Chapter 8
Soil Biota, Soil Health and Global Change

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8.1 Soil Health and Soil Biota

The concept of soil health is intuitively simple because of the obvious connections with human health. Scotland's Macaulay Institute have taken up this anthropomorphic approach in their soil health knowledge and outreach programme titled "dirt doctors" in which they ascribe human health and behavioural traits to the major soil types in Scotland (www.macaulay.ac.uk/news/dirtdoctors). The term "soil health" has, however, created some challenges when applied in contexts other than for communication and knowledge transfer. From a technical perspective, soil health is difficult to measure and therefore hard to manage; from a political perspective, it is hard to ascribe a value to, particularly with respect to public good benefits. From an economic viewpoint, it is ascribed significance only when plant production systems decline or fail. The "soil health as a useful concept" debate will therefore continue to generate new or slightly modified definitions reflecting the objectives of the particular interest group. For example, the policy context defines soil health as "A goal for land owners and managers that embraces an accountable system of soil management for maintaining and improving soil functions and productivity for a range of purposes across generations. Healthy soil is a soil that is managed as an ecosystem on a 'fit-for-purpose' basis and within its capabilities" (*A policy framework for investment by the Department of Primary Industries, Victoria, Australia June 2007*). A popular and enduring technical definition is provided by Doran et al (1996) as "the capacity of a living soil to function, within natural or managed ecosystem boundaries, to sustain plant and animal productivity, maintain or enhance water and air quality, and promote plant and animal health". A more contemporary definition embraces a broader ecosystems context; a soil that is capable of supporting the production of food and fibre, to a level and with a quality

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sufficient to meet human requirements, together with continued delivery of other ecosystem services that are essential for maintenance of the quality of life for humans and the conservation of biodiversity (Falkowski et al. 2008; Kibblewhite et al. 2008; also see Chap. 1 and Preface of the book).

Collectively, the challenges associated with the soil health concept reflect the reality; soils *are* a complex ecosystem and the "health status" of that ecosystem depends not only on the prevailing farming system (e.g. a healthy soil for viticulture may be different from a healthy soil for grain production) but also on many interacting physical, chemical and biological factors operating on temporal and spatial scales that may lack relevance for human needs and activities. Understanding the complexity of functions and interactions within the soil ecosystem therefore is not without challenges. Soils are, afterall, *are* the most diverse ecosystem on the planet (Torsvik et al. 1990; Torsvik and Øvreås 2002; Venter et al. 2004), and although the knowledge of these systems is growing exponentially (see Sects. 8.3 and 8.4), the community composition of the soil biota, particularly the micro-organisms, remains largely unclassified (Chen et al. 2008; Keller and Zengler 2004), with the underpinning ecological concepts, rudimentary and sometimes misattributed (Bardgett et al. 2005).

Notwithstanding these challenges, the requirement for greater acknowledgement and understanding of the soil as an ecosystem that provides essential services for society is, however, critical. The already widespread degradation of soils (EU 2002) and the growing population pressures for food will require an estimated 63% increase in average cereal yields by 2050, placing even more pressure on land already under agriculture (Lal 2009). Global change will add to this pressure thereby further highlighting the need for more robust knowledge to underpin both political and landholder risk management strategies for soil-based food production industries.

The soil biota is linked to the soil health concept through its role in the mediation of processes that provide agricultural goods (e.g. nutrients and disease control for food and fibre production) and ecosystem services (water quality and supply, erosion control, atmospheric composition and climate regulation, pollutant attenuation and degradation, non-agricultural pest and disease control and biodiversity conservation) (Kibblewhite et al. 2008). It is therefore imperative when addressing issues of global change impacts on soil health to consider the trilogy of interrelated properties: the physical, chemical *and* the biological (see Chaps. 1 and 2).

8.2 Soil Biota: Multiple Roles and Responses to Under Global Change

Soil biota has many and varied roles in all global change. It has a direct causal role, it can also contribute to mitigation and can be changed (either adversely of beneficially) by global change. Both the causal and mitigation roles relate to the capacity of microbes such as bacteria, archaea and fungi to produce *and* consume all the greenhouse gases, NO, N_2O, CH_4 and CO_2, respectively (Fig. 8.1). In other words, these gases are both starting substrates and by-products of energy-generating pathways

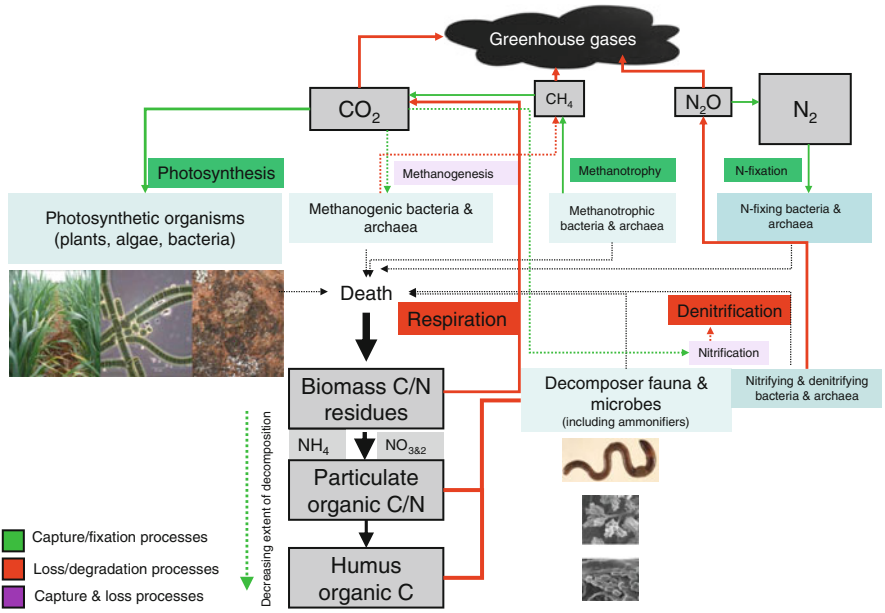

Fig. 8.1 The microbial carbon and nitrogen cycles illustrating the multiple microbial capture and loss pathways associated with the generation of greenhouse gases

