

#### 4. DECOMPOSITION: THE ROLES OF VARIOUS FUNCTIONAL GROUPS OF ORGANISMS

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Decomposition of organic matter is largely a biological process, regulated by decomposer organisms, the physicochemical environment and the resource quality. The process is inseparably linked with the synthesis of new organic compounds (biosynthesis of decomposer tissues and humification) and the release of elements (mineralization) (Swift et al., 1979). The organisms involved in decomposition cover a wide range of sizes: micro-organisms (bacteria, fungi), microfauna (protozoa, nematodes), mesofauna (e.g. enchytraeids, mites, collembola, termites) and macrofauna (e.g. earthworms). Most of the process takes place below-ground and at the soil surface. Decomposition can be studied in terms of the contribution of the organisms involved at the level of the individual, the population and/or the community. Because it is impossible to study every species in soil (since there are so many) species are often assembled in functional groups, i.e. groups that are considered to have approximately the same function in soil. In theory such species may belong to different taxonomical orders. Functional groups, however, are defined such that they must be roughly homogeneous in habitat, food, feeding mode and

ecophysiology of the organisms (Hunt et al, 1987; Moore et al., 1988). As a consequence the boundaries usually occur between orders or lower taxa. The subdivision in functional groups is very much determined by our taxonomic and ecological knowledge of those groups, which in turn is largely determined by the techniques to isolate and quantify organisms from soil. Protozoa, e.g., can be isolated from soil but are very difficult to quantify, (Stout et al., 1982) while it is assumed that most of the bacteria and fungi from soil are not isolated by current techniques at all (Paul and Clark, 1989). This is one reason why decomposition is often studied in terms of sum parameters (microbial biomass, soil respiration, enzyme activity, net element mineralization).

Whereas sum parameters may allow a reliable description of decomposition, they are less useful for explaining and predicting the process. Various efforts to that end have been made starting from the food web concept. Many food web studies of natural and agro-ecosystems (figure 1) resulted in the same figure of approximately 30% for the contribution of the soil fauna to the transfer of nitrogen in soil, with protozoa being the most important animal group, followed by nematodes (Verhoef and Brussaard, 1990). The contribution to carbon transfer is mostly relatively high as compared to nitrogen transfer if the C:N ratio of the food is higher than that of the consumer. Depending on conversion efficiencies nitrogen is usually immobilized. The contribution to carbon transfer is mostly relatively low as compared to nitrogen transfer if the C:N ratio of the food is approximately the same as that of the consumer or smaller. Again depending on conversion efficiencies, nitrogen is usually mineralized (Wood, 1989). This reasoning may, however, be open to criticism if the organism selects a subset from the available food for ingestion, with a C:N ratio different from that of the total food.

Soil food web studies have already advanced theory in ecology in which detritus-based food webs received little attention until recently (Moore and Hunt, 1988; Moore et al., 1989). For explaining and predicting decomposition, however, several limitations of current food web research have still to be overcome.

Firstly, pathogens are not explicitly accounted for, only implicitly, viz. in the nominal death rate parameters, and some groups such as root herbivores and root symbionts

like mycorrhizas, which are wide-spread in nature, are seldom addressed. The same holds for gut symbionts.

Secondly, it is unknown what the composition is (e.g. C:N:P:S ratio) of the organic material actually used by microorganisms i.e. what enters the food web from detritus or from root-derived material. This is a fundamental problem which may not be solved until it is possible to quantify the biomass and activity of various physiological groups of bacteria and fungi. Perhaps genetic marking and recapture techniques are a first step that may eventually lead to an identification method of such physiological groups.

Associated with the question of the composition of food actually ingested is the fact that there is only scant knowledge on the effects of so-called secondary plant products (phenolics, terpenoids, alkaloids) on the palatability of organic matter for microorganisms and soil animals. These substances have a function in protection of the living plant against diseases and herbivores, but they continue to exert effects after the plant parts have entered the dead organic matter pool. It seems likely that there is an evolutionary selective advantage in being able to cope with such substances and it would be interesting to know at what cost in terms of assimilation and production efficiencies of the decomposer organisms adaption to such substances takes place and, indeed, how the evolutionary "necessity" to adapt determines the structure of the decomposer community and the rate of the decomposition process. The same holds, likewise, for the array of defense substances, such as antibiotics, used by soil microbes and animals in the chemical warfare that structures below-ground biological interactions. Thirdly, non-symbiotic mutualistic relationships other than consumption/predation, such as comminution, dispersal and priming of substrates are not accounted for in current food web research.

