Biol Fertil Soils (1989) 8:1–6

Biology and Fertility of Soils

Abiotic controls on the functional structure of soil food webs

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Summary. The hypothesis that the trophic structure of soil food webs changes as a result of the abiotic environment was examined by reviewing studies of soil biota. In dry soils with a water potential below −1.5 MPa, most bacteria, protozoans, and many species of nematodes are not active. These taxa persist in the soil in a state of anhydrobiosis. Because soil fungi grow at soil water potentials of −6.0 to −8.0 MPa, soil food webs in dry environments appear to be fungal-based and fungal grazers in dry environments appear to be predominantly fungiphagous mites. There is indirect evidence that some species of fungiphagous mites remain inactive in dry soils in a state of "cryptobiosis". In habitats where there is insufficient vegetative cover to shade and modify the soil surface, the functional soil food web consists of fungi and a few taxa of soil acari for extended periods of time.

Key words: Bacteria – Fungi – Protozoans – Nematodes – Mites – Water potential – "Cryptobiosis" – Anhydrobiosis – Trophic structure – Food web

Soil food webs are characterized by structural similarity in most environments. That general structure is one in which only a small fraction of the soil fauna is dependent upon primary producers such as soil algae (Fig. 1). Most of the soil food web is based on energy and nutrients in the detrital organic-matter pool used by bacteria and fungi (Hunt et al. 1987). Depending on soil characteristics such as porosity and clay content, populations of bacteria, yeasts, and fungi grow on the dead plant material. This microflora is grazed by a variety of herbivores such as protozoans (flagellates, amoebae, ciliates), nematodes and microarthropods (Acarina, Collembola, Psocoptera, and other insects), and these prey upon each other as well as serving as prey for a variety of larger predators like mesostigmatid mites (Hunt et al. 1987).

In moist, thermally neutral environments all components of this generalized food web are active and thus the trophic relationships are as complex as the taxonomic composition of the biota in a particular soil. This generalization is supported by the results of a one-season field experiment with irrigation near Uppsala, Sweden, in which there were changes in soil respiration and biomass of bacteria and fungi but no measurable effect on species of grazers in the soil food web (Schnürer et al. 1986). In less favorable environments, not all taxa of the generalized food web are active at all times. Walter et al. (1988) recognized the importance of abiotic controls on the functioning of soil food webs in short-grass prairie in suggesting that the ability of microarthropods to use moisture-dependent prey such as nematodes is important when modeling the dynamics of this system. This leads to the general hypothesis: The taxonomic composition, hence trophic structure, of the *active* components of soil food webs varies through time as a function mainly of soil water potential and soil temperature. In the light of this hypothesis we further hypothesize that abiotic controls on soil food webs should be most important in extreme hot and cold deserts and vary in importance in other ecosystems (Table 1).

Extending results of experimental studies to other geographical areas

When the tests of hypotheses have been derived from a limited number of studies in one or a few locations, the applicability of these data to other geographical areas may be questioned. Most of the data on which this review is based are from studies in the Chihuahuan Desert. However, it is proposed that the