necessary for microbial growth and integral to fundamental biogeochemical cycles and a whole range of ecosystem goods and services (Falkowski et al. 2008; Kibblewhite et al. 2008). These processes are cyclic, dynamic and adaptive and are regulated by temperature (ambient and soil), moisture availability, soil and plant management. The soil biota is likely to be affected directly (e.g. physiological stress and adaptation responses) and indirectly (e.g. through habitat modification) by global change scenarios. These scenarios include elevated temperature (projected increase from 1990 of 1.4–5.8°C by 2100), elevated atmospheric CO_2 (projected increase from 368 ppm in 2000, to between 540 and 970 ppm by 2100), elevated atmospheric N (projected increase of N_2O from 316 ppb in 2000) and fluctuating CH_4 concentrations (e.g. a rapid rise from about 700 ppb in 1,750 to about 1,775 ppb in 2005, followed by a projected decline), and precipitation changes by an average of 20% on current levels (Solomon et al. 2007). Soil biota can also provide solutions for mitigation and adaptation to global change. An example of this is where sensitive species can be used to predict impending biogeochemical changes or where new species can displace existing species to reduce loss of greenhouse gases to the atmosphere. The following sections will provide further detail of some of the key roles that soil biota play in global change.

8.2.1 Soil Microbiota and Greenhouse Gas Production

Anthropogenic disturbance of the biogeochemical cycles is perhaps today's greatest environmental challenge, and C and N cycling are probably most profoundly

affected. These cycles, while highly interdependent, differ in the microbes that mediate the underlying processes and specifically those involved in greenhouse gas emissions. The functional and taxonomic differentiation of these microbes will inform greenhouse gas mitigation options.

8.2.1.1 N-Gas Production

Nitrogen is a key nutrient for plant growth and plays a critical role in plant community structure and composition in many environments. There are nine forms of nitrogen in soil, differing in their degree of oxidation (Paul 2007). Nitrous oxide (N_2O) and to a lesser extent, nitric oxide (NO) are important greenhouse gases that are generated from plant and microbial (organic) N forms which are converted into N-gases, N_2O and N_2, through NO as the obligatory intermediate. It has been estimated that two-thirds of N_2O originate from soil and that of the 12 sources identified in the USA, agricultural soil management generates almost 70% of emissions (http://www.epa.gov/nitrousoxide/sources.html; cited 18 Dec 2010). Two highly coupled, microbially mediated processes that generate N_2O and NO are nitrification and denitrification. Nitrous oxide is emitted from soil during the processes of nitrification and denitrification. Nitrification is the microbial oxidation of NH_4^+ (to NH_3^+) to NO to NO_2^- to NO_3^- and of NH_4^+ (to NH_3^+) to gaseous forms, NO and N_2O. Although nitrification represents a key step in the conversion of ammonia nitrogen into its gaseous forms, this process is less relevant to N_2O emissions. Furthermore, a commonly held view is that nitrifier numbers are typically low in soils. Denitrification is the reduction of NO_3^- to NO, N_2O, and N_2 in anaerobic soil conditions (water filled pore space >60%). The identification of the microbial species associated with nitrification and denitrification is ongoing and being rapidly facilitated by microbial genome sequencing technologies (Cavicchioli et al. 2007; Green et al. 2010).

Nitrification is the most complex of the two processes being carried out most energy efficiently by autotrophic nitrifiers that derive C-energy from CO_2 or carbonate and less efficiently by heterotrophic nitrifiers that derive C-energy from organic matter. The autotrophic nitrifiers are divided into two discrete taxonomic groups, the ammonia oxidisers (to NH_3^+ to NO_2^-) and the nitrite oxidisers (NO_2^- to NO_3^-). The ammonia oxidisers have been classified as bacteria belonging exclusively to the Betaproteobacteria and specifically to genera, *Nitrosomonas*, *Nitrosolobus*, *Nitrospira* and *Nitrosovibrio* (Paul 2007; Prosser 1986). The nitrite oxidisers are more broadly distributed in the Proteobacteria with *Nitrobacter* in the Alphaproteobacteria, *Nitrospina* and *Nitrospira* in Deltaproteobacteria and *Nitrosococcus* in the Gammaproteobacteria. The fungi are considered to be the most numerous and efficient heterotrophic nitrifiers and include the common soil fungi *Fusarium*, *Aspergillus* and *Penicillium* (Lin et al. 2008; Prosser 1986; Zhang et al. 2002); however, it is known that the production of N_2O in heterotrophic nitrification is not energy generating and thought to be a result of the release of oxidases and peroxidases during cell lysis and lignin degradation. More recently, a whole third domain discovered in the late 1970's, the Archaea, has been implicated in nitrification. While

largely taxonomically unresolved, the ammonia oxidisers are described as archaeal ammonia oxidisers (AOA) and the nitrite oxidisers as Nitrospira-like and Nitrotoga-like nitrite oxidisers. Of significance is the assertion that these archaeal nitrifiers are dominant in many natural and agricultural soil systems (Cavicchioli et al. 2007; Wagner 2009).

