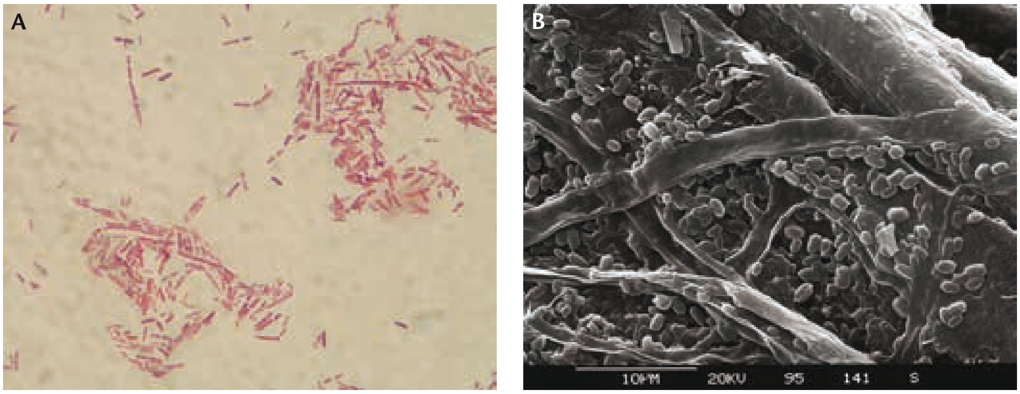

Fig. 3.2. Bacteria are the most numerous organisms in soil. They perform a huge range of functions, including: mineralisation of nutrients from organic matter; transformation of elements such as carbon, nitrogen, sulphur and phosphorus; antibiotic production; nitrogen fixation; and degradation of organic wastes and pollutants. (A) Rod-shaped bacteria under a light microscope. (B) A photograph taken with an electron microscope showing bacterial cells and colonies decomposing residues from a cereal crop.

The primary role of bacteria is to decompose organic matter. Labile compounds such as sugars, starches, fats and proteins are rapidly metabolised, while more recalcitrant compounds (e.g. cellulose, hemicelluloses, lignin and chitin) are utilised more slowly. The actinobacteria, a group of bacteria with slender branching filaments, play an important role, as they are able to break down an enormous variety of organic compounds.

During the decomposition process, nutrients held in an organic form are mineralised, which means they are converted into inorganic forms that can be utilised by plants. In the case of nitrogen (N), for example, enzymes produced by bacteria break down proteins, chitin and other nitrogen-containing materials into smaller molecules that are then metabolised to produce ammonium. A relatively small group of nitrifying bacteria then convert ammonium to nitrate.

In addition to modifying soil fertility through their roles in decomposing organic matter and transforming mineral nutrients, bacteria have other important roles in soil. Many bacteria influence plant growth by producing hormones that stimulate root growth, toxins that impair root function, or antibiotics that are detrimental to root pathogens. Free-living nitrogen-fixing bacteria use decomposing plant residues and carbon compounds released from roots as an energy source, and are able to convert nitrogen (N_2) from the atmosphere into ammonia. Another group of bacteria form a symbiotic association with plants in which the bacteria receive a continuous supply of photosynthates for growth, and in return, the plant receives a supply of fixed nitrogen. The best known example is the association between leguminous plants and *Rhizobium*, a relationship that provides almost 50% of the nitrogen used in agriculture (see Box 3.1).

