Belowground Food Webs in a Changing Climate

Chapter · September 2006

DOI: 10.1201/9781420003826.ch5

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5 Belowground Food Webs in a Changing Climate

Joseph C. Blankinship and Bruce A. Hungate

CONTENTS

5.1 INTRODUCTION

Amidst a network of tunnels and pores, soil organisms recycle carbon and nutrients. They mix plant litter and detritus, causing changes in soil structure that can ultimately influence the amount of water and oxygen available for plant roots. They are also eaten by aboveground predators, providing direct connections between below- and aboveground food webs. Root herbivory is very difficult to quantify, but likely just as important as leaf herbivory. As we gain an appreciation for the importance of mycorrhizal fungi, an appreciation of organisms that graze on these fungi seems to follow.

In spite of the importance of these activities in contributing to ecosystem functioning, soil organisms — and the feeding relationships between soil organisms collectively referred to as the *belowground food web* — have received much less attention than their aboveground counterparts. After all, it's dark down there. This makes wildlife viewing a bit problematic. Ecological processes at this microscale are difficult to mimic in the laboratory and difficult to monitor in the field, and sampling inevitably alters habitats. Belowground food webs have also received less attention because of their often overwhelming concentration of biodiversity and

complex feeding interactions among organisms resulting from the strong prevalence of omnivory. Life-history traits, pathogens, lateral gene transfer between microorganisms, and symbioses also introduce interesting possibilities of complicating our understanding of belowground food webs.

Climatic change experiments provide an important avenue for understanding belowground food webs. Anthropogenic climatic change is a perturbation through which we can investigate how organisms collectively influence soil resource availability, and whether the trophic structure and species composition of the food web modifies these influences. Adjustments may occur in the activity, abundance, diversity, and distribution of organisms in the soil profile, allowing the belowground community to tolerate novel conditions. Can a species adapted to cold Arctic tundra tolerate warmer summer temperatures and increased soil moisture due to the melting of permafrost? Can a drought-adapted species tolerate even longer droughts? Can a community take advantage of increased plant root production and exudation by harvesting more energy under elevated atmospheric CO_2? Changes at the level of individual species within food webs may, in some cases, have negligible effects of trophic interactions. In other cases, such changes may be important, altering belowground trophic structure and plant resource availability. Trophic interactions between belowground organisms determine the amount of energy available for carbon and nutrient cycling, litter mixing, and aboveground food webs. How will current rates of anthropogenic climatic change affect these trophic interactions?

5.2 CURRENT PARTICIPANTS AND MECHANISMS

Although most belowground food web analyses have been performed in intensively managed arable soils (Scheu 2002), it is expected that many of the same participants (organisms) and mechanisms (processes) operate in relatively unmanaged soils. For example, it is expected that soil structure has a similar influence on belowground food webs in both managed and unmanaged ecosystems, such that fine-textured soils provide greater physical protection for bacteria against protozoan grazing than coarse-textured soils (Rutherford and Juma 1992). Spatial heterogeneity in soil resources is assumed to influence all belowground food webs. Similarly, indirect effects mediated by plants, such as changes in microclimate and litter production, are expected to influence all belowground food webs. However, it is also expected that management practices and greater perturbation in agroecosystems have accumulated differences in soil structure, resource availability, and plant interactions that could significantly modify the activity, abundance, diversity, and distribution of organisms in the soil profile. In order to identify differences between intensively managed and relatively unmanaged ecosystems, we first need a basis for comparison.

Food web diagrams display trophic interactions between organisms in one of three forms (Scheu et al. 2002). In simplest form, a food web diagram displays *connectivity* between different species (e.g., a protozoan and a bacterium) or different feeding guilds (e.g., herbivores and carnivores). Connectivity food webs display who eats whom and nothing more. Improved understanding can be displayed in the second type of food web diagram, which includes *energy flow*. While connectivity diagrams indicate how energy is transferred between organisms, energy flow diagrams indicate

how much energy is transferred. This additional information can help identify the dominant pathways of energy transfer within a food web. The third and most detailed food web diagram includes *interaction strengths* between organisms. Interaction strength food webs display the per capita effect a predator exerts on its prey or vice versa. This form of food web diagram is truly functional and can be applied to field conditions in order to understand possible food web responses to perturbation. In a majority of natural ecosystems, our understanding of belowground food webs remains at the stage of connectivity diagrams.

The trophic structure of a food web depends on the abundance, distribution, and feeding preferences of individual organisms. In order to study trophic interactions between these organisms, ecologists organize individuals into populations of species, and species into feeding groups. A *feeding group* (or "guild") consists of populations that eat a similar substrate. For example, *detritivores* are a feeding group that eats the common substrate of detritus (unrecognizable dead plant and animal material). Likewise, *herbivores* eat live plant material, *bacterivores* eat bacteria, *fungivores* eat fungi, and *predators* eat live animals. The feeding group is the basal entity of any food web and ideally includes all species that perform a functionally equivalent role in the food web. When different species obtain their energy through the same number of feeding transfers from primary production, they belong to the same *trophic level.* Low trophic levels are closely connected to primary producers and eat organisms that have participated in a small number of feeding transfers. High trophic levels (or predators) eat organisms that have participated in a larger number of feeding transfers. *Trophic structure* refers to the distribution of biomass and energy in different trophic levels in a food web. Biomass distribution can take the form of an upright or inverted trophic pyramid depending on instantaneous rates of bottom-up and top-down forces. Energy distribution always forms an upright pyramid with more energy processed at lower trophic levels.

Species probably do not aggregate into discrete, homogeneous trophic levels (Polis and Strong 1996). In reality, omnivory, diets shifts, and spatial heterogeneity in resources blur the boundaries between discrete trophic levels. *Omnivores* (organisms that eat multiple types of substrates) complicate the concept of trophic levels. Omnivores are food generalists and cannot be placed into a single trophic level. Similarly, ontogenetic (e.g., age) and environmentally induced changes (e.g., wildfire) in the diet of species may confuse the concept of discrete trophic levels (Polis 1984). Spatial heterogeneity in soil structure and the distribution of populations means that just because two populations are in the same general location, feeding transfers are not necessarily occurring. For example, a bacterium may be able to escape predation by hiding in soil pores that are too small for protozoa to enter (Rutherford and Juma 1992). Rather than discrete levels, trophic structure is more accurately described as a continuum of feeding transfers or a "trophic spectrum" (Darnell 1961).

For some food webs, the collection of trophic transfers can be usefully organized into linear food chains. But such food chains likely oversimplify trophic dynamics in soil, where a web pattern more accurately reflects the complex connections between different trophic levels. Trophic systems are often described as either plant-based (live plant material) or detritus-based (i.e., dead plant and animal material), depending on what is viewed as the ultimate source of energy (after the sun!). In

reality, these two systems form one food web, as live plant material senesces and joins the detritus-based trophic system. Or a carnivore connects the two trophic systems by eating root herbivores in the plant-based system and detritivores (e.g., earthworms) in the detritus-based system.

While plant- and detritus-based trophic systems emphasize bottom–up effects (i.e., lower to higher trophic levels) of biomass and energy transfer within food webs, trophic cascades emphasize top–down effects (i.e., higher to lower trophic levels). Much like the overlapping boundaries and connections between trophic levels and food chains, bottom–up and top–down effects are intertwined and operate simultaneously in most food webs. A population may be limited by resource availability on one soil particle (i.e., bottom–up), predation on an adjacent soil particle (i.e., top–down), or by both on yet another soil particle (i.e., bottom–up and top–down forces can affect populations simultaneously). A *trophic cascade* occurs when changes in abundances at one trophic level alters abundances at a lower trophic level across more than one link in a food web (Pace et al. 1999). The green world hypothesis (Hairston et al. 1960) postulates strong top–down control in aboveground food webs. If a food chain has an odd number of trophic levels, the world is *green* because (in the case of a three-level system) predators reduce herbivore abundances, releasing plants from grazing pressure. If a food chain has an even number of trophic levels (for example, four), the world is *barren*, because secondary predators reduce abundances of primary predators, which then reduces predation on herbivores, and more plants are ultimately eaten. There is evidence that trophic cascades also occur in belowground food webs. For example, in a desert plant litter, the removal of predatory mites from a model system increased the abundance of bacterivorous nematodes, and decreased the abundance of bacteria (Santos et al., 1981). In this case, the presence or absence of the fourth trophic level cascaded down the food chain to affect the second trophic level. However, when applied to more complex field systems, there are reasons to believe that trophic cascades are less common belowground than aboveground (McLaren and Peterson 1994; Rypstra and Carter 1995). First, omnivory rates are probably higher belowground, which makes it rare for a predator species to significantly reduce abundances of one prey species before switching to a different prey species, among the wide array of soil biodiversity. Second, spatial heterogeneity in the soil profile may prevent trophic cascades by providing refugia for prey species. And third, trophic cascades may be absent because of high microbial turnover rates in detritus-based trophic systems. Detritivores are dominated by bacteria and fungi, which have high reproductive rates that may compensate for the effects of top–down grazing. For example, bacterial abundances can be unaffected by food chain length, and fungal abundances can actually be higher in the presence of predators (Mikola and Setälä 1998).