Depending on the relative abundance of functional groups and the quality of the substrate mutualistic relationships have often been shown to increase the microbial activity. This means that a hitherto unknown part of the decomposition, ascribed to microorganisms, could rightfully be credited to soil animals. Hence, in food web simulations, the contributions of soil microorganisms to element transfer is overestimated and that of animals underestimated. Deletion of a functional group in food web simulation is one way to better estimate the importance of that group for

element transfer (De Ruiter et al., 1992). This has led to as much as an order of magnitude increase in the estimation of nitrogen transfer by some groups, but the proportional contribution remains low in most (but not all) cases. However, apart from consumption/predation, mutualistic effects are still not accounted for by this technique.

Soil food web research has, in practice, been research on the decomposition of litter or crop residues. The litter layer, however, is only one of several habitats where decomposition occurs. Decomposition is already initiated above-ground by microorganisms on senescing leaves. Small pools in tree stems and branches are ecosystems in themselves where most of the organic matter produced or introduced is decomposed. Belowground, the rhizosphere, soil aggregates, worm channels and termite and ant mounds are important habitats where decomposition takes place in addition to the litter layer. On the axis from litter layer to insect mounds the habitat is, to an increasing degree, created by the biota itself: microorganisms → soil aggregates; roots → rhizosphere; worms → channels; insects → mounds.

The organisms creating those habitats also create microhabitats for other organisms with which they often have close mutualistic relationships. On this axis current food web theory is increasingly difficult to apply as long as mutualistic interactions cannot be adequately accounted for.

Bearing these limitations in mind one may wonder if food web simulations will ever reliably represent decomposition and mineralization processes. There is some evidence they will. In our research on integrated and conventional farming systems (Brussaard et al., 1988; Kooistra et al., 1989), we are encouraged by the close agreement between the nitrogen mineralization during the growing season as simulated from food web interactions with that observed from incubation studies of field soil (De Ruiter et al., 1992). The clue to this finding may be the sampling strategy by which all (micro)habitats present on the study site were well represented in space and time. We sampled at five points in time during the growing season at the scale of individual plants (Brussaard et al., 1990). We used our organism estimates to

simulate the nitrogen mineralization on a tens of  $m^2$  scale over the entire growing season, i.e. on one level of scale beyond. If the objective would have been to explain the decomposition or mineralization process on the scale of the individual plant, we should have sampled the microsites below the plant scale with a frequency accounting for the speed at which processes occur in the rhizosphere, soil aggregates, worm channels, etc. In other words, at a certain hierarchical level decomposition and mineralization are explained from the level below, given the right sampling strategy. If beginners' luck has been involved in our result, it probably was in the frequency and timing of sampling.

Food web simulations may be feasible, but are they necessary? This depends on the scale at which one is interested in the decomposition process. On a scale of regions and millennia the climate and edaphic properties such as clay and organic matter content are usually good enough predictors of the decomposition process. The smaller the scale, the more important vegetation and resource quality are, followed by the structure of the decomposer community (Lavelle et al., 1992). All factors acting on a certain scale influence all scales below. Factors at lower levels may, however, also modify those at higher levels, perhaps resulting in a genuinely cybernetic system on the earth scale (cf. the Gaia debate). Irrespective of the spatial and temporal scale, however, knowledge on the working mechanisms and effects of the chemicals that soil organisms ingest is important, if we want to know which type of human-imposed stress, and how much of it, can be added without violating the decomposition process as a whole. Whatever the stress factor is, in many cases the composition of the organic matter entering the soil is altered by it, e.g. by increased N or S deposition or greenhouse gases. One example may clarify this point. In the case of added xenobiotics less effect on sum parameters than on individual parameters has often been observed, probably due to the functional replacement of sensitive species by less sensitive species. In the long run, however, this has been shown to lead to ever simpler soil communities, in which the energetic costs of adaptation by the surviving species grow increasingly higher up to the point that the limits to the functioning of the system have been reached (Van Capelleveen, 1987). To prevent this we have to increase our insight into the ecophysiology, population biology and adaptive capabilities of the organisms assembled in functional groups, so as to formulate norms for setting boundaries on man-induced stress.

This may be one of the main incentives for the EC to foster the application and further development of decomposition studies. It is my feeling that for the biological part of this research food web theory is a useful framework and food web modelling a useful tool. Further development of this area will undoubtedly benefit from and contribute to ecological theory, which may, indeed, be one of the main incentives to foster decomposition research for the ESF.

To summarize, the following research priorities can be identified:

1. Ecological studies and simulation of mutualistic relationships among decomposer organisms in key (micro)habitats
2. Identification of the composition of organic materials actually entering the food web and ingested within the food web at the functional group level
3. Evolutionary and ecological effects of secondary plant products on decomposer organisms and the decomposition process
4. Isolation and quantification of soil microorganisms at the physiological group level

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Figure 1.

The soil food web at the field site of the Dutch Programme on Soil Ecology of Arable Farming Systems, the Lovinkhoeve experimental farm, Marknesse, The Netherlands. Arrows from each box to the detritus pool omitted. (From: De Ruiter et al., 1992).

