Climate change and multitrophic interactions in soil: the primacy of plants and functional domains

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Abstract

Soil multitrophic interactions transfer energy from plants as the predominant primary producer to communities of organisms that occupy different positions in the food chain and are linked by multiple ecological networks, which is the soil food web. Soil food web sequesters carbon, cycles nutrients, maintains soil health to suppress pathogens, helps plants tolerate abiotic and biotic stress, and maintains ecosystem resilience and sustainability. Understanding the influence of climate change on soil multitrophic interactions is necessary to maintain these essential ecosystem services. But summarising this influence is a daunting task due to a paucity of knowledge and a lack of clarity on the ecological networks that constitute these interactions. The scant literature is fragmented along disciplinary lines, often reporting inconsistent findings that are context and scale-dependent. We argue for the differentiation of soil multitrophic interactions along functional and spatial domains to capture cross-disciplinary knowledge and mechanistically link all ecological networks to reproduce full functionalities of the soil food web. Distinct from litter mediated interactions in detritosphere or elsewhere in the soil, the proposed ‘pathogen suppression’ and ‘stress tolerance’ interactions operate in the rhizosphere. A review of the literature suggests that climate change will influence the relative importance, frequency and composition of functional groups, their trophic interactions and processes controlling these interactions. Specific climate change factors generally have a beneficial influence on pathogen suppression and stress tolerance, but findings on the overall soil food web are inconsistent due to a high level of uncertainty. In addition to an overall improvement in the understanding of soil multitrophic interactions using empirical and modelling approaches, we recommend linking biodiversity to function, understanding influence of combinations of climatic factors on multitrophic interactions and the evolutionary ecology of multitrophic interactions in a changing climate as areas that deserve most attention.

Keywords: biological control, carbon sequestration, endophyte, mycorrhiza, plant growth promotion, rhizosphere, soil borne plant pathogens, soil food web, soil health, suppressive soil

Received 9 January 2012; revised version received 6 February 2012 and accepted 10 February 2012

Introduction

Soil multitrophic interactions involve plants, herbivores, predators, endophytes, pathogens, decomposers and other functional groups that occupy different positions in the food chain and perform vital functions to deliver ecosystem services that support life and cultural services not associated with material benefits [United Nation’s Millennium Ecosystem Assessments, (MEA, 2005)]. As the dominant primary producer in terrestrial and soil ecosystems, plants are the main source of food for all organisms at higher trophic levels, such as herbivores at level 2, predators at levels 3 and beyond. Soil multitrophic interactions mediate > 80% of processes to sequester carbon, decompose organic matter, cycle nutrients, maintain soil fabric and structure and regulate the population of pest and pathogens (Barrios, 2007; Kabouw et al., 2011). Therefore, it is essential to determine whether climate change will adversely influence multitrophic interactions to affect ecosystem services.

The estimated number of species in soil is 100 000 for protozoa; 500 000 for nematodes; 7000 for earthworms; and a significant proportion of the 1.5 million fungal species (Susilo et al., 2004; Coleman & Whitman, 2005). The number of bacterial species range between 6000 and 50 000 (Van Der Heijden et al., 2008). With 55–98% of the total biodiversity on Earth (Beed et al., 2011), few other ecosystems can match the size, complexity or the biodiversity of the soil biota. The complex interactions involving this biodiversity (McCann, 2007) in a heterogeneous...
soil environment (Wolfe & Klironomos, 2005; Wardle, 2006) makes soil multitrophic interactions scale-dependent (Van Der Putten et al., 2004) and difficult to understand (Van Der Putten et al., 2001; Pritchard, 2011). This is reflected in the limited literature on soil multitrophic interactions (De Román et al., 2011; Johnson et al., 2011; Van Dam & Heil, 2011). The complexity also obscures understanding of essential processes such as the temperature sensitivity of soil carbon decomposition and feedbacks to climate change, despite much research (Davidson & Janssens, 2006; Conant et al., 2011).