Denitrification by contrast is relatively straightforward and the denitrifiers are the most important producers of the major greenhouse gases, and are also the most physiologically diverse encompassing the organotrophs, chemo- and photolithotrophs, N_2-fixers, thermophiles, halophiles and various pathogens. These facultatively anaerobic bacteria are represented by more than 60 genera of bacteria of culturable species, particularly *Pseudomonas* and *Algaligenes*, *Bacillus*, *Agribacterium* and *Flavibacterium* (Paul 2007) and unculturable phyla Acidobacteria and Thermomicrobia (Morales et al. 2010).

Edaphic factors including soil water content, temperature, pH, salinity, plant species and availability of organic carbon influence the rate of N-gas generation. The literature contains many examples demonstrating the degree to which these factors influence actual and potential nitrification and denitrification either by direct measurement of gas efflux (Chen et al. 2010; Davidson et al. 2008; Falloon et al. 2009; Gu et al. 2009; Ma et al. 2010; Reth et al. 2005) or by the measurement of the abundance of specific enzymes associated with each process using quantitative-PCR (Q-PCR)-based approaches (Colloff et al. 2008; Liu et al. 2010; Morales et al. 2010; Okano et al. 2004; Rotthauwe et al. 1997; Wakelin et al. 2007). Knowledge of how these edaphic factors selectively regulate the nitrifier and denitrifier communities, particularly those that use NO_3^- as the electron acceptor, will provide soil management strategies for reducing N loss via denitrification (Faulwetter et al. 2009; Siciliano et al. 2009; Zhang et al. 2009). Modification of soil moisture and oxygen content and C:N input ratios (quality and quantity) by altering soil structure and residue input regimes respectively is likely to have a significant impact on the magnitude and scale of biological N-loss. Currently, however, N_2O efflux reduction strategies focus mainly on the use of nitrification inhibitors, an old strategy for reducing N-fertiliser loss (McGuinn 1924). In the contemporary context of global change, there has been a renaissance in the types of inhibitors and modes of application. These are either nitrification or urease inhibitors, the former reducing the availability of NO_3^- for denitrification, and the latter slowing the hydrolysis of urea to ammonium, resulting in less availability of substrate for nitrification (Malla et al. 2005; see Chap. 10). The efficacy and environmental impacts of nitrification inhibitors are highly dependent on soil texture, water and temperature with largely benign effects on physical– chemical and biological soil properties reported (Cuttle 2008; Edmeades 2004; Granli and Bockman 1994; O'Callaghan et al. 2010).

8.2.1.2 C-Gas Production

Carbon, like nitrogen, is a key nutrient and has many forms differing in their degree of oxidation. The global soil organic carbon pool is estimated to be ~1,395 $\times$ 10^{15} g

(Post et al. 1982), and accumulation is controlled principally by net primary productivity while losses are mainly a function of the biological stability of the various chemical forms. These forms are lignin, cellulose, tannins, starches, sugars and the gases, carbon dioxide (CO_2) and methane (CH_4). The two principal C-loss pathways are through microbial respiration (see Chap. 7) and methanogenesis.

The degradation of organic C in soil and the generation of CO_2 in the process of aerobic respiration are carried out by the heterotrophic microbial community with the assistance of the micro-, meso- and macrofauna. It is widely estimated that the vast majority of the microbial community have a predominantly heterotrophic existence, and the soil biota is collectively regarded as the "waste management crew" in that they balance intake of CO_2 by photosynthetic processes and release it back into the environment by respiration processes (Paul 2007). The age and quality of the organic matter can influence the rate of release of CO_2 back into the atmosphere, with the particulate organic matter being the most readily decompose and the humus being more slowly decomposed (Hernández and Hobbie 2010; Skjemstad et al. 2004). The addition of labile sources can stimulate the decomposition of more recalcitrant C via a priming effect on the microbial community (Blagodatskaya et al. 2007; Blagodatsky et al. 2010; Kuzyakov 2010). Furthermore, the activity of specific groups of soil biota such as enchytraeids (Annelida: Oligochaeta) can also facilitate release of CO_2 from older C pools (Briones et al. 2010).

The generation of CH_4 in the relatively more complex microbial process of methanogenesis is also a respiration process that uses CO_2 and other forms of C instead of oxygen. Methane is roughly 25 times more effective as a greenhouse gas than carbon dioxide (IPCC 2007) and thus even at lower atmospheric concentrations contributes about half the radiative climate forcing of CO_2 (Beerling et al. 2009). Large quantities of CH_4 are annually produced (methanogens) and consumed (methanotrophs) by interdependent microbial communities ("consortia") living in the soil and ocean sediment. Methane can be produced by both acetotrophic and hydrogenotrophic methanogens, and differences in environmental conditions affect the composition of these communities (Demirel and Scherer 2008). Cultured methanogens are grouped into the orders Methanobacteriales, Methanococcales, Methanomicrobiales, Methanosarcinales (Whitman et al. 2001) and uncultured methanogens are obligate archaeal anaerobes that may represent new orders with complex interactions with other anaerobes and the physical and chemical environment (Liu and Whitman 2008). Like methanogens, methanotrophs have many uncultivated members that are either aerobic or more most recently, anaerobic CH_4 oxidising archaea (ANME) (Alperin and Hoehler 2009). The aerobic methanotrophs belong to two groups; type I (Methylococcaceae) or type II (Methylocystaceae) with molecular studies indicating that many are still uncultivated (Chen et al. 2009). Peatlands, considered to be highly significant carbon reservoirs, have active methanogenesis and methanotrophy with a dominance of the Methylocystis-related species of methanotrophs (Chen et al. 2008). The degree to which methanogenesis is coupled with methanotrophy ultimately determines how much CH_4 is released into the atmosphere. The extent to which each group contributes to CH_4 emissions and the regulatory role of soil physical and chemical conditions is of major interest (Andert et al. 2009).