A *trophic transfer* refers to the feeding of one organism on another, or on detritus. These individual trophic transfers collectively form the food web. Although simple in theory, trophic transfers are difficult to quantify, especially in a spatially heterogeneous and opaque environment such as soil. A single trophic transfer consists of three components — consumption, assimilation, and production — that determine the amount of energy and biomass that are transferred during a feeding event. The more energy or biomass that is transferred, the higher the *trophic efficiency*.

Consumption efficiencies in belowground food webs are generally lower than in aboveground food webs because deterministic biological interactions, such as predation, are restricted to small spatial scales with inherent restrictions in perception and locomotion (Ekschmitt and Griffiths 1998). This is expected to reduce consumption efficiencies and lead to overestimations of the overall energy and biomass cycled through belowground food webs. On the other hand, detritivores have extremely high consumption efficiencies because they repeatedly ingest, defecate, and reingest the same detritus. Generally, about 1% of available energy consumed at one trophic level successfully contributes to production at the next highest trophic level (Colinvaux and Barnett 1979).

Size is often used to categorize soil organisms. Organisms with a body width less than 0.1 mm are referred to as microflora or microfauna. Larger organisms between 0.1 and 2 mm are referred to as mesofauna, and the largest organisms greater than 2 mm are macrofauna. Size can be a useful means of characterizing a belowground food web, much like characterizing soil texture by sieving. An organism must generally have a large enough mouth to physically consume another organism. A small organism may be able to escape predation by having exclusive access to small pores within a soil particle, and has a larger surface-to-volume ratio to absorb soluble substrates more rapidly. On the other hand, a larger organism has a smaller surface-to-volume ratio and is more resistant to desiccation. Therefore, the distribution of different body sizes in a belowground food web provides information about how trophic transfers occur in a particular soil.

Food web diagrams are models of what ecologists suspect — either through experiments or observations — to be happening. The two main types of food web models are those that are organism oriented or process oriented (Paustian 1994). *Organism-oriented food web models* describe the flow of matter or energy through different groups of organisms that are organized by taxonomy or trophic levels (Figure 5.1). *Process-oriented food web models* describe the activities mediating the transformations and storage of matter or energy (Figure 5.2).

With such a wide variety of organisms participating in the belowground food web — "if [only] we are willing to sweep our vision down from the world lined by the horizon to include the world an arm's length away" (Wilson 1994) — it is understandable that the subject of soil biodiversity is of considerable interest. Biological diversity within litter and soils may be orders of magnitude greater than aboveground diversity, but it has not been fully documented in any ecosystem (Adams and Wall 2000). Accurate descriptions of biodiversity are often hampered by extraction methods, choice of sampling depth, selective sorting, and insufficient taxonomic resolution (André et al. 2002). These factors introduce bias and tend to underestimate soil biodiversity. For example, the most commonly used extraction methods have efficiencies around 40%, and most studies focus on a selected half of microarthropods (mites or springtails) (André et al. 2002). Taxonomic resolution seems to be related to organism size, with smaller organisms, such as bacteria and fungi, being the least resolved.

One of the central motivations for studying biodiversity has been to identify connections with ecosystem function. Biodiversity may be important in maintaining current ecosystem function and in providing insurance for future ecosystem function

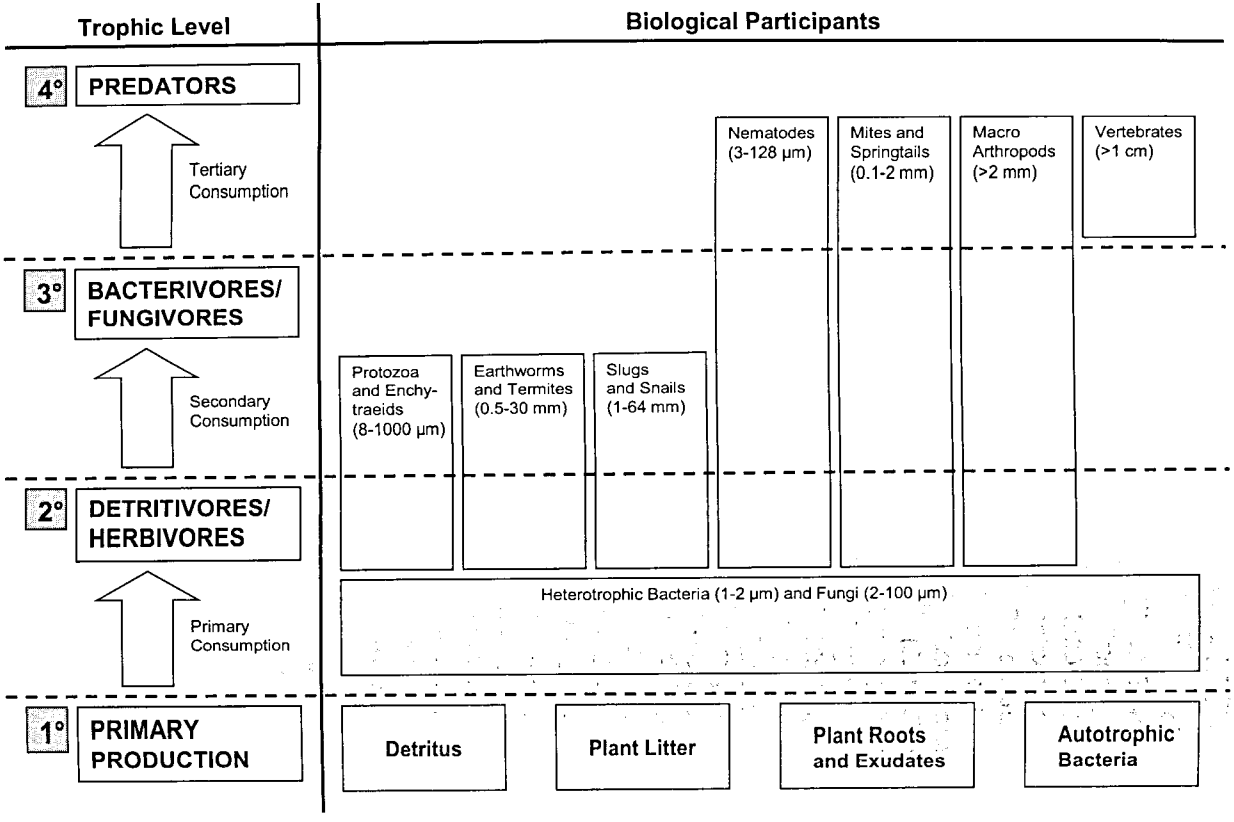

FIGURE 5.1 Organism-oriented belowground trophic level model. Size ranges refer to body widths.

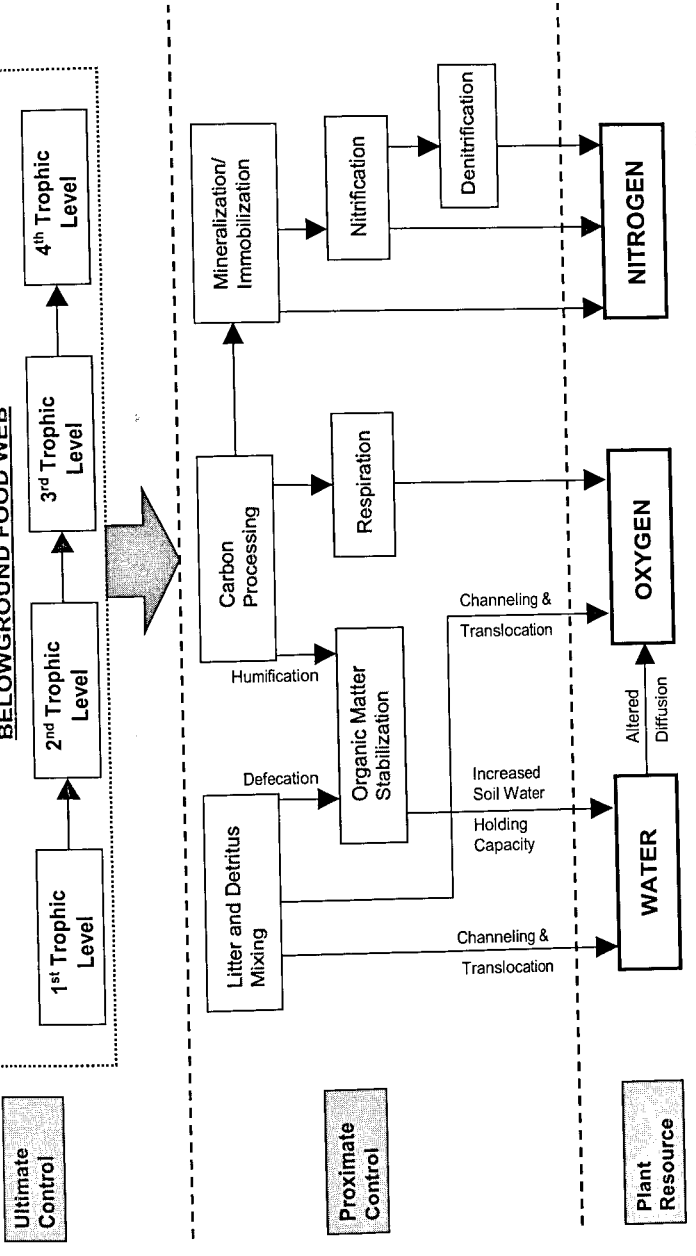

FIGURE 5.2 Process-oriented belowground food web model showing controls on soil water, oxygen, and nitrogen availability.

during perturbation (e.g., climatic change) (Bengtsson et al. 1997). *Functional redundancy* describes a hypothesis in ecology in which different species perform the same function in nature, so that changes in species diversity do not affect ecosystem function (Loreau 2004). In the case of food webs, *function* refers to the trophic level in which the organism participates. If two species are functionally redundant, then in theory, one species can go extinct without any changes in net energy transferred between trophic levels. In model systems, there is strong evidence that belowground trophic structure can affect ecosystem function. For example, in the absence of predatory mites, fungivorous nematodes decreased fungal biomass, which leads to a 40% reduction in decomposition rates (Santos et al. 1981). In more complex systems, however, functional redundancy within trophic levels is expected to compensate for any losses of individual species. Another study showed that the presence of bacterivorous nematodes on C and N mineralization seemed to vary with time (with an initial increase followed by a longer-term decrease) and litter quality (Bouwman et al. 1994). The third trophic level appeared to indirectly affect C mineralization via changes in bacterial activity, and directly affect N mineralization via digestion and excretion.

