Chapter 3 Impact of Climate Change on Soil Microbial Community



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Abstract As climate changes endlessly, it becomes more important to understand possible reactions from soils to the climate system. It is a known fact that microorganisms, which are associated with plant, may stimulate plant growth and enhance resistance to disease and abiotic stresses. The effects of climate change factors, such as elevated CO₂ drought, and temperature on beneficial plant-microorganism interactions are increasingly being explored. Organisms live in concert with thousands of other species, such as some beneficial and pathogenic species which have little to no effect on complex communities. Since natural communities are composed of organisms with very different life history traits and dispersal ability, it is unlikely that all of the microbial community will respond to climatic change factors in a similar way. Among the different factors related to climate change, elevated CO_2 had a positive influence on the abundance of arbuscular and ectomycorrhizal fungi, whereas the effects on plant-growth-promoting bacteria and endophytic fungi were more variable. The rise in temperature effects on beneficial plant-associated microorganisms were more variable, positive, neutral, and negative, which were equally common and varied considerably with the temperature range. Likewise, plant-growth-promoting microorganisms (i.e., bacteria and fungi) positively affected plants subjected to drought stress. In this chapter, we explore how climatic change affects soil microbes and plant-associated microorganisms.

3.1 Introduction

Microbial communities are groups of microorganisms that share a common living space. The microbial populations that form the community can interact in different ways, for example, as predators and prey or as symbionts. The community includes both positive (like symbiosis) and negative (like antibiosis) interactions.

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Microorganisms are the backbone of all ecosystems, even then in some zones, they are unable to process photosynthesis due to absence of light. In such zones, chemosynthetic microorganisms provide carbon and energy to the other organisms. Soil microbial communities play an important role in agro-ecosystem functioning and are on the field scale essential for plant nutrition and health. Moreover, they are involved in turnover processes of organic matter, breakdown of xenobiotics and formation of soil aggregates. These soil microbial communities are responsible for the cycling of carbon (C) and nutrients in the ecosystem and their activities are regulated by biotic and abiotic factors such as the quantity and quality of litter inputs, temperature, and moisture. Atmospheric and climatic changes will affect both abiotic and biotic drivers in ecosystems and the response of ecosystems to these changes. Soil microbial communities may also regulate feedbacks from ecosystem to the atmosphere. The response of the microbial communities that regulate ecosystem processes is less predictable. These microbes play an important role in biogeochemical cycles. The nitrogen cycle, the phosphorus cycle, the sulfur cycle and the carbon cycle all depend on microorganisms. The nitrogen gas, which makes up 78% of the earth's atmosphere, is unavailable to most organisms, until it is converted to a biologically available form by the microbial process of nitrogen fixation.

Climate change factors, such as atmospheric CO₂ concentrations, temperature, and altered precipitation regimes, can potentially have both direct and indirect impacts on soil microbial communities. The response of soil microbial communities to changes in atmospheric CO_2 concentrations can be positive or negative. Increasing temperatures can increase microbial activity, processing, and turnover, causing the microbial community to shift in favor of representatives adapted to higher temperatures and faster growth rates (Bradford et al. 2008). How multiple climate change factors interact with each other to influence microbial community responses is poorly understood. For example, elevated atmospheric CO_2 and precipitation changes might increase soil moisture in an ecosystem, but this increase may be counteracted by temperature (Dermody et al. 2007). Similarly, temperature may increase microbial activity in an ecosystem, but this increase may be eliminated if changes in precipitation lead to a drier soil condition or reduced litter quantity, quality, and turnover. Similarly, changes in soil moisture and ecosystem temperature do not always lead to predictable or significant changes in bacterial and fungal abundance (Chen et al. 2007; Kandeler et al. 2006).

