

Elevated temperatures and carbon dioxide concentrations: effects on selected microbial activities in temperate agricultural soils

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Received: 6 May 2009 / Accepted: 25 June 2009 / Published online: 8 July 2009
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Abstract Human activities have increased greenhouse gas concentrations in the atmosphere. Research has demonstrated this increased concentration will affect our climate by causing increases in temperature and altered weather patterns. The effects of climate change have been studied, including effects on some ecosystems throughout the world. There are studies that report changes in the soil due to climate change, but many did not extend their research to the microorganisms that inhabit soils. In our analysis of soil microorganisms that may be affected by climate change, two microbial outcomes emerged as having particular ecological and societal importance. Perturbations in the soil environment could lead to community shifts and altered metabolic activity in microorganisms involved in soil nutrient cycling, and to increasing or decreasing survival and virulence of soil-mediated pathogenic microorganisms. Alterations in CO₂ concentrations and temperature may alter soil respiration, soil carbon dynamics, and microbial community structure. Microbial-mediated processes that play an important role in the nitrogen cycle may also be influenced as a result of climate change. The potential for an increase in frequency of horizontal gene transfer due to changing climatic factors is of concern due to possible evolutionary changes in soil-borne pathogen populations, including the spread of virulence factors and genes that aid in environmental survival. We suggest that soil microbial communities in temperate agricultural systems continue to be researched for alterations to community structure, specifically the increase or decrease of soil activity and respiration,

nitrification and denitrification, pathogen survival and alterations to horizontal gene transfer.

Keywords Agriculture · Activity · Bacteria · Biosphere · Carbon dioxide · Climate change · Emissions · Environment · Gene transfer · Global warming · Microorganisms · Nutrient cycles · Pathogens · Respiration · Soil

Introduction

Global climate change alters the biosphere. Although changes to terrestrial and aquatic ecosystems are predicted, agricultural soils are of specific interest due to the large area of the Earth's surface they cover for food production, and their importance in the release and sequestering of greenhouse gases, irrigation and fertilizer impacts on water and nutrient cycles, and their diverse communities of microorganisms. Tilman et al. (2001) estimated in 2000 there were 1.54×10^9 ha of cropland, 3.47×10^9 ha of pasture, and 2.80×10^8 ha of irrigated land worldwide, which are estimated to increase by 18.5, 13.4, and 47.1% by 2050, respectively. Agricultural soils play a central role in the global carbon and nitrogen cycles. For example, cultivated soils under conventional tillage practices release about ten times more nitrous oxide than poplar forest soils (Robertson et al. 2000).

Agricultural soils contain a diverse community of endogenous plant pathogens (Manning and Tiedemann 1995) and manure amendments to these soils can provide a source of potential human and animal pathogens (Kudva et al. 1998; Wells et al. 1999; Gagliardi and Karns 2000). For these reasons, it is necessary to understand how the complex agricultural soil environment and soil microbial

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communities will respond to global climate change (Fig. 1). Agricultural soils in temperate regions will be focused on because: (1) the effects of global climate change are predicted to increase winter temperatures (Intergovernmental Panel on Climate Change (IPCC) 2007), altering the soil environment in these regions and; (2) research regarding the effects of climate change on the agricultural soil environment has occurred in temperate regions.

Anthropogenic factors such as fossil fuel usage and land use changes have increased the concentrations of greenhouse gases in the atmosphere over the last century (IPCC 2007). Increases in the human population, increases in agricultural production and global industrialization over the last century have increased the rate of addition of greenhouse gases to the atmosphere. Well-mixed greenhouse gases such as CO₂, N₂O, CH₄, and halocarbons, in addition to water–vapor feedback and solar irradiance, contribute to increases in the mean global temperature, which is predicted to continue increasing (IPCC 2007). The average global concentration of atmospheric CO₂, the predominant greenhouse gas of anthropogenic origin, was about 380 ppm in 2005, which exceeds the previous maximum concentration for the past 650,000 years by about 80 ppm (IPCC 2007). Agriculture is the predominant source of nitrous oxide emissions, accounting for more than a third of all N₂O emissions (IPCC 2007). Nitrous oxide has a global warming potential of about 300 times CO₂ (IPCC 2007). The global atmospheric N₂O concentration was 319 ppb in 2005, an increase from the pre-industrial estimate of 270 ppb. Other changes to surface reflectance due to land use changes, cloud cover and

atmospheric concentrations of sulfate aerosols decrease the global mean temperature. The result is an increase in the global mean temperature and a decrease in global inter-annual temperature variability (Michaels et al. 1998; Jones et al. 1999a). However, regional changes may become increasingly variable. As the mean temperature rises, some studies have shown the frequency of extreme warming events will increase (Bonsal et al. 2001; Manton et al. 2001; Wang and Gaffen 2001), although these data have been debated (Jones et al. 1999b; Kunkel et al. 1996, 1999; Karl and Knight 1997). On a regional scale, extreme temperature and precipitation events are expected to increase in duration and severity (Karl and Knight 1998; Groisman et al. 1999; Gruza et al. 1999; Easterling et al. 2000; Haylock and Nicholls 2000; Dai et al. 1998). The anthropogenic alteration of global atmospheric gas concentration, temperature ranges, and precipitation events will affect the soil environment, and in some cases may alter soil microbial communities.

While the IPCC (2007) Working Group II report—*Impacts, Adaptation and Vulnerability* offers an analysis of ecosystem effects of climate change, terrestrial microbial communities were not discussed. To understand the effects of climate change on soil microorganisms, it is necessary to elucidate how the soil environment may change. Data suggest that an increase in soil moisture content due to rainfall is likely in some areas (Karl et al. 1995; Dai et al. 1998). For example, increased soil moisture decreases gas exchange and porosity, and indirectly changes both pH and soil redox potential. Other areas may experience drought conditions with different outcomes on soil microorganisms.

