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Controls of the Microbial Loop: Biotic Factors

MICROBIAL ECOLOGY

The Microbial Loop Concept as Used in Terrestrial Soil Ecology Studies

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Abstract. Components and processes in the aquatic microbial loop are compared with the composition and functioning of the soil microbial loop. Relative to their bacterial and/or fungal food sources, many of the soil water-film fauna (e.g., protozoa, nematodes) are conspicuous by low biomasses and high turnover rates of carbon and mineral nutrients. Comparisons with production and turnover rates of aerial (pore-inhabiting) fauna are made, and the highly patchy nature of soil microhabitats is shown to be similar to that of aquatic (marine) habitats.

My principal objectives are to compare and contrast the concept of the microbial loop in aquatic ecosystems (e.g., Sherr and Sherr [20] and Bratbak et al. [2]) with the microbial loop as it has been used in soil ecology studies. As described by Sherr and Sherr [20], the structure of the microbial loop in aquatic systems was set forth in early papers of Larry Pomeroy relating to the ocean's food web. I suggest that Pomeroy has had an even more marked impact on an appreciation of the incredible diversity of microbial interactions, which occur in all ecosystems, as was discussed in his earlier seminal paper [17]. Turnover rates in seven different ecosystems, ranging from the rumen to coral reefs, forests, and oceanic plankton, were compared. Pomeroy noted that one needs to consider the turnover times of available versus total biomass of essential elements when considering the fate of standing stocks of principal nutrients, such as nitrogen and phosphorus.

This Pomeroy paper [17] is one of the earliest to make the case for the major influences of protozoa as one of the principal microbial grazers in all terrestrial systems. Numerous other authors have come along in the 24 years since this landmark paper and tested their ideas against his early suppositions and suggestions for future work. Interestingly, but not surprisingly, the roles of microfauna and microbial turnover rates and patterns are still honored more in the breach than in mainstream practice. The following is a brief historical perspective on studies of soil protozoa.

Studies of the effects of protozoa date from the early work of Russell and Hutchinson [18], who performed partial-sterilization experiments to see if they could mimic the putative effects of protozoan grazing. Are protoza feeding so heavily on bacteria that they significantly affect soil health? This struck a responsive chord, resulting in studies carried out in virtually every decade of this century

[6, 8, 10, 14, 22–24], showing the impacts of protozoa on bacterial and fungal production and nutrient remineralization. The general consensus is that protozoan grazing stimulates mineralization, with subsequent plant uptake of N enhanced by ca. 15–20% over control systems that lack protozoa.

Raoul Francé, a German sociologist, made analogies between aquatic plankton and the small and medium-sized organisms in the soil, which he termed "Das Edaphon" [12]. This euphonious term was appealing, and gave a feeling of synonymy between systems, but did not, however, lead to any insightful experiments. Ironically, John Stout, a pioneer soil protozoologist in New Zealand derived independently the terrestrial plankton concept [21]. Stout noted the considerable amount of water present in water films, and suggested that at least part of the available energy of the system is released in the form of soluble nutrients from frass, honey dew, or other products of phytophagous arthropods, and from dead plant litter. An additional significant source of these labile compounds comes from rhizosphere exudates and exfoliates as well [5]. Stout makes the prescient statement: "It is this pool of soluble nutrients which constitutes the main substrate of microbial proliferation, supports the terrestrial plankton, and which directly or indirectly provides the basic nutrients of the great majority of soil animals" [20] (Fig. 1). Stout included the following biota in the terrestrial nannoplankton: zymogenous microflora (bacteria and yeasts), microfauna (herbivores), including protozoa, rotifers, nematodes, copepods, and microdrili such as enchytraeids, and microfauna (predators) (Fig. 1, [21]).

The biochemical competence of the soil protozoan fauna should be considered as well. A constitutive bacteriolytic enzyme, a hexosaminidase, was isolated from a culture containing *Acanthamoeba castellanii* (Drozanski, 1972, cited by [19]). Indeed soil amoebae with chitinase and cellulase enzyme activities have been isolated [25]. Many amoebae and some ciliates are able to lyse fungal cell walls, with three enzymatic systems capable of degrading the chitin polymer: lysozymes, exochitinases, and endochitinases [15]. These competencies are especially important as researchers [3, 4] extend their work into biological control mechanisms; several amoebae were shown to be significant control agents of *Gaeumannomyces graminis tritici,* the notorious "take-all" fungus of South Australian wheatlands.