8.2.2 Soil Biota and Greenhouse Gas Capture

Just as there are biological processes responsible for the generation of greenhouse gases, so are there biological processes that capture or sequester greenhouse gases, or their precursors, thereby countering emissions. The preceding section provides a good example of how methanotrophs use the CH_4 generated by the methanogens and convert it into a more environmentally benign C-form (see Chap. 10). Biological processes that capture or sequester greenhouse gases are therefore of great relevance. For example, soil biota can theoretically capture soil C through processes such as deep residue burial (e.g. dung beetles and earthworms), microbial photosynthesis (light carbon fixation), microbial chemosynthesis (dark carbon fixation), microbial methanotrophy (see Sect. 8.2.1.2) and humification (the diversion of litter into humus through microbial and chemical reactions) (Albrecht et al. 2010; Novis et al. 2007; Prescott 2010; Vargas-García et al. 2010). The extent to which these processes occur in various soil ecosystems and the assemblages of soil microbes that mediate these specific C-capture processes requires a systems approach and a highly integrated research effort.

8.2.3 Novel Applications for Soil Microbes in Global Change Mitigation Strategies

An emergent role for microbes is their potential as sensitive indicators of adverse effects of mitigation strategies. For example, geosequestration, the process of deep ocean subsurface deposition of CO_2, is an important strategy for reducing atmospheric CO_2. The environmental impact of CO_2 leakage from these deep reservoirs into near-surface terrestrial environments is largely unknown. A CO_2GeoNet project team (http://www.co2geonet.com, cited 18 Dec 2010) is using the abundance and diversity of "environmentally important" bacteria living in deep ocean sediment to provide sensitive indicators for the leakage of CO_2 from deep reservoirs into near-surface terrestrial ecosystems (Krüger et al. 2009). This study suggests that the different CO_2 gradients select for distinctive and measurable microbial communities that shift towards anaerobic and acidophilic species under elevated CO_2 concentrations. It is proposed that these communities can provide a sensitive and reliable fingerprint of the extent of leakage. Another study by Cunningham and co-workers (2009) is using engineered microbial biofilms which are capable of precipitating crystalline calcium carbonate to form a plug that may result in the long-term sealing of preferential leakage pathways.

8.2.4 The Impact of Global Change on Soil Biota

The impact of global change and specifically elevated temperature and carbon dioxide on soil processes has largely focused on the measurement and predictive

modelling of greenhouse gas emission trends over space and time. A better mechanistic understanding of many global change processes and the opportunities for adaptation and mitigation could be obtained from a greater focus on microbial physiology and metabolism, the factors controlling microbial assemblages, and of their spatial and temporal distribution (Scow and Louise 1997). A limited number of multidimensional, multinational programmes have been established to map trends in greenhouse gas evolution (e.g. NitroEurope; http://www.nitroeurope.eu and the Austrian research network, MICDIF; http://www.nfn.oberwalder.info/NFN). These programmes incorporate the measurement of microbial community diversity and function as important components of understanding greenhouse gas efflux patterns that are linked to global change scenarios.

There are two investigative approaches for assessing the likely impacts of global change on soil microbial diversity. The first is the use of free air carbon dioxide enrichment experiments (usually abbreviated as FACE) which are field-based facilities of defined area containing a representative plant ecosystem that is exposed to ambient or elevated CO_2 with or without elevated ambient temperature. There are numerous examples of FACE experiments (e.g. BioCON, University of Minnesota; http://www.biocon.umn.edu, TasFACE; University of Tasmania; http://www.utas.edu.au). An alternative approach is to focus on ecosystems that are particularly vulnerable such as the high altitude forests (N-enrichment threats) and Polar Regions. The microbial communities in both these regions can be viewed as sentinels and as amplifiers of global change factors and polar regions in particular are regarded as ideal model ecosystems for exploring microbial changes associated with elevated temperature and CO_2 (Vincent 2010). Other reasons cited for the focus on polar regions are that soils are poorly developed with a simplified soil food-web structure, and that significant warming has already occurred with greatest global warming rates being recorded here (Rinnan et al. 2009; Robinson 2009). There are many more studies that examine the effects of temperature and CO_2 separately, and for this reason they are treated separately below.

8.2.4.1 Elevated Temperature

Global surface temperatures have increased 0.76°C from the average calculated from 1850 to 1899, to the current average calculated from 2001 to 2005. Eleven of the last 12 years have been the warmest experienced since instrumental records began in 1850 (Houghton et al. 2007). Several studies have demonstrated the impacts of elevated temperature (eT) on gross soil biological processes such as respiration and decomposition with a clear trend for enhanced rates of decomposition with increasing temperature in medium- to long-term studies. For example, organic matter decomposition rates in Maritime Antarctic terrestrial ecosystems (Antarctic Peninsula regions of Anchorage and Signy Islands) were contrasted with those at the cool temperate Falkland Islands. Higher temperatures applied in field studies led to small increases in organic matter breakdown in both ecosystems with effects more strongly influenced by local substratum characteristics (especially

soil N availability) and plant functional type than by large-scale temperature differences. It was concluded that substantial warming (4–8°C) is required before significant effects can be detected (Robinson 2009). Studies have also indicated that warming effects are influenced by the plant rhizosphere and season. For example, an increase in temperature 3°C above ambient did not effect root rhizosphere respiration as much as bulk soil respiration. Furthermore, there was a significant stimulation of belowground respiration during the coldest part of the year when plant productivity was low. These findings have clear consequences for the modelling of belowground respiration and emphasise the need for separating root and bulk soil respiration fluxes and for accounting for seasonal effects (see Chap. 7). Most importantly, they suggest that the warming-induced increase in decomposition will reduce C storage in the soils of temperate ecosystems (Hartley et al. 2007; Kirschbaum 1995; Zhang et al. 2005).

