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Decomposition pathways and successional changes

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Summary – In soils, energy and nutrient pathways are primarily mediated by bacteria or fungi. Bacteria-dominated systems rapidly transfer nutrients, directly and *via* consumers, to plants. In contrast, fungal-based decomposition channels are slower; they are driven by more complex organic resources. There are strong linkages between nematodes and their fungal or bacterial food sources. On one hand, consumer organisms affect rates of energy and nutrient release from their prey; on the other hand, they may regulate the prey biomass. The nature and abundance of available resources can be monitored by faunal analysis of fungal- and bacterial-feeding nematodes (f/b ratio, channel index). The resources change constitutively with time. Readily decomposable portions are rapidly consumed by bacteria and their predators so that the recalcitrant fraction becomes proportionally greater. That change is mirrored by corresponding increase in fungal decomposition and reflected in the nematode fauna. We discuss the relationship of nematode trophic structure with the nature of the incoming organic material and the prevailing state of the physical environment. For example, decomposition pathways of natural forests are predominantly fungal and those of agricultural systems are bacterial. We discuss the significance of the pathways in relation to the structure and functions of the entire soil food web.

Decomposition processes are important for energy flux in terrestrial ecosystems. By recycling plant material and mineralising nutrients therein, the below-ground decomposer system provides the basis for soil fertility and plant life. However, regardless of their significant importance, cryptic below-ground systems have received little attention.

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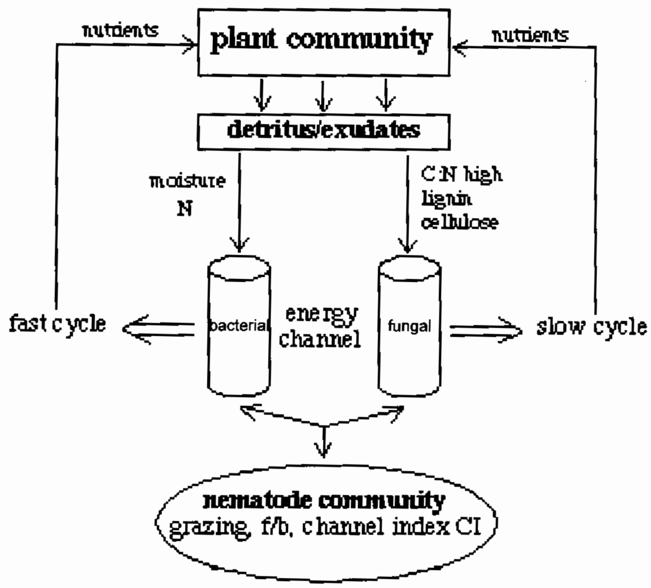

Fig. 1. *Energy and nutrient pathways in a detritus system in relation to plant derived inputs and nematode community influences (f/b: ratio of numerical abundances of fungal- and bacterial-feeding nematodes).*

This is largely because the processes mediated by the systems are particularly complex and difficult to address, either experimentally or through direct observation.

Products of plant photosynthesis provide food sources for soil organisms. Fungi, bacteria, and root herbivores are the starting points for three different energy channels through the soil food web. In detritus systems, plant litter and root exudates serve as substrates for decomposition processes, and the pathways of energy and nutrients are primarily controlled by microorganisms in the bacterial and fungal energy channels (Fig. 1). Systems dominated by bacteria are best described as fast cycle systems. The turnover rate of bacteria and their consumers is high, leading to a rapid nutrient transfer to plants. In contrast, fungal-based energy channels represent a slow cycle. They are driven by more complex organic resources. Further, saprophytic fungi have longer generation times than bacteria and react more slowly to grazing (Scheu & Setälä, 2002).

Nematodes are one of the most abundant groups of biota in the soil. The bacterial and mycelial grazers among them are key intermediaries in decomposition processes and nutrient cycling, and thereby they indirectly affect primary production. Nematodes are tightly linked to their food sources and the nature and abundance of available resources can be monitored by analysis of the nematode fauna, for example by the fungal to bacterial feeder ratio or the channel index (Sohlenius & Sandor, 1987; Ferris *et al.*, 2001).