While taxonomic descriptions of biodiversity are one means of organizing soil organisms for food web analyses, trophic levels are the preferred categories by providing additional information about how different species function within the soil environment. Food web stability depends more on the number of trophic levels than on species richness (de Ruiter et al. 1998) and changes in trophic structure are known to affect ecosystem function (Chapin III et al. 1997). The functional importance of a soil organism is hypothesized to be inversely related to the trophic position of the organism (Laakso and Setälä 1999). In other words, feeding interactions are most likely to influence ecosystem-level processes when they occur near the bottom of the food web (Setälä 2002).

5.3 EFFECTS OF CLIMATIC CHANGE

Our knowledge of climatic change impacts on soil organisms lags behind other branches of terrestrial ecology (Ingram and Freckman 1998). As noted earlier, the entire belowground food web is rarely investigated at the same time, and rarely in relation to climatic change. Little is known about how changes in belowground trophic structure currently influence ecosystem function, and we cannot yet rule out the possibility that functional redundancy within trophic levels increases the resistance and resilience of belowground food webs to anthropogenic climatic change. Through studying belowground food webs in the context of climatic change, we hope to improve our predictions of future conditions. Climatic change experiments can also help improve our understanding of current interactions between community structure and activity. Specific mechanisms for changes in ecosystem processes may become clearer as we begin to identify the responses of individual trophic groups. Because the entire belowground food web has never been studied in a single climatic change experiment (the closest attempts include: Klironomos et al. 1996; Cotrufo and Gorissen 1997; Yeates et al. 1997; Lussenhop et al. 1998; Rillig et al. 1999b;

Taylor et al. 2004), it is necessary to combine the results of separate studies in order to understand how climatic change affects trophic structure.

Climatic change can affect soil carbon and nitrogen cycling (see Chapter 2), and the organisms in charge of the cycling are living within a complex food web. Thus, documenting food web responses may help us explain observed changes in soil biogeochemistry. Why is a particular ecosystem process not affected by climatic change? Through measuring the abundance, diversity, distribution, and efficiency of trophic transfers, we may be able to account for adjustments made by the belowground food web that allow the community to resist climatic change. If the process does change, is it simply because of changes in abiotic factors, or are changes in trophic interactions partly responsible? Are there any common global patterns of response to climatic change factors, or do results appear to be context dependent?

5.3.1 Direct vs. Indirect Effects of Climatic Change on Belowground Food Webs

Changes in precipitation, temperature, and atmospheric CO_2 can affect the belowground food web through both direct and indirect mechanisms (Table 5.1). Direct effects occur when a climatic change factor alters the abiotic environment and immediately elicits a physiological or behavioral response from soil organisms. For example, many organisms increase rates of respiration when temperature increases. Indirect effects occur when a climatic change factor (or two or three) interacts with an ecosystem property to affect soil organisms. For example, enhancing carbon input to soil can stimulate ammonium consumption by soil heterotrophs, thereby reducing ammonium availability to nitrifying bacteria. Accumulating experimental evidence indicates that effects of climatic change on soil food webs are primarily indirect responses to changes in vegetation (Wardle et al. 1998).

Altered abundance and annual distribution of precipitation can directly affect soil organisms through three types of mechanisms. First, altered precipitation may affect metabolic rates. Second, some soil organisms (such as protozoa and nematodes) depend on water films between soil particles for mobility. If precipitation increases, it will be easier for these organisms to move around and perhaps consume previously inaccessible resources. If precipitation decreases, less mobility is expected. And third, altered precipitation may change the vertical distribution of populations in the soil profile, allowing a population to move down in the soil profile where it is wetter (to escape desiccation) or up in the soil profile where it is drier (to escape drowning).

Altered precipitation can also have indirect effects. Repeated drying cycles have been shown to decrease soil aggregate stability (Soulides and Allison 1961; Young et al. 1998), indicating that reduced precipitation can indirectly affect organisms through changes in soil structure. Altered precipitation can indirectly affect soil aeration by influencing oxygen consumption rates through respiration, and positively affect plant root production and turnover (Norby and Jackson 2000), which represents a change in available surface area for microbial colonization and herbivory in the rhizosphere. Altered precipitation can also influence plant community composition (Lloret et al. 2004) and phenology, which may indirectly affect belowground communities through changes in litter abundance, quality, and host species.

TABLE 5.1
Direct and Indirect Effects of Climatic Change on Belowground Food Webs

	ALTERED PRECIPITATION	ELEVATED TEMPERATURE	ELEVATED CARBON DIOXIDE
DIRECT EFFECTS	Δ metabolism Δ mobility Δ vertical distribution of populations	Δ metabolism Δ vertical distribution of populations Δ latitudinal distribution of pops.	none
INDIRECT EFFECTS	Δ soil structure Δ O_2 availability Δ plant root production/turnover Δ plant species composition Δ length/timing of growing season	Δ soil moisture Δ soil structure Δ plant root production/turnover Δ plant species composition Δ length/timing of growing season	↑ plant litter and root production Δ plant species composition Δ soil structure ↑ soil moisture Δ length/timing of growing season

Elevated temperature can directly affect soil organisms by influencing metabolic rates or shifting spatial distributions. Changes in distribution may occur within the soil profile (e.g., as organisms seek deeper, cooler temperatures) or between latitudes and altitudes.

Warming can also have indirect effects. Elevated temperatures can alter soil water content, reducing it directly by enhancing evapotranspiration (Goyal 2004) or altering it indirectly through changes in plant senescence (e.g., Zavaleta et al. 2003a). Freeze-thaw cycles (which are expected to become more common during the winter in colder ecosystems and less common in warmer ecosystems) tend to break apart soil particles and decrease aggregate stability (Soulides and Allison 1961; Oztas and Fayetorbay 2003). This could indirectly affect soil organisms through changes in soil structure (e.g., porosity for diffusion of oxygen) and habitat stability. Like altered precipitation, elevated temperature can change plant root production and turnover, often increasing both (Pregitzer et al. 2000a), and change plant species composition. Experiments suggest that warming reduces plant species richness through the loss of less abundant species (Chapin III et al. 1995; Lloret et al. 2004), and it is unknown whether belowground biodiversity follows this change in aboveground biodiversity. And finally, growing seasons begin earlier, measured either through date of budbreak (Farnsworth et al. 1995; Norby et al. 2003) or snowmelt (Price and Waser 1998), when average conditions are warmer. In colder ecosystems, this provides a longer growing season for plants, and probably for higher belowground activity too.

Soil organisms are not expected to directly respond to elevated atmospheric CO_2 because soil CO_2 concentrations are already quite high and are unlikely to significantly change with atmospheric CO_2 (Lavelle et al. 1997). Plant responses to elevated CO_2, however, are likely to indirectly affect belowground food webs. First, elevated CO_2 has been shown to increase plant litter abundance (Owensby et al. 1999; Ferris et al. 2001; Dijkstra et al. 2002), plant root production (King et al. 1996; Owensby et al. 1999; Pregitzer et al. 2000b; Arnone et al. 2000), and plant root exudation (Paterson et al. 1997). Changes in root production and exudation are expected to directly affect belowground herbivores and microbes that can metabolize labile carbon substrates. Second, elevated CO_2 can affect plant species composition (Zavaleta et al. 2003b), which may modify belowground communities. Third, elevated CO_2 can influence soil structure by altering the size and stability of soil aggregates (Rillig et al. 1999a). Elevated CO_2 tends to increase mycorrhizal production of glomalin (Rillig et al. 1999a), a protein that is known to play a role in binding soil aggregates, but net effects on aggregate size (and soil porosity?) may be ecosystem specific. For example, in a sandstone grassland, elevated CO_2 increased aggregate size (Rillig et al. 1999a), while in a calcareous grassland, elevated CO_2 reduced aggregate size (Niklaus et al. 2003). Elevated CO_2 has been shown to increase soil moisture (Field et al. 1997; Niklaus et al. 1998; Hungate et al. 2002; Nelson et al. 2004), and influence the length and timing of the growing season (Badeck et al. 2004), which are certain to affect biological activity.

