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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

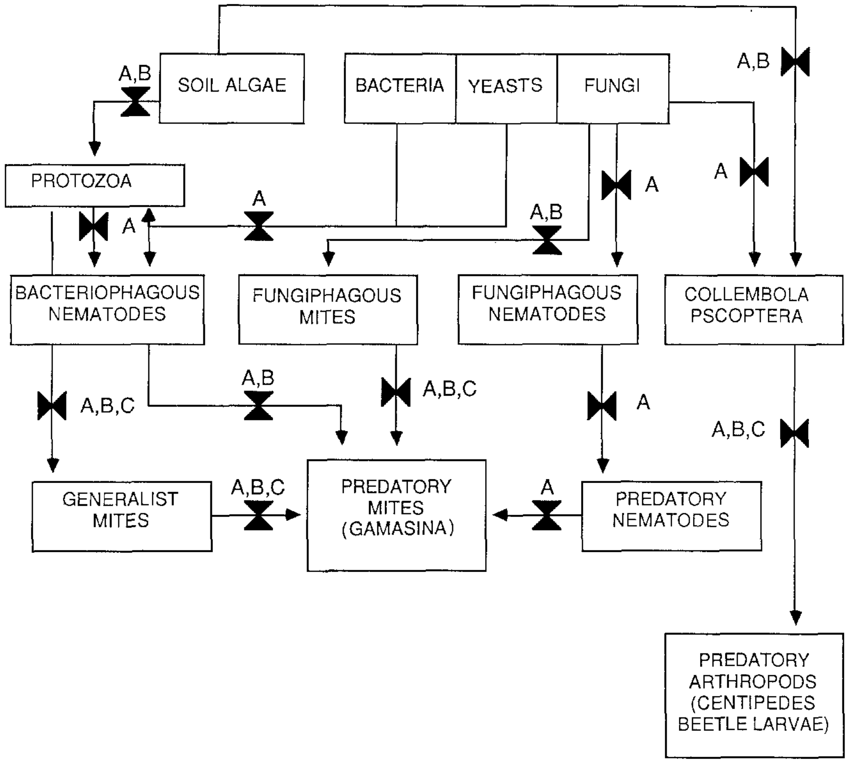

Fig. 1. The structure of a generalized food web indicating the abiotic controls of interactions among components of the food web. *A*, moisture control of activity; *B*, temperature control of activity; *C*, diurnal migration

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. 1981 a; 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