Alterations to the soil microbial community due to climate change may have environmental, economic and societal impacts. Ecological concerns arising from shifts in the soil environment, agricultural and human health effects are due to impacts of climate change on microbial communities and biogeochemical processes. Specific concerns regarding alterations to the microbial community include the altered activities of microorganisms in soil nutrient cycling and the survival, persistence, and movement of soil-borne microbial pathogens to areas where they were previously not present, or not a problem in agricultural crop production.

Numerous groups and species of microorganisms may be affected by climate change. However, to the best of our knowledge, a synthesis of data pertaining specifically to nutrient cycling microorganisms and microbial pathogens in soil requires additional research. Some reviews have been compiled examining the effects of climate change on plant pathogens in agricultural systems (Manning and Tiedemann 1995; Chakraborty et al. 1998; Coakley et al. 1999; Rosenzweig et al. 2001; Fuhrer 2001). This subject

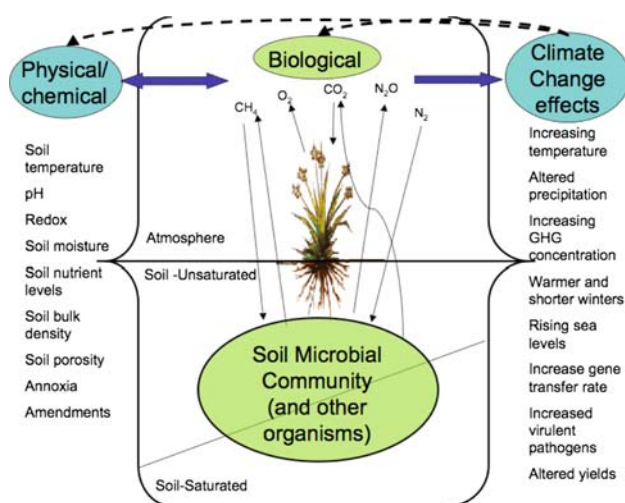


Fig. 1 Some complex interactions between climate change and soil microbial communities. Climate change affects soil microbial communities and vice versa under dynamic biological, chemical and physical conditions

will be not be covered in this review to avoid repetition, although information will be provided when new information forthcoming after these reviews were published, is available.

Effect of climate change on microbial-mediated soil nutrient cycling

Climate change and soil microbial processes are linked through the complex bidirectional interaction of the soil and atmosphere. Microbial processes in soil release greenhouse gases (e.g., CO₂, N₂O, CH₄) and soil serves as a sink for carbon in agricultural soils (Cole et al. 1996). The soil microbial community also regulates the cycling of nutrients essential to maintaining a productive and fertile soil system. Climate change can affect the soil system in numerous, interacting ways (see Fig. 1). In this section we focus on the effects of increasing temperature and increasing atmospheric CO₂ concentrations. The changes in the soil microbial community due to climate change will be linked to temperate agricultural systems to serve as an example of how the changes in the soil community will also affect humans.

Effect of temperature on microbial processes

Direct effects of increased soil temperature include accelerated losses of CO₂ and CH₄ from soil by increasing the activity of plant roots and soil heterotrophs (Pendall et al. 2004). Soil respiration contributes up to 10% of atmospheric CO₂ (Raich and Potter 1995) and other greenhouse gases. A global temperature increase of 2°C is predicted to increase soil carbon release by 10 petagrams (Pg; 10¹⁵ g) of carbon per year world-wide (Luo et al. 2001). While the terrestrial biosphere is currently acting as a carbon sink for CO₂ emissions of both natural and industrial origins, Cox et al. (2000) suggested that after 2050 the sink will become a source, increasing CO₂ concentrations in the atmosphere. Higher soil temperatures have been associated with increased net plant productivity, which may provide more substrates for heterotrophs in the long term, if other resources are not limiting (Trumbore 1997).

Under controlled conditions, soil respiration (heterotrophic and autotrophic) can increase as a result of elevated soil temperatures and thus a direct link between soil respiration and temperature, and potentially a means of positive feedback to global climate change has been postulated. There have been large-scale and long-term studies that contradict this relationship between respiration and temperature in soil. Some of these studies have observed a stabilization of soil respiration under increased temperatures in natural systems (McHale et al. 1998; Luo et al.

2001; Stromgren 2001; Melillo et al. 2002; Zhang et al. 2005). There are several hypotheses as to why this occurs: potential changes in microbial community structure may change overall microbial temperature sensitivity (Balser et al. 2006), changes in substrate availability associated with concurrent changes in temperature and water content (Eliasson et al. 2005; Davidson and Janssens 2006), decreases in plant litter quality and quantity over time (Rustad et al. 2001), and changes in relative abundance of labile carbon versus soil organic carbon (Fierer et al. 2005). A possible explanation for the acclimation of soil microbial respiration to temperature in a natural system is a combination of these factors to differing degrees in each individual system, and a model better describing the response of soil respiration to temperature needs to be proposed (see Davidson and Janssens 2006).

There have been studies that confirmed the positive relationship between temperature and microbial respiration in soil (Giardina and Ryan 2000; Dalias et al. 2001; Sanderman et al. 2003; Eliasson et al. 2005; Fang et al. 2005). These findings have been applied to modeling experiments which suggest results of the short-term soil-warming experiments are compatible with long-term sensitivity of soil organic carbon (SOC) turnover (Kirschbaum 2004; Knorr et al. 2005). Using different modeling techniques, both investigations concluded that long-term soil warming will affect SOC turnover, and agree there is a possibility of positive feedback between global warming and atmospheric release of SOC, more than was initially suggested (Kirschbaum 2004; Knorr et al. 2005). These findings refute those that suggest that increased SOC turnover is a transient process, which returns to “pre-warming” conditions after 1–3 years, due to acclimation. To better understand the relationship between atmospheric temperature increases and microbial respiration in soil, more large-scale, long-term field-based studies are required.