While Earth’s climate has always changed over time, since the industrial revolution, human-induced CO₂ emission has risen from 280 mg kg⁻¹ in 1750 to 379 mg kg⁻¹ in 2005. The radiative forcing due to greenhouse gas emissions has increased global surface temperatures by 0.74 °C over the past century and this is projected to continue by between 0.15 and 0.3 °C per decade, depending on the emission scenario (IPCC, 2007). Recent observations indicate that between 2000 and 2007 emissions have risen by 3.4% per year, exceeding almost all projections from the Intergovernmental Panel on Climate Change (Raupach & Canadell, 2010). Rising sea levels, shrinking glaciers and increased rainfall in the middle and high latitudes of the Northern Hemisphere but a decrease over the sub-tropics are among other projected changes. Heat waves and heavy precipitation may become more frequent and tropical cyclones may be more intense in the 21st century (IPCC, 2007).

Historically, reduced agricultural production under cooling has caused price inflation, famine and war, reducing human populations (Zhang et al., 2007). The ‘fertilization effect’ of rising CO₂ concentration can increase crop biomass and grain yield (Ainsworth & Long, 2005), potentially increasing food production. But yield increases are moderated by interactions, including multitrophic interactions controlling water and nutrient availability, and pest and disease outbreaks. These and other biophysical elements will combine with social and economic factors to determine food security under future climates (Chakraborty & Newton, 2011).

For individual species, rising CO₂ and temperature will modify its biology and shift its geographical range, and some will face extinction if these rises continue beyond their tolerance limit. But influences on individual species cannot be used to project influences on multitrophic interactions, which involve many species/fuctional groups linked by networks of ecological interactions that operate simultaneously (Olff et al., 2009). With more than one species carrying out the same function, there is redundancy. This richness of species that underpins soil resilience (Wakelin et al., 2010), also contributes to the variability inherent in most studies on multitrophic interactions. Despite proposed frameworks for community interactions (Hassall et al., 2006; Gilman et al., 2010) very little published works have considered the influence of climate change on soil multitrophic interactions. Reviews have mostly covered some theoretical (Newman, 2007) and empirical aspects (Van Der Putten et al., 2004; Blankinship & Hungate, 2007; Brussaard et al., 2007; Pritchard, 2011) of climate change and multitrophic interactions.

This review argues for a clear differentiation of multitrophic interaction networks that comprise the ‘amorphous’ soil food web and a renewed focus on the primacy of plants as the mediator of climate change impacts on soil multitrophic interactions. We recognise and describe two distinct spatial and functional domains under ‘stress tolerance’ and ‘pathogen suppression’ as components of soil food web. We briefly review recent literature on the influence of climate change on these multitrophic interaction networks to synthesise cross-disciplinary knowledge. We recommend four major lines of enquiry to help guide future research. The review aspires to stimulate debate and discussion rather than offer an exhaustive review of literature on the potential influence of climate change on soil multitrophic interactions.

**Multitrophic interactions in soil: the need for clear differentiation of multitrophic interaction networks**

Microbial activity does not occur uniformly throughout the soil but in ‘hot spots’ of specialised ecological niches like the rhizosphere and detritosphere (environment surrounding decomposing litter), and physical, chemical and biological heterogeneity support and maintain these niches. Functional dynamics of biological processes can be better understood by focusing on ‘hot spots’ (Blackwood & Paul, 2003; Wakelin et al., 2010).