Fungi

Although bacteria are the most abundant component of the soil microbiota, fungi sometimes contribute much more to total microbial biomass. However, regardless of whether bacteria or fungi predominate in a particular soil, their collective contribution to the soil biomass far exceeds that of algae, protozoans, nematodes and other soil animals. The advantage fungi have over other microbes is that their filamentous hyphae enable them to

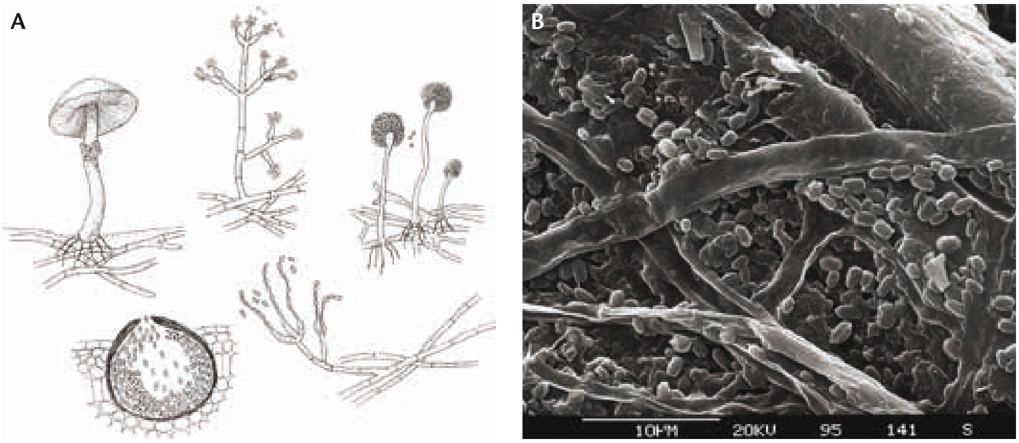

Fig. 3.3. Fungi play many different roles in soil, including decomposition of organic matter and parasitism of plants, insects, nematodes and other fungi. (A) Some of the fungi commonly found in soil. (B) An electron micrograph showing fungi binding plant residues to soil particles.

forage for food. Batteries of enzymes are released, and they break down plant residues and other organic materials into simpler forms that can be absorbed by the mycelial network.

Most farmers hearing the word ‘fungus’ will think of the mushrooms they eat, or the many fungal pathogens that attack the leaves and roots of their crops. However, there are many other groups of fungi in soil, and they play many different roles in the soil environment (Fig. 3.3). Some are plant pathogens (see Chapter 4); some are responsible for decomposing plant residues such as straw, wood and bark; some improve soil structure and aeration by binding soil particles together; some are parasitic on other soil organisms; and mycorrhizal species form mutualistic associations with plant roots that aid nutrient uptake. Both fungi and bacteria are also a food source for microbe-feeding fauna, and are therefore of great significance to the numerous groups of small animals that live in the soil food web.

Archaea

These microorganisms are considered more primitive than bacteria and are found in diverse environments such as marine and fresh water, sediments, and in soil under forests, grasslands and agricultural crops. Because archaea are very difficult to culture, knowledge of their diversity, distribution and occurrence has largely been achieved through the use of DNA tools and various techniques in molecular biology.

While archaea are frequently present in soils in relatively small numbers compared with bacteria, some archaea play an important role in nitrogen cycling, as they oxidise ammonium to nitrite and nitrate in a process known as nitrification. Another group of archaea produces methane, an important greenhouse gas, and its production from organic matter decomposition leads to carbon loss. Archaea are generally anaerobic and are most commonly found in wet environments such as rice paddy fields.

Cyanobacteria and algae

These organisms were once classified together as ‘soil algae’. However, they are not closely related. Cyanobacteria have a prokaryotic cell structure (i.e. their cells lack a distinct nucleus and membrane-bound organelles) and so they belong in the Kingdom Bacteria. In

Fig. 3.4. In this undisturbed remnant vegetation in north-western Victoria, soil crusts are formed by cyanobacteria. The cyanobacterial crust is visible as black clumps on the soil surface, with cyanobacterial cells binding the sandy orange calcarosol soil together. This helps trap nutrients and moisture, and stabilises the soil in this low-rainfall region. Many lichens (visible here as white cup structures a few millimetres wide) and algae also grow among the cyanobacterial crust.

contrast, algal cells have a nucleus like most other organisms (i.e. they are eukaryotic). Nevertheless, cyanobacteria and algae have many similarities: both are microscopic in size, they are the main photosynthetic microbes in soil, and they are able to withstand extreme environments.