3.2 Impact of Climate Change on Soil Microbial Communities

Climate change is a change in the statistical distribution of weather patterns that lasts for an extended period of time (i.e., decades to millions of years). Impact of climate change on soil microbial communities results in increasing atmospheric CO_2 concentration, temperature, and drought. Climate change has both positive and negative effects on soil microbial communities. Majority of studies showed that elevated CO_2 had a positive influence on the abundance of arbuscular and ectomycorrhizal fungi whereas the effects on plant-growth-promoting bacteria and endophytic fungi were more variable. In most cases, plant-associated microorganisms had a beneficial effect on plants under elevated CO_2 .

Climate change is caused by various factors such as biotic processes, variations in solar radiation received by earth, plate tectonics, and volcanic eruptions. Certain human activities are also responsible for ongoing climate change, often referred to as global temperature. It will show direct and indirect impacts on terrestrial ecosystems, both above and below the ground. On the surface of the soil, the effects of global change will be largely direct: elevated atmospheric carbon dioxide as well as changes in temperature, precipitation, and nitrogen availability, which will all alter the growth of plant species. Below the surface of the soil, disturbances often act quickly like microbial metabolic activities can be changed by many ecosystem-scale factors such as nitrogen deposition, elevated carbon dioxide (Dhillion et al. 1996; Ajwa et al. 1999; Mayr et al. 1999). The response to climate change is more complex. Plant responses affect the type and amount of carbon entering the soil system as well as the physical architecture of the plant root zone.

Through their diverse metabolic activities, soil microbial communities are the major drivers of soil nutrient cycling and their importance in mediating climate change and ecosystem functioning should not be underestimated (Balser et al. 2001). Climatic change involves increasing atmospheric CO_2 concentration, temperature, precipitation, and drought. It can alter the relative abundance and function of soil communities because soil community members differ in their physiology, temperature sensitivity, and growth rates (Lennon et al. 2012; Briones et al. 2014; Delgado-Baquerizo et al. 2014).

3.2.1 Impact of Elevated CO₂

Altered environmental conditions due to climate change are likely to induce changes in plant physiology and root exudation. Particularly elevated CO₂ leads to increase in C allocation at the root zone and potentially alters root exudation compositions. Alterations might include changes in the availability of chemo attractants or signal compounds as well as a different C/N ratio or nutrient availability (Kandeler et al. 2006; Haase et al. 2007). Photosynthetically derived carbon (C) into the rhizosphere through root exudation, making root exudates, is a key factor in increasing microbial abundance and activity in the rhizosphere compared to bulk soil (Lynch 1990; Kapoor and Mukerji 2006). Low-molecular-weight C compounds present in root exudates, including sugars, organic acids (OAs), and amino acids are readily assimilated by microorganisms and are proposed to play a primary role in regulating microbial community dynamics in the rhizosphere (Bais et al. 2006).

Root exudates play a key role in plant-microorganism interactions by influencing the structure and function of soil microbial communities. Model exudate solutions, based on organic acids (OAs) (quinic, lactic, maleic acids) and sugars (glucose, sucrose, fructose), previously identified in the rhizosphere of *Pinus radiata*, were applied to soil miniature. OAs caused significantly greater increases than sugars in the detectable richness of the soil bacterial community. The greater response of bacteria to OAs may be due to the higher amounts of added carbon, solubilization of soil organic matter, or shifts in soil pH. The impact of climate change on root exudates like model solutions such as OAs, which plays a significant role in shaping soil bacterial communities therefore, this may have a significant impact on plant growth (Shi et al. 2011).

Climate change may significantly impact the diversity and activities of such plantassociated microbial communities (Drigo et al. 2008). Consequently, microorganisms known for their beneficial effects on plant growth or health might also be impaired, in terms of exhibiting their desirable properties and their colonization capacity under certain conditions. The majority of studies performed so far have indicated that elevated CO_2 conditions will lead to increased colonization of PGPF (plant-growth-promoting fungi). It is also important to note that elevated CO_2 concentrations may induce AMF (arbuscular mycorrhizal fungi) community composition changes (Klironomos et al. 2005). AMF are known to enhance plant nutrient uptake (mostly phosphate) or confer other benefits in exchange for rhizosphere carbohydrate compounds (Koide 1991; Newsham et al. 1995).