The literature mostly ignores the networks of ecological interactions comprising soil food web that operate simultaneously to perform specific functions. Classifying soil food web according to energy channels (Moore et al., 1988; Holtkamp et al., 2008), trophic controls (Scherber et al., 2010) or size-based templates (Olff et al., 2009) have not improved understanding. On the other hand, disciplinary research in ecology, soil microbiology, plant pathology, and others, offers understanding of specific aspects of soil multitrophic interactions but overlooks important processes and mechanisms that operate at different scales. Food webs are more than the sum of their trophic elements (Cohen et al., 2009) and the failure of mathematical models to predict climate change impacts on soil food web (Smith et al., 1998) is a reflection of knowledge gaps. This has
prompted calls for an integration of disciplinary knowledge (Van Der Putten et al., 2004; Shennan, 2008).

Plants directly or indirectly control and mediate all soil multitrophic interactions. Root exudates, sloughed off root tissue and rhizodeposition attract bacteria, fungi and nematodes as pathogens or parasites of live roots. As plants die, canopy and root litter continue to supply nutrients to these and other microbes operating as saprophytes and other functional groups. Plants determine the composition of fungal and bacterial communities in the rhizosphere through the production of specific flavonoids in root exudates (Straney et al., 2002). Other specific chemical signals control associations between plant roots and mycorrhizae (Shefferson et al., 2007), and pathogens and plant growth promoting organisms (Haas & Defago, 2005). Glucosinolate produced by cruciferous plants decomposes in soil into compounds that act as a fumigant against soil-borne pathogens (Gimsing & Kirkegaard, 2009) and other microbes such as nitrifying bacteria (Brown & Morra, 2009).

The role of overall biodiversity in soil multitrophic interactions is not well understood. This is unlike in terrestrial multitrophic interactions where a loss of biodiversity affects the delivery of ecosystem services (Hooper et al., 2005; Cardinale et al., 2006; Scherber et al., 2010). This poor understanding is largely because only 0.1% of soil fungi and bacteria have been cultured and assigned clear metabolic roles (Barrios, 2007). The difficulty of linking biodiversity to function persists despite the use of metagenomics (Elsas et al., 2008) and other molecular tools to expand our knowledge of biodiversity (Beed et al., 2011) and the functional potential of species or communities (Phillips et al., 2003; Montero-Barrientos et al., 2010). Although increased activity of more diverse soil food web points to the importance of biodiversity in soil multitrophic interactions (Krumins et al., 2006), the effect of species richness decreases with trophic distance (Scherber et al., 2010) and biodiversity may have a different rate at each trophic level.

There is some evidence that microbial diversity per se is not necessary at least for soil carbon sequestration (King, 2011). Carbon is sequestered in soil aggregates (Blanco-Canqui & Lal, 2004) and Arbuscular mycorrhizae (AM) (Bedini et al., 2009), saprophytic fungi and bacteria contribute to the formation and stabilization of soil aggregates (Gupta, 2011). Differences in community composition do not explain differences in organic matter content of soils (Kim et al., 2007).

In this review we recognise two distinct spatial and functional domains under ‘stress tolerance’ and ‘pathogen suppression’ as components of soil food web (Fig. I) to help improve understanding of the constituent multitrophic interactions and to reinforce the primacy of plants as the driver of multitrophic interactions (Scherber et al., 2010; Johnson et al., 2011). Multitrophic interactions involved in pathogen suppression operate in the rhizosphere where bacteria, fungi, nematodes, protozoa and possibly other microbes perform specific functions to help suppress infection and colonisation of plant roots by pathogenic microbes. Multitrophic interactions that impart stress tolerance to plants also operate in the rhizosphere and involve mycorrhizae, endophytic fungi, bacteria and viruses. This distinction is not to detract from the important role of soil food web or its network of multitrophic interactions but to propose a framework to help synthesise cross-disciplinary knowledge. All trophic processes including parasitism, predation, competition and mutualism are essential elements of the overall soil food web (Susilo et al., 2004; Lambers et al., 2009), but only specific combinations of microbes and trophic processes deliver stress tolerance or pathogen suppression. Also, the same group of organisms can participate in different multitrophic interaction networks. Necrotrophic fungi, for instance, use enzymes and other chemicals to decompose organic matter but use a very different set of virulence factors to invade living plant tissue as a pathogen.