Because light is needed for photosynthesis, most cyanobacterial and algal cells are found in the upper few millimetres of soil. Population densities are highest in regions of high rainfall, but cyanobacteria and algae also occur in semi-arid and arid environments, where they cover more than 70% of the soil surface (Fig. 3.4). Their role in soil is to provide carbon and nitrogen, chelate nutrients, increase mineral weathering rates and influence local hydrological cycles. In deserts, they interact with lichens and other organisms to form soil crusts that stabilise soils, help retain nutrient-rich dust and enhance soil structure. Because they form the base of the food chain, they also provide food for larger soil organisms such as protozoans, nematodes and microarthropods.

Protozoa

Soil protozoans are single-celled organisms that range in diameter from 5 to 100 μm and commonly reach densities of 10^4–10^6 per gram in the surface layers of soil. Populations are much lower further down the soil profile, as levels of organic matter are lower and so fewer food sources are available.

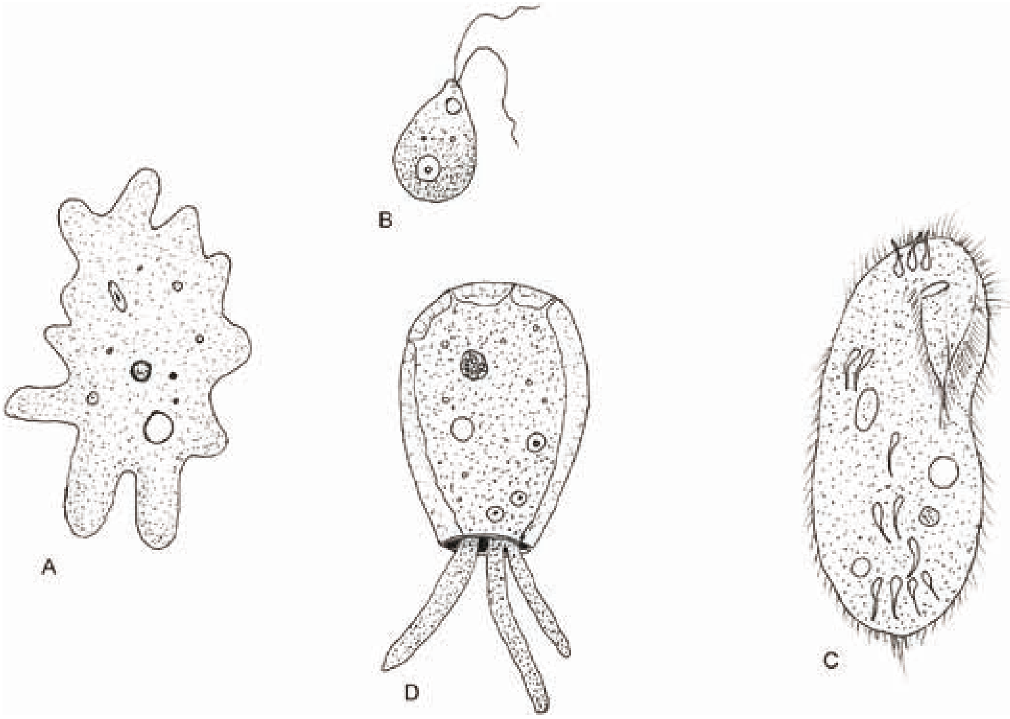

Fig. 3.5. Several types of single-celled protozoans occur in soil: (A) jelly-like amoebae; (B) groups that move using whip-like flagella or (C) numerous small cilia; and (D) testate forms with a hard shell.