Decomposition pathways

The abundance of structural carbon compounds, such as cellulose, has significant effects on long-term patterns of decomposition. The C/N ratio of organic material in the soil is another important determinant (Dilly & Irmler, 1998). Pathways with a strong bacterial component generally occur in moist soils that are N-rich and contain readily decomposable substrate. These conditions promote rapid decomposition (fast cycle). In bacterial-based energy channels, the major grazers of microbes are protozoa and nematodes.

The fungal decomposition pathway is favoured by a high C/N ratio in the soil, especially if recalcitrant materials predominate (Rosenbrock *et al.*, 1995). Fungi have better substrate assimilation efficiency than bacteria and are able to break down complex polyaromatic compounds such as lignin and humic or phenolic acids. Major grazers in this system are fungal-feeding microarthropods, which form an abundant and species-rich community (Beare *et al.*, 1997; Scheu & Setälä, 2002). In the absence of microarthropods, fungal-feeding nematodes become system regulators (Parker *et al.*, 1984).

Plants provide two quite different sources for the detritus food web. Root exudates and plant debris both support bacterial and fungal energy channels in organic matter decomposition. Root exudates may be the source for a separate short, fast energy channel. In the rhizosphere, the interaction between plants, microbes and grazers forms a loop. Protozoa, in particular, are important in liberating nutrients bound in microbial biomass for plant uptake. As there is little evidence of extensive consumption of these grazers by top predators (Scheu & Setälä, 2002), carbon could become fixed at this level and not progress to the remainder of the food web.

The energy channels in soil are not distinctly separated. There is a dynamic balance between the fungal and bacterial pathways. The channels run simultaneously and there is transfer of carbon between them. The situation is therefore not simple to model. While it has been stressed that biotic and abiotic systems must be studied in concert (Moore *et al.*, 1998), functional groups, the basic units of an ecosystem model, are usually defined by taxonomic relationships and not by ecosystem function. To construct a food web model it is necessary to: *i*) determine the functional groups of bacteria, fungi and fauna in the detritus food web with primary focus on ecological functions rather than taxa; *ii*) link the functional groups to successional changes during decomposition processes; and *iii*) assess which nutritional relationships are derived from successional coincidences. In this procedure, the functional groups provide a link between species interactions and energy flow.

Succession

During soil organic matter decomposition, substrates change with time. Readily decomposable compounds are rapidly consumed by bacteria so that the recalcitrant fraction becomes proportionally greater. This change is mirrored by a corresponding increase in fungal decomposition. Among fungi, substrate is initially colonised by pioneer saprophytic species, mainly sugar fungi, which utilise simple soluble nutrients (Dilly & Irmler, 1998). They are followed by the more specialised polymer degraders, which utilise cellulose, hemicelluloses or chitin. In later successional stages, the fungal flora comprises species able to break down recalcitrant compounds. They are accompanied by secondary opportunistic invaders. Similarly, bacteria show successional changes during litter degradation (Dilly & Irmler, 1998). In the initial phase, generalist bacteria, with cellulolytic or proteolytic enzymes, dominate. Later there is a relative increase of nitrifiers.

The coincidence of functional groups of bacteria and fungi during succession influences the structure and function of the detritus food web. Bacteria and fungi form the major food source for the grazing soil fauna, including nematodes. There are strong trophic linkages, for example feeding preferences of fungivore nematodes for specific fungal species are well known (Chen & Ferris, 2000; Ruess *et al.*, 2000). The changes among primary decomposers result in a related succession of functional groups of nematodes during decomposition. The initial phase is dominated by bacterial feeders, while the dominance of fungal-feeding nematodes increases later (Freckman, 1988).