Soil microorganisms mediate numerous biogeochemical processes (van Elsas et al. 2007) connected to global climate change (e.g., CO₂ and N₂O emissions). Microbial biomass often responds positively to increases in temperature (Pendall et al. 2004), although this depends on other environmental factors, such as soil water content (Hungate et al. 1997), and nitrogen availability (Diaz et al. 1993). Zogg et al. (1997) observed that both substrate pools for microbial respiration and the abundance of biomarker Gram-positive and Gram-negative bacteria differed significantly among temperature treatments (5–25°C). This provides evidence for a shift in the function and composition of microbial communities in response to soil warming. Such changes following annual increases associated with global climate change may alter patterns of soil organic matter (SOM) decomposition. Communities of free-living and symbiotic microorganisms in non-rhizosphere and

rhizosphere soil locations may change in community structure and activity to mediate carbon cycle responses to soil warming, and in doing so, will increase turnover rates of soil organic carbon.

A changing climate will likely alter microbial mediated nitrification and denitrification dynamics in the soil environment. In a meta-analysis of climate change effects on nitrification and denitrification, Barnard and Leadley (2005) concluded that increased temperature had no effect on nitrifying enzyme activity (NEA) or net nitrification; however, there were only a small number of studies reviewed. Nitrification generally has an optimum temperature range between 20 and 35°C. Avrahami and Conrad (2003) observed that the proportion of N₂O associated with nitrification, decreases at elevated temperatures. In this study community shifts were observed in the ammonia-oxidizing bacteria (AOB) during a long-term incubation study (20 weeks) even when there was no net growth (Avrahami and Conrad 2003). Temperature did not have an effect on denitrifying enzyme activity (DEA) (Barnard and Leadley 2005). Their review demonstrates that laboratory studies can show a positive response of denitrification to temperature, whereas field and mesocosm experiments did not show this positive response, suggesting an acclimation of denitrification to temperature over time and under natural conditions. This reinforces the need for long-term field experiments studying the effects of global climate change on the microbial communities involved in soil nutrient cycling, so that researchers can discern if acclimation is actually occurring in the environment, and what the consequences of acclimation are.

Effects of elevated CO₂ on microbial processes

There are studies that describe increased atmospheric CO₂ concentrations effects on soil microbial respiration. A meta-analysis by De Graaff et al. (2006) was completed for open top chambers (OTC) and free-air carbon dioxide enrichment (FACE) studies on mineral soils. Observations from long-term and replicated experiments were weighted more heavily in the analysis. Microbial respiration increased by 17.1% under elevated CO₂ (ranging from 430 to 750 ppm) for herbaceous plant species. Microbial carbon (C) also increased by 7.7% in this same analysis. There was no difference between soils treated with nitrogen (N) and those that were not. The increase in microbial respiration was attributed to an increase in plant productivity associated with elevated CO₂, thus providing more C substrate to soil microorganisms (De Graaff et al. 2006). Conversely, other laboratory and field studies have shown that no change in soil respiration results from increases in atmospheric CO₂ (Billings and Ziegler 2005; Pinay et al. 2007).

Since elevated CO₂ generally stimulates plant production, it is possible that microbial biomass in bulk or non-rhizosphere soil would also increase under elevated CO₂. The majority of studies reviewed reported increases in microbial biomass. Drissner et al. (2007) researched the effects of increased atmospheric pCO₂ over nine years on the function and structural diversity of soil microorganisms in a FACE system with *Trifolium repens* (white clover) and *Lolium perenne* (perennial ryegrass). Under 60 Pa pCO₂, soil microbial biomass increased by 48.1% in the spring, and 23.1% in the autumn. These results contrast findings by Kandeler et al. (2006), who observed no significant changes in microbial biomass; however, this does not mean the bacterial communities are not affected by elevated CO₂, since changes (i.e., gene expression, enzyme activity) can occur without alterations in biomass size.

Elevated CO₂ has significant effects on enzyme activity in microbial communities in bulk soil. Drissner et al. (2007) examined the activities of a selection of enzymes involved in cycling carbon, nitrogen and phosphorus. In the spring, increases were observed in invertase (36.2%), xylanase (22.9%), urease (23.8%), protease (40.2%), and alkaline phosphomonoesterase (54.1%) activities. In the autumn, however, activities of these enzymes were 3–12% less (Drissner et al. 2007). These results highlight the importance of examining parameters beyond microbial biomass size. Knowledge of both the size and activity of a microbial community is essential to measure the changes in function of the community.

Influence of increased CO₂ on the rhizosphere

Because of the high level of biological activity in the rhizosphere, it has been hypothesized that interactions in the rhizosphere may be more sensitive to the effects of global climate change compared to non-rhizosphere soils (Xu and Chen 2006). The rhizosphere is the zone of soil influenced by plant roots. Viewed as the most chemically and biologically active location in soil, the rhizosphere is the location where the majority of plant-soil-microorganism interactions occur. The high level of microbial activity in the rhizosphere is due to rhizodeposition, the input of organic constituents from living roots to surrounding soil, including sloughed off cells, decomposition of root biomass, and root exudates such as amino acids, organic acids, sugars, polysaccharides and proteins (Walker et al. 2003). Rhizodeposition supports microbial communities surrounding the roots, which are important to ecosystem function since they reside in the key interface between plant carbon production and carbon flow to the terrestrial ecosystem (Paterson et al. 1997). Of equal importance, the activity of rhizosphere microbial communities directly influences plant growth, through mineralization or immobilization of plant nutrients,

mutualistic symbioses, or pathogenic interactions. Since the concentration of CO₂ in soil can exceed the concentration in the atmosphere a combination of increased atmospheric CO₂, soil warming or altered weather conditions may have significant direct and indirect effects on rhizosphere soil microbial communities.

Most of the articles reviewed reported increases in rhizosphere microbial biomass under increased CO₂ concentrations. Zak et al. (1993) reported a 121% increase in microbial biomass in the rhizosphere of *Populus euramericana* (Poplar) when exposed for 22 weeks to 690 ppm CO₂ in open top chambers. In contrast, other studies reported no change, or decreases in microbial biomass. For example, in a nine-year, FACE study by Bazot et al. (2006), soil microbial biomass in a rhizosphere soil of *L. perenne* was not significantly affected under increased CO₂ concentrations when sampled in spring. However in autumn sampling, microbial biomass had decreased by 46%. Though these investigations yielded different results, it should be noted these were conducted under varying experimental conditions (laboratory or field), length of study (months vs. years), plant species and characteristics of soil use (agriculture, pastoral, forest), which precludes a direct comparison of their results.

