

14 Microbes and Microfauna Associated with Biological Soil Crusts

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14.1 Introduction

Microbial populations play a critical role in the regulation of nutrient cycling and energy flow in ecosystems, as they mediate decomposition and subsequent mineralization rates which, in turn, regulate nutrient availability and primary production (Zak and Freckman 1991). Even in regions where water is considered limiting, nutrient availability can restrict plant growth (Romney et al. 1978). Extreme temperatures and/or low soil moisture restrict soil food web development. As soil favorability increases, edaphic taxa generally appear in the following order: pigmented bacteria > actinomycetes > algae and cyanobacteria > fungi, protozoa, other bacteria > lichens > mosses and microarthropods (Cameron et al. 1970).

The trophic structure of soil food webs is very important in soil nutrient cycles. Soil primary producers are lichens, mosses, green algae, and cyanobacteria. These organisms, along with plant material, are both grazed directly and decomposed by soil biota. During decomposition, early-colonizing yeast and bacteria are grazed by nematodes and protozoans, while mites control nematode numbers. Later stages of decomposition are dominated by fungi, which are grazed by nematodes, collembola, and mites. Thus, trophic relationships among soil biota become major regulators of decomposition and mineralization in soils (Ingham et al. 1985).

There is also a synergy between bacteria, fungi, protozoa, and cyanobacteria. Grazing by protozoa stimulate cyanobacterial nitrogen fixation (Ghabbour et al. 1980). Addition of heterotrophic bacteria and fungi to soils significantly increases cyanobacterial biomass (Schiefer and Caldwell 1982). Bacteria and fungi release nutrients and scavenge cyanobacterial "wastes", including O₂, enhancing cyanobacterial N fixation (see Chap. 19). Nitrogen provided by the cyanobacteria, in turn, increases microbial decomposition activity (Lynch and Harper 1983). The objective of this chapter is to discuss the relationship between biological soil crusts and other heterotrophic components of the soil food web, such as bacteria, fungi, protista, nematodes, and soil invertebrates.

14.2 Biological Soil Crusts as a Food Source for Other Soil Food Web Components

Bacteria and Fungi. Bacteria are generally numerically dominant in desert soil food webs. Bacteria that can form desiccation-resistant structures are the most common genera in deserts (Kieft 1991). Bacteria are the major decomposer/consumers of soil-crust cyanobacteria (J.S. States, unpubl.). Fungi occur in smaller number than bacteria, but often have similar biomass in desert soils (see Chap. 13). Fungi can form desiccation-resistant spores and grow in air-filled soil pores (Kieft 1991). Yeasts and molds are less prominent in hotter deserts than cold deserts (Cameron and Blank 1967). Fungi specialize on more recalcitrant material than bacteria, and thus are more common in shrub communities and on litter with higher C:N ratios (Kieft 1991). Actinomycetes, especially *Streptomyces*, use the cyanobacterium *Microcoleus* as a food source, and in preference to *Scytonema*. While common soil fungi are found on all crust types, unique saprotrophic fungi are involved in the decomposition of lichens and bryophytes (J.S. States, unpubl.).

Protista. Protists, including amoebae, ciliates, and flagellates are also important in soil food webs, and eat soil cyanobacteria and algae (Tchan and Whitehouse 1953; Whitford 1996). *Nasula picta* and *Thecamoeba* have been observed eating *Microcoleus* in surface soils collected from under *Spinifex* plants in a hot Australian desert (S.S. Bamforth, pers. comm.).

Nematodes. Nematodes are important consumers in soil food webs. Functional groups include bacterivores, omnivore-predators, plant-feeders, and fungivores. Numbers and types of nematodes present are dependent on the amount and type of food sources (Yeates 1979; Zak and Freckman 1991). Nematodes are known to feed on algae and cyanobacteria (Table 14.1; Tchan and Whitehouse 1953).

Arthropods. Arthropods are the most abundant herbivores and detritivores in many terrestrial ecosystems, and are important in regulating rates of decomposition and mobilization of nutrients (Parkinson 1983). Mites are the major group found in deserts, and can constitute up to 90% of the microfauna (Wallwork 1972). Microarthropods feed on algae, fungi, cyanobacteria (specifically *Microcoleus*), bacteria, other invertebrates, and plant detritus, and thus are important regulators of soil microflora (Table 14.1). Microarthropods are also important in the dispersal of soil microflora. They carry bacteria and fungal cells and spores, lichen fragments, and soredia on their bodies (Bailey 1976; Parkinson 1983; Steinberger 1991).

Table 14.1. Soil arthropod taxa that feed (+ = degree of feeding) on cyanobacteria, algae, and fungi from the Chihuahuan Desert and shortgrass steppe. (After Walter 1988 and J. States, unpubl.)

Taxon	Degree of feeding	Habitat	
		Desert	Steppe
Coleoptera			
<i>Anotylus</i> sp.	+++		×
Collembola			
<i>Hypogastura scotti</i>	+++		×
<i>Folsomia elongata</i>	+++		×
Oribatida			
<i>Pilogalumna</i> sp.	+++		×
<i>Haplozetes</i> sp.	+++		×
<i>Ceratozetes</i> sp.	+++		×
<i>Pergalumna</i> sp.	+++	×	
<i>Peloribates</i> sp.	+++	×	
<i>Oppia</i> sp.	+++	×	
Astigmata			
<i>Tyrophagus zachvatkini</i>	+++		×
<i>Tyrophagus similis</i>	+++		×
Endeostigmata			
<i>Alicorhagia fragilis</i>	++		×
<i>Alicorhagia usitata</i>	++		×
Prostigmata			
<i>Eupodes</i> spp.	+++	×	×
<i>Linopodes</i> sp.	+++	×	
<i>Paratydeus</i> sp.	+	×	
Tydeidae	+++	×	×
Tardigrades	++	×	×

Macroarthropods are also important in desert ecosystems. However, few are known to be dependent on biological soil crusts directly for habitat or food. Exceptions include a species of isopod, two snails, Australian termites, and a mole cricket, each of which feeds on biological soil crusts. Fecal material from these species can be an important source of nitrogen for the ecosystems in which they occur (Steinberger 1991).