Viruses probably play some significant roles in microbial ecologies of soil environments. Farrah and Bitton [11] observed that: "Lytic phages could act to restrict the growth of susceptible bacteria, and other phages could transmit genetic information between bacteria. However, there is limited information on their numbers and activities in soil." Pantastico-Caldas et al. [16] found that temperate phages in desert systems (which dominated in their studies) were inactivated on soil particles at acid pH (4.5–6). These phages had essentially no effect on populations of soil bacteria in Arizona soils, but persisted at low densities in their hosts, in contrast to the often-cited impacts of virulent phages on *Escherichia coli* in liquid chemostat cultures.

The principal influences of protozoa vs. other meso- and macrofauna were summarized by Coleman et al. [9] (Table 1), drawing, in part, on earlier work of Clarholm [7]. In short, protozoan activities within the water-film communities are extensive, with an average 10–12 turnovers per year. Protozoa, particularly amoebae and flagellates, probably have more impact on soil microbial C and N turnover on a per unit mass basis than any other fauna.

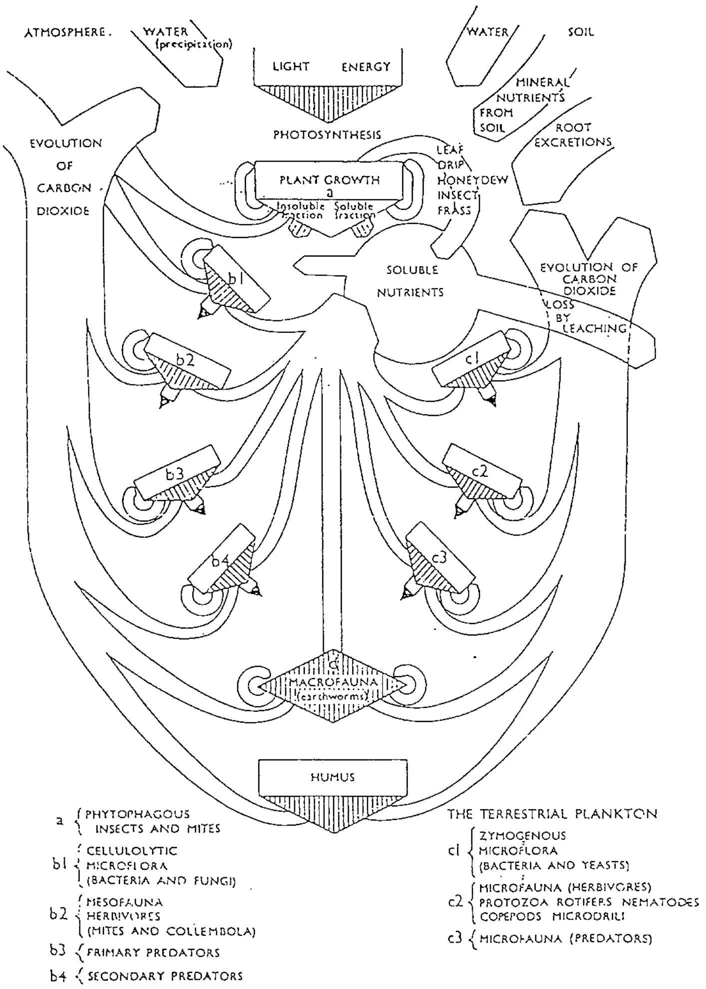
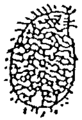
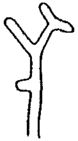
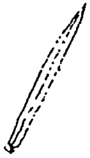
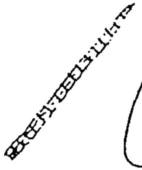
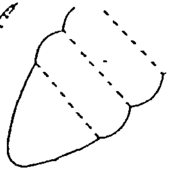


Fig. 1. The relations of the terrestrial plankton to the other fauna and flora and to the flow of energy and supply of nutrients in a forest organic cycle [21].

Another insight from our recent studies in the Georgia Agroecosystem project was developed by Beare et al. [1]. The context and location-specific nature of the milieu needs to be considered when determining the function of the microbial loop. There are at least five quite different "spheres" of influence, including not only the well-known rhizosphere and detritusphere, but also regions influenced by termites, earthworms (drilosphere), and the macro- and microaggregates, or aggregatusphere (Fig. 2). Although only a minor proportion of the total soil volume, these "hot spots" are where most of the trophic and nutrient regeneration activities occur, with impacts on aggregate status as well. For example, Hu et al. (unpublished) measured higher mannose/xylose ratios (indicating greater microbial than plant contribution to carbohydrates) in soil microaggregates with fungal hyphae present vs. those with