In addition to determining the effect of increased atmospheric CO₂ on rhizosphere microbial biomass, it is necessary to examine the effect on microbial community structure. Under elevated atmospheric CO₂, plants modify the rhizosphere and regulate the microflora (Paterson 2003); carbon flow into the soil increases, which can stimulate the growth and activity of microorganisms that rely on plant carbon sources. This has been the focus of investigations utilizing both molecular and metabolic approaches. In a study by Tarnawski et al. (2006), community function of *L. perenne*- and *Molinia coerulea* (purple moor grass)-associated *Pseudomonas* populations were altered following 8 years of increased pCO₂ (60 Pa) using the FACE system. This study, which utilized metabolic approaches, observed that the population density of *Pseudomonas* spp. was not significantly affected by an increased CO₂ concentration (60 Pa). However, certain functional groups in the population were stimulated such as siderophore-producing *Pseudomonas* spp. in the rhizosphere under increased CO₂ (Tarnawski et al. 2006). Siderophore production is important in root colonization by *Pseudomonas* spp., plant growth promotion, and in some cases, phytopathogenesis (Tarnawski et al. 2006).

Molecular techniques have been used to examine microbial community structure changes in the rhizosphere due to elevated CO₂. Marilley et al. (1999) observed an increased dominance of *Pseudomonas* spp. in the rhizosphere of *L. perenne* and decreased dominance of *Pseudomonas* spp. in the the rhizosphere of *T. repens* in the same FACE system used in the Tarnawski et al. (2006)

study. Pseudomonads are important rhizosphere bacteria that influence many plant–microbe interactions such as the colonization of plant roots by phytopathogens. Increases or decreases in their relative abundance in the rhizosphere has the potential to alter plant- and human-pathogen survival and distribution in both natural and agricultural soil ecosystems. To our knowledge, Marilley et al. (1999) published one of the only studies that observed a change in rhizosphere bacterial community as a result of increased atmospheric CO₂. Other groups using techniques such as phospholipid fatty acid profile analysis (Zak et al. 1996), community DNA hybridization and % G+C base profiling (Griffiths et al. 1998) reported no changes in rhizosphere community structure as a result of increasing atmospheric CO₂ (692, 718 ppm, respectively). These different observations indicate the importance of furthering research in this area, and applying several methods to elucidate community alterations. It is apparent that research conducted with different soils and plants under different conditions can produce different research outcomes.

Rhizosphere fungal communities respond differently to increases in atmospheric CO₂ compared to rhizosphere bacterial communities. In an investigation by Jones et al. (1998) fungi responded differently between ambient (350–400 ppm) and elevated (550–600 ppm) atmospheric CO₂ treatments. Not only did functional groups such as cellulose decomposers increase in biomass, but fungal taxonomic composition differed significantly between ambient and elevated CO₂. This finding was supported by Brant et al. (2006), who reported that increased long-term carbon input into soil (7 years) resulted in increased fungal:bacterial biomass ratio in soil compared to the control soil with normal carbon inputs.

Effect of increased CO₂ on mycorrhizal fungi colonization

Arbuscular mycorrhizal fungi (AMF) are the most widespread group of mycorrhizae and act as a sink for about 10% of plant photosynthate (Staddon and Fitter 1998). AMF are important for plant growth as they mediate competition between plant hosts and transfer nutrients to plant hosts via large surface area arbuscules. Because mycorrhizal colonization is dependent on host-plant photosynthesis, it has been speculated that increased atmospheric CO₂ will result in greater mycorrhizal colonization of plant roots (Diaz et al. 1993).

Some studies have reported significant alterations in AMF growth and colonization patterns. In research using the FACE system, the effect of 7 years of altered atmospheric pCO₂ (60 Pa) on root colonization of *L. perenne* (perennial ryegrass) and *T. repens* (white clover) by AMF was examined (Gamper et al. 2004). AMF root colonization

was increased in both plant species, with significant effects on colonization intensity and hyphal colonization. In addition, increased numbers of AMF spores in the soil of each plant monoculture were observed (Gamper et al. 2004). Similar responses were reported in Hartwig et al. (2002), although the study length was only 9 weeks. These results are in agreement with the hypothesis that higher availability in plant roots may stimulate symbiosis. In contrast, earlier studies reported little or no response of AMF colonization to increases in atmospheric CO₂ (Jongen et al. 1996; Staddon et al. 1998). Absence of AMF colonization response to CO₂ may be the result of not conducting experiments under free-air conditions, or with plants and AMF communities that were adapted to long-term increased pCO₂ conditions.

Ectomycorrhizae are symbiotic relationships formed between fungi (predominantly Basidiomycetes and Ascomycetes) and long-lived woody perennial plants. Though only a small fraction of plant species (about 8,000) are involved in these symbioses, ectomycorrhizae are important since they occupy a large global area (Finlay 2007). The reported effects of increased CO₂ on colonization are variable, and seem to depend on the particular plant-fungi association (Staddon and Fitter 1998). In *Pinus densiflora* seedlings infected with the ectomycorrhiza, *Pisolithus tinctorius*, and grown under increased atmospheric CO₂ (60 Pa), ectomycorrhizal development was stimulated under increased CO₂, and a resulting synergistic effect on plant growth was observed (Choi et al. 2005). A synergistic effect was probably observed due to increased carbohydrate availability in the root system, which benefits the fungi, increasing its capacity for nutrient uptake, thus benefiting the host plant (Staddon and Fitter 1998). Increased mycorrhizal colonization may act as a sink for fixed carbon, increasing the capacity of the plant's response to increased atmospheric CO₂.