Soil food web

Soil food web is the network for the transfer of energy among and between communities of organisms living all or part of their lives in the soil ecosystem (Barrios, 2007; Blankinship & Hungate, 2007). In its simplest form, soil food web shows ‘connectivity’ between various species, groups or feeders; while food webs showing the ‘transfer of energy’ between organisms at various trophic levels are at the next level of complexity; and webs showing per capita ‘interaction strengths’ between organisms are among the most detailed to offer functional insights. However, there is a lack of integration of horizontal and vertical complexity and biodiversity within and between trophic levels, respectively, and their interactions (Duffy et al., 2007). Consequently, knowledge of soil food web is fragmented. Models incorporating elements of belowground interactions suffer from deficiencies and are not often validated using independent data (Matthews et al., 2004).

Energy flows from primary producers to higher trophic levels via one of three basic channels, (a) bacterial channel of saprophytic and pathogenic bacteria and their consumers; (b) fungal channel of saprophytic, mycorrhizal and pathogenic fungi; and (c) the root energy channel of herbivores, nematodes, bacteria, micro-arthropods and their consumers (Moore et al., 1988; Holtkamp et al., 2008). However, food webs are dynamic energy flow systems without a fixed structure over time and both bacterial and fungal energy channels...
operate simultaneously in most soil food webs with temporal and spatial variation (Hassall et al., 2006). The dominance of fungal or bacterial energy channels are often determined by the quality and quantity of soil organic matter (Holtkamp et al., 2008). Soil food webs with bottom-up trophic control where biomass and energy transfers from lower to higher trophic levels (Scherber et al., 2010) are influenced by nutrient availability.

Multitrophic interactions involved in pathogen suppression

Soil-borne pathogens are responsible for 90% of diseases that affect major crops in the USA (Lewis & Papavizas, 1991) and together with parasitic nematodes inflict enormous loss to agriculture each year (Lumsden et al., 1995; Bird & Kaloshian, 2003). Fungal pathogens in soil are necrotrophs that derive nutrition from dead organic substrates but have the capacity to infect and kill live plant roots by producing toxins and other substances. Their broad host range and saprophytic ability allows them to sustain large populations.

Plant pathogens are important in the structure and function of food webs (Borer et al., 2007; Holdo et al., 2009; Olofsson et al., 2011), but their importance extends beyond food webs. At the ecosystem level, pathogens influence the structure, composition and evolution of plant communities (Dobson & Crawley, 1994; Roy et al., 2004; Kardol et al., 2006) affecting the

Fig. 1 A conceptual diagram of plant-mediated influences of climate change on soil food web and feedback to global climate showing important niches (in capital), and processes and mechanisms (in italics) involved in the network of multitrophic interactions between plants as the primary producer and soil organisms in the overall soil food web and its two constituent multitrophic interactions involved in pathogen suppression and stress tolerance (delineated by dotted line). Arrows with solid lines represent known interactions and arrows with dashed lines represent processes and interactions that are not clearly understood.

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delivery of ecosystem services (Cheatham et al., 2009) including carbon exchange (Olofsson et al., 2011). The soil borne pathogen *Phytophthora cinnamomi* has altered some Australian forest communities by replacing susceptible *Eucalyptus* trees with resistant sedge and grass communities while another soil borne pathogen, *Phellinus weirii*, has been a major agent for forest disturbance in North America (Alexander, 2010).

Soil health and pathogen suppressiveness are two important aspects that function due to multi-species interactions between organisms at different trophic levels (Verhage et al., 2010), but their multitrophic nature has not always been explicitly demonstrated. Soil quality and soil health are related concepts used to designate the functional and/or productive status of soil. There is considerable scientific debate about the concepts and indicators to measure soil quality and health (Van Bruggen & Semenov, 2000; Janvier et al., 2007). Using keystone species like *Rhizobium*, or soil dwelling nematodes and their trophic groups provide workable estimates of soil health, but methods that combine physical, chemical and biological parameters, make them cumbersome and expensive (Van Bruggen & Semenov, 2000; Pattison et al., 2008).