Protozoans are commonly sub-divided into four groups: flagellates, naked amoebae, testate amoebae and ciliates (Fig. 3.5). They reside in water-filled pores and move in water films, where they feed primarily on bacteria, although fungal feeders and predators are known. Protozoans multiply rapidly when populations of their bacterial prey increase (e.g. following a rainfall event or when organic matter is added to soil), but when conditions become unfavourable or the soil begins to dry, they survive by forming resistant structures known as cysts.

Because protozoans feed prolifically on bacteria, their presence affects the composition and activity of the microbial community, particularly in the rhizosphere, where a ready supply of bacterial prey is always available. However, their main effect is on nutrient supply. A large proportion of the nutrients ingested by protozoans (~60%) are excreted into the soil environment in mineral form, where they are available for uptake by plants.

Nematodes

Nematodes are the most numerous multicellular animals in soil, with most fertile agricultural soils having at least 5 million nematodes/m^2. They are one of the smallest soil animals, with most species between 300 and 800 μm long, and ranging from 10 to 20 μm wide. Like protozoans, they move and feed in water films around soil particles.

Soil nematodes feed mainly on bacteria and fungi, but plant-parasitic, omnivorous and predatory species also occur (Fig. 3.6). Some bacterial-feeding nematodes ingest their prey by sucking bacteria through a tube-like or funnel-shaped mouth, while other species use

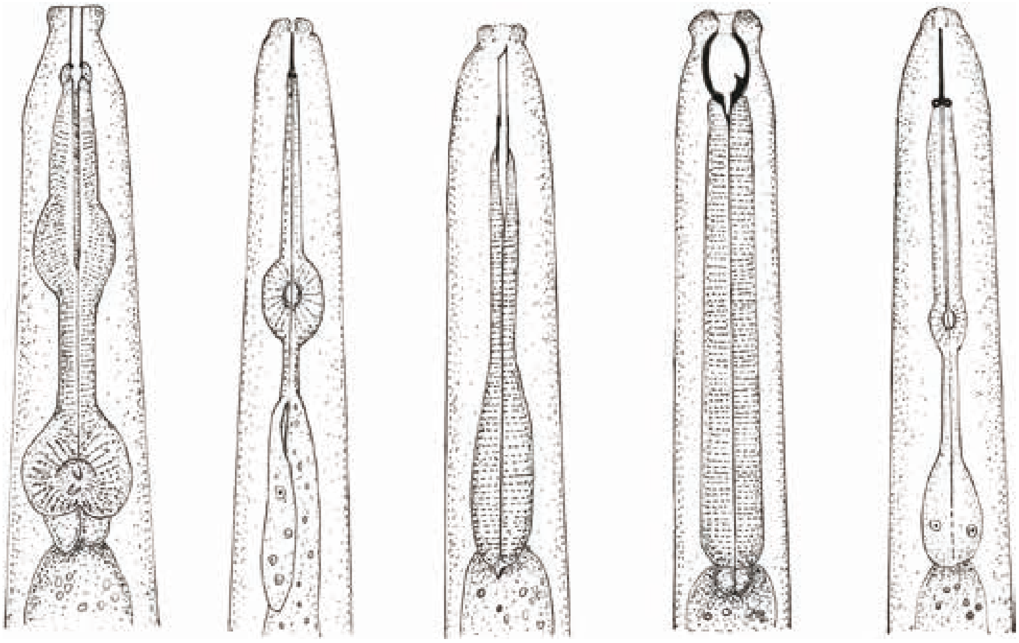

Fig. 3.6. Mouthparts and the oesophageal regions of five different nematode feeding groups. From left to right: Bacterial-feeder; fungal-feeder, omnivore, predator, and plant parasite.

prominent lips to scrape bacteria off surfaces. Most fungal feeders use a delicate spear to pierce fungal hyphae and spores (Fig. 3.7). The subsequent effects of these nematode feeding activities (changes in the microbial community and nutrient excretion) are similar to those of protozoans.