A limited number of studies have examined the impact of eT on soil biological communities. For soil fauna, global warming and changes in the quality and quantity of litter are the main factors that are expected to increase mesofaunal biomass and diversity and alter life history features (Coûteaux and Bolger 2000). Microbial communities are more adaptable to eT and responses can vary depending on the historical exposure of the community to a range of soil temperatures (Waldrop and Firestone 2006). In an Antarctic climate gradient experiment, where eT was applied in open top chambers, bacterial communities adapted to the mean annual temperature of their environment. It was also estimated that the predicted increase of 2.6°C for the Antarctic Peninsula would increase the minimum temperature for bacterial growth by 0.6–1°C. Interestingly, the temperature sensitivity of bacterial communities increased with mean annual soil temperatures suggesting that communities from colder regions were less temperature sensitive than those from warmer regions (Rinnan et al. 2009). These adaptive responses have also been demonstrated in laboratory-based experiments for both fungal and bacterial communities over a wide range of temperatures (5–50°C) and particularly above the optimum for microbial growth (about 30°C). Increasing soil temperature above this optimum resulted in an increase in the optimum for bacterial and fungal growth with minor effects on growth below this optimum, although lower temperatures selected for communities growing better at the lowest temperature (Barcenas-Moreno et al. 2009). This adaptive response to eT has been correlated with changes in community structure with distinct microbial heterotrophic communities observed at different temperatures (Andrews et al. 2000) and declines in soil fungi and Gram-negative bacteria relative to Gram-positive bacteria (Feng and Simpson 2009). These changes in community structure have also been associated with decreases in microbial biomass, enzyme activities and microbial respiration (Waldrop and Firestone 2006). Feng and Simpson (2009), however, cautioned about the confounding effects of substrate utilisation in elevated temperature response studies concluding that faster exhaustion of available nutrient sources at higher temperatures rather than temperature per se primarily regulated microbial biomass, and that SOM quality intimately controls microbial responses to global warming.

It is clear that soil fauna and microbes respond directly and to varying degrees to eT, but other factors such as substrate availability and quality also play a role in this response (see Chap. 5). The thermal acclimation potential of soil communities in various global ecosystems needs to be resolved using high resolution approaches to accurately predict the likely outcome of prolonged temperature increases. Furthermore, a focus on eT impacts on key soil functional guilds associated with the provision of ecosystem goods and services and specifically greenhouse gas loss and capture mechanisms is also required. Technologies that resolve microbial community structure and function will provide unprecedented insight into eT in global ecosystems (see Sect. 8.4).

8.2.4.2 Elevated CO_2

The effects of elevated CO_2 (eCO_2) are mainly considered to be beneficial for plants, and hence by association, for soil biota too, since plant ecosystems respond to rising CO_2 concentrations with increased photosynthesis, growth and resource allocation. This in turn is thought to affect all soil dwelling species as a result of quantitative and qualitative alterations in C and other nutrients, and in water availability (Coûteaux and Bolger 2000; Drigo et al. 2007; Hu et al. 1999; Kanerva et al. 2008; Moscatelli et al. 2005; Yuan et al. 2006). Given the complexities and highly interactive associations in soil, the response to eCO_2, as with eT, is likely to be variable and unlike eT, mainly indirect.

Comprehensive reviews have highlighted the major impacts of eCO_2 on soil fauna (Coûteaux and Bolger 2000) and microbial communities (Waldrop and Firestone 2006; Zak et al. 2000). In contrast to the effects of eT, the effects of eCO_2 are largely indirect and influenced by litter quality and quantity, seasonality of substrate supply and global warming (Coûteaux and Bolger 2000). Zak and colleagues (2000) summarised data from 47 published reports on soil microbial C and N cycling under eCO_2 in an attempt to generalise whether process rates increase, decrease or remain unchanged. This synthesis focussed on changes in soil respiration, microbial respiration, microbial biomass, gross N mineralisation, microbial immobilisation and net N mineralisation, representing important control points for the belowground flow of C and N. With few exceptions, and as with eT, the rates of soil and microbial respiration were more rapid under eCO_2, indicating that (1) greater plant growth under eCO_2 enhanced the amount of C entering the soil, and (2) additional substrate was being metabolised by soil micro-organisms (see Chap. 7). In contrast, microbial biomass, gross N mineralisation, microbial immobilisation and net N mineralisation under eCO_2 were highly variable, and it was concluded that there were insufficient data to predict how microbial activity and rates of soil C and N cycling will change as the atmospheric CO_2 concentration continues to rise (Zak et al. 2000). There has, however, been significant research activity in the last 20 years and not surprisingly the whole spectrum of soil biological responses to eCO_2 (e.g. stimulatory, inhibitory, no effect, transient and disparate) have been reported and mainly from