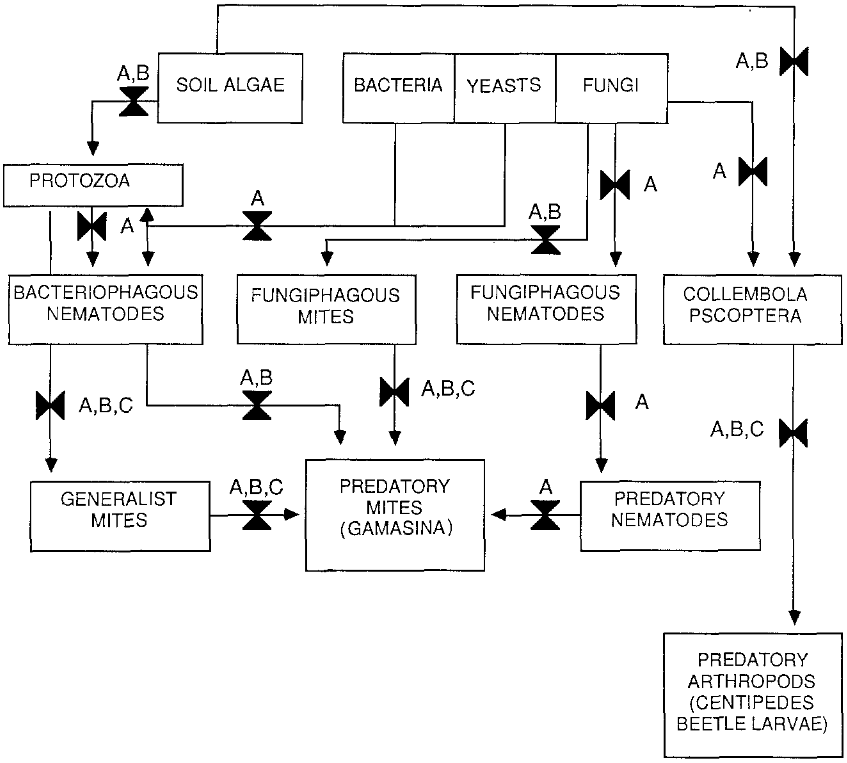

Fig. 1. The structure of a generalized food web indicating the abiotic controls of interactions among components of the food web. *A*, moisture control of activity; *B*, temperature control of activity; *C*, diurnal migration

Table 1. Hypothesized relative importance of abiotic controls on soil food webs in a variety of ecosystems. Index of importance: 1, unimportant; 10, most important. The index of importance is a relative numerical scale based on the intensity of solar radiation, temperature, duration of rainless periods, and extent of vegetative canopy and litter layer modifying soil microclimate

Moist, closed canopy forest	1
Forest gap	5
Clear-cut forest	7
Tall-grass prairie	5
Short-grass prairie	7
Savanna (tropical)	7
Chaparral	8
Hot desert	10
Cold desert	9
Tundra	3

data reviewed here are generally applicable to dryland ecosystems and that these results can be extended to other ecosystems. The soil biota of the warm dryland ecosystems share numerous taxa that are identical at the generic level and possibly even the same species (Wood 1971; Coineau and Massoud 1977; Coineau et al. 1978; Wallwork and Steinberger 1985; Steinberger et al. 1988). In studies comparing ecosystem processes in the Chihuahuan Desert in North America with those in the Negev Desert, Israel, we found a remarkable similarly in these processes and in the biota mediating the processes (Buyanovsky et al. 1982; Steinberger and Whitford 1988). Where comparative studies of physiological adaptations have been carried out with soil fauna from widely separated dryland areas, the same physiological responses have been documented (Greenslade 1981; Poinsot-Balaguer 1984). The data on microorganisms reviewed by Griffin (1972) were from studies on several continents, and hence should be reasonably general in their applicability. While it is possible that some taxa of the soil biota in some unstudied dryland region may have adaptations that would lead to different functional responses by the soil food web to abiotic constraints, until there is evidence of different responses the data reviewed here can be considered to be generally applicable.