5.3.2 Effects of Altered Precipitation

A number of experiments have investigated effects of moisture on soil organisms (Table 5.2), but field manipulations of precipitation are rare. Some soils are treated in the field, others are treated in the laboratory, and others are treated through latitudinal or altitudinal transplantation (e.g., Sohlenius and Boström 1999). Some soils are treated for 24 hours (e.g., Kang et al. 2003) while others are treated for 13 years (e.g., Lindberg and Persson 2004). But at this point in our understanding, it would be premature to ignore any type of experimental design.

The second trophic level of the belowground food web tends to respond positively to elevated precipitation and negatively to reduced precipitation. Wetter conditions increase the abundance (Clarholm 1981) and biomass (Lundgren and Söderström 1983; Gallardo and Schlesinger 1995; Fierer and Schimel 2002) of bacteria and fungi. It is hypothesized that elevated precipitation favors bacterial-based food chains over fungal-based food chains because of differences in physiology (Wardle et al. 1998). Drier conditions have been shown to decrease bacterial and fungal biomass, but only in the more exposed surface litter layer (Salamanca et al. 2003), which is most vulnerable to drying. While individual bacterial cells may not be migrating deeper, this does illustrate that population distributions within a soil profile can be shifted by changes in precipitation. Repeated wetting events also tend to decrease bacterial and fungal biomass (Taylor et al. 2004), which is probably caused by cell death upon wetting and subsequent consumption by other detritivores. Altered microbial substrate utilization under elevated precipitation (Papatheodorou et al. 2004) indicates changes in metabolism, but there is no evidence of changes in microbial community structure (Wilkinson et al. 2002). Similarly, snail and slug community structure is unaffected by altered soil moisture (Sternberg 2000). Earthworms (Presley et al. 1996) and herbivorous nematodes (Todd et al. 1999) tend to prefer wetter conditions. Collectively, experiments provide evidence that elevated precipitation tends to increase production at the second trophic level, and reduced precipitation has the opposite effect.

The third trophic level tends to be unresponsive to elevated precipitation and to respond negatively to reduced precipitation. Despite increased production by the second trophic level under wetter conditions, there is little evidence of population explosions in the third trophic level. While protozoa do increase in abundance (Clarholm 1981), perhaps in response to a favored bacterial-based food web, there are no changes in abundances of enchytraeids (Lindberg et al. 2002), nematodes (Sohlenius and Wasilewska 1984; Todd et al. 1999; Sohlenius and Boström 1999; Papatheodorou et al. 2004), or microarthropods (Lindberg and Persson 2004). When a positive effect of elevated precipitation on nematodes was found, it only occurred in surface litter (Freckman et al. 1987), suggesting that surface nematodes are most likely to be limited (either via mobility or physiology) by water availability. Nematode diversity appears to be unaffected by wetter conditions (Sohlenius and Wasilewska 1984; Papatheodorou et al. 2004), and microarthropod diversity can be positively affected (Tsiafouli et al. 2005) or unaffected (Lindberg and Persson 2004). The third trophic level tends to be more responsive to reduced precipitation. In most cases, drier conditions decrease the biomass of organisms in the third trophic level. For example, drying

TABLE 5.2
Effects of Altered Precipitation on Belowground Trophic Structure

Trophic Level	Ecosystem Type	Type of Manipulation	Duration of Manipulation	Results	Reference
II. Detritivores/Herbivores	warm desert	wetting	10 days	increase in microbial biomass-N	Gallardo and Schlesinger, 1995
	boreal forest	wetting	17 days	increase in abundance of bacteria	Clarholm, 1981
	boreal forest	*ambient precipitation*	2 years	increase in abundance of bacteria with increase in organic soil water content, no change in abundance of bacteria in mineral soil	Lundgren and Söderström, 1983
	grassland	wetting	6 months	altered microbial substrate utilization	Papatheodorou et al., 2004
	coniferous forest	wetting	4 months	no change in microbial community structure using PLFA	Wilkinson et al., 2002
	deciduous forest	drying	1 year	no change in microbial biomass	Salamanca et al., 2003
	grassland	drying-rewetting *laboratory incubation*	10 days	decrease in microbial biomass-C with rewetting	Kieft et al., 1987
	grassland, oak woodland	drying-rewetting *laboratory incubation*	2 months	increase in microbial biomass with increased drying-rewetting frequency	Fierer and Schimel, 2002
	coniferous forest	wetting *constant vs. fluctuating*	5 months	decrease in microbial biomass with fluctuating irrigation	Taylor et al., 2004
	grassland	wetting	4 years	increase in abundance of herbivorous nematodes	Todd et al., 1999
	wetland	drying and wetting *laboratory incubation*	1 year	increase in survivorship of earthworms at intermediate soil water contents, increase in fecundity of earthworms at high soil water contents	Presley et al., 1996
	grassland	drying and wetting	2 years	no change in species composition of slugs and snails	Sternberg, 2000
	deciduous forest	drying and wetting *laboratory incubation*	24 hours	decrease in soil respiration with extreme drying and wetting	Kang et al., 2003
	grassland	drying and wetting *laboratory incubation*	16 days	decrease in soil respiration with drying	Fierer et al., 2003
	deciduous forest	drying and wetting *laboratory incubation*	4 months	no change in soil respiration	Zak et al., 1999
	polar tundra, taiga	drying-rewetting *laboratory incubation*	24 hours	decrease in soil respiration with drying, increase in respiration with rewetting	Gulledge and Schimel, 1998
	grassland, oak woodland	drying-rewetting *laboratory incubation*	2 months	increase in soil respiration with increased drying-rewetting frequency in grassland, decrease in soil respiration with increased drying-rewetting frequency in oak woodland	Fierer and Schimel, 2002

TABLE 5.2 (CONTINUED)
Effects of Altered Precipitation on Belowground Trophic Structure

Trophic Level	Ecosystem Type	Type of Manipulation	Duration of Manipulation	Results	Reference
III. Bacterivores/Fungivores	boreal forest	wetting	17 days	increase in abundance of amoebae	Clarholm, 1981
	boreal forest	drying and wetting	8 and 10 years	decrease in abundance of enchytraeids with drying	Lindberg et al., 2002
	grassland	wetting	6 months	no change in abundance or species diversity of bacterivorous nematodes	Papatheodorou et al., 2004
	warm desert	wetting	1 year	no change in abundance of nematodes in detritus, increase in abundance in litter	Freckman et al., 1987
	grassland	wetting	4 years	no change or decrease in abundance of microbivorous nematodes	Todd et al., 1999
	polar tundra	drying and wetting *transplantation*	1 year	no change in abundance of nematodes	Sohlenius and Boström, 1999
	boreal forest	wetting	8 years	no change in abundance or species dominance of nematodes, increase in vertical distribution of nematodes upwards into litter	Sohlenius and Wasilewska, 1984
	grassland	drying and wetting	4 months	decrease in abundance of nematodes with both drying and wetting	Bakonyi and Nagy, 2000
	coniferous forest	wetting *constant vs. fluctuating*	5 months	decrease in abundance of nematodes with fluctuating irrigation	Taylor et al., 2004
	polar tundra	wetting	4 years	increase in abundance of mites and springtails	Convey et al., 2002
	deciduous forest	wetting	6 months	no change in abundance of springtails	Ferguson and Joly, 2002
	boreal forest	wetting	13 years	no change in abundance or species composition of mites and springtails	Lindberg and Persson, 2004
	coniferous forest	wetting *constant vs. fluctuating*	5 months	no change in abundance of mites or springtails	Taylor et al., 2004
	polar tundra	wetting	1 year	decrease in abundance of mites and springtails with thicker winter ice layer	Coulson et al., 2000
	coniferous forest	drying	6 years	springtails recovered faster to drought than mites	Lindberg and Bengtsson, 2005
	coniferous forest	drying and wetting	4 months	decrease in species richness of mites and springtails with drying increase in species richness of mites and springtails with wetting decrease in species richness of mites and springtails with decreasing wetting frequency	Tsiafouli et al., 2005
	boreal forest	drying and wetting	8 and 10 years	decrease in abundance of mites and springtails with drying decrease in diversity of mites with drying, increase in diversity of mites with wetting	Lindberg et al., 2002
IV. Carnivores	deciduous forest	wetting	6 months	no change in growth rate of predacious mites	Ferguson and Joly, 2002
	boreal forest	wetting	13 years	no change in abundance of predatory macroarthropods	Lindberg and Persson, 2004
	boreal forest	drying and wetting	8 and 10 years	decrease in abundance of macroarthropods with drying	Lindberg et al., 2002

decreases abundances of enchytraeids (Lindberg et al. 2002), nematodes (Bakonyi and Nagy 2000), and microarthropods (Lindberg et al. 2002). In the case of enchytraeids, this response is consistent with the fact that they have no special protection mechanisms against evaporation (Didden 1993). There is also evidence that microarthropod diversity decreases under reduced precipitation (Lindberg et al. 2002; Tsiafouli et al. 2005), perhaps because some species are better adapted to drier conditions. Like the second trophic level, the third trophic level appears to be negatively affected by reduced precipitation, suggesting that drier conditions may cause bottom–up resource limitation for higher trophic levels. More importantly, drier conditions can directly affect soil habitat quality (e.g., water potential and water film thickness), independently reducing biological metabolism and mobility at each trophic level.