experiments conducted at FACE facilities globally. For example, inhibitory responses to eCO_2 have been recorded for methanotrophy from a coniferous forest free-air CO_2 enrichment (FACE) site with net CH_4 consumption (soil methanotrophic activity), being 47% lower despite similar moisture, temperature, NO_3^- and NH_4^+ contents. It was concluded that a reduction in the strength of the CH_4 soil sink may ultimately affect the atmospheric CH_4 budget and, consequently, future climates (Phillips et al. 2001). Other studies have demonstrated little or no changes in microbial activity in response to eCO_2. This has been reported for N_2 fixation (Billings and Ziegler 2005), for rhizosphere populations of bacteria, NH_4^+-oxidising bacteria and *Rhizobium leguminosarum bv. trifolii* (Drigo et al. 2007; Schortemeyer et al. 1996), for microbial biomass nitrogen, rates of nitrogen mineralisation and nitrification, bacterial substrate utilisation and extracellular enzyme activities (Sinsabaugh et al. 2003), for total PLFA biomass, profiles and specific subgroups for 16S rRNA gene clone libraries (Kanerva et al. 2008), extracellular enzyme activity and potential soil N mineralisation and nitrification (Austin et al. 2009), and for arbuscular mycorrhizal fungi (AMF) measurements (hyphal length, glomalin-related soil protein) (Clark et al. 2009). Many more studies have demonstrated either variable or transient shifts in soil microbial communities. The wide range of responses is commonly attributed to the confounding influence of the plant response to eCO_2 in terms of compositional change in litter, in seasonality and in competition with the microbial community for nutrients. For example, microbial enzyme activities associated with N or P mineralisation only increased when plant nutrient limitation was strongly exerted under eCO_2 (Kang et al. 2005) and soil microbial population shifted to a more fungal dominated community with reduced plant residue N quality (Drigo et al. 2007; Kandeler et al. 2008). Seasonality related to plant biomass quantity and fertilisation were important overriding factors in determining changes in the nematode abundance and diversity (Li et al. 2009). Furthermore, increased competition between the plant and the microbial community for nutrients and particularly nitrogen has also been demonstrated under eCO_2 (Freeman et al. 1998; Insam et al. 1999).

The impacts of eCO_2 are also complicated by the multiple interactions within microbial communities. For example, a study of a grassland microcosm soil by Barnard and co-workers demonstrated how soil nitrifying enzyme activity had a tendency to increase while denitrifying enzyme activity decreased under eCO_2, but a possible large immobilisation of N by soil micro-organisms concurrently may have reduced soil nitrate concentrations under eCO_2, leading potentially to decreased nitrate leaching and denitrification (Barnard et al. 2005). Free-living bacterial-feeding protozoa increased or decreased under eCO_2 depending on whether mycorrhiza was present or absent (Rønn et al. 2002). A similar disparate response to eCO_2 was observed for rhizosphere bacterial and fungal communities depending on the presence of mycorrhiza (Drigo et al. 2007, 2009). Other examples of highly interactive effects of eCO_2 are related to water availability and faunal lifecycles (Coûteaux and Bolger 2000), soil drying and the capacity of mycorrhizal fungi and plant growth

promoting bacteria to contribute to aggregate stability (Kohler et al. 2009), and soil type on rhizosphere nematode and mycorrhizal fungi (Drigo et al. 2007).

8.3 Specific Challenges for Resolving the Role of Soil Biota in Global Change

The soil biota remains the most elusive and challenging component of soil health in terms of precise measurement of who is present and active and meaningful interpretation of global change impacts. Several challenges will be highlighted related to: (1) community structure (who is there) to function (what they are doing), (2) microhabitat diversity and scale and (3) applying ecological rules.

8.3.1 Soil Communities: Structure and Function

Describing the soil biota according to a range of parameters such as size, abundance, and taxonomic and functional guilds is the first step in elucidating the relative impact of physicochemical factors related to climate, geomorphic soil class, major land-use and soil management. The cataloguing of assemblages according to their taxonomy is a work-in-progress with estimates of only 1% of bacterial and viral, 5% of fungal, 12% of collembolan, 15% of mite and 50% of earthworm species having been described (Gatson and Spicer 2004; Hawkesworth 2001; Lavelle 1996; Williamson et al. 2005). The capacity to identify single species (or genomes) and entire microbial communities (or metagenomes) through DNA-based sequencing technologies is increasing knowledge of taxonomy of soil biota at an unprecedented rate (Sect. 8.4). But is taxonomy enough? Of all the technical definitions of soil health, biological function rather than taxonomy is highlighted. There are several levels of functional classification of soil biota from the low resolution or food-web-based categories of ecosystem engineers, litter transformers, phytophages and parasites, micro-predators and microflora (Lavelle 1996) to categories based on gene abundance linked to enzyme targets and to phylogenetically linked gene expression (Tringe and Hugenholtz 2008). While the food-web-based functional categories take into account the potential top–down regulatory controls of larger organisms (e.g. the ecosystem engineers) over smaller ones, a higher resolution classification is required to more precisely attribute soil health functions and the organisms involved in agroecosystem goods and services (Kibblewhite et al. 2008b; Van Der Heijden et al. 2008). The linkage of soil biological community structure to function and then to ecosystem goods and services is the ultimate goal. Not only will this assist in creating a societal value for specific functions associated with soil health, it will also enable more targeted management of these soil functions to improve soil health to achieve multiple outcomes in a global change context.