Successional changes within the nematode community are confounded by the effects of drought, accumulation of recalcitrant substrates and a higher C/N ratio in the soil. This implies a linkage of nematode grazers not only to the available food resources, but also to abiotic factors in their soil environment. For instance, Griffiths *et al.* (1995) showed that decreasing moisture favours fungal- rather than bacterial-feeding nematodes, possibly due to their ability to tolerate dry conditions.

The pattern of succession of bacterial-feeding nematodes followed by fungal feeders is a common feature of organic matter decomposition in nutrient-rich habitats and depends on nematode life-history strategies. Each stage in primary succession has a specific nematode assemblage, which reflects its biotic and abiotic characteristics. Primary succession is initiated by suspension-feeding Rhabditidae (Bouwman & Zwart, 1994). They are typical enrichment opportunists, with a *c-p* value of one. Major characteristics of these nematodes are large body size and high fecundity. These enrichment opportunists are slowly followed by nematodes with higher *c-p* values, particularly the epistrate-grazing Cephalobidae. They belong to the general opportunists, and are characterised by having smaller bodies and lower fecundity (Bongers, 1990; Bongers & Bongers, 1998). An important feature of the *c-p* 2 nematodes is that they are well adapted to dry conditions in the soil environment (Griffiths *et al.*, 1995). The Cephalobidae are accompanied in time by the fungal feeders of the suborder Aphelenchina, especially the Aphelenchidae (Bouwman & Zwart, 1994; Niles & Freckman, 1998).

Nematodes as indicators

The coincidence of functional groups of bacteria, fungi and their nematode grazers during succession provides an opportunity to monitor the nature and abundance of available resources in pathways during decomposition. The consumer organisms can be used as indirect measures. Thus, the composition of the nematode assemblage may serve as an indicator for changes among the bacteria and fungi that are often more difficult to study.

Two different approaches are commonly used. One is based on nematode trophic structure solely. This is the ratio f/b, the numerical abundance of fungal- to bacterial-feeding nematodes. The other is the channel index (CI), which integrates nematode feeding groups and *c-p*-scaling into a matrix classification of functional guilds (Ferris *et al.*, 2001). The guilds represent a grouping of taxa with the same feeding habits, and inferred function, in the food web. Members of a guild respond similarly to food web enrichment or to environmental perturbations. The channel index is calculated on the percentage of the opportunistic grazers of bacteria and fungi weighted by their fecundity and life course characteristics (Ferris *et al.*, 2001).

System-predominant pathways

The predominant decomposition pathways in soils of different systems vary. For example, forest ecosystems are fungal-dominated whereas agroecosystems are generally bacterial dominated. The major factor influencing decomposition processes is the dominant vegetation at a site. Plants may act as hosts for soil nematodes, deliver a variety of food resources and, as roots or litter form an important microhabitat in the soil, affect environmental conditions. Due to their position in the soil food web, plant-feeding nematodes show the most pronounced association to the nature of the plant community. Bacterial and fungal feeders respond secondarily to changes in the microbial community, which is directly affected by the input of detritus.

Wasilewska (1979) investigated the distribution of nematode trophic groups in different ecosystem types. The study showed a distinct increase of the fungal to bacterial feeder ratio from grassland to agricultural field to forest with 0.19 to 0.38 to 0.74, respectively. This indicates a more bacterial-based decomposition in grasslands and a more fungal-dominated pathway in forests, whereas agroecosystems are intermediate.

A literature survey of Ruess (2003) on a range of studies in grasslands, crop-fields and forests revealed no distinct differences in the fungal to bacterial feeder ratio between these soil systems as values of f/b overlapped. The channel index increased significantly in forest soils compared to both grasslands and fields. In summary, the data suggest that neither the fungal to bacterial feeder ratio nor the channel index is reliable as a predictor for different ecosystems. However, the hypothesis requires further testing to determine whether there is a sampling time or depth component that should be considered.