Responses of fourth trophic level participants to climatic change are rarely studied. After more than a decade of treatments in a boreal forest, predatory macroarthropods responded negatively to drier conditions and showed no response to wetter conditions (Lindberg et al. 2002; Lindberg and Persson 2004). This pattern of response is similar to the third trophic level. Over the range of experiments conducted to date, soil organisms at all trophic levels appear to be more sensitive to reduced precipitation than elevated precipitation. Only the hardiest species survive, as demonstrated by the reduced abundance and diversity of soil organisms in the world's deserts (Wall and Virginia 1999). It should also be noted that most field studies simulate reductions in precipitation of 25 to 100%, which are more extreme than the 15 to 20% reductions predicted in some areas during the next century (Intergovernmental Panel on Climate Change [IPCC] 2001). Therefore, treatments tend to overestimate the effects of reduced precipitation. Rather, some experiments may be more useful in understanding responses to extreme drought events, which are expected to become more common in the future.

5.3.3 Effects of Elevated Temperature

Predicted magnitudes of global warming are unlikely to have large direct effects on the biomass or community structure of broad taxonomic groups of soil organisms (Wardle et al. 1998), except at the boundaries of a specie's tolerance range. *Tolerance range* (which may also be applied to soil moisture) describes the extent to which a species can grow and reproduce in different climates and survive through extreme weather events. If temperatures are above the upper limit of an organism's tolerance range, enzymes may be denatured by extreme temperatures. Alternatively, warming in colder ecosystems may release organisms from temperature limitation. Environmental tolerance ranges of soil organisms are rare in the literature, and knowledge of this physiological trait may help soil ecologists explain changes in trophic structure by climatic change, and help agriculturists manage these changes in temperature- or water-stressed croplands.

While larger manipulations of temperature in the laboratory tend to decrease microbial biomass (Joergensen et al. 1990; Grisi et al. 1998; Cole et al. 2002; Jonasson et al. 2004) (Table 5.3), the few longer-term field manipulations of warming either show an increase (Ruess et al. 1999) or no effect (Bardgett et al. 1999). Fungi

TABLE 5.3
Effects of Elevated Temperature on Belowground Trophic Structure

Trophic Level	Ecosystem Type	Type of Manipulation	Duration of Manipulation	Results	Reference
II. Detritivores/Herbivores	grassland, tropical forest	*laboratory incubation* (15 and 35°C)	5 months	decrease in microbial biomass with increase in temperature	Grisi et al., 1998
	subarctic heathland	*laboratory incubation* (10 and 12°C)	6 months	decrease in microbial biomass-C and -N with increase in temperature	Jonasson et al., 2004
	grassland	*laboratory incubation* (15-35°C)	8 months	decrease in microbial biomass with increase in temperature, decrease in turnover time of microbial biomass with increase in temperature	Joergensen et al., 1990
	peatland	*laboratory incubation* (12-18°C)	2 months	decrease in microbial biomass with increase in temperature	Cole et al., 2002
	grassland	*laboratory incubation* (0-25°C)	23 days	no change in microbial biomass	Contin et al., 2000
	mesocosm (weedy field)	+ 2°C	9 months	no change in microbial biomass	Bardgett et al., 1999
	coniferous forest	*laboratory incubation* (0-45°C)	2 days	increase in ratio of bacterial to fungal growth rates at higher temperatures	Pietikainen et al., 2005
	subarctic heathland	+ 0.4-2°C	5 years	no change in microbial immobilization of C, N, or P	Jonasson et al., 1999
	subarctic heathland	+ 0.9-2°C	6 years	increase in microbial biomass-C, increase in active fungal biomass	Ruess et al., 1999
	deciduous forest	*laboratory incubation* (5-25°C)	4 months	altered microbial community composition using PLFA and LPS-OHFA	Zogg et al., 1997
	grassland	+ 1°C	1 year	increase in arbuscular mycorrhizal fungi hyphal length and colonization	Rillig et al., 2002
	grassland	+ 3°C	1 year	no change in arbuscular mycorrhizal fungi colonization	Heinemeyer et al., 2003
	wetland	*laboratory incubation* (15-28°C)	1 year	increase in survivorship of earthworms at intermediate temperatures, increase in fecundity of earthworms at intermediate temperatures	Presley et al., 1996
	N/A	*laboratory incubation* (12-35°C)	3 months	increase in growth rate of earthworms with increase in temperature	Viljoen and Reinecke, 1992
	deciduous forest	*laboratory incubation* constant vs. fluctuating T	1 year	decrease in earthworm cocoon production under fluctuating temperature	Kostecka and Butt, 2001
	deciduous forest	*laboratory incubation* constant vs. fluctuating T	4 months	decrease in earthworm mortality and cocoon production under fluctuating temperature	Uvarov, 1993
	grassland	+ 3°C	2 years	increase in abundance and activity of snails and slugs, no change in species composition of snails and slugs	Sternberg, 2000
	deciduous forest	*laboratory incubation* (5-25°C)	1 day	increase in soil respiration with increase in temperature	Kang et al., 2003
	grassland	*laboratory incubation* (10-35°C)	16 days	increase in soil respiration with increase in temperature	Fierer et al., 2003
	deciduous forest	*laboratory incubation* (5-25°C)	4 months	increase in soil respiration with increase in temperature	Zogg et al., 1997
	polar tundra	*laboratory incubation* (4.3 and 9.6°C)	5 months	increase in soil respiration, increase in litter decomposition rate (mass loss)	Hobbie, 1996
	deciduous forest	*laboratory incubation* (5-25°C)	4 months	no change in soil respiration	Zak et al., 1999
	polar tundra, taiga	*laboratory incubation* (freeze-thaw cycles)	5 days	increase in soil respiration	Schimel and Clein, 1996
	boreal forest	*laboratory incubation* (freeze-thaw cycles)	1 month	no change in soil respiration	Sulkava and Huhta, 2003

TABLE 5.3 (CONTINUED)
Effects of Elevated Temperature on Belowground Trophic Structure

Trophic Level	Ecosystem Type	Type of Manipulation	Duration of Manipulation	Results	Reference
III. Bacterivores/Fungivores	peatland	*laboratory incubation* (12-18°C)	2 months	decrease in abundance of enchytraeids with increase in temperature	Cole et al., 2002
	polar tundra	+ 2°C	3 months	increase in abundance of enchytraeids	Briones et al., 1997
	boreal forest	*laboratory incubation* (freeze-thaw cycles)	1 month	increase in abundance of enchytraeids	Sulkava and Huhta, 2003
	coniferous forest	+ 2-4°C	6 years	no change in abundance of enchytraeids	Haimi et al., 2005
	polar tundra	+ 2.2°C	1 year	increase in abundance of nematodes, especially microbivorous nematodes	Convey and Wynn-Williams, 2002
	alpine tundra, subalpine forest	*slope aspect* (+ 2.2°C)	1 year	increase in abundance of nematodes on south-facing slopes (N Hemisphere)	Hoschitz and Kaufmann, 2004
	subarctic heathland	+ 0.9-2°C	6 years	increase in abundance of nematodes, decrease in diversity of nematodes	Ruess et al., 1999
	N/A	*laboratory incubation* (15 and 23°C)	2 months	increase in growth and fertility rate of a nematode species with increase in temperature	Popovici, 1973
	grassland	+ 6-9°C	4 months	no change in abundance of nematodes, decrease in diversity of nematodes	Bakonyi and Nagy, 2000
	N/A	*laboratory incubation* (5-30°C)	6 days	no change in nematode respiration, increase in movement of nematodes with increase in temperature	Dusenbery et al., 1978
	polar tundra	*transplantation* mean annual T between -0.7 and +7.9°C	1 year	decrease in abundance of nematodes with increase in mean annual temperature	Sohlenius and Boström, 1999
	grassland	*laboratory incubation* (5-40°C)	1 month	decrease in abundance of bacterivorous nematodes at extreme low and high temperatures, optimal growth temperature different for different species	Anderson and Coleman, 1982
	N/A	*laboratory incubation* (10-35°C)	1.5 months	decrease in generation time of fungivorous nematodes with increase in temperature	Pillai and Taylor, 1967
	boreal forest	*laboratory incubation* (freeze-thaw cycles)	1 month	increase in abundance of microarthropods	Sulkava and Huhta, 2003
	polar tundra	+ 2.2°C	8 years	increase in abundance of mites and springtails, increase in proportion of small individuals	Kennedy, 1994
	polar semi-desert, heathland	10% increase in summer heat budget	3 years	no change in abundance of mites or springtails in tundra heath, increase in abundance of springtails in polar semi-desert	Coulson et al., 1996
	polar tundra	*laboratory incubations* (freeze-thaw cycles)	3 months	no change in abundance of mites or springtails	Sjursen et al., 2005
	polar tundra	30% increase in time above 0°C	2.25 years	no change in abundance of mites or springtails	Sinclair, 2002
	coniferous forest	+ 2-4°C	6 years	no change in abundance of oribatid mites, decrease in abundance of acaridid mites	Haimi et al., 2005
	polar tundra	*laboratory incubation* (2-12°C)	10 months	increase in mortality of mites with increase in temperature, increase in growth rate and molting rate of mites with increase in temperature	Convey, 1994
	polar tundra	+ 0.4°C	4 years	decrease in abundance of microarthropods (especially springtails)	Convey et al., 2002
	subalpine meadow	+ 1°C	2.5 years	increase in mesofaunal biomass and diversity during cool wet summer, decrease in mesofaunal biomass and diversity during warmer drier summer	Harte et al., 1996
IV. Carnivores	N/A	N/A	N/A	N/A	N/A