8.3.2 Microhabitat Diversity and Scale

The extreme heterogeneity of the soil microhabitat arises because of inherent geomorphological and hydrogeological soil features, as well as the non-uniform effect of external conditions (e.g. climate and nutrient inputs). One consequence of a large diversity of microhabitats is that the predicted impact of a disturbance (e.g. eCO_2 and eT) on a given species may not be the same even over a small area (Bardgett et al. 2005). This can be problematic when applying the "sentinel or indicator" species concept because the relative sensitivities to say, eT for example, may differ over a small spatial scale due to the large habitat diversity, and the identified sensitive species may therefore not be present in a closely located soil ecosystem (Bünemann et al. 2006). Examples of important mechanistic questions like "how will global change factors such as elevated CO_2 and temperature influence soil N and C turnover?" will require more targeted examination at smaller scales where intracellular and intercellular interactions occur. Clearly, soil biological processes occur at a much lower scale (micrometre to metre), and the compositing of samples across an area can mask effects (Manter et al. 2010). Important agronomic issues that are likely to be impacted by global change such as disease spread and suppression and nitrogen mineralisation and fixation and are mediated by specific rhizosphere biological processes will also require a much finer scale of investigation (from micrometre to metre) (Watt et al. 2006). Another important consideration relates to the way some microbes transcend scale in their exploitation of soil niches. A good example is where the prey, a fungus, extends hyphal networks across a larger scale (metres) than their predators (springtails and mites), which may extend only a few centimetres (Wall et al. 2005). This suggests that in some cases, several scales must be considered simultaneously to explain soil N and C turnover.

The impact of global change on these functions must therefore apply sampling strategies and statistical approaches that take into account heterogeneity of microhabitat (Baker et al. 2009) and interpolates across scale to account for the principal that the sum of soil functions at the micrometre scale, controlled by spatial organisation (of soil), affects metre scale function (Herrmann et al. 2007).

8.3.3 Applying Ecological Rules

Soil is a complex ecosystem and the soil biological community performs multiple, highly interactive functions that collectively reflect soil health status. These are nutrient cycling, pesticide degradation, disease control and plant growth promotion. Soil ecosystems behave differently to aboveground or plant-based ecosystems, so that the rules that are generally applied to ecosystem processes do not always hold when applied belowground (Wall et al. 2005). These "conceptual anomalies" must be considered in monitoring strategies and in the interpretation of data to assess the

impacts of human activities and global change. One feature of belowground communities is "functional interdependency". This concept was highlighted in a review co-chaired by Handelsman et al. (2007), who described the ability of microbes to eat rock, to breathe metals, transform the inorganic to the organic and crack the toughest chemicals as a microbial bucket brigade. "Each microbe performs its own task, and its end product becomes the starting fuel for its neighbor". This concept is more specifically illustrated as syntrophy (or literally, "feeding together"), which is where two or more species with contrasting nutritional characteristics require each other to function (Paul 2007). In syntrophy, one species may produce a product or environment that is essential for a second species to function. In most cases, the nature of syntrophic reactions involves H_2 being produced by one partner and consumed by another. This "interspecies H transfer" allows anaerobic microbes to grow in aerobic environments. There are many examples of syntrophic systems including the nitrification–denitrification coupling (see Sect. 8.2.1.1) and the degradation of ethanol to CH_4 and CO_2 (*Desulfovibrio* spp. and a methanogen, *Methanobacterium* spp.) (Fenchel and Finlay 1995).

Another concept worthy of note in the context of global change is functional redundancy, where one function can be carried out by a range of different microorganisms. It is generally used to explain the different levels of stability in soil ecosystems. The underlying principle is that microbial communities with functionally redundant species may display similar levels of indicator enzyme activities across a range of environmental conditions (Marschner et al. 2003; Perez-Piqueres et al. 2006). Loss or reduction in the population size of a particular species following normal disturbance events (e.g. eCO_2 and eT) thus does not impair key functional characteristics of the soil such as biodegradation, nitrogen transformations, disease suppression and plant growth promotion.

Community ecological concepts related to interdependency, including symbioses or syntrophies and redundancy, must therefore guide experimental design, measurement and interpretation when elucidating roles of soil biota in global change. The proceeding section describes how emergent biotechnological and biostatistical approaches are providing unprecedented access to the soil microbial communities with all the complexities associated with temporal-spatial scale and functional interdependencies.

8.4 Enabling Technologies and Applications in Global Change

The unprecedented growth in knowledge of soil biota and particularly of the microbial component can be attributed to the arrival of sequencing and scanning technologies and greatly enhanced computational power to generate and process large, multiparametric datasets. Many of the emergent biotechnologies will provide "warp speed" advancement in knowledge of soil biological systems by virtue

of the following features: (1) they are rapid throughput, allowing for parallel detection of a range of features of interest (species, functions), (2) they integrate large data sets and reveal relationships between these datasets in a visual output format and (3) they provide high level visualisation of mechanistic information.

8.4.1 Soil "Omics" Technologies

The suffix "ome" is derived from the Greek word for "all" or "every". The original term was "genomics" referring to the study of the genetic material contained in an organism or cell. Many technologies are now described using the "omics" suffix, and several are beginning to be applied to the study of soil biological systems. For example, metagenomics studies the DNA of communities of soil organisms (answers who is in the community), and transcriptomics studies the RNA (and answers simultaneously who is there and what is functioning). Proteomics is the study of proteins in an organism. Metabolomics is the study of the entire range of metabolites, the precursors and products of enzymatic activity and can provide an overview of the metabolic status of a biological system (Yu Lin et al. 2006).