The composition of microbial communities correlates with plant physiology and is likely to be driven by root exudation or metabolite patterns. This indicates that the colonization of plant-associated microorganisms depends on the availability of certain compounds produced by the plant acting as the primary nutrient source, as chemo attractants or signal molecules. Consequently, at elevated CO₂ concentrations in particular, but also under conditions of increased temperature or drought, different genotypes of PGPF or PGPB show potential for different functional activities in the plant environment (Waldon et al. 1989; Marilley et al. 1999; Drigo et al. 2009). However, because of altered community structures, beneficial microorganisms might have to compete with different microbial communities and therefore might show an altered colonization behavior. In addition to the potential effects of climate change on microbial colonization characteristics, microbial activities may be affected (Kandeler et al. 2006; Haase et al. 2008). Microbial communities showing different activities or producing altered signals in the long term either may result in the establishment of altered communities or in the elicitation of different plant responses.

Considering the fact that plant-beneficial microorganisms such as mycorrhizal fungi and nitrogen-fixing bacteria provide up to 80% N and up to 75% P and that an extremely high number of plant species are completely dependent on microbial symbionts for growth and survival, it is evident that alterations in the plant-beneficial microbial communities may ultimately influence plant diversity and functioning of soil microbiota. Furthermore, the abundance or the activity of microorganisms with biocontrol activities may be altered and thereby plant pathogen populations may be affected (Compant et al. 2010). Under elevated CO_2 conditions, nutrients such as N might be limiting, leading to the need for enhanced fertilizer input in agriculture, in

such cases plant growth-promoting microorganisms supporting nutrient acquisition such as mycorrhizae or N-fixing bacteria may gain increasing importance.

Overall, these results suggest that elevated CO_2 may interact with the plant– fungal symbiosis and may lead to increased endophyte infection frequency, although with lowered toxin production (Brosi et al. 2009). The impact of CO_2 on the host plant and its endosymbionts may additionally change the plant carbohydrate content.

3.2.2 Impact of Temperature

Temperature changes are often coupled with changes in soil moisture, which may explain some inconsistent results from experiments exploring how microbial communities respond to climatic change. For example, rates of microbial activity at warmer temperatures can be limited by diffusion and microbial contact with available substrates (Zak et al. 1993). While bacterial communities may respond rapidly to moisture pulses, the slower-growing fungal community may lag in their response (Bell et al. 2008; Cregger et al. 2012, 2014). Global changes such as temperature are directly altering microbial soil respiration rates because soil microorganisms, and the processes they mediate are temperature sensitive. The role of elevated temperature in microbial metabolism has received considerable attention (Bradford 2013; Frey et al. 2013; Hagerty et al. 2014; Karhu et al. 2014). Q_{10} is often used in climate change models to account for microbial temperature sensitivity; however, using this relationship masks many of the interactions that influence the temperature sensitivity of microbial processes, such as decomposition. Therefore, using only Q₁₀ to account for temperature sensitivity in models may lead to poor predictions. Further, while decomposition of soil organic matter, soil respiration, and growth of microbial biomass generally increase with temperature (Bradford et al. 2008). The transient effects of temperature on soil communities have been hypothesized. The soil carbon substrates are depleted by increased microbial activity and because of tradeoffs as microbial communities either acclimate, shift in composition, or constrain their biomass to respond to altered conditions and substrate availability (Allison and Martiny 2008; Bradford 2013). Experimental temperature can initially alter the composition of microbial communities, and shift the abundance of Gram-positive and Gram-negative bacteria (Zogg et al. 1997).

While plant species migrations in response to climate change are well described (Grabherr et al. 1994; Walther et al. 2002; Parmesan and Yohe 2003) most studies fail to address the ability of associated soil microorganisms to shift their range to maintain the positive or negative relationship between the plant and the soil community (van der Putten 2012). Shifts in microbial activity can in turn lead to changes in decomposition, nitrogen mineralization and organic carbon storage. Nitrogen deposition is likely to decrease mycorrhizal fungal biomass while increasing bacterial and saprotrophic fungal biomass (Treseder 2004; Rinnan et al. 2007) and has the potential to increase carbon cycling by increasing the activity of microbial enzymes related to carbon cycling. Soil biota may be poor dispersers, therefore they may respond to climate change at a different rate than plants (van der Putten 2012).