Effect of elevated CO₂ on C and N cycling in soil

Soil C:N ratios increased under elevated atmospheric CO₂ (430–750 ppm) by 4.1% for woody plant species with no added effect of soil N (De Graaff et al. 2006). Elevated CO₂ increased soil N in systems with herbaceous plant species (De Graaff et al. 2006). Luo et al. (2004) theorized that under enhanced CO₂, available mineral N decreases due to increased C storage in the soil (the formation of SOM requires a certain ratio of C, N and other nutrients and thus an increase in C storage would require a certain amount of N storage). De Graaff et al. (2006) observed an increase in soil C by 1.2% per year under elevated CO₂ (430–750 ppm); however, the increase depended on soil N, with soils under low N (0–30 kg ha⁻¹) showing no change in soil C and those amended with N (>30 kg ha⁻¹) resulted in an increase of soil C. Another review by Van Groenigen

et al. (2006) reported that soils receiving greater than 30 kg N ha⁻¹ had an increase in soil C under elevated CO₂ levels (450–800 ppm).

Eckersten et al. (2001) reported increased productivity and decreased soil C over a long-term period under increased CO₂ levels from 353 to 515 ppm. Other studies have shown a decrease in soil C (Calabritto et al. 2002; Cardon et al. 2002; Hoosbeek et al. 2004; Dijkstra et al. 2005). One possible explanation for a decrease in soil C is that priming, which is the stimulation of soil organic matter decomposition, is occurring caused by the addition of labile substrates. This effect may be short term. The current evidence suggests that nutrient addition in the form of fertilizer or N₂-fixation is necessary for net soil C sequestration to take place under elevated atmospheric CO₂ (Hungate et al. 2003; Luo et al. 2004). In agricultural systems where this is likely to occur, C sequestration may be possible, however; soil C losses from soil disturbances must be managed. Low disturbance practices such as zero tillage could be implemented if net soil C sequestration is to occur under elevated atmospheric CO₂.

De Graff et al. (2006) also observed an increase in N immobilization by 22% and increased microbial N contents by 7.7% under increased CO₂ (430–750 ppm) and it was suggested that microbial N immobilization was a factor that caused acclimation of plant growth to elevated CO₂. Schneider et al. (2004) reported that nitrogen availability limited plant yields in a nine-year FACE study. Thus nitrogen limitation may be avoided if the ecosystem has sufficient N stocks, N inputs (N₂-fixation or fertilizer) or if N losses are reduced (Luo et al. 2004).

Research by Zak et al. (1993) suggested a positive feedback mechanism occurs between increases in CO₂ and increases in plant root growth, microbial activity, and the availability of nitrogen in the rhizosphere. Increased size and activity of microbial biomass has been observed in some studies (Drissner et al. 2007; Marilley et al. 1999). Over time, increased microbial activity may result in more nitrogen available for competing plant roots, or for denitrifying bacteria (Hungate et al. 1997). This supports the positive feedback mechanism suggested by Zak et al. (1993). For example, under increased atmospheric CO₂ and ample soil nitrogen, plant yields increase, resulting in increased carbon input into soil, and increased rhizodeposition. This stimulates microbial enzymatic activity, which may mobilize more nitrogen, making it available to the plant, causing further plant yield increases.

Effect of elevated CO₂ on nitrification, denitrification and N₂ fixation

In both field and mesocosm studies with both woody and herbaceous species it was reported that nitrifying enzyme

activity (NEA) decreased, gross nitrification did not change, and net nitrification increased under elevated CO₂ (550–750 ppm) (Barnard and Leadley 2005). This may be explained either by changes in NH₄⁺ levels because of changes in mineralization, or by increased water content associated with soils under elevated CO₂. Horz et al. (2004) also reported shifts in the AOB community structure and abundance under simulated global change using a FACE system for grasses and forbs. The total abundance of AOB decreased under elevated CO₂ (700 ppm) and was further decreased under elevated CO₂ and precipitation (50% above ambient).

Denitrification is a central process in the N cycle that has shown responses to simulated climatic changes. It is an anaerobic process that is influenced by oxygen, carbon and nitrate availability. Barnard and Leadley (2005) summarized that increasing CO₂ has a negative effect on denitrifying enzyme activity (DEA). Other studies have shown a decrease in soil NO₃⁻ under elevated CO₂ (Niklaus et al. 1998, 2001; Johnson et al. 2001; Tschlerko et al. 2001; Barnard et al. 2004a, c). However, a study by Tarnawski et al. (2006), which utilized metabolic approaches, observed that denitrifying *Pseudomonas* spp. in the *Pseudomonas* population were stimulated under increased CO₂ in bulk soil, even though the density of *Pseudomonas* populations were not significantly affected. In the same study, however, rhizosphere-associated denitrifying *Pseudomonas* spp. were decreased under increased CO₂, which was due to N limitation (Tarnawski et al. 2006).

Results of studies examining links between elevated CO₂ and N₂-fixation are not conclusive. In the meta-analysis by De Graaff et al. (2006) it was reported that elevated CO₂ (430–750 ppm) had no effect on N₂-fixation but when non-N nutrients were supplied there was a significant increase in N₂-fixation by 51%. It has been shown in short term pot experiments that N₂-fixers generally respond to increased CO₂ more than non N₂-fixers (Poorter 1993; Soussana and Hartwig 1996; Lüscher et al. 2000; Poorter and Navas, 2003; Ainsworth and Long 2005). Others have found no increase in N₂-fixation under increased CO₂ (Arnone 1999; West et al. 2005). These were longer-term studies and suggest that increased N₂-fixation may not be sustained in the long term under elevated CO₂. For example, Hungate et al. (2004) found that N₂-fixation increased in the leguminous vine *Galactia elliptica* in the first year of the study but this effect disappeared by the third year and for subsequent years of the study. This effect was attributed to decreased foliar concentrations of molybdenum (Mo) (key component of nitrogenase) potentially caused by a decrease in pH and increase in organic matter in soil caused by elevated CO₂, which would increase the adsorption of Mo to soil particles and decrease its availability to the plant.