8.4.1.1 Soil Metagenomics

The soil metagenome is defined as the collective genomes (bacterial, archaeal, fungal and viral) in or recovered from soil and starts with the extraction of both DNA and RNA (Daniel 2004, 2005; Handelsman et al. 1998). Soil metagenomics is by far the most widely embraced of the new technologies to apply to soil addressing a serious shortcoming of conventional soil microbiology, the inability to identify the vast majority (99%) of soil organisms and the functions they perform (Chen et al. 2008; Keller and Zengler 2004; Xu 2006). It is therefore providing an unprecedented view of the taxonomic diversity, metabolic potential and ecological role of soil microbial communities enabling powerful resolution of the multiple ways in which soil microbes can benefit society. The importance of this technology lies within the emergent ecological concept that vital ecosystem services (e.g. mitigation of CO_2 plant growth promotion and disease suppression, nutrient cycling and bioremediation) are undertaken by a whole community of microbes working together in a self-organised pattern. Understanding the dynamic role of microbial communities is currently an unmet challenge. Metagenomics technologies will have a central role in answering some big questions that have been eloquently posed by Handelsman et al. (2007) and subcommittee members. These are:

- How resilient are microbial communities in the face of rapid global change?
- Can microbial communities, versatile as they are, help to buffer and mediate key elemental cycles now undergoing rapid shifts?

- Can changes in microbial communities serve as sensors and early-alarm systems of environmental perturbations?
- To what extent can we manage microbial communities to modulate the effects of human activities on natural elemental cycles sensibly and deliberately?

These questions will be answered neither by culturing microbes nor by sequencing single genomes or conserved genes (e.g. 16S and 18S rRNA). Considerable momentum is now building for global coordination of soil metagenomics research efforts to ensure consistency in (1) sampling strategies to address spatial and temporal variability, (2) DNA extraction procedures to maximise representation and (3) interpretation of output sequence data (http://www.terragenome.org).

While metagenomics provides an overarching community approach for understanding anthropogenic impacts, there are some specific and elegant tools that will allow the linkage of community structure with function and specifically the construction of gene-to-metabolite networks related to functions such as greenhouse gas production and C sequestration. There are several emergent enabling technologies that will greatly assist in this aim. The two receiving most attention and therefore worthy of mention are metatranscriptomics and stable isotope probing (SIP) or SIP-coupled techniques.

8.4.1.2 Soil Metatranscriptomics

Transcriptomics refers to the measurement of the transcriptome or the set of all messenger RNA (mRNA) molecules, or transcripts, produced by a cell. "Meta"transcriptomics is therefore the transcriptome of functions derived from a population of cells that would occur in soil. Because RNA is extracted in this analysis, the active or expressed subset of genes that are being transcribed under certain soil environmental conditions, rather than those simply present (as with DNA extraction) are measured. Expression profiling can be used to assess active groups of soil microbes present under certain environmental conditions (Urich et al. 2008) and to detect biocatalysts and other resource material associated with a range of applications including alternative energy production (Ferrer et al. 2009; Warnecke and Matthias 2009).

8.4.1.3 Stable Isotope Probing

SIP particularly when combined with other molecular technologies is a powerful approach for linking community function and structure. SIP is a technique that is used to identify the micro-organisms in environmental samples that use a particular growth substrate. The method relies on the incorporation of a substrate, including bacteria, that is highly enriched in a stable isotope, such as ^{13}C or ^{15}N and the identification of active micro-organisms by the selective recovery and analysis of isotope-enriched cellular components from the microbial community (Dumont and Murrell 2005; Dumont et al. 2006; Friedrich 2006; Manefield et al. 2002; Radajewski et al. 2000). Some examples of SIP-coupled technologies that are relevant to global change studies are SIP of phospholipid fatty acids (PLFA-SIP)

and rRNA (RNA/DNA-SIP) to analyse the metabolically active methanotrophic community in soil and water (Boschker et al. 1998; Cebron et al. 2007; Qiu et al. 2008), to detect benzoate-utilising denitrifying bacteria (Gallagher et al. 2005) to assess the primary production functions in a dark environment (Chen et al. 2009) and to determine the role of earthworms in soil CH_4 emissions (Hery et al. 2007). Finally, and most recently, the coupling of SIP and metagenomics has enabled a genome-wide analysis of methylotrophs and has been used to target a novel methylotroph, *Methylotenera mobilis*, and to reconstruct its metabolism (Chen et al. 2009; Kalyuzhnaya and Lapidus 2008).

8.5 Future Needs

Soil biota is a critical element in the search for new knowledge leading to improved prediction and management of adverse impacts of global change. There are outstanding needs and challenges that must take account of three key facts (Chapin et al. 2009): (1) soil is the most diverse ecosystem on the planet, (2) only 1% of the soils microbial diversity is catalogued and (3) ecological concepts that apply to aboveground plant communities do not always apply belowground. These highlight that knowledge of soil biota per se and as mediators of global change processes is relatively rudimentary. The timely arrival of "omics" technologies has provided high resolution, purpose built tools for providing unprecedented access to the hidden majority and has spawned a new science discipline in bioinformatics. It will generate new and/or modified ecological rules and hence a much needed framework for understanding a whole range of anthropogenic impacts. Also critical to a renewed focus on soil biota is the need for greater intellectual organisation, and strong leadership and advocacy from the global Research and Development community. Once achieved, research efforts can be coordinated to generate shared outcomes such as: (1) new knowledge of the underlying soil biological processes and the multiple regulators that control responses to eCO_2 and eT *in a relevant time frame and spatial context*, (2) deep exploration of the mainly "hidden" microbial community for alternative bioenergy applications, and (3) data for enhanced predictive modelling capability to ensure that the current anthropogenic impacts can be managed efficiently and cost-effectively.

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