Increased temperature causes the soil water to decrease in some areas (Le Houerou 1996), leading to enhanced drought in several regions of the world, whereas others are known to support plant growth and to increase plant tolerance to biotic and abiotic stresses (Bent 2006). Many of these plant-growth-promoting microorganisms colonize the rhizosphere, the portion of soil attached to the root surface and influenced by root exudates and by microorganisms (Bent 2006; Lugtenberg and Kamilova 2009; Prasad et al. 2015). Some microorganisms can also enter the root system of their hosts and enhance their beneficial effects with an endophytic lifestyle (Stone et al. 2000).

In the majority of cases, the responses of AMF to increased temperature had a positive impact on their colonization and hyphal length. In some cases however, no effects or negative effects of enhanced temperature on AMF were reported (Compant et al. 2010). AMF may respond to higher temperatures with enhanced growth and plant colonization for majority of strains (Furlan and Fortin 1973; Graham et al. 1982; Fitter et al. 2000). This was demonstrated, for instance, in strains of *Glomus intraradices, Glomus mossae*, and many others (Baon et al. 1994; Monz et al. 1994). Temperature may also significantly alter the structure of the AMF hyphal network and induce a switch from more vesicles responsible for storage in cooler soils to more extensive mycorrhizal hyphal networks, indicating growth in warmer soils (Hawkes et al. 2008). This is linked to faster carbon allocation to the rhizosphere and an increased respiration of the extra mycorrhizal mycelium at a high soil temperature (Heinemeyer et al. 2006).

3.2.3 Impact of Drought

Drought stress might be an additional consequence of climate change. High temperature leads to drought or soil moisture stress. Soil moisture related to the microbial community is more highly unpredictable and complex than temperature, and less investigated. Drought amplifies the differential temperature sensitivity of fungal and bacterial groups (Briones et al. 2014). Even with small changes in soil moisture availability (30% reduction in water holding capacity), soil fungal communities may shift from one dominant member to another while bacterial communities remain constant. Interactions among microbes and background temperature and moisture regimes in any given location influence microbial composition and function with changing climate.

Despite logical mechanisms by which microbial communities may be altered by changes in soil moisture. Generally, drought reduces AMF colonization, but in some cases this kind of response might be dependent on strains as reported by Davies et al. (2002), who demonstrated that drought enhanced arbuscular formation and hyphae development of the *Glomus* sp. strain ZAC-19, whereas colonization by a *Glomus fasciculatum* strain was reduced.

Drought is frequently responsible for reduced plant growth in roots and aerial plant parts, which makes the plant susceptible to other pathogens attack. This may lead to changes in the allocation of photosynthates in the rhizosphere as well as in ectomycorrhizal mycelium (ECM) formation. However, plants may change the type of mycorrhiza colonizing their hosts during longer exposure to drought as it was shown by Querejeta et al. (2009). The beneficial association between some strains of AMF and plants may thus reduce the severe effects of water limitation to plants. Moreover, some AMF may resist drought stress better than others.

Different mechanisms may thus be responsible for ECM-induced stress tolerance. Improved performance of mycorrhizal seedlings under drought stress conditions may also be linked to better P and K nutrition as well as to a more extensive root system with mycelial strands as demonstrated with *Picea sitchensis* and *P. involutus* (Lehto 1992). The consequences of drought stress tolerance induced by ECM may in addition affect belowground litter quality and quantity as well as accumulation of organic matter in soils.