The amount of data on soil C and N dynamics suggests that climate change will have an impact on the future of nutrient cycling in soil. CO₂ emissions from soils will possibly increase under increasing CO₂ concentrations and temperatures whereas N₂O emissions from nitrification and denitrification may decrease. This may be due to increases in the ratio of C to N in the soil. Microbial biomass is likely to increase under elevated CO₂ and temperature, as well as the ratio of fungi to bacteria.

Some temperate agricultural systems may deteriorate due to climate change without strict nutrient management. The progressive nitrogen limitation (PNL) theory suggested by Luo et al. (2004), points to decreases in plant production in the long-term without added nutrients. This process can be delayed in short-term studies by a number of ecosystem responses, indicating the need for long-term studies to fully understand the processes. There is evidence of significant changes to microbial communities involved in soil nutrient cycling, although more studies on community structure change and function should be attempted to complement the studies measuring gas emissions. Although there has been research on the compounding effects of all potential climate change variables, more research is necessary to understand the extent that climate change will affect the soil microbial system.

Effect of climate change on soil-mediated pathogens

Apart from the microbial processes likely to be affected due to climate change, impacts of climate change on plant and human health including infectious diseases have been focal areas (MacMichael et al. 2006; Harvell et al. 2002). Climate change may have an influence on pathogen survival in soil, host physiology and resistance, and host-pathogen interactions. The overall impact of climate change on plant pathogens has been reviewed (Coakley et al. 1999; Garrett et al. 2006), but a paucity of information exists on the effect of climate change on the fate of fecal-borne pathogens in the environment.

Microorganisms that have the ability to survive and grow in variable environments will have the greatest fitness if current climate trends continue. The term “soil-mediated bacterial pathogens” is used in this paper to designate soil-borne pathogens and pathogens from fecal matter that can persist for unknown periods of time, and also can be transported through soil by water flow.

Fecal pathogens in the soil environment

Pathogen contamination of potable water and food supplies has gained attention due to several incidences of disease outbreaks (Smith and Perdek 2003). Livestock infected

with zoonotic organisms can excrete pathogens in their feces and as a result, animal waste has been implicated as a source of infection in some human food-borne illness (Bach et al. 2002) and water-related illness. Animal manure application to agricultural lands is a major source of pathogenic microorganisms in surface and ground water systems (Reddy et al. 1981; Goss et al. 1998; Jamieson et al. 2002; Bach et al. 2002; Joy et al. 1998; Patni et al. 1984). Fecal pathogens can contaminate potable water via soil. The impact of predicted climate change on growth and survival of these pathogens and their virulence is worthy of study. Alteration of biotic and abiotic factors in the soil environment due to climate change may have an impact on growth and survival of zoonotic-based pathogens. Although some research has been performed on the impacts of climatic change on survival of these microorganisms, information deduced from field research and the food industry may be of value to better understand how pathogenic bacteria may react to a warming climate.

Effect of soil CO₂ concentration and temperature on survival of zoonotic pathogens

The concentration of CO₂ in soil is higher (10–50 times) than in the atmosphere, therefore increasing levels of atmospheric CO₂ may not directly influence below-ground processes (Van de Geijn and Van Veen 1993). Most below-ground responses are likely due to the indirect effects, such as faster root growth and increased rhizodeposition. Zak et al. (1993) suggested the existence of a positive feedback between atmospheric CO₂ enrichment and an increase in root growth, microbial activity, and nitrogen (N) availability in the rhizosphere, when N is available. This may have a positive effect on autochthonous microorganisms, as well as pathogens.

The majority of the literature examined for this review described an inverse relationship between temperature and bacterial mortality, with higher temperatures decreasing the survival times of enteric bacteria and die-off doubling with a 10°C increase in temperature (Reddy et al. 1981; Thomas et al. 1999). Minimum temperature for growth of *E. coli* is 7.5°C (Smith et al. 1994); however, *E. coli* can survive over a wide range of temperatures. Survival of pathogens in soil and water varies among different microorganisms. Kudva et al. (1998) reported that *E. coli* survived longer in sheep and cattle manure at temperatures below 23°C whereas Howell et al. (1995), observed greater *E. coli* survival at warmer conditions. Wang et al. (1996) observed that *E. coli* O157:H7 survived for 7–8 weeks at 37°C and 8–9 weeks at 28°C and retained its ability to produce verotoxins. In the laboratory, *E. coli* O157:H7

survived for at least 8 weeks in moist soil at 25°C (Mubiru et al. 2000). Under fluctuating environmental temperatures (–6.5 to 19.6°C) this microorganism was detected for up to 99 days (Bolton et al. 1999). Wang et al. (1996) observed a strain variation in survival and growth characteristics of pathogens in feces. This has also been suggested by Doyle (1991), indicating that *E. coli* O157:H7 can persist for extended periods of time under a wide range of environmental temperatures.

Salmonella can adapt to gradually increasing temperatures. Spinks et al. (2006) observed that increasing the growth temperature from 20 to 37°C increased heat resistance of *S. typhimurium* at 55°C by about threefold. Thermotolerance of *Salmonella* is also induced by competitive flora. A high concentration of competitors is perceived by *Salmonella* cells as a signal to induce stationary-phase gene expression mediated by RpoS (σ^S) (Duffy et al. 1995) which can be an additional advantage for the survival of this microorganism among increasing competing flora under elevated temperatures. Smith et al. (1994) showed that exposure of *E. coli* and *Salmonella* to polar, marine, low temperature conditions in Antarctica for 56 days, shifted the optimum and permissible growth temperatures downward. This suggests that the long-term exposure of fecal pathogens to stressful conditions may lead to adaptation to the environment.

Further, according to the projections of IPCC (Houghton et al. 2001) for terrestrial ecosystems, winter temperatures are expected to increase more than the summer temperatures. Low winter temperatures are crucial to the die-off of pathogens in the soil environment. Higher winter temperatures coupled with higher soil organic matter content as a result of climate change may enhance the survival of pathogens in the soil environment.