Temperature. Temperatures that exceed the boundaries of the biokinetic zone for most organisms impose severe constraints on the functional structure of soil food webs. Temperatures greater than 40 °C occur regularly in surface soils and litter exposed to direct insolation in arid and semi-arid tropical and subtropical ecosystems. These high temperatures, which are accompanied by extremely dry conditions, preclude the activity of virtually all organisms (Whitford et al. 1981a; Freckman and Whitford, unpublished data, 1984). The effects of temperatures higher than 40 °C are considered later. In the polar regions, surface vegetation (mosses, etc.) and litter are frozen for much of the year. During the short periods of thaw, the soil biota includes representatives of taxa characteristic of more temperate systems (Chernov et al. 1977; Douce and Crossley 1977). Species of microarthropods in these extreme environments may exhibit cold-hardiness through a capacity for supercooling (Somme 1976–1977, 1978; Block 1981). These animals are thus allowed brief periods of activity when temperatures are above 0 °C and passively survive the intervening periods of temperatures below 0 °C. In polar and subpolar environments, water is usually available during periods of thaw. However, in some environments water availability may be reduced during a thaw, which may affect taxa that require water films in order to remain active. Drier microhabitats in the arctic were dominated by Acarina (Prostigmata and Cryptostigmata) while wetter sites were dominated by Collembola (Douce and Crossley 1977). There are insufficient data to establish a range of threshold conditions for polar soil food webs that would allow prediction of the functional structure of the webs under a variety of environmental conditions.

Water potential thresholds: Microorganisms

The detrital organic-matter pool, the soil microflora and the partially decomposed organic matter resulting from their metabolic activity are the base of soil food webs. Griffin (1972) reviewed the limited data on germination and growth of soil microflora over a range of matric potentials. Numerous fungi are capable of spore germination at soil water potentials between −10 MPa and −50 MPa. The latent period for spore germination apparently increases at lower water potentials. Growth of bacteria is generally limited to soil water potentials greater than −10 MPa (Griffin 1972) and most bacteria require intact water films for their growth. Schnürer et al. (1986) found there was no change in fungal biomass but a marked decrease in bacterial biomass during a 1-week period of soil drying. In addition, bacteria tend to be limited by the availability of suitable sources of energy (Schnürer 1986, exhibiting negligible respiration at soil water potentials below −1.5 Mpa (Griffin 1980). Many soil fungi are capable of relatively rapid growth in soil at −6.0 to −8.0 MPa. As soils dry there is rapid reduction in bacterial growth and biomass while fungi continue to grow (Parker et al. 1984). Therefore in seasonally dry or arid environments, soil food webs are primarily fungus-based, not based on soil bacteria except during the periods when soil water potentials are greater than −1.5 MPA.

Despite the limited data on the physiological attributes of most taxa of soil biota, and especially those of desert habitats, some generalizations can be made from experimental studies in which soil moisture and/or soil temperature were manipulated. One difficulty in interpreting field studies is the possibility that the migratory behavior of organisms within the soil column could affect the trophic structure of the food web (Metz 1971). Many field studies do not allow for a distinction between emigration from the soil core being examined and physiologically inactive organisms. However, in terms of the trophic relations within a food web at a given location, this distinction is unnecessary because the end result is the same, i.e., a change in the proportions of species in the food web.

Table 2. Effects of supplemental rainfall and surface litter quantity on population densities (number per 10 g soil) of soil protozoans in a desert soil 12 and 24 days after the initial watering (Parker et al. 1984)

Experimental conditions (litter/moisture)	Flagellates		Ciliates		Amoebae	
	12 days	24 days	12 days	24 days	12 days	24 days
0 g/wet	250	1 144	250	250	5 800	50 970
0 g/dry	590	1 004	350	360	2 200	20 350
150 g/wet	450	3 050	380	2 530	2 680	15 040
150 g/dry	710	5 150	260	250	4 470	18 070

Total populations 20% lower than in short-grass prairie

Water potential threshold: Protozoa

In experimental studies using simulated rainfall, marked effects were found on the proportions of the community of grazers active in the soil. Rainfall had little effect on the densities of ciliates but had marked effects on amoebae and flagellates which increased by an order of magnitude 24 days after the initiation of frequent watering (Table 2; Parker et al. 1984). The numerical responses of protozoans were not as important, however, as the percentage of the population in the inactive or cyst form. Parker et al. (1984) reported that at 0.5–2.8% soil water content all protozoans were encysted, at 8.5% soil moisture between 64% and 91% were active, and at 12% soil moisture 96% of the protozoans were active. Using the data in Parker et al. (1984) and water-extraction curves for these soils from Schlesinger et al. (1987), we calculated that 50% of the protozoan population was encysted at a soil water potential of −0.1 MPa, and that virtually the entire protozoan population was inactive at −0.4 MPa. Thus, although desert soils may harbor relatively high densities of protozoans, these populations are active for only a few days during the year.