There are some microsymbionts, such as the strains of the taxa *Atkinsonella*, *Balansia*, *Balansiopsis*, *Echinodothis*, *Epichloë*, *Myriogenospora* (White 1994), *Parepichloë* (White and Reddy 1998), *Neotyphodium* (Glenn et al. 1996), and certain endophytic fungi that can colonize entirely within plant tissues and may grow within roots, stems, and/or leaves, emerging to sporulate at plant or host-tissue senescence (Sherwood and Carroll 1974; Carroll 1988; Bacon and De Battista 1991).

Water may act in concert with nitrogen addition to increase decomposition of plant tissues (Henry et al. 2005). Increased moisture, or alleviation of water stress, can also alter the lignification of plant cell walls (Henry et al. 2005), increase grassland productivity, and impact on soil carbon. Soil moisture coupled with elevated carbon dioxide also decreases abundance of ammonium oxidizing bacteria, potentially altering the soil nitrogen cycle (Horz et al. 2004). Temperature with elevated carbon dioxide may act additively to increase soil respiration (Niinisto et al. 2004; Van Veen et al. 1991; Hungate et al. 1997). Although there have been few reports on the interactions between elevated temperature and moisture, there is evidence to suggest that together they may lead to shifts in the structure of methane-oxidizing bacterial communities (Horz et al. 2005).

3.3 Conclusion and Future Prospects

Climate change will affect soil microbial communities' structure and functions both directly and indirectly. Directly through changing the physical structure of the soil and carbon allocation and indirectly by changing land use. Soil microbes are essential components in the agricultural ecosystem responses to climate change through which the process of cycling of nutrients and soil carbon allocation occurs. Temperature interacts with changes in water and nitrogen availability. All climate change factors such as temperature, increasing CO_2 concentration, precipitation, and drought impact will be both positive and negative. However, most of the cases it has a positive effect on the microbial community. Although, in order to clearly understand the exact mechanism of impact on climate change on soil microbial community, some other factors which show impact on soil microbial communities and models need to be studied.

References

- Ajwa H, Dell CJ, Rice CW (1999) Changes in enzyme activities and microbial biomass of tallgrass prairie soil as related to burning and nitrogen fertilization. Soil Biol Biochem 31:769–777
- Allison SD, Martiny JBH (2008) Resistance, resilience, and redundancy in microbial communities. Proc Natl Acad Sci USA 105:11512–11519
- Bacon CW, De Battista J (1991) Endophytic fungi of grasses. In: Arora DK, Rai B, Mukerji KG, Knudsen GR (eds) Handbook of applied mycology Vol. 1. Soil and plants. Dekker, New York, pp 231–256
- Bais HP, Weir TL, Perry LG, Gilroy S, Vivanco JM (2006) The role of root exudates in rhizosphere interactions with plants and other organisms. Annu Rev Plant Biol 57:233–266