tend to show a positive response to warming (Ruess et al. 1999; Rillig et al. 2002), perhaps due to their close association with increased root production. Increased turnover rates of microbial biomass (Joergensen et al. 1990) and altered microbial community composition (Zogg et al. 1997) have also been found at elevated temperatures. Warming tends to increase soil respiration (Hobbie 1996; Zogg et al. 1997; Fierer et al. 2003; Kang et al. 2003), which indicates that soil organisms metabolize carbon at faster rates. This is consistent with increased microbial turnover rates and decreased microbial biomass. Warming also tends to increase growth rates of earthworms (Viljoen and Reinecke 1992), and increase the abundance and activity of slugs and snails (Sternberg 2000). While laboratory experiments tend to show a negative effect of warming on the second trophic level, field experiments show no effect or a positive effect. This contradiction represents an area for future research. Is 2 to 3°C warming during the next century enough to cause long-term changes in bacterial and fungal metabolic rates, or are moisture, nutrient availability, and litter quality more important controls? Responses may depend on ecosystem-specific changes in soil moisture by warming. For the time being, it is appropriate to accept the hypothesis that predicted magnitudes of warming will only have small effects on production at the second trophic level.

The third trophic level tends to be positively affected by warming. Enchytraeids, which are most important in high latitude ecosystems, can respond positively to warming in the field (Briones et al. 1997) and to freeze–thaw cycles in the laboratory (Sulkava and Huhta 2003), but effects can also be absent (Haimi et al. 2005) or negative (Cole et al. 2002). Temperature is expected to influence the species composition and population density of enchytraeids, but probably not their presence or absence, as there seem to be species adapted to most climates (Didden 1993). Warming increases nematode abundances, both in field manipulations (Ruess et al. 1999) and along environmental gradients (e.g., north- to south-facing slopes) (Hoschitz and Kaufmann 2004). Microbivorous nematodes (i.e., nematodes that eat bacteria and fungi) seem especially favored under warmer conditions (Convey and Wynn-Williams 2002). This result is consistent with the higher microbial turnover rates and lower microbial biomass. Warming also tends to decrease nematode diversity (Ruess et al. 1999; Bakonyi and Nagy 2000), increase nematode growth and fertility rates (Popovici 1973; Pillai and Taylor 1967) and increase nematode mobility (Dusenbery et al. 1978). If nematode diversity decreases, bacterivorous and fungivorous nematodes are probably the ones taking advantage of warmer conditions, and represent another example of how climatic change can modify belowground trophic structure. Responses to warming are less consistent among microarthropods. In some cases, warming increases microarthropod abundances (Kennedy 1994; Coulson et al. 1996); in other cases, warming decreases microarthropod abundances (Convey et al. 2002; Haimi et al. 2005) or has no effect (Coulson et al. 1996; Sinclair 2002; Haimi et al. 2005; Sjursen et al. 2005). This variability may be a result of interannual variation. In a subalpine meadow, experimental warming increased mesofaunal biomass during a cool wet summer, but decreased mesofaunal biomass during a warm dry summer (Harte et al. 1996). This suggests that precipitation may be more important than temperature in controlling abundances of soil fauna, and is consistent with the strong negative effects of drought described earlier.

Soil predators in the fourth trophic level are rarely investigated in warming experiments, and represent a wide open area for future research. However, it should also be noted that some of the experiments presented in the third trophic level can also apply to the fourth trophic level. Some nematodes and microarthropods also eat other soil animals. Because most studies do not differentiate between bacterivores, fungivores, and predators, it is difficult to identify exactly what changes in abundances mean in terms of trophic structure. In general, changes in abundances of fourth trophic level participants are expected to positively track changes in the third trophic level, but it is not yet known whether increases in third trophic level production by warming increases production at higher trophic levels.

5.3.4 Effects of Elevated Atmospheric Carbon Dioxide

Carbon dioxide (CO_2) enrichment experiments are numerous compared to precipitation and warming experiments, and range in scale from laboratory mesocosms to field treatments surrounding forests (Table 5.4). Fortunately, soil organisms are often studied in these experiments, with a similar pattern of focus as those found in precipitation and warming experiments: Most studies pay attention to the second trophic level, fewer studies pay attention to the third trophic level, and almost nobody pays attention to the fourth trophic level.

In most studies, second trophic level participants do not show a response to elevated CO_2. For example, no effects of elevated CO_2 were found on bacterial abundances (O'Neill et al. 1987; Klironomos et al. 1996; Schortemeyer et al. 1996; Rillig et al. 1997; Treonis and Lussenhop 1997; Rillig et al. 1999b; Schortemeyer et al. 2000) or microbial biomass (Hungate et al. 1997; Jones et al. 1998; Lussenhop et al. 1998; Schortemeyer et al. 2000; Zak et al. 2000; Niklaus et al. 2003; Sonnemann and Wolters, 2005). When effects are found, the response tends to be positive (Zak et al. 1993; Marilley et al. 1999; Insam et al. 1999; Sonnemann and Wolters 2005), especially in the rhizosphere where C exudation occurs (Cotrufo and Gorissen 1997; Jones et al. 1998). Microbial immobilization of C and N tends to increase under elevated CO_2 (Berntson and Bazzaz 1997; Hungate et al. 1997; Niklaus 1998; Hungate et al. 1999; Williams et al. 2000), but net mineralization has also been observed (e.g., Zak et al. 1993). Mycorrhizal fungi, plant symbionts that can be ambiguously placed in the second trophic level, seem to take the greatest advantage of increased root C exudation under elevated CO_2, as indicated by increased root colonization (Godbold et al. 1997; Kasurinen et al. 2005) and hyphal length (Klironomos et al. 1996; Klironomos et al. 1997; Runion et al. 1997; Sanders et al. 1998; Rillig et al. 1999b). Nonmycorrhizal fungi tend to be less affected (Klironomos et al. 1996) or negatively affected (Klironomos et al. 1997), probably reflecting their greater distance from the root source of C exudation. Organisms that are closely associated with roots and root exudates (e.g., mycorrhizal fungi and rhizospheric bacteria) seem to be especially responsive to the carbon pulse from plants at the onset of CO_2 exposure, but effects can disappear over time. Sometimes microbial diversity (Mayr et al. 1999; Phillips et al. 2002) and activity (Rillig et al. 1997; Mayr et al. 1999; Schortemeyer et al. 2000) change under elevated CO_2, while other times structure (Jones et al. 1998; Insam et al. 1999; Bruce et al. 2000; Niklaus et