Also of importance is the effect the indigenous soil microorganisms have on bacteria added to soils in manure sand biosolids. The influence of the indigenous microbial community on pathogens is an important area of research. For example, it was reported *E. coli* O157:H7 survived significantly longer in manure-amended autoclaved soil than in manure-amended non-autoclaved soil (Jiang et al. 2002). However, the abiotic conditions also differed in these substrates, so that competition with the microbial community had probably changed. From a public and environmental health perspective, scientists, regulators and policy makers will need to re-examine survival of *E. coli* (and other pathogens) in the environment to better understand their persistence, reproduction, gene expression, antibiotic resistance and toxin production. Risks from particular pathotypes are not easily predicted if there is a lack of knowledge on pathogens in diverse soil and aquatic environments.

Pathogen evolution by horizontal gene transfer (HGT)

Horizontal gene transfer plays a central role in bacterial evolution (Ochman and Moran 2001). The transfer of genetic material has three primary mechanisms in bacterial cells—conjugation, transduction, and transformation. Conjugation is the process by which plasmid DNA is directly transferred from a donor cell to a recipient cell through a conjugation bridge. Many toxin and antibiotic resistance genes have been spread throughout the bacterial community in this manner. Transduction is the transfer of DNA between bacterial cells by a bacteriophage, which may code for toxins, adherence, and nutrient acquisition systems. Transformation occurs when competent bacterial cells take up free DNA from the soil environment. Bacteria can acquire genes required for survival in the soil environment by horizontal gene transfer, which is thought to be important for pathogens adapting to new or changing habitats (Barkay et al. 1993; Tschape 1994; Lilley and Bailey 1997; Ochman and Moran 2001). Environmental selection pressures have been proposed to be one of the primary factors that may increase the probability of HGT events, most notably when transferred plasmids confers some type of growth advantage to the hosts (Hill and Top 1998; Hohnstock et al. 2000; Van Elsas and Bailey 2002). Horizontal gene transfer has played a prominent role in evolution of bacterial genome and diversification and speciation of enterics (Ochman et al. 2000). Enterohemorrhagic *E. coli* O157:H7 is an example of HGT producing a novel pathogen (Whittam et al. 1988). In this serotype, a shiga-like toxin (verocytotoxin) from *Shigella dysenteriae* was transferred to opportunistic pathogenic strains of *E. coli*, in multiple events (Whittam et al. 1988). The *E. coli* O157:H7 verocytotoxin is hypothesized to also serve as an iron acquisition system (Chart 2000). Karch et al. (1999) states that such dual-use toxin/siderophores in pathogenic *E. coli* can also be thought of as conferring metabolic fitness in the environment. Evolutionary selection for the inclusion of pathogenic islands into the genome may also confer metabolic fitness that allows bacterial pathogens to survive in diverse and changing environments.

Effect of soil temperature on horizontal gene transfer (HGT)

Climate change is predicted to increase soil temperature most notably in temperate and sub-arctic environments, which may alter the frequency of HGT events in the microbial community of these soils. The optimal temperature for HGT in soil is dependent on the characteristics of both the transferred plasmid and its host (Dröge et al. 1999). Some plasmids mediate temperature-dependent transformation efficiency, such as pQM85, which had a maximum

transformation frequency at 10°C between *Pseudomonas putida* strains, much less than the optimum growth temperature of its host (Fry and Day 1990). Horizontal gene transfer generally occurs over a wide temperature range but is reduced in frequency at temperature extremes (Dröge et al. 1999). Optimum bacterial temperature ranges also affect HGT frequency, as gene transfer is more efficient at 5°C for psychrotrophic strains (Day et al. 1992) and more efficient at about 30°C for mesophilic microorganisms. The plasmid HGT frequency between *E. coli* and *Rhizobium meliloti* in sterile soil was greatest at 30°C, with a conjugation frequency of 6.7×10^{-6} transformants recipient cells⁻¹ for transfers between strains of *R. meliloti*, and 5.1×10^{-6} transformants recipient cells⁻¹ for transfers between *E. coli* donors and *R. meliloti* (Lafuente et al. 1996). Lafuente et al. (1996) showed that for these bacterial pairings, transfer frequency increased by an order of magnitude when the temperature was increased from 20 to 30°C, although bacterial biomass remained relatively constant over these temperatures. The transfer frequency decreased from 30 to 40°C as both donor and recipient cell viability declined. These data indicate that small alterations in temperature will not dramatically increase the frequency of horizontal gene transfer until a threshold temperature of about 21°C is reached for these specific strains. Above this threshold, Lafuente et al. (1996) showed that a 1°C increase in temperature has the potential to double HGT frequency. Soil surface temperatures within this range are common in the tropics and in the summer months in temperate zones. The number of days per annum with temperatures above this threshold may increase due to climate change in temperate soils. Due to the low frequency of HGT in the soil, it is difficult for researchers to study the effects of climate change directly, but efforts should be made to test these principles in long-term microcosm studies. In a laboratory experiment, plasmid HGT frequency between *E. coli* and *Pseudomonas putida* strains increased linearly from 50 to about 230 transfer events after 5 h of incubation when the temperature was raised from 5 to 29°C. At 35.5°C, plasmid transfer events decreased considerably (Johnsen and Kroer 2007). In plate transformation assay studies, natural transformation occurred optimally at high temperatures. High frequency transformation of *Azotobacter vinelandii* occurred in a range between 26–37°C, and natural transformation was optimal at 30°C (Page and Sadoff 1976). Similarly, high frequency transformation of *Pseudomonas stutzeri* occurred between 20 and 37°C (Lorenz and Wackernagel 1992). However, it is unlikely that similar frequencies would be observed in natural soils, as the degradation of extracellular DNA in these environments would be rapid. Soil temperature increases should be examined further for its ability to increase the frequency of genetic exchange between soil microorganisms.

