasible by recognizing abiotic, microbial, and soil fauna components of the decomposition constant (Seastedt, 1984). There are three main methods for measuring the mass loss of a given substrate due to the effects of the biota: (1) litterbag studies, (2) chemical treatments, and (3) radioisotope techniques. Litterbag studies exclude invertebrates of a particular size by varying the mesh size of the bags. This method could fail to predict accurately faunal contributions to the percentage of mass remaining, because small mesh-sized bags can change the microclimate of the confined litter, and fragments of litter from bigger mesh-sized bags can escape (Seastedt, 1984). Naphthalene is a chemical treatment commonly used to repel litter microarthropods from the soil surface. However, naphthalene application can stimulate microbial activities (González et al., 2001). Therefore, manipulative experiments based on faunal exclusions using biocides need to be judiciously interpreted. Carbon isotope techniques represent a practical tool for measuring the turnover rate of organic matter when used in combination with plants of different isotopic origin. This method promises to help quantify the effects of soil fauna on the labile and recalcitrant portions of the soil organic carbon pool over the long term.

The range of values for the contribution of soil fauna activities to litter decomposition varies widely along latitudinal gradients, because it is dependent on confounding effects of the size, abundance, diversity, and functionality of the fauna (e.g., Hansen, 1999; Heneghan et al., 1999; Irmler, 2000; González and Seastedt, 2001). Anderson (1977) argued that small animal species tend to have large geographic distribution patterns as a result of the size and ubiquity of the microsites they occupy, whereas larger ones show greater discontinuity in distribution (Figure 16.7). There is also evidence of trophic separation of *Cryptostigmata* according to mean body size. For example, Anderson (1977) analyzed the gut content of 12 species and found that the largest mite generally fed on leaf litter and the smallest species were mycophagous (Figure 16.8). Heneghan et al. (1999) showed that the decomposition of oak litter proceeds faster in Puerto Rican and Costa Rican forests than in a temperate forest in North Carolina. In this study, microarthropods had little effect on the decomposition in the temperate forest, whereas their influence was pronounced at the tropical sites, in spite of similar or even lower species diversity.

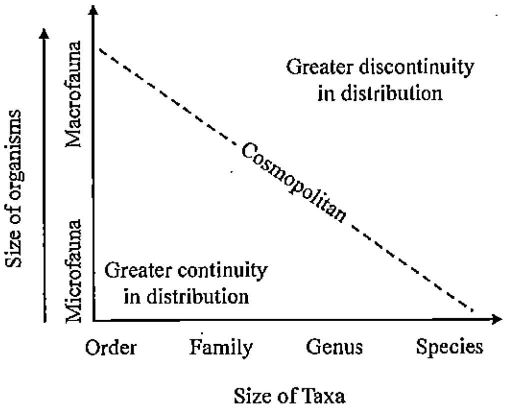

Figure 16.7. Biogeographical distribution of soil animals in relation to body size and taxonomic level. Modified from Anderson (1977).

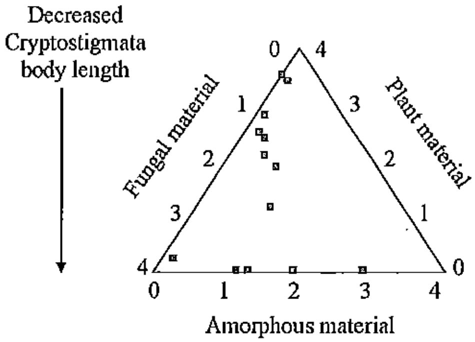

Figure 16.8. Cumulative mean proportions of the major food items selected by the most abundant *Cryptostigmata* species. Modified from Anderson (1977).

Therefore, the results from Heneghan et al. (1999) point to the importance of the faunal assemblage structure as a major determinant of decomposition rates in the tropics.

Swift et al. (1979) hypothesized that soil macrofauna were more abundant in the tropics than in temperate ecosystems. Macrofauna eat larger amounts of litter than microfauna. In fact, faunal effects on litter breakdown can be up to 66% in a tropical wet forest, a site of high abundance of macrofauna and diversity of functional groups (González and Seastedt, 2001). Anderson (1977) theorized that most classes and orders of soil animal communities are cosmopolitan, families are more restricted in distribution, and genera and species show a high degree of endemism (Figure 16.7). It is because of the cosmopolitan distribution of microarthropods that they are often represented as a constant in most field studies on litter decomposition (Heneghan et al., 1998). Still if we deem the tremendous lack of taxonomic expertise and comparative studies of soil organisms and ecosystem processes across geographical zones, we realize the extent of uncertainty in our understanding of this aspect of the global carbon cycling.