Bacterial- and fungal-feeding nematodes have very short life cycles (often only 5–15 days) and so populations respond quickly when a new food source becomes available. In contrast, the omnivorous and predatory nematodes respond much more slowly when prey numbers increase, as they are much larger (commonly 1–3 mm long) and often have generation times of weeks or months. Omnivorous nematodes use a retractable spear to feed on algal cells, protozoans, nematodes and other invertebrates, while most of the predatory nematodes have a broad mouth armed with teeth that is used to capture and consume nematodes and other small animals.

Plant-parasitic nematodes obtain their sustenance by inserting their feeding spear into root cells. However, species vary markedly in their capacity to damage the root system. Some feed superficially on root hairs and other root cells but have no impact on plant growth. Others are more damaging, as they feed on root tips and prevent roots from growing normally. A third group move into the root and feed with at least some part of their body embedded in root tissue. They are all important pests of agricultural crops and are discussed in Chapter 4.

Mites and collembolans

The predominant components of the soil mesofauna are mites and collembolans (also known as springtails). These small arthropods, which generally range in size from 0.2 to 2 mm, are the third most abundant group of soil animals after the protozoans and nema-

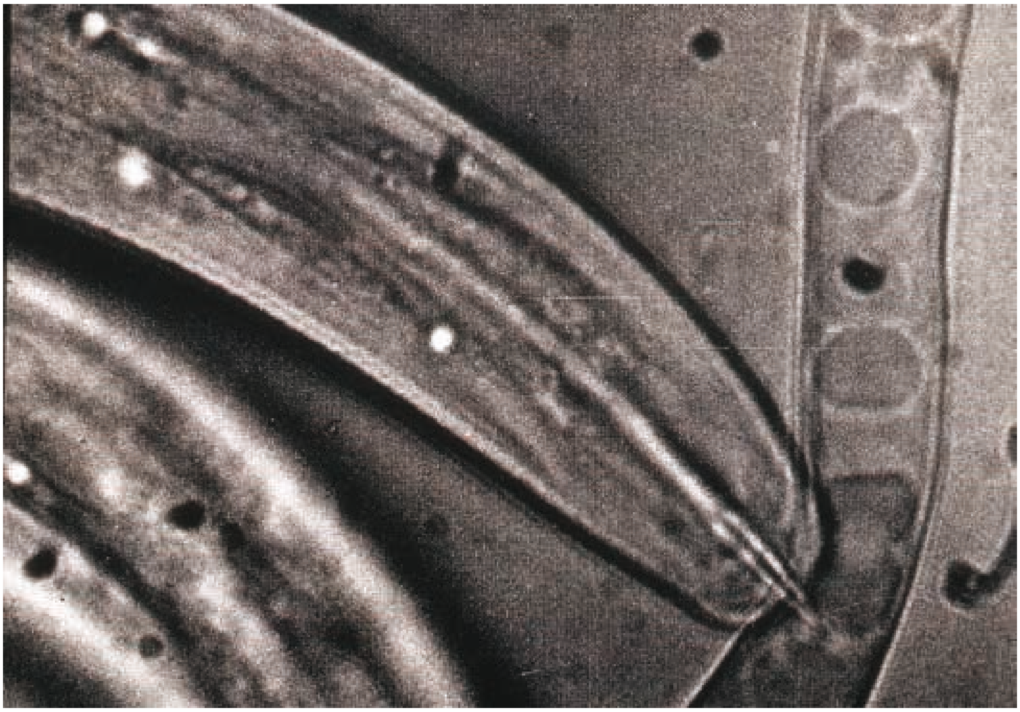

Fig. 3.7. *Aphelenchus avenae* feeding on a fungus. This nematode is one of the most common fungal-feeding nematodes in Australian soils. In the laboratory it thrives on *Rhizoctonia solani*, an important plant pathogen.

todes (Fig. 3.8). Fertile grassland soils with high levels of organic matter may support as many as 300 000 microarthropods per square metre. However, populations are much lower in arable fields due to the negative impact of tillage and compaction.