TABLE 5.4
Effects of Elevated Atmospheric CO_2 on Belowground Trophic Structure

Trophic Level	Ecosystem Type	Magnitude of Manipulation *as compared to ambient reference of 370 ppm*	Duration of Manipulation	Results	Reference
II. Detritivores/Herbivores	mesocosm (deciduous)	+35 Pa (partial pressure)	5 months	no change in microbial biomass in rhizosphere	Lussenhop et al., 1998
	mesocosm (weedy field)	+200 ppm	9 months	no change in microbial biomass	Jones et al., 1998
	grassland	+360 ppm	1 year	no change in microbial biomass	Hungate et al., 1997
	scrub oak woodland	+390 ppm	2 years	no change in microbial biomass in bulk soil	Schortemeyer et al., 2000
	mesocosm (deciduous)	+35 Pa	2.5 years	no change in microbial biomass	Zak et al., 2000
	grassland	+230 ppm	6 years	no change in microbial biomass	Niklaus et al., 2003
	mesocosm (grassland)	+330 ppm	2 months	increase in microbial biomass in rhizosphere	Cotrufo and Gorissen, 1997
	mesocosm (deciduous)	+322 ppm	5 months	increase in microbial biomass C in rhizosphere and bulk soil	Zak et al., 1993
	mesocosm (herbaceous)	+330 ppm	1 month	no change in abundance of bacteria	Treonis and Lussenhop, 1997
	mesocosm (sagebrush)	+330 ppm	3 months	no change in abundance of bacteria	Klironomos et al., 1996
	mesocosm (woody shrub)	+380 ppm	4 months	no change in abundance of bacteria in rhizosphere	Rillig et al., 1997
	mesocosm (deciduous)	+320 ppm	6 months	no change in abundance of bacteria in rhizosphere	O'Neill et al., 1987
	mesocosm (grassland)	+230 ppm	1.5 years	no change in abundance or biomass of bacteria in rhizosphere	Schortemeyer et al., 1996
	scrub oak woodland	+390 ppm	2 years	no change in abundance of bacteria in rhizosphere	Schortemeyer et al., 2000
	grassland	+74 ppm	3 years	increase in bacterial biomass	Sonnemann and Wolters, 2005
	grassland	+330 ppm	6 years	no change in abundance of bacteria	Rillig et al., 1999b
	mesocosm (grassland)	+35 Pa	3 months	increase in abundance of bacteria in rhizosphere	Marilley et al., 1999
	mesocosm (tropical)	+240 ppm	1.5 years	increase in abundance of bacteria	Insam et al., 1999
	mesocosm (weedy field)	+200 ppm	9 months	increase in abundance of saprophagous fungi	Jones et al., 1998
	mesocosm (deciduous/coniferous)	+330 ppm	8 months	increase in ectomycorrhizal colonization	Godbold et al., 1997
	mesocosm (grassland)	+230 ppm	5 months	increase in length of arbuscular mycorrhizal fungi	Sanders et al., 1998
	mesocosm (deciduous)	+350 ppm	3 years	increase in mycorrhizal fungi infection rate no change in ratio of fungi to bacteria	Kasurinen et al., 2005
	grassland	+74 ppm	3 years	no change in fungal biomass	Sonnemann and Wolters, 2005
	grassland	+330 ppm	6 years	increase in total fungal hyphal length	Rillig et al., 1999b
	mesocosm (coniferous)	+350 ppm	1.6 years	increase in density of ectomycorrhizal fungi	Runion et al., 1997
	mesocosm (deciduous)	+330 ppm	1.2 years	increase in hyphal length of arbuscular mycorrhizal fungi, decrease in hyphal length of non-mycorrhizal fungi	Klironomos et al., 1997
	grassland	+190 ppm	3 years	no change in arbuscular mycorrhizal fungal spore production	Wolf et al., 2003
	mesocosm (sagebrush)	+330 ppm	3 months	no change in abundance of non-mycorrhizal fungi, increase in abundance of arbuscular mycorrhizal fungi	Klironomos et al., 1996
	mesocosm (grassland)	+350 ppm	4 months	increase, no change, or decrease in arbuscular mycorrhizal fungi depending on plant species	Rillig et al., 1998
	mesocosm (weedy field)	+200 ppm	9 months	no change in bacterial community composition using DNA profiles	Jones et al., 1998
	mesocosm (annuals)	+200 ppm	10 months	no change in bacterial community structure using DGGE	Bruce et al., 2000
	mesocosm (tropical)	+240 ppm	1.5 years	no change in microbial community composition using CLPPs and PLFA	Insam et al., 1999
	grassland	+230 ppm	6 years	no change in microbial community composition using PLFA	Niklaus et al., 2003
	deciduous forest	+190 ppm	3 years	altered microbial community composition using PLFA	Phillips et al., 2002
	alpine meadow	+310 ppm	4 years	altered microbial community composition using CLPPs	Mayr et al., 1999
	grassland	+360 ppm	1 year	increase in microbial N immobilization	Hungate et al., 1997
	mesocosm (deciduous)	+330 ppm	1 year	increase in microbial N immobilization	Berntson and Bazzaz, 1997

TABLE 5.4 (CONTINUED)
Effects of Elevated Atmospheric CO_2 on Belowground Trophic Structure

Trophic Level	Ecosystem Type	Magnitude of Manipulation *as compared to ambient reference of 370 ppm*	Duration of Manipulation	Results	Reference
	scrub oak woodland	+350 ppm	1.2 years	increase in microbial immobilization rate	Hungate et al., 1999
	mesocosm (deciduous)	+35 Pa	2 years	increase in microbial C immobilization	Mikan et al., 2000
	grassland	+230 ppm	3 years	increase in microbial N immobilization	Niklaus, 1998
	grassland	+370 ppm	8 years	increase in microbial C and N immobilization	Williams et al., 2000
	deciduous forest coniferous forest	+195 ppm	3 years	no change in microbial N immobilization	Zak et al., 2003
	mesocosm (deciduous)	+322 ppm	5 months	increase in N mineralization	Zak et al., 1993
	mesocosm (grassland)	+330 ppm	8 months	no change in microbial substrate utilization in rhizosphere	Van Ginkel et al., 2000
	deciduous forest	+195 ppm	2 years	no change in soil extracellular enzyme activities, no change in microbial substrate utilization	Sinsabaugh et al., 2003
	scrub oak woodland	+390 ppm	2 years	decrease in microbial activity using FDA hydrolysis	Schortemeyer et al., 2000
	mesocosm (woody shrub)	+380 ppm	4 months	altered microbial substrate utilization using CLPPs	Rillig et al., 1997
	alpine meadow	+310 ppm	4 years	altered microbial enzyme activity	Mayr et al., 1999
	grassland	+74 ppm	3 years	no change in abundance of herbivorous nematodes	Sonnemann and Wolters, 2005
	mesocosm (deciduous)	+35 Pa	5 months	decrease in abundance of earthworms	Lussenhop et al., 1998
	mesocosm (grassland)	+330 ppm	1.3 years	increase in abundance of earthworms	Yeates et al., 1997
	deciduous forest	+190 ppm	3 years	increase in soil respiration	Phillips et al., 2002
	grassland	+370 ppm	8 years	increase in soil respiration	Williams et al., 2000
III. Bacterivores/Fungivores	mesocosm (deciduous)	+35 Pa	5 months	increase in abundance of protozoa	Lussenhop et al., 1998
	mesocosm (herbaceous)	+330 ppm	1 month	increase in abundance of flagellates, decrease in abundance of amoebae	Treonis and Lussenhop, 1997
	grassland	+330 ppm	6 years	no change in abundance of protozoa	Rillig et al., 1999b
	mesocosm (grassland)	+330 ppm	1.3 years	increase in abundance of enchytraeids	Yeates et al., 1997
	coniferous forest	+350 ppm	6 years	no change in abundance of enchytraeids	Haimi et al., 2005
	grassland	natural CO_2 vent (370 to 3900 ppm)	N/A	decrease in abundance and diversity of nematodes, increase in dominance of bacterivorous nematodes	Yeates et al., 1999
	mesocosm (grassland)	+330 ppm	1.3 years	increase in abundance of bacterivorous nematodes	Yeates et al., 1997
	grassland	+330 ppm	4 years	no change in abundance of bacterivorous or fungivorous nematodes, decrease in nematode diversity	Hungate et al., 2000
	mesocosm (sagebrush)	+330 ppm	3 months	increase in abundance of nematodes	Klironomos et al., 1996
	mesocosm (weedy field)	+200 ppm	9 months	increase in abundance of springtails, altered species composition of springtails	Jones et al., 1998
	coniferous forest	+350 ppm	6 years	no change in abundance of of oribatid mites decrease in abundance of acaridid mites	Haimi et al., 2005
	grassland	+230 ppm	6 years	no change in abundance of mites or springtails	Niklaus et al., 2003
	mesocosm (deciduous)	+330 ppm	1.2 years	no change in abundance of mites, decrease in abundance of springtails	Klironomos et al., 1997
	grassland	+330 ppm	6 years	increase in abundance of mites and springtails	Rillig et al., 1999b
	mesocosm (grassland)	+180 ppm	N/A	increase in attractivity of invertebrate (sciarid fly) to fungi in litter	Frouz et al., 2002
	mesocosm (sagebrush)	+330 ppm	3 months	no change in abundance of microbivorous arthropods	Klironomos et al., 1996
IV. Carnivores	mesocosm (grassland)	+330 ppm	1.3 years	increase in abundance of predatory and omnivorous nematodes	Yeates et al., 1997
	mesocosm (sagebrush)	+330 ppm	3 months	no change in abundance of predatory arthropods	Klironomos et al., 1996
	grassland	+74 ppm	3 years	decrease in abundance of predatory nematodes	Sonnemann and Wolters, 2005
	grassland	+230 ppm	6 years	decrease in abundance of predatory and omnivorous nematodes	Niklaus et al., 2003

al. 2003) and activity (van Ginkel et al. 2000; Sinsabaugh et al. 2003) remain the same. Sometimes earthworm abundances decrease (Lussenhop et al. 1998), while other times abundances increase (Yeates et al. 1997).

These varied results, and results from precipitation and warming experiments, stress that climatic change effects on belowground trophic structure are strongly ecosystem dependent. The belowground food web operates with the context of a particular set of climatic variables, plant community properties, and physical soil properties. And even though all dirt kind of looks the same, the communities living within different soils do not have the same responses to climatic change factors. There are quite a few examples of the same trophic level responding differently to the same climatic change factor in the same type of ecosystem. This suggests that responses of belowground structure to climatic change may be controlled by different bottom–up and top–down forces. And these different trophic forces can vary within the same soil over time, probably due to seasonal and annual variation in microclimate.