- Balser TC, Kinzig A, Firestone MK (2001) Linking soil microbial communities and ecosystem functioning. In: Kinzig A, Pacala S, Tilman D (eds) The functional consequences of biodiversity: empirical progress and theoretical extensions. Princeton University Press, Princeton, NJ, pp 265–294
- Baon JB, Smith SE, Alston AM (1994) Phosphorus uptake and growth of barley as affected by soil temperature and mycorrhizal infection. J Plant Nutr 17:479–492
- Bell C, McIntyre N, Cox S, Tissue D, Zak J (2008) Soil microbial responses to temporal variations of moisture and temperature in a Chihuahuan Desert grassland. Microb Ecol 56:153–167
- Bent E (2006) Induced systemic resistance mediated by plant growth-promoting rhizobacteria (PGPR) and fungi (PGPF). In: Tuzun S, Bent E (eds) Multigenic and induced systemic resistance in plants. Springer, Berlin, pp 225–258
- Bradford MA (2013) Thermal adaptation of decomposer communities in temperature soils. Front Microbiol 4:333. https://doi.org/10.3389/fmicb.2013.00333
- Bradford MA, Davies CA, Frey SD, Maddox TR, Melillo JM, Mohan JE, Reynolds JF, Treseder KK, Wallenstein MD (2008) Thermal adaptation of soil microbial respiration to elevated temperature. Ecol Lett 11:1316–1327
- Briones MJI, McNamara NP, Poskitt J, Crow SE, Ostle NJ (2014) Interactive biotic and abiotic regulators of soil carbon cycling: evidence from controlled climate experiments on peatland and boreal soils. Glob Chang Biol 20:2971–2982
- Brosi GB, Nelson JA, McCulley RL, Classen AT, Norby R (2009) PS 45–40: Global change factors interact with fungal endophyte symbiosis to determine tall fescue litter chemistry. The 94th ESA annual meeting, PS 45–40
- Carroll G (1988) Fungal endophytes in stems and leaves—from latent pathogen to mutualistic symbiont. Ecology 69:2–9
- Chen X, Tu C, Burton MG, Watson DM, Burkey KO, Hu S (2007) Plant nitrogen acquisition and interactions under elevated carbon dioxide: impact of endophytes and mycorrhizae. Glob Chang Biol 13:1238–1249
- Compant S, Cl'ement C, Sessitsch A (2010) Colonization of plant growth-promoting bacteria in the rhizo- and endosphere of plants: importance, mechanisms involved and future prospects. Soil Biol Biochem 42:669–678
- Cregger MA, Schadt CW, Mc Dowell NG, Pockman WT, Classen AT (2012) Response of the soil microbial community to changes in precipitation in a semiarid ecosystem. Appl Environ Microbiol 78:8587–8594
- Cregger MA, Sanders NJ, Dunn RR, Classen AT (2014) Microbial communities respond to experimental temperature, but site matters. Peer J 2
- Davies FT Jr, Olalde-Portugal V, Aguilera-Gómez L, Alvarado MJ, Ferrera-Cerrato RC, Boutton TW (2002) Alleviation of drought stress of Chile ancho pepper (Capsicum annuum L. cv. San Luis) with arbuscular mycorrhiza indigenous to Mexico. Sci Hortic 92:347–359
- Delgado-Baquerizo M, Maestre FT, Escolar C, Gallardo A, Ochoa V, Gozalo B, Prado Comesana A (2014) Direct and indirect impacts of climate change on microbial and biocrust communities alter the resistance of the N cycle in a semiarid grassland. J Ecol 102:1592–1605