Table 1. Average standing crop and energetic parameters for microorganisms, mesofauna, and earthworms in a lucerne ley and Georgia no-tillage agroecosystem (modified from [1], [7], [13]) (From [9])

	Naked amoebae	Flagellates	Ciliates	Bacteria	Fungi	Microbivorous nematodes	Collembola	Mites	Enchytraeids	Earthworms
										
Typical size in soil	30 μm	10 μm	80 μm	0.5–1 × 1–2 μm	0–2.5 μm 1.0–5.5 μm	0 to ~40 μm	0–5000μm	0–1000μm	0–1000μm	0–5000μm
Mode of living	in water films on surfaces	free-swimming in water films		on surfaces	free and on surfaces	in water films free and on surfaces	free	free	free	free in soil
biomass (kg dw ha^1)	95%	5% 50^a	<1%	500–750^b	700–2700^c	1.5–4^d	0.2–0.5^d	2–8^d	1–8^d	25–50^d
% active	0–100			15–30	2–10	0–100	80–100	80–100	?	0–100
Estimated turn-over times, season^{-1}		10		2–3	0.75	2–4	2–3	2–3	?	3
No of bacteria division^{-1} × 10^{-3}	3–8	0.6–1	20–2000							
Minimum generation time in soil (h)		2–4		0.5	4–8	120	720	720	170	720

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[a] MPN technique

[b] Direct counts plus size-class estimations

[c] Direct estimation of total hyphal length and diameter

[d] Extractions and sorting

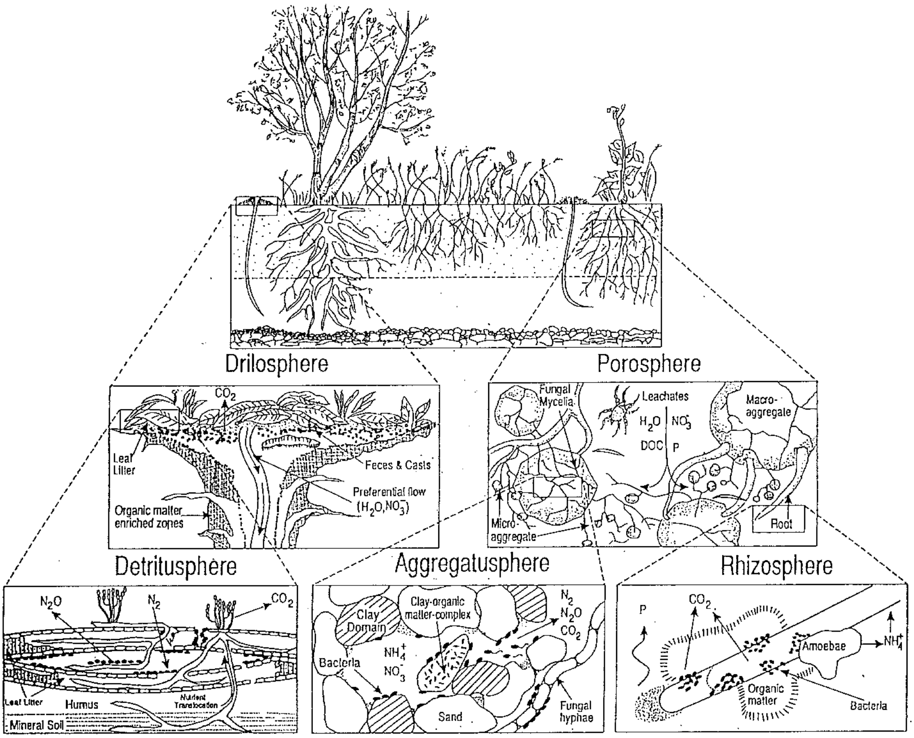

Fig. 2. "Spheres" of influence, being "hot spots" of activity in many soil systems. "Drilosphere," portion of the soil which is earthworm burrow-influenced; "porosphere," that portion which contains water-films and channels between aggregates; "aggregatusphere," the micro- and macroaggregates which contain bacteria, fungi, and some micro- and mesofauna feeding upon them; "rhizosphere," the region of soil directly root-influenced; "detritusphere," the litter, fermentation, and humification layers above the mineral soil, which are havens for microbes (including mycorrhizae) and fauna feeding upon them [1].

markedly reduced hyphal biomass in our field mesocosm studies. The fungi significantly enhanced stability of water-stable aggregates as well [1].

It is important to note than many insights into soil function are possible if soils are viewed as being an opaque aquatic milieu. The insights of Pomeroy have aided in achieving a synthesis between the aquatic and terrestrial microbial loops.

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