14.3 Distribution of Food-Web Organisms in Desert Soils Relative to Biological Soil Crusts

On a regional level, the distribution, size, and composition of soil food-web components are controlled by regional rainfall and temperature patterns. On a local scale, the occurrence of different taxa is controlled by the distribution of soil moisture, temperature, and organic matter, all of which are influenced by the presence of biological soil crusts (Binet 1981; Whitford 1996).

Distribution of soil microorganisms is correlated with distribution of soil organic matter. In deserts, where soil organic matter is very low (generally <1%), occurrence of microorganisms is expected to be closely tied to that of biological soil-crust development, as crusts are a major source of soil C and N in these ecosystems. This is especially true in plant interspaces, where input of plant litter is low (see Chaps. 18, 19). Indeed, studies worldwide have generally found numbers of bacteria, fungi, protozoa, nematodes, and microarthropods greatest at the soil surface, except in extreme environments and in soils next to plant roots (Antarctica, hyperarid deserts; Table 14.2). This difference is especially pronounced in plant interspaces

Studies directly addressing the influence of biological soil crusts on soil microflora have shown similar results (Table 14.2). In gypsum soils on the Colorado Plateau, USA, soil surfaces (0–2 cm) in lichen-crusting plant interspaces were found to have larger bacterial and fungal populations than underlying soils (2–5 cm). Adjacent alluvial soils with no lichens showed no significant differences between surface soils and subsurface soils (K.B. McKnight et al., unpubl.). In general, crusts on sandy soils had greater active bacteria and fungi than underlying soils (4–6 cm) in interspaces and under plants (J. Belnap, unpubl.). In Tunisia, Skujins (1984) reported that microbial biomass is greater, but species diversity less, in surface than in subsurface soils.

In Great Basin, US, alluvial soils, indicators of microbial activity (dehydrogenase activity, respiration, and proteolysis) were five to ten times higher in the upper 3 cm of soil that contained soil-crust organisms than the rest of soil profile (Rychert and Skujins 1973) although plate counts measured fewer organisms at the surface (Kovda et al. 1979). This was also seen by Bolton et al. (1993). No significant differences were seen in heterotroph, actinomycete, or fungal numbers between surface and subsurface soils. However, indicators of microbial activity were much higher in the surface soils (microbial C, N, ATP, respiration, dehydrogenase with glucose, and phosphatase).

Soils experiencing extreme cold and hot temperatures are exceptions to this pattern, as they tend to have higher microbial numbers below, rather than at, the soil surface. Bacteria, fungi, and protozoa numbers were higher at 2–15 cm than 0–2 cm in Antarctic dry valleys (Cameron et al. 1970). Higher

microbial numbers are found at depth in some hot Middle East deserts (Binet 1981). Cameron and Blank (1967) found fungal populations greater at depth at two of six sites in the Mojave Desert.

Biological soil crusts provide habitat for larger organisms as well. Microbial-feeding nematodes are highest in surface soils on the Colorado Plateau, Great Basin, Sonoran, and Mojave Deserts in the US (Zak and Freckman 1991; J. Belnap, unpubl.). Yeates (1979) reported a high correlation of nematode abundance and moss cover ($r^2=0.86$; $P<0.001$). In both polar regions, microarthropods occur commonly in mosses and lichens at the surface (Crawford 1981). In warm deserts, mosses provide habitat for cryptostigmatid, prostigmatid, and mesostigmatid mites, as well as collembolans, nematodes, rotifers, tardigrades, and some protozoans (Yeates 1979). Microarthropod numbers are found to be greatest at soil surfaces in Australian, Great Basin, Mojave, Colorado Plateau, and Chihuahuan Deserts (Wood 1971; Whitford et al. 1981; Steinberger 1991; Rundel and Gibson 1996; J. Belnap, unpubl.). Franco et al. (1979) found 80% of collected microarthropods in the top 10 cm of soils during most of the year in the Mojave. Probstigmata mites, tardigrades, isopods, snails, mole crickets, tenebrionid beetles, protozoans, termites, and ants have all been recorded feeding on cyanobacteria, lichens, and mosses (Bailey 1976; Ghabbour et al. 1980; Loria and Herrnstadt 1980; Rogers et al. 1988; Steinberger 1991).

Limited data indicate that the level of crust development influences microorganism numbers. In Colorado, USA, lichen-moss crusts supported three times as many bacterial-feeding nematodes and seven times as many fungal-feeding nematodes as adjacent cyanobacteria-only crusts (Anderson et al. 1984). In the Arctic, crusts with liverworts had more bacteria and fungi than crusts with only cyanobacteria (Smith and Griggs 1932).

14.4 Conclusion

As can be seen from the above discussion, there is strong evidence that biological soil crusts are important in the maintenance of desert soil food webs. Early successional crusts (those dominated by cyanobacteria) support a less complex decomposition biota than crusts with lichen and bryophyte species. The role of the biological soil crusts appears especially important in the large interspaces between plants, as these areas have limited input of organic matter. In addition, plant roots are continuously extracting nutrients from interspace soils, reducing their fertility over time. Biological soil crusts help maintain the fertility of these interspaces by contributing both carbon and nitrogen to the interspace areas, thus partially counteracting the tendency of nutrients and microorganisms to concentrate under shrubs.

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