Natural and undisturbed habitats

Wasilewska (1994) studied the trophic structure of soil nematode communities in grassland sites. A sequence of developmental stages from newly established to permanent meadows was analysed. Both indices, the fungal to bacterial feeder ratio as well as the channel index clearly increased with meadow age. For young meadows (less than 4 years), f/b and CI averaged as 0.27 and 12.5, respectively. In permanent and old meadows (aged from 4-12 years) means of f/b and CI were 0.55 and 30.3, respectively. This implies a more fungal-dominated decomposition pathway with time. In the first years of succession, meadows showed a higher metabolic activity and primary production, whereas there was greater organic matter and higher humification in older meadows. This indicates a shift from bacterial- to fungal-dominated decomposition processes during succession, which was reflected by the increase in both indices.

The f/b ratio and the CI are also useful tools to assess changes in decomposition channels along a transect. Hánel (1992) investigated a meadow-spruce forest ecotone. There was a clear increase in fungal-based energy transfer, indicated by f/b and CI, along the transect. This corresponded to an increase in fungal abundance from meadow to forest measured in the study. Indices showed changes due to sampling date, but not consistently with similar trends. As always, seasonal variation warrants consideration in interpreting such data.

Environmental disturbance

Besides succession or transect analyses in undisturbed habitats, the indices of nematode trophic structure may also offer valuable information on changes in soil decomposition pathways due to perturbation. Ruess *et al.* (1996) investigated the effects of soil acidification in a spruce forest site. Regular application of acid rain for 3 years decreased soil pH and increased the length of fungal hyphae and the ergosterol content of the soil. The latter is a measure of the active fungal biomass. This change in favour of fungi in the primary decomposition channels was reflected by a higher f/b and CI. The fungal to bacterial feeder ratio increased from 0.43 to 0.70 and the channel index from 59 to 86 in control and acidified plots, respectively.

Similar responses were observed in grassland sites with disturbance by either acid or alkaline emissions (Valocká & Sabová, 1997). Increasing levels of pollution intensity due to the distance of the pollution source were investigated. The perturbations resulted in a change in soil pH, *i.e.*, pH decreased in acid and increased in alkaline plots. Such shifts are likely to be followed by a shift in bacterial and fungal pathways in the soil. At the control site, the fungal to bacterial feeder ratio was 0.73 and the channel index was 25. A change to the fungal-based energy channel occurred in the acidified plots, indicated by an increase of f/b and CI to 2.48 and 71, respectively. In contrast, alkaline emissions led to a shift to the bacterial energy channel and reduced f/b to 0.10 and CI to 5.

Conclusions

Successional changes in the detritus food web, driven by the nature of available resources and by environmental conditions, are reflected in successional changes in the abundance of enrichment-opportunist bacterivore nematodes, less volatile general opportunist bacterivores, and fungivores. The shift from bacterial to fungal feeders during primary succession in nutrient-rich habitats gives a general picture of resource availability during organic matter degradation. The bacterial-feeding Rhabditidae and Cephalobidae, with their different life strategies, can be used to determine different stages in decomposition processes.

Succession of functional groups of nematodes therefore may serve as link between microorganisms and energy flow in soils. Analysis of the nematode community structure provides a valuable tool to assess the nature of decomposition pathways. Simple ratios of trophic groups or functional guilds are useful for studying matter and energy flow within the below-ground detritus-based food web. Indices like the fungal to bacterial feeder ratio or the channel index are most useful for tracking successional changes or disturbance within a system. However, f/b and CI may not be predictors for different ecosystems. Clearly, such indices are estimators that are based on the numerical response of organisms to availability of appropriate resources. It would be misleading to imply that they provide a quantitative measure of the component flow of carbon and energy through bacterial and fungal decomposition channels. Nevertheless, they form a basis for interpretation of the likely conditions of soil food webs.

Bacterial- and fungal-based energy channels in soil run simultaneously and are not distinctly separated. There may be time lags in response or cross exchange of energy and nutrients; they are dynamic features of the soil environment.

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