- Dermody O, Weltzin JF, Engel EC, Allen P, Norby RJ (2007) How do elevated CO₂, warming, and reduced precipitation interact to affect soil moisture and LAI in an old field ecosystem? Plant Soil 301:255–266. https://doi.org/10.1007/s11104-007-9443-x
- Dhillion S, Roy J, Abrams M (1996) Assessing the impact of elevated CO₂ in a Mediterranean model ecosystem. Plant Soil 187:333–342
- Drigo B, Kowalchuk GA, van Veen JA (2008) Climate change goes underground: effects of elevated atmospheric CO₂ on microbial community structure and activities in the rhizosphere. Biol Fertil Soils 44:667–679
- Drigo B, van Veen JA, Kowalchuk GA (2009) Specific rhizosphere bacterial and fungal groups respond to elevated atmospheric CO₂. ISME J 3:1204–1217
- Fitter AH, Heinemeyer A, Staddon PL (2000) The impact of elevated CO₂ and global climate change on arbuscular mycorrhizas: a mycocentric approach. New Phytol 147:179–187
- Frey SD, Lee J, Melillo JM, Six J (2013) The temperature response of soil microbial efficiency and its feedback to climate. Nat Clim Chang 3:395–398
- Furlan V, Fortin J-A (1973) Formation of endomycorrhizae by Endogone calospora on Allium cepa under three temperature regimes. Nat Can 100:467–477
- Glenn AE, Bacon CW, Price R, Hanlin RT (1996) Molecular phylogeny of Acremonium and its taxonomic implications. Mycologia 88:369–383
- Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. Nature 369:448-448
- Graham JH, Leonard RT, Menge JA (1982) Interaction of light and soil temperature with phosphorus inhibition of vesicular–arbuscular mycorrhiza formation. New Phytol 91:683–690
- Haase S, Neumann G, Kania A, Kuzyakov Y, Römheld V, Kandeler E (2007) Elevation of atmospheric CO₂ and Nnutritional status modify nodulation, nodule-carbon supply, and root exudation of *Phaseolus vulgaris* L. Soil Biol Biochem 39:2208–2221
- Haase S, Philippot L, Neumann G, Marhan S, Kandeler E (2008) Local response of bacterial densities and enzyme activities to elevated atmospheric CO₂ and different N supply in the rhizosphere of *Phaseolus vulgaris* L. Soil Biol Biochem 40:1225–1234
- Hagerty SB, van Groenigen KJ, Allison SD, Hungate BA, Schwartz E, Koch GW, Kolka RK, Dijkstra P (2014) Accelerated microbial turnover but constant growth efficiency with temperature in soil. Nat Clim Chang 4:903–906
- Hawkes CV, Hartley IP, Ineson P, Fitter AH (2008) Soil temperature affects allocation within arbuscular mycorrhizal networks and carbon transport from plant to fungus. Glob Chang Biol 14:1181–1190
- Heinemeyer A, Ineson P, Ostle N, Fitter AH (2006) Respiration of the external mycelium in the arbuscular mycorrhizal symbiosis shows strong dependence on recent photosynthates and acclimation to temperature. New Phytol 171:159–170
- Henry HA, Clelad EE, Field CB, Vitousek PM (2005) Interactive effects of CO₂, N deposition, and climate change on plant litter quality in a California annual grassland. Oecologia 142:465–473
- Horz HP, Barbrook A, Field CB, Bohannan BJM (2004) Ammonia-oxidizing bacteria respond to multifactorial global change. Proc Natl Acad Sci USA 101:15136–15141
- Horz HP, Rich V, Avrahami S, Bohannan BJM (2005) Methane-oxidizing bacteria in a California upland grassland soil: diversity and response to simulated global change. Appl Environ Microbiol 71:2642–2652
- Hungate BA, Lund CP, Pearson HL, Chapin FS (1997) Elevated CO₂ and nutrient addition alter soil N cycling and N trace gas fluxes with early season wet-up in a California annual grassland. Biogeochemistry 37:89–109
- Kandeler E, Mosier AR, Morgan JA, Milchunas DG, King JY, Rudolph S, Tscherko D (2006) Response of soil microbial biomass and enzyme activities to the transient elevation of carbon dioxide in a semi-arid grassland. Soil Biol Biochem 38:2448–2460
- Kapoor R, Mukerji KG (2006) Rhizosphere microbial community dynamics. In: Mukerji KG, Manoharachary C, Singh J (eds) Microbial activity in the rhizosphere. Springer, Berlin, pp 55–66

- Karhu K et al (2014) Temperature sensitivity of soil respiration rates enhanced by microbial community response. Nature 513:81–84
- Klironomos JN, Allen MF, Rillig MC, Piotrowski J, MakvandiNejad S, Wolfe BE, Powell JR (2005) Abrupt rise in atmospheric CO₂ overestimates community response in a model plant–soil system. Nature 433:621–624
- Koide R (1991) Nutrient supply, nutrient demand and plant response to mycorrhizal infection. New Phytol 117:365–386
- Le Houérou HN (1996) Climate change, drought and desertification. J Arid Environ 34:133-185
- Lehto T (1992) Mycorrhizas and drought resistance of Picea sitchensis (bong) Carr. I. in conditions of nutrient deficiency. New Phytol 122:669–673
- Lennon JT, Aanderud ZT, Lehmkuhl BK, Schoolmaster DR Jr (2012) Mapping the niche space of soil microorganisms using taxonomy and traits. Ecology 93:1867–1879
- Lugtenberg B, Kamilova F (2009) Plant-growth-promorting Rhizobacteria. Annu Rev Microbiol 63 (1):541–556
- Lynch JM (1990) Introduction: some consequences of microbial rhizosphere competence for plant and soil. In: Lynch JM (ed) The rhizosphere. Wiley, West Sussex, pp 1–10
- Marilley L, Hartwig UA, Aragno M (1999) Influence of an elevated atmospheric CO₂ content on soil and rhizosphere bacterial communities beneath Lolium perenne and Trifolium repens under field conditions. Microb Ecol 38:39–49
- Mayr C, Miller M, Insam H (1999) Elevated CO₂ alters community-level physiological profiles and enzyme activities in alpine grassland. J Microbiol Methods 36:35–43
- Monz CA, Kunt HW, Reeves FB, Elliot ET (1994) The response of mycorrhizal colonization to elevated CO₂ and climate change in *Pascopyrum smithii* and *Bouteloua gracilis*. Plant Soil 165:75–80
- Newsham KK, Fitter AH, Watkinson AR (1995) Multifunctionality and biodiversity in arbuscular mycorrhizas. Trends Ecol Evol 10:407–411
- Niinisto SM, Silvola J, Kellomaki S (2004) Soil CO₂ efflux in a boreal pine forest under atmospheric CO₂ enrichment and air temperature. Glob Chang Biol 10:1–14
- Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42
- Prasad R, Kumar M, Varma A (2015) Role of PGPR in soil fertility and plant health. In: Egamberdieva D, Shrivastava S, Varma A (eds) Plant growth-promoting Rhizobacteria (PGPR) and medicinal plants. Springer International Publishing, Switzerland, pp 247–260
- Querejeta JI, Egerton-Warburton LM, Allen MF (2009) Topographic position modulates the mycorrhizal response of oak trees to interannual rainfall variability. Ecology 90:649–662
- Rinnan R, Michelsen A, Baath E, Jonasson S (2007) Fifteen years of climate change manipulations alter soil microbial communities in a subarctic heath ecosystem. Glob Chang Biol 13:28–39
- Sherwood M, Carroll G (1974) Fungal succession on needles and young twigs of old-growth Douglas fir. Mycologia 66:499–506
- Shi S, Condron L, Larsen S, Richardson AE, Jones E, Jiao J, O'Callaghan M, Stewart A (2011) In situ sampling of low molecular weight organic anions from rhizosphere of *Pinus radiata* grown in a rhizotron system. Environ Exp Bot 70:131–142
- Stone JK, Bacon CW, White JF (2000) An overview of endophytic microbes: endophytism definded. In: Bacon CW, White JF (eds) Microbial endophytes. Dekker, New York, pp 3–29
- Treseder KK (2004) A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO2 in field studies. New Phytol 164:347–355
- van der Putten WH (2012) Climate change, aboveground-belowground interactions and species range shifts. Annu Rev Ecol Evol Syst 43:365–383
- van Veen K, Liljeroth E, Lekkerkerk J (1991) Carbon fluxes in plant-soil systems at elevated atmospheric carbon dioxide levels. Ecol Appl 1:175–181
- Waldon HB, Jenkins MB, Virginia RA, Harding EE (1989) Characteristics of woodland rhizobial population from surface- and deep-soil environments of the Sonoran Desert. Appl Environ Microbiol 55:3058–3064

- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389–395
- White JF Jr (1994) Taxonomic relationships among the members of the Balansiae (Clavicipitales). In: Bacon CW, White JF Jr (eds) Biotechnology of endophytic Fungi of Grasse. CRC Press, Boca Raton, FL, pp 3–20
- White JF Jr, Reddy PV (1998) Examination of structure and molecular phylogenetic relationships of some graminicolous symbionts in genera Epichloë and Parepichloë. Mycologia 90:226–234
- Zak DR, Pregitzer KS, Curtis PS, Teeri JA, Fogel R, Randlett DL (1993) Elevated atmospheric CO₂ and feedback between carbon and nitrogen cycles. Plant Soil 151:105–117
- Zogg GP, Zak DR, Ringelberg DB, MacDonald NW, Pregitzer KS, White DC (1997) Compositional and functional shifts in microbial communities due to soil temperature. Soil Sci Soc Am J 61:475–481