Water potential threshold: Nematodes

Nematodes are grazers on protozoans, bacteria, yeasts, and fungi. Like protozoans, nematode activity may be severely restricted in dry soils because nematodes enter a state of anhydrobiosis when water is limited (Demeure et al. 1979; Demeure and Freckman 1981; Freckman 1982; Freckman et al. 1987). Basically, anhydrobiotic nematodes are desiccated worms that return to activity and can begin to breed as soon as there are free water films which re-hydrate the anhydrobionts. In a series of simulated rainfall experiments Freckman et al. (1987) found that continuously moist soil had a significant effect only on the phytophagous and omnivore-predator nematodes. Nematodes responded like the protozoans with respect to the percentage of the population that was anhydrobiotic at various soil water potentials. The soil water potential at which 50% of the population was anhydrobiotic was −0.4 MPa, with 99% of the population anhydrobiotic at between −3.0 and −5.0 MPa. Thus for both nematodes and protozoans, soil water potentials well above the permanent wilting point of −1.5 MPa will shift a large fraction of the population into an inactive state. Populations of nematodes may be active in surface litter layers for only a few hours after rain and for only 48–72 h in the soil following a summer rain event (Whitford et al. 1981 a).

Temperature and water potential effects: Microarthropods

Microarthropods have been extracted from desert soils with undetectable gravimetric soil water (Whitford et al. 1981). Diurnal patterns of abundance of various groups of microarthropods have also been documented. There is a virtual absence of active microarthropods in surface litter in the middle of the day, with the peak abundance in the coolest part of the day, i.e., 1–2 h after sunrise. Shortly before sunrise in the Chihuahuan Desert, surface litter may have up to 6% water by weight but by midday there is no detectable water (Whitford et al. 1981 a). In the upper 20 cm of soil, the abundance of active taxa varies through the day, with groups like tydeid mites exhibiting great variation while nanorchestids and oribatids exhibit no discernible patterns and little change throughout the day (Whitford et al. 1981 a).

In a recent study MacKay et al. (1986) used a combination of shading and irrigation to change soil temperature and soil water in order to examine the effects of the changes on microarthropods inhabiting litter accumulations. High soil moisture and lowered soil temperature had marked effects on the populations of fungiphagous and litter-feeding mites. The population densities of these mites increased 8–10 times, but there were virtually no changes in the densities of predatory mites. The combination of water and shade was no more effective than shade alone on some species like the small fungivore, *Tarsonemus* sp., whereas both shade and water were required to increase the densities of collembolans and psocopterans. Other mites, like the algal-feeding *Speleorchestes* sp., responded neither to shade nor to water.

Some of these patterns are best understood in relation to cryptobiotic behavior in various groups of microarthropods. Some taxa of microarthropods exhibit what may be referred to as "cryptobiosis", since we have no physiological characterization of the state. Cryptobiosis is literally "hidden life". It is used here to distinguish those organisms that are not extracted from soil unless the soil is wet. However, after soil samples have been extracted and the dry soil is rewetted, additional numbers of some taxa are obtained (Table 3). MacKay et al. (1987) interpreted increased numbers of a species in the soil under litter at midday as evidence of diurnal migration. Diurnal migration was found in a predator, *Spiniladella cronini*, and a generalist-algavore, *Speleorchestes* sp. However, the densities of some species that did not increase in the sublitter soil apparently exhibited some form of cryptobiosis (Table 3) and large numbers were extracted after rewetting.