Now, let us return to elevated CO_2 effects on the third trophic level, where there are again few consistent responses. The longer-term field studies, however, tend to find a lack of response among third trophic level participants. In some instances, abundances of protozoa (flagellates) increase (Treonis and Lussenhop 1997; Lussenhop et al. 1998), in other instances abundances (amoebae) decrease (Treonis and Lussenhop 1997). Enchytraeid abundances have been shown to increase (Yeates et al. 1997) or not change (Haimi et al. 2005). Nematode abundances may increase (Klironomos et al. 1996), decrease (Yeates et al. 1999), or not change (Hungate et al. 2000). Nematode diversity tends to decrease (Yeates et al. 1999; Hungate et al. 2000). Decreased diversity could reflect a greater dominance of a few species of bacterivorous nematodes (Yeates et al. 1997; Yeates et al. 1999), and illustrates how changes in trophic diversity may be hidden beneath undetectable changes in abundances or biomass. Elevated CO_2 can increase (Rillig et al. 1999b), have no effect (Klironomos et al. 1997; Niklaus et al. 2003; Haimi et al. 2005), or decrease (Haimi et al. 2005) abundances of mites. Springtails respond positively (Jones et al. 1998; Rillig et al. 1999b), negatively (Klironomos et al. 1997), or not at all (Niklaus et al. 2003). And microbivorous arthropods show no response (Klironomos et al. 1996). There is interesting evidence that elevated CO_2 can affect the third trophic level through changes in the second trophic level (Jones et al. 1998). In a model system, elevated CO_2 increased abundances of saprophagous fungi, probably due to increased soil carbon availability. This change in fungal composition affected the next highest trophic level, as indicated by increased springtail abundances, and a change in springtail diversity to a community probably dominated by species well suited at eating newly dominant saprophagous fungal species. This is a rare example of how climatic change may affect belowground trophic structure in a single (model) ecosystem.

Once again, climatic change effects on the fourth trophic level are understudied in comparison to lower trophic levels, and no consistent responses to elevated CO_2 are apparent yet. Predatory and omnivorous nematodes have been found to increase (Yeates et al. 1997) or decrease (Niklaus et al. 2003; Sonnemann and Wolters 2005) in abundance. These different responses may be caused by differences in length of experimentation, with the increase reflecting about a year of treatments and the

decrease reflecting 6 years of treatments. Increased microbial turnover may be a relatively short-lived source of energy for bacterivores, fungivores, and predators, and trophic structure may eventually return to more of an upright biomass pyramid as omnivory compensates for increased abundance of predators. On a shorter time scale, predatory arthropods showed no response after three months at elevated CO_2 (Klironomos et al. 1996).

5.4 CONCLUSIONS

The belowground food web is biologically complex, functionally important, and apparently responsive to climatic change. However, knowledge of belowground food webs, especially in unmanaged ecosystems, lags behind that of aboveground and aquatic food webs. While soil organisms sometimes respond to climatic change through adjustments in population size, adjustments may also occur in activity (e.g., trophic efficiencies), diversity, and spatial distribution—properties of belowground food webs that are rarely examined.

Figure 5.3 attempts to summarize results from over 100 studies. Organisms were sampled in different ecosystems, with different soil types, and at a particular microclimate in time. They had also experienced a wide variety of experimental designs. The responses of the second, third, and fourth trophic levels are based on changes in abundance or biomass, and the consistency and availability of data. The first conclusion is that there does not seem to be a common global response of trophic structure to climatic change. There are some cases (e.g., reduced precipitation) in which most studies agree, but there is usually an exception. If there are already exceptions, given the low availability of studies, we can expect to find more exceptions in the future. Because of context-dependent responses, the generalized responses in Figure 5.3 are expected results, but may not be the case in every ecosystem on every sampling date. The benefit of the doubt is given to a "no response," if there is a large proportion of studies that found a lack of response or if there is not strong enough evidence to assign a common directional response. However, arrows are displayed if multiple studies agree on a directional response.

5.4.1 Summary of Climatic Change Effects

It is expected that belowground food web responses to climatic change are dominated by direct effects in the cases of altered precipitation and elevated temperature (e.g., changes in metabolism, mobility, and vertical distribution), and by indirect effects in the case of elevated atmospheric CO_2 (e.g., changes in root production, soil structure, and soil moisture).

Despite greater abundances of second trophic level participants under elevated precipitation, population sizes in the third and fourth trophic levels tend to remain the same. What is the fate of this increased production at the bottom of the food web? Higher trophic levels probably use this extra production to metabolize faster or move around more, which may result in a change in ecosystem function (e.g., faster decomposition). Because most of the data on belowground food web participants are based on snapshot views of abundances, we need to be careful in

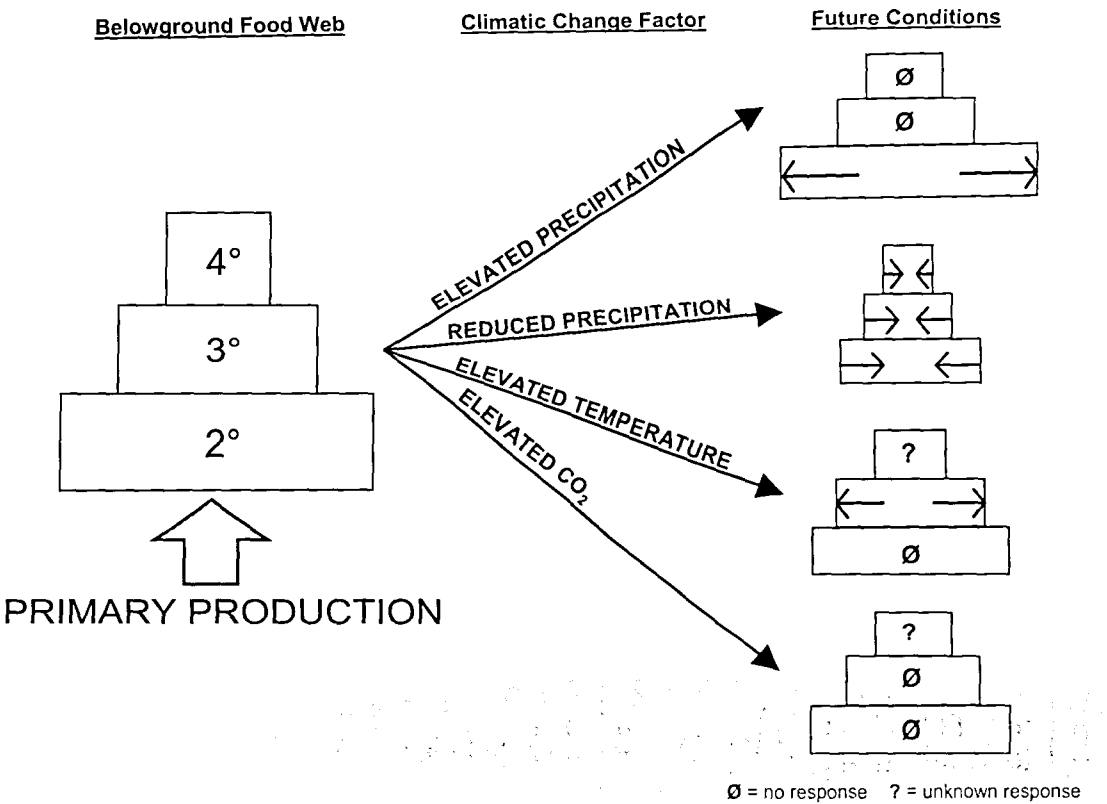

FIGURE 5.3 Climatic change effects on belowground trophic structure showing common or unknown responses of second, third, and fourth, trophic levels. It is important to note that these responses are generalized and that different ecosystems can display different responses.

interpreting a lack of response. There could be an associated change in activity, which is the main concern of any land manager.

All trophic levels tend to be negatively affected by reduced precipitation, but it is unknown whether this is caused by individual responses of organisms to water stress and reduced mobility, or a bottom–up effect associated with a reduction in secondary production. Warming tends to have little effect on the second trophic level and a positive effect on the third trophic level. The third trophic level may respond positively to warming because of physiological preferences or accelerated microbial turnover rates. Under elevated atmospheric CO_2, no consistent changes are observed in abundances of second trophic level participants, but there are instances when increased carbon input by plants under elevated CO_2 cascade up to higher trophic levels. When no change is found, it is possible that third trophic level grazing and fourth trophic level predation hide any increases in second trophic level abundances. By understanding mechanisms for climatic change effects on belowground trophic structure, we can increase our understanding of more general mechanisms for climatic change effects on ecosystem functions.

5.4.2 Research Needs

Sampling belowground structure requires a significant amount of time and effort for isolating and identifying the high diversity of dirty microscopic organisms. Results from different ecosystems show that it is more likely to be worth the time and effort if multiple trophic levels are studied in a single ecosystem. Other issues include biological dormancy, which allows organisms to survive through extremely hot, cold, wet, and dry conditions. Lateral gene transfer can occur between microorganisms, allowing a species to acquire a novel gene, and perhaps participate in a different trophic level or tolerate a new climate. Organisms can be omnivorous or picky in their food selection. And bottom–up and top–down trophic interactions appear to have different effects in different ecosystems. While abundances have laid the foundation for our understanding of belowground food webs, methods accounting for net energy flow and greater soil biodiversity will improve our ability to predict responses to climatic change. We need to examine all trophic groups at the same time, in the same ecosystem, and under different microclimates. Climatic change does not always change belowground trophic structure, but it can in certain contexts. And climatic change factors may interact to produce unique responses. Through long-term ecosystem-specific studies, we can figure out where and when changes in belowground trophic structure will be most important in the future.

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