Soil Fauna–Microbial Interactions

Soil fauna can affect plant litter decomposition through interactions with microbial communities (Figure 16.6). These interactions are multiform, because they are greatly influenced by the direction and magnitude of the activities of the soil organisms involved. Indirect effects of soil fauna on microbial communities can be generally considered positive because soil fauna increase the surface area for microbial use, stimulate microbial populations in their gut, and increase the dispersal of spores on their integument (Anderson, 1987). However, soil fauna can feed on the microbial biomass and alter their turnover rates. The net effect of soil fauna and microbial interactions on nutrient mineralization would be, for the most part, dependent on the feeding behavior of the soil fauna on the microorganisms. For example, oribatid mites (*Cryptostigmata*) may stimulate fungal growth by grazing on senescent hyphae (Griffiths and Bargett, 1997), but, depending on the foraging intensity, net microarthropod effects on microbial activity can also be negative (González et al., 2001). Hanlon and Anderson (1979) reported inhibition of soil microbial respiration as the number of grazing collembolans was increased beyond an optimal number.

In addition to feeding methods, faunal effects on microbes can be considered in terms of relative body size (Visser, 1985; Anderson, 1987). Anderson states that the "indirect physical effect of animals on microbial populations and activities increase with body size." Concordingly, Visser (1985) argued that microarthropods have a high chance of selective feeding on the microbial population. González et al. (2001) found that exclusion of soil fauna resulted in a higher microbial biomass and lower maximum growth rate of microbes in subalpine forests. Given the dominance and abundance of microarthropods in the subalpine forest, soil fauna could affect ecosystem processes primarily through direct interactions with the microorganisms in this site. In contrast with the results found in the subalpine forests, González et al. (2001) found that exclusion of soil fauna in two tropical forests (dry and wet) did not affect the biomass and maximum growth rates of microorganisms; suggesting a larger net regulatory effect of soil fauna on microbes in the tropics via indirect mechanisms.

It is known that the main energy sources for bacteria are fresh aboveground litter, root-derived carbon, and small organic matter molecules that have been enzymatically processed by fungi (Clarholm, 1994). Yang and Insam (1991) found a higher fraction of bacterial biomass in an AB horizon that in the A horizon in soils from a tropical rain forest in China, supporting the idea that fungal biomass is more abundant in the initial stages of decomposition than in the later stages. Soil fauna can selectively feed on the microbial population, and we need to account for the superimposed effects of grazing by the soil fauna on the nutrient release from organic particles. Therefore, the intimacy of the fauna–microbial association can be related not only to body size but also to the formation of biogenic structures and the digestive process (Figure 16.9; Lavelle, 1997).

Concluding Remarks

More than 20 years have passed since Swift et al. (1979) presented a conceptual trilateral model of plant litter decomposition. It remains the most robust and widely

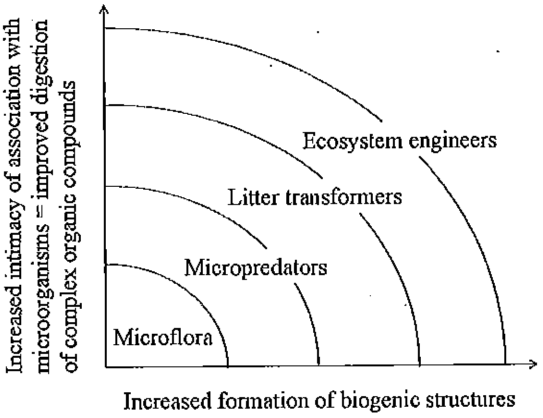

Figure 16.9. Interactions among micro- and macro-organisms in soils. As the size of organisms increases, their relationships with microflora gradually shift from predation to external and internal mutualism, and they produce biogenic structures of increasing strength. When present, larger organisms tend to be more competitive than smaller ones, but their activity is more frequently limited by low temperature and moisture conditions. Modified from Lavelle (1997).

accepted model, as demonstrated by its citation in most introductory paragraphs of studies and reviews dealing with the topic. Yet quantitative efforts of modeling keep treating biotic effects on decomposition like a black box. Soil biologists have long recognized that a tangle of confounding effects is imbedded within the overall organismal portrait. Soil fauna, microorganisms, and their interactions are important regulating factors of decomposition, and their relative hierarchical control varies spatially and temporally.

In recent years, there has been a tremendous advancement in understanding the particular roles and effects of soil organisms on ecosystem processes driven by micro- and mesocosms studies. There is still the need for comprehensive and manipulative field studies that try to tease apart the distinct effect of fauna and microorganisms. This is not an easy task, for the interactions of the abundance, diversity, activity, and functionality of soil organisms (fauna and microorganisms) are at play.

Kinetic methods have been proven useful in determining soil microbial communities and functional groups. They can be used for assessing inhibitory effects of soil fauna on microorganisms or as tool for determining competition for resources within the microbial compartment. Methods of soil fauna exclusion in the field should be carefully evaluated. The application of biocides to litter and soil surfaces is a popular technique to quantify soil fauna effects on plant litter decomposition and mineralization rates. However, this technique is likely to have a nontarget impact on the microbial community that might mask soil fauna effects.

The recent advancement in the study of soil microbial–faunal interactions has opened a new dimension in the understanding of soil biology and ecosystem ecology. Many scientists are currently puzzling with biodiversity issues that relate to ecosystem process and function. The field of soil biology is not exempt from this trend in ecology. The implications of soil biodiversity to ecosystem functioning should be carefully examined. The biocomplexity of the activities and interactions of soil organisms can have profound effects on the functioning of systems and the globe.

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