Predicted outcome of climate-change-induced alterations to pathogens in the soil environment

Climate change may increase environmental variability through a number of mechanisms. Average temperature increases are predicted, as are extremes in temperature fluctuations and precipitation events. This in turn would alter soil temperature, moisture, pH and nutrient availability. Prokaryotic cells are programmed for cell division. They do this by responding to the environmental stimuli by regulating gene expression. Various signal transduction systems and regulatory mechanisms that exist in fecal bacteria may allow them to adapt to variable environmental stimuli.

Variability in the soil environment would select for bacteria with genes that confer metabolic fitness in a range of environments. These genes may be spread through the soil microbial community by horizontal gene transfer. Genes that confer environmental fitness, such as those coding for nutrient acquisition systems or siderophores, may also confer virulence. If a variable soil environment increases the prevalence of environmental fitness genes, researchers may observe (1) an increase in survival of pathogenic bacteria in soil, or the introduction of novel pathogens, (2) an attenuation or decrease in virulence of pathogens in soil since bacteria that lack loss of function mutations in anti-virulence genes may be selected for in a variable climate, and (3) movement of pathogens from an environmental niche (which typically limits virulence) to host tissue, with a subsequent narrowing of niche specificity and increase in virulence brought about by release from the selective pressure of life in soil. These hypotheses are not mutually exclusive, nor are they exclusive to host-species, since humans and animal pathogens, as well as plant pathogens, may be altered at the genetic level by climate change. Although such events are hypothetical, efforts should be made to monitor the soil microbial community for such genetic changes in soil-borne pathogens, including the HGT of environmental fitness genes as a result of climate change.

Although we have considered individual effects of climate change for simplicity, these effects may have confounding effects. In this section, we used available information from the research on zoonotic pathogens in the food industry under controlled environments and the other research conducted under laboratory conditions, as there is little information available in soil environments under varying climatic conditions. Caution should be exercised when extrapolating the results of short-term experiments under laboratory conditions, in predicting ecosystem responses. There is a necessity for more research on these aspects of the soil environment. Moreover, there is a paucity of knowledge of gene expression in pathogens, (especially toxin production) under diverse and fluctuating environmental conditions.

Conclusions

Climate change confronts us on a global scale in our common, shared, biosphere (Trevors and Saier 2009). It challenges researchers to elucidate the complex causes and outcomes, and the ecological, economic and societal significance of its effects. Studies investigating how soils were altered by temperature and CO₂ concentrations were examined to provide an understanding of how climate change can alter the soil environment. A paucity of data exists on the effect of climate change on the soil environment, and therefore it is recommended that large-scale (multi-year, multi-site) field experiments be implemented to examine the interactions between the aforementioned factors and their effects on soil microbial communities. In addition to field studies, microcosm studies designed to test environmental alterations due to climate change within the magnitudes predicted by climate researchers may yield an understanding of how the changing climate can affect soil geochemical parameters and the subsequent response of the soil microbial community.

In trying to understand how soil microorganisms may be affected by climate change, two microbial outcomes emerged as having particular ecological and societal importance. Perturbations in the soil environment could lead to community shifts and altered metabolic activity in microorganisms involved in soil nutrient cycling, and to increasing or decreasing survival and virulence of soil-mediated pathogenic microorganisms. Soil microorganisms have ecological importance in nutrient cycling, which affects both atmospheric gas concentrations and influences the fertility of agricultural soils. Alterations in CO₂ concentrations and temperature may alter soil respiration, soil carbon dynamics, and microbial community structure. Nitrification and denitrification, bacterial-mediated processes that play an important role in the nitrogen cycle, may also change as a result of climate change. Of particular importance is the alteration of the environment directly under the influence of plant roots, known as the rhizosphere. The rhizosphere provides a unique energy-rich habitat for microorganisms involved in greenhouse gas cycling as well as microbial pathogens. Increased temperature and CO₂ as a result of climate change can increase root exudation, sloughing, and CO₂ release into the rhizosphere, altering the microbial community and activity.

Alterations of the global climate may have positive or negative societal impacts. Crop plants in temperate agricultural systems may benefit from higher yields due to increases in temperature and atmospheric CO₂ concentrations, but may be put at risk of nutrient deficiency and increased soil-mediated pathogen survival and virulence. Agricultural soils contain important species and plant and animal pathogens. These microorganisms may be

endogenous to soil, or be transported into soil by manure applications or microbial inoculants. Soil-borne and soil-mediated pathogens may survive in soil for increasing durations as a result of climate change, and may be transported into previously uncolonized niches or regions. The potential for an increase in frequency of horizontal gene transfer due to changing climatic factors is of concern due to possible evolutionary changes in soil-borne pathogen populations, including the spread of virulence factors and genes that aid in environmental survival. We therefore suggest that soil microbial communities in temperate agricultural systems continue to be researched for alterations to community structure, specifically the increase or decrease of soil activity and respiration, nitrification and denitrification, pathogen survival and alterations to horizontal gene transfer. In addition, very little knowledge is available on microbial gene expression (e.g., nitrous oxide production, Saleh-Lakha et al. 2008, 2009; toxin production in microbes) under diverse, interacting and fluctuating environmental conditions and diverse pure culture conditions. This should be a priority research area as the molecular based methods are available to complete such research. Gene expression/proteomics approaches applied to microorganisms in pure cultures and soils are immensely valuable as gene expression specifies a cell's identity and governs its present activities until differential gene expression is again altered by changes in the surrounding environment. The total genetic information in a single g of soil is not even known.

As outlined in Fig. 1, the complex, random and non-random interactions between physical, chemical and biological factors and the amount of gene expression under changing environmental conditions in soils will require an immense international, collaborative research effort to better understand climate change, soils, the atmosphere and how agriculture will feed an already hungry planet. Transformations of energy and matter in living organisms are under the control of genetic instructions, and the universe obeys the laws of thermodynamics with increasing entropy. Climate change and how organisms evolve or become extinct under a changing environment, is simply natural selection, evolution and the fundamental laws of thermodynamics being obeyed on the Earth.

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