Table 3. Comparisons of selected taxa of microarthropods extracted from soils that were wet after extraction and were incubated at 20 °C for 24 h then re-extracted (data from MacKay et al. 1987)

Taxa	Soil layer			
	0.5 cm		5–10 cm	
	Pre-wetting	Post-wetting	Pre-wetting	Post-wetting
Fungivores				
Siteroptes sp.	1.6 ± 2.3	18.0 ± 23.3	1.0 ± 1.4	6.2 ± 11.6
Tarsonemes sp.	12.0 ± 24.1	40.6 ± 70.6	0 ± 0	7.8 ± 15.8
Predators				
Cunaxa sp.	0 ± 0	0.8 ± 1.0	0 ± 0	0.8 ± 0.8
Spinibdella cronini	1.0 ± 0.7	0.6 ± 0.9	0.8 ± 0.8	0.2 ± 0.4

Values given are mean ± SD numbers per 500 g soil

Based on this review of data, it is clear that abiotic factors, especially temperature and soil water content, control the functional structure of soil food webs. The importance of the abiotic controls is magnified at the litter-soil interface where the thermal and hydric environment changes rapidly in a daily cycle. In arid and semi-arid ecosystems (deserts, grasslands, and savannas) and in forest gaps, clear-cuts, post-fire systems, etc., the soil surface with whatever litter layer exists is exposed to the drying and heating effects of direct sunlight. In closed-canopy systems the litter-soil interface environment is considerable moderated. Thus, depending upon the degree of aridity in the system, the active food web that is processing leaf litter at the soil surface may be limited to a few species of fungi and mites that are active for a few hours each day (Whitford et al. 1981a; Freckman et al. 1987; MacKay et al. 1987). We found no change in the percentage of anhydrobiotic nematodes in litter in the Chihuahuan Desert over the daily cycle of litter moisture from 0% to 6% by mass (Freckman and Whitford, unpublished data, 1984). Bacteria, protozoans, and nematodes are active in the subaquatic phase of the porosphere (Vannier 1987) which persists for only a few hours in litter on the soil surface in a desert (Whitford et al. 1981a).

In the soil, however, the subaquatic phase persists for a number of days following a rain event (Whitford et al. 1981a). The primary energy source for biota living within the soil is dead roots and rootlets. In ecosystems where abiotic controls of food webs are important (Table 1) soil organic-matter contents are low and the soil microarthropod fauna is dominated by prostigmatids (Seastedt 1984). These factors suggest that the soil food web functioning in the Chihuahuan Desert is a good model for the other open systems listed in Table 1. Even in forested ecosystems that are clear-cut, the soil microfauna of open environments are prostigmatid mites and decomposition rates are reduced, which suggests changes in the functional structure of those soil food webs (Seastedt and Crossley 1981; Whitford et al. 1981b; Blair and Crossley 1988).

Hunt et al. (1987) concluded that food webs in the short-grass steppe were similar to those in the northern Chihuahuan Desert. Thus the functional relationships of the soil food web model of Hunt et al. (1987) are applicable when soil water potentials remain below -0.4 MPa and soil temperatures remain below 30 °C. During the extended periods when the soil environment is beyond those boundaries, the functional soil food web will be largely reduced to a few species of fungi and a small group of fungiphagous prostigmatid mite species. The importance of the soil biota that are active in the edaphic state (Vannier 1987) of the soil (i.e. little free water, soil relative humidity close to 100%) is borne out by the findings of Parker et al. (1984) that fungiphagous mites, not nematodes or protozoans, were primarily responsible for N mineralization of decomposing roots in the Chihuahuan Desert. Thus models focusing on the functioning of soil food webs must incorporate the abiotic controls shown in Fig. 1 in order to examine the role of soil animals in C and N mineralization.

Acknowledgements This review is based on a symposium paper on soil food webs at the Ecological Society of America annual meeting, Columbus, Ohio, August 1987. This paper is a contribution of the Jornada Long Term Ecological Research Program supported by Grant BSR 8612106 from the U.S. National Science Foundation.

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Received August 4, 1988