There is enormous taxonomic diversity within the mites and collembolans, with hundreds of different families and thousands of species. Thus, the feeding habits of most species are not known. Some consume a variety of substrates, others are fungivores or detritus feeders, while others prey on nematodes and other soil animals.

Mites and collembolans are most commonly found in the upper soil layers and both are favoured by situations where there is a discrete litter layer. Because soil porosity decreases with increasing depth and microarthropods can only move in pores that are larger than themselves, larger species are mainly confined to surface soil. Thus, smaller species become relatively more abundant as depth increases.

Enchytraeids, symphylans, tardigrades and other mesofauna

In addition to mites and collembolans, many other small invertebrates live in terrestrial habitats. Perhaps the most important are the enchytraeids, also known as 'potworms' (Fig. 3.9). They occur at very high densities in natural soils, where there is usually a distinct litter layer, but are also found in agricultural soils. Although they are much smaller than earthworms, they are anatomically similar and appear to play a similar role in soil. Enchytraeids ingest organic matter together with microorganisms associated with decaying litter and roots, but mainly survive on fungal mycelium.

Fig. 3.8. Various microarthropods commonly found in soil: (A, B) mites; (C) centipede; (D) springtail and (E) isopod.

Symphylans and tardigrades are also relatively common in soil. Symphylans are small, white, elongate animals,, and, because they have many legs, they resemble centipedes. Although generally omnivorous, some species feed on plant roots and may become pests of agricultural crops. Tardigrades, also known as 'water bears', have a varied diet, but are sometimes important predators of nematodes. However, they are best known for their recuperative powers after being exposed to major changes in their environment (e.g. extreme cold, rapid drying or the removal of oxygen). This resilience when faced with major changes in their physical or chemical environment is a feature of many soil organisms, as it allows them to survive spells of unfavourable conditions and reactivate when the environment improves.

In addition to the mesofauna already mentioned, a diverse group of small animals can also be found in most soils. However, these organisms are unlikely to have a significant impact on soil ecology, as they are generally present at population densities of less than a few thousand per square metre. Examples include rotifers, which are usually considered aquatic organisms, and primitive insects such as proturans and diplurans.

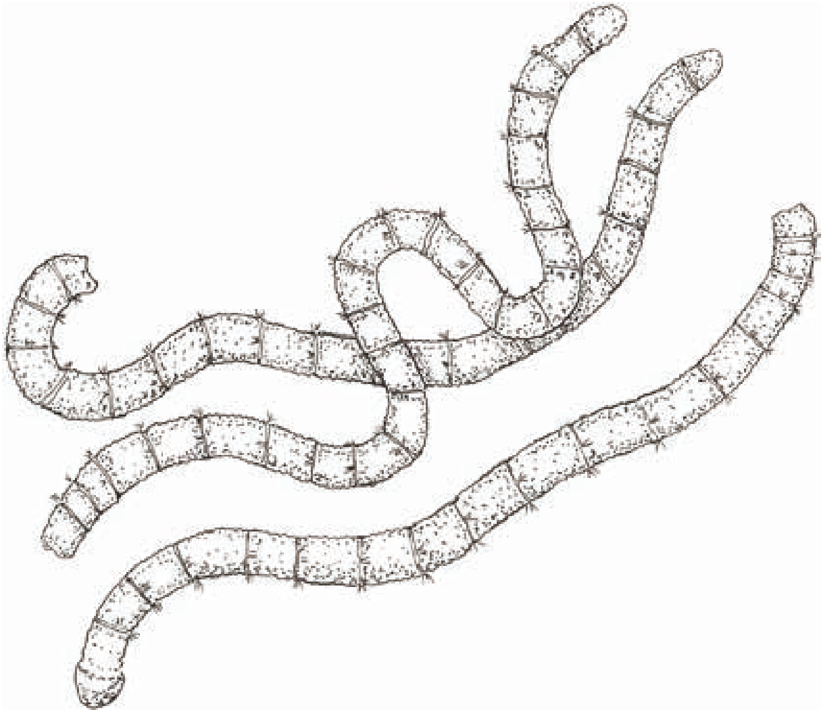

Fig. 3.9. Enchytraeids (potworms) have much the same role in soil as earthworms, but tend to be more abundant in acid soils. Because most species are 5–15 mm long, they are large enough to be visible with the naked eye.