Suppressive soils are ‘soils in which disease severity or incidence remains low, in spite of the presence of a pathogen, a susceptible host, and climatic conditions suitable for disease development’ (Baker & Cook, 1974). Soils suppressive to fungal and bacterial pathogens and nematodes have been described. Different mechanisms have been postulated to explain suppressiveness including microbial diversity and composition, population size of certain groups or species, competition for nutrients, antibiosis and predation by amoebae (Chakraborty et al., 1983).

*Pseudomonas*, *Lysobacter* and other bacteria and non-pathogenic *Fusarium* and *Trichoderma* species are implicated in the suppression of fungal pathogens including *Gaeumannomyces graminis* var. *tritici*, *Pythium ultimum* and *Thielaviopsis basicola* (Haas & Defago, 2005; Borneman & Becker, 2007; Postma et al., 2010). Antibiosis, induced systemic resistance (ISR) and specific pathogen-antagonist interactions are three modes of action involved in pathogen suppression by bacteria (Haas & Defago, 2005). Strains of the fungus, *Trichoderma harzianum* commonly found among rhizosphere organisms also trigger ISR (Shoresh et al., 2010). ISR makes plants more resistant to necrotrophic fungal pathogens, some viruses and insects, and it extends to parts of a plant. Some Actinobacteria form endophytic relationships to protect roots from infection by several fungal pathogens (Franco et al., 2007).

The protection of host roots by ISR and antibiotic production also promotes plant emergence and growth. These changes in plant composition and signalling pathways link soil microbe – plant interactions to aboveground trophic processes such as herbivory (Pineda et al., 2010). Other changes such as pathogen-induced mycotoxin in cereals makes straw attractive to earthworms and leads to its rapid decomposition (Wolfarth et al., 2011).

**Multitrophic interactions involved in stress tolerance**

Mutualism by mycorrhizae and endophytes confers benefits such as nutrient acquisition and stress tolerance to their plant hosts (Frey-Klett et al., 2007). Mycorrhizae mediate plant nutrient foraging, carbon allocation and root architecture, changes in soil structure and soil carbon storage (Staddon et al., 2002), and shift plant communities by suppressing non-mycorrhizal species (Cameron, 2010; Klironomos et al., 2011). Ectomycorrhizal fungi (EM) proliferate outside the root and form a sheath around the root as a physical barrier to protect against pathogens by antibiotics and by inducing fungistatic compounds (Duchesne, 1994). AM form arbuscules as sites of energy transfer between the host and fungus, and vesicles or hyphal swellings as storage organs (Rillig, 2007). AM enhance nutrient uptake by the plant, prevent root infection by pathogens and stimulate plant defence by lignification (Azcón-Aguilar & Barea, 1997). AM increase host plant fitness by modulating multitrophic interactions (Hoffmann et al., 2011).

An example of multitrophic interactions involving AM and EM is their association with members of *Pseudomonas*, *Bacillus*, *Klebsiella* and *Streptomyces* as mycorrhiza helper bacteria (Frey-Klett et al., 2007). This association makes the mycorrhizal symbiont more effective in mobilising soil nutrients, fixation of atmospheric nitrogen and the protection of roots against soil borne pathogens.

Endophytic fungi reside entirely within plant tissues and emerge to sporulate at plant senescence (Bacon et al., 1991). This association, ranging from mutualistic to parasitic, can confer tolerance to environmental stress such as heat and water stress (Rodríguez et al., 2009). Endophytes enhance survival and primary production of host plants (Newsham, 2011), prompting suggestions for their use for climate change mitigation (Redman et al., 2011).

Many endophytes produce alkaloids and other secondary fungal metabolites that offer resistance to intense grazing from animals, insect herbivores and pathogens (Pineda et al., 2010). A typical example of multitrophic interaction involving an endophyte is the symbiosis between a virus-infected *Curvularia protuberata* and its grass host * Dichanthelium lanuginosum* (Márquez et al., 2007). Neither the fungus nor its host...
plant can grow in geothermal soils above $38^\circ C$, but when the fungus is infected by a virus, the plant can grow at soil temperatures of $50^\circ C$. This thermotolerance allows the plant to thrive in soils where annual temperatures fluctuate between 20 and $50^\circ C$.

Climate change influence on soil multitrophic interactions

Recent reviews have dealt with climate change influence on some aspects of soil food web such as, beneficial and harmful organisms (Companet et al., 2010; Pritchard, 2011), genetic resources of soil micro-organisms (Beed et al., 2011), soil community response to warming and precipitation (Briones et al., 2009; Hawkes et al., 2011), rhizosphere microbial community response to rising atmospheric CO$_2$ (Drigo et al., 2008), and climate change influence on mycorrhizae (Nannipieri, 2011) and plant pathogens (Chakraborty & Newton, 2011). With only a single review dealing with soil food web (Blankinship & Hungate, 2007), a comprehensive analysis of climate change impact on soil multitrophic interactions has been lacking.

Influences will be mediated through qualitative changes in plant

Climate change influence on soil organisms and their multitrophic interactions will be mostly plant mediated (Johnson et al., 2011). Qualitative changes in physiology, tissue composition and signalling pathways under rising CO$_2$ may influence soil multitrophic interactions. As CO$_2$ levels in soil pores often exceed projected future atmospheric concentrations by several fold (Flechard et al., 2007), CO$_2$ may not directly influence multitrophic interactions. Plants with increased root growth and root to shoot ratio at elevated CO$_2$ will modify root architecture, exudation of labile compounds in the rhizosphere and root turnover rate (Pritchard, 2011) to influence plant-pathogen and plant-mycorrhiza interactions (Melloy et al., 2010; Eastburn et al., 2011; Pickles et al., 2012). Unlike CO$_2$ warming will directly influence multitrophic interactions if rises in soil temperature exceed the buffering capacity of soils. Indirect influences of temperature will be mediated through changes in the quality, quantity, species composition and structure of plant communities.

Of particular interest are the large number of plant genes and gene networks and some hormones that are regulated in a coordinated manner in response to infection by fungal pathogens, cold or drought stress (Singh et al., 2002; Eastburn et al., 2011) and insect herbivory (Verhage et al., 2010), albeit with different signalling pathways (Ramirez et al., 2009). Table 1 lists some examples of changes to the structure, composition and signalling pathways of plants under climate change and their influence on plant-microbe interactions from a multitrophic interactions perspective. This list is neither exhaustive nor definitive, as plants can respond in a different way to heat and drought stress when applied together compared with each stress being applied separately (Rizhsky et al., 2002). A comprehensive list of host-pathogen changes in response to elevated CO$_2$ and O$_3$ has recently been published (Eastburn et al., 2011).

Root maintenance respiration increases with rising soil temperature, increasing root turnover and reducing root longevity (Pritchard, 2011). Root production and turnover increases with raised soil water content, leading to increased root surface area for microbial colonization and herbivory (Gill & Jackson, 2000). The composition, diversity and productivity of plant communities change with changing precipitation pattern to influence belowground interactions (Suttle et al., 2007) including those involving mycorrhizae and pathogens.

Geographical distribution of plants will change with changing temperature and precipitation. One estimate projects a 51% reduction in the 32 million hectares of highly productive area under wheat, covering northwestern Mexico, the Indo-Gangetic plains and the Nile valley (Ortiz et al., 2008). Changed distribution will cause habitat fragmentation and expose plant communities to new stresses if soils and other conditions are unsuitable in areas with suitable climate. The poleward shift of plant species and changes in species assemblages due to warming of about 3 $^\circ C$ can be more important for soil organisms than the direct effects of warming (Wardle, 2002). At least in the short-term there will be an uncoupling of above and belowground multitrophic interactions, and new networks may evolve (Van Der Putten et al., 2010).

Climate change influence on soil food web

Increased abundance and altered quality of plant litter at elevated CO$_2$ will influence microbial decomposition of litter and the release of nutrients. In general, decreased nitrogen concentration and increased carbohydrate and phenolics increase the carbon/nitrogen ratio of plant litter at high CO$_2$. While some studies show a delayed degradation of plant litter produced at high CO$_2$ (Ulajnen et al., 2003), a meta-analysis failed to show any overall delay in litter degradation (Norby et al., 2001). However, as most studies have used soil respiration as an indicator of microbial activity, the influence of altered litter quality on the structure and function of soil communities and their subsequent influence on soil food web remains unclear. Herbivores
Table 1  Selected examples of changes in plant form and function under elements of climate change with demonstrated/potential effect on microorganisms involved in multitrophic interactions in soil, with arrows indicating an increase (↑) or decrease (↓) in plant response

<table>
<thead>
<tr>
<th>Plant</th>
<th>Element of climate change</th>
<th>Change(s) in plant response</th>
<th>Influence relating to multitrophic interactions</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arabidopsis thaliana</td>
<td>Drought</td>
<td>↑Abscisic acid ↑Stomatal closure</td>
<td>Induced resistance to pathogens</td>
<td>(Jakab et al., 2005)</td>
</tr>
<tr>
<td>Arabidopsis thaliana</td>
<td>Drought</td>
<td>↑Abscisic acid ↑Methyl jasmonate</td>
<td>Reduced disease incidence by fungal pathogen Botrytis cinerea</td>
<td>(Ramírez et al., 2009)</td>
</tr>
<tr>
<td>Hordeum vulgare and others</td>
<td>Drought</td>
<td>↑Shoot and root biomass ↑Shoot N</td>
<td>Reduced effect of drought by earthworm Aporrectodea caliginosa Reduced aphid abundance Increased number of parasitoid</td>
<td>(Johnson et al., 2011)</td>
</tr>
<tr>
<td>Brassicaceae family</td>
<td>Elevated CO₂</td>
<td>↑Glucosinolate ↑Stomatal conductance ↑Phenolics &amp; tannins ↑Plant defence against pathogen</td>
<td>Reduced soil microbial population Reduced foliar disease incidence by fungal pathogen Phyllosticta minima</td>
<td>(Schonhof et al., 2007) (McElrone et al., 2005)</td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>Elevated CO₂</td>
<td>↑Leaf nicotine ↑Phytoalexin Glyceollin in resistant plants ↑Plant defence against pathogen Phytophthora sojae from β-glucan elicitor</td>
<td>Increased resistance to potato virus Y Potentially increased resistance to fungal pathogen Phytophthora sojae from β-glucan elicitor</td>
<td>(Matros et al., 2006) (Braga et al., 2006)</td>
</tr>
<tr>
<td>Nicotiana tabacum</td>
<td>Elevated CO₂</td>
<td>↑Nitrogen concentration ↑Net photosynthesis ↑Papillae production ↑Silicon accumulation</td>
<td>Reduced fungal leaf spot by Cercospora and Septoria Reduced fungal penetration by Blumeria graminis</td>
<td>(Strengbom &amp; Reich, 2006) (Hibberd et al., 1996)</td>
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<tr>
<td>Glycine max</td>
<td>Elevated CO₂</td>
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<tr>
<td>Solidago rigida</td>
<td>Elevated CO₂</td>
<td>↑Nitrogen concentration ↑Net photosynthesis</td>
<td></td>
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<tr>
<td>Hordeum vulgare</td>
<td>Elevated CO₂</td>
<td>↑Nitrogen concentration ↑Phenolics</td>
<td>Potentially delayed litter degradation</td>
<td>(Lindroth, 2010)</td>
</tr>
<tr>
<td>Several species</td>
<td>Elevated CO₂</td>
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and soil invertebrates feeding on plant tissue containing high levels of secondary or structural compounds show reduced growth, development and population densities, with potential impacts on soil food web (Lindroth, 2010). Herbivory also increases due to compensatory feeding on plant tissue with reduced nutritional value (Schadler et al., 2007).

A high carbon/nitrogen ratio of plant litter and the exudation of organic carbon compounds may shift soil food webs from bacteria to fungi-dominated (Drigo et al., 2007), increasing fungal abundance across different ecosystems (Janus et al., 2005; Lipson et al., 2006). Mycorrhiza and heterotrophic fungi may also be boosted by increased photosynthesis and transfer of carbon to fine roots (Bardgett et al., 2008), but this will be moderated by shifts in the composition and diversity of the vegetation. Some plants may selectively enrich certain fungi by secreting toxins in soil (Van Der Putten, 2009).

Findings on bacteria are variable. Some CO2-enrichment studies show a stimulation of rhizosphere bacteria including nitrogen-fixing rhizobia and increased size and number of root nodules (Compant et al., 2010; Pritchard, 2011) and increased bacterial biomass (Drigo et al., 2008), while others show no general trend (Zak et al., 2000).

Elevated CO2 can boost population size, colonisation, and/or diversity of AM and EM fungi (Compant et al., 2010). A meta-analysis of 65 field studies where mycorrhizal response to CO2 enrichment was measured for > 2 months, showed a 47% increase in growth of AM or EM (Treseder, 2004). AM association supplies all of the plant phosphorous nutrition in some crops (Smith et al., 2004). The boost in AM population could further improve the acquisition of phosphorous, nitrogen, zinc and other nutrients (Cavagnaro et al., 2011). But the benefit to mycorrhizal association from CO2 enrichment will be determined by phosphorous and nitrogen availability in soil.

At the second trophic level there is no significant and consistent response of high CO2 in the majority of over 50 studies (Blankinship & Hungate, 2007). At the third trophic level, population size and/or diversity of some root feeding nematodes (Yeates & Newton, 2009) and collembolans increase with CO2-enrichment. But other studies show no change (Hungate et al., 2000), or enrichment of nematodes only under low fertility (Li et al., 2009), pointing to the complexity of these interactions. Eight out of 15 studies of the third trophic level showed increased abundance or activity, six showed no change and one showed a reduction of bacterivores and/or fungivores but individual groups such as protozoa, enchytraeid and nematodes did not show any consistent trend (Blankinship & Hungate, 2007). In one long-term study, the effect of elevated CO2 on fungal communities was transmitted to higher trophic levels and influenced the abundance and species composition of fungal feeders (Jones et al., 1998). Nevertheless, the relationships between community structure and CO2 enrichment are complicated by spatial heterogeneity and other factors (Ge et al., 2010).

Soil microbial activity and mineralization are increased in warmer soils (Gill & Jackson, 2000) before acclimation reduces temperature sensitivity (Balser et al., 2006), but changes in litter quality and physiology of soil organisms at high temperatures modify these (Heinemeyer et al., 2006). Fungal populations and nematodes grazing on fungi and bacteria generally increase due to warming, while nematode diversity is reduced despite increased growth, fertility and mobility (Convey & Wynn-Williams, 2002; Blankinship & Hungate, 2007). Soil water content can modify the effect of rising temperatures. The algal-feeding Entoedrulaimus that prefers a moist habitat, increases under warming in preference to microbe-feeding nematodes (Simmons et al., 2009). Increasing soil temperature generally decreases soil microbial biomass in controlled experiments but long term