The macrofauna: millipedes, centipedes, spiders, termites, ants, scorpions and earthworms

These large soil animals are the most familiar members of the soil fauna, as they are readily visible to the naked eye. Given that this group of animals span a wide range of taxonomic groups, it is not surprising that their feeding habits are very diverse, and may involve the consumption of organic debris and associated microorganisms, predation on large and small arthropods, plant feeding and opportunistic consumption of many different substrates.

Of all the animals in soil, earthworms have perhaps the greatest impact on the soil environment because they are capable of moving large quantities of soil. In some situations, the amount of soil that is relocated is equivalent to bringing a layer of soil 1–5 mm thick to the surface every year. Thus, earthworms create macropores, are involved in soil formation, play an important role in litter decomposition and redistribute organic matter within the soil profile (Fig. 3.10). Earthworms also stimulate the microflora by making plant litter more accessible to microbes, by producing nutrient-rich casts, and by improving aeration and soil moisture conditions. Some species live in leaf litter on the soil surface, others make horizontal burrows in the upper soil layer, while anecic species build permanent burrows deep into the mineral layer of soil.

Because earthworms are highly sensitive to disturbance caused by tillage implements, their populations and biomass are almost always much higher in natural soils than in conventionally cultivated agricultural soils. They are also sensitive to contaminants, and have proved to be one of the best indicators of the presence of pesticides and pollutants in soil.

Fig. 3.10. Earthworms are an important component of the soil macrofauna. They have several roles in soil, but one of the most important is to create macropores (see arrows) that allow air to diffuse, water to infiltrate, and smaller animals to move throughout the soil profile.

The soil food web

The previous section on soil biodiversity highlights the fact that soil organisms do not exist in isolation. Enormous numbers of bacteria, fungi, protozoans, nematodes, microarthropods and other organisms co-exist in soil, where they interact with each other in closely knit communities. The term 'soil food web' is used to describe this complex and biologically diverse living system. Energy to drive the system comes from the sun and is used by plants to convert CO_2 and minerals into energy-rich compounds through a process known as photosynthesis. Organisms within the soil food web then compete for this resource and, during the process, the food energy is transferred from one organism to another. Each organism is consumed by the next member of the food chain and it, in turn, is then preyed on by one of its predators.

Perhaps the best way of understanding the way organisms interact within food webs is to view the system pictorially. Thus, in Fig. 3.11, a group of organisms known as producers (predominantly plants, but also algae and some bacteria) use energy from the sun to convert CO_2 from the atmosphere into organic compounds. Some of that organic matter falls to the ground and is found on the soil surface as plant residue. Most of the organisms in the soil are consumers (i.e. they obtain their energy from plants, plant residues or other organisms, either by eating them or feeding on their waste products). The food sources for each organism dictate its trophic level in the food chain, with organisms feeding on plants viewed as occupying a lower trophic level than organisms that prey on other organisms.

In soil, plants are the dominant primary producers and consequently form the base of the food web. Organisms that consume roots (herbivores) or organic matter derived from plants (detritivores) form the next trophic level. In turn, they are consumed by predators (a

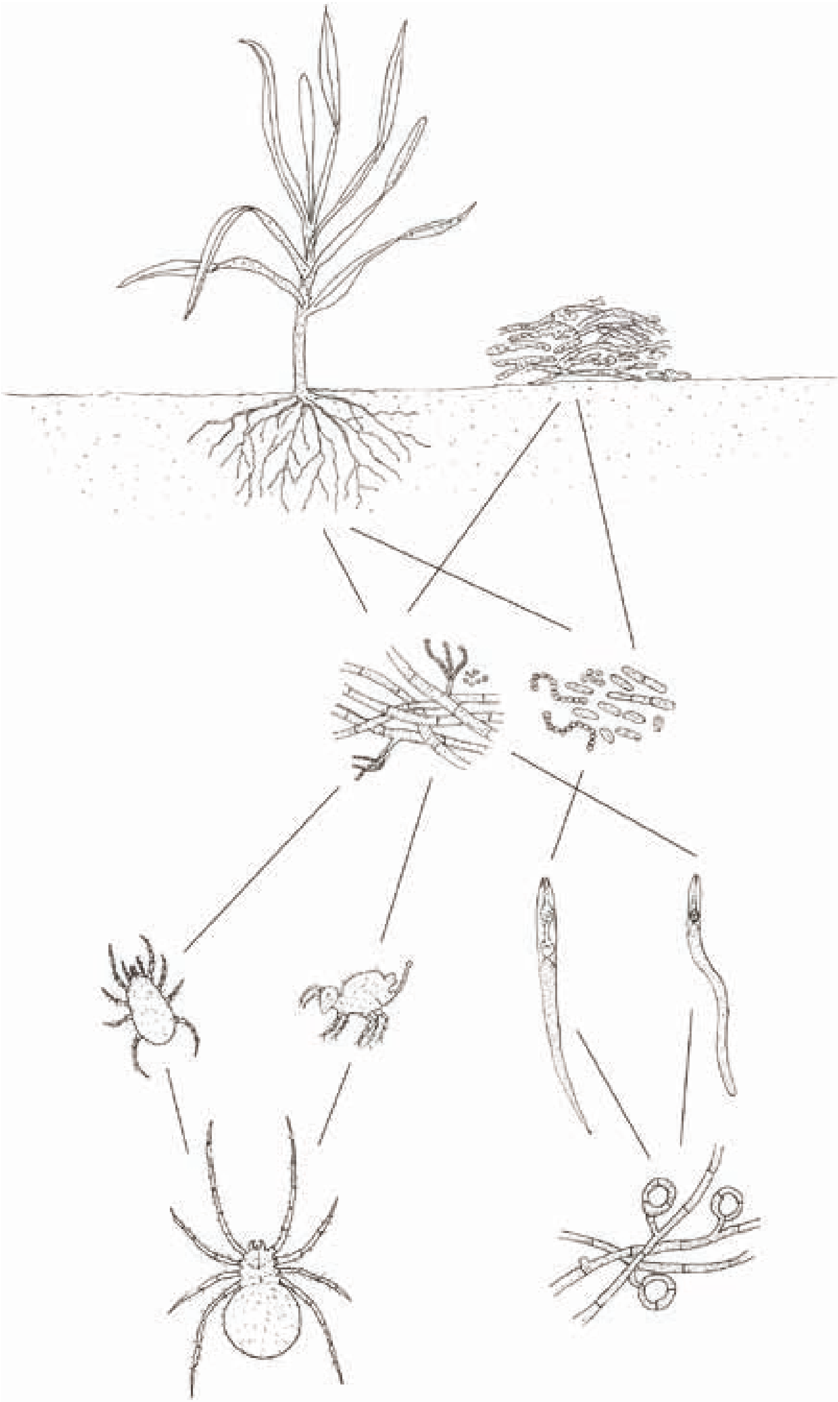

Fig. 3.11. A simplified version of the soil food web. Living plants and organic matter derived from plants is the energy source that sustains all soil organisms. Fungi and bacteria live on roots and plant residues, but they are a food source for small arthropods and nematodes. In this example, these organisms are then consumed by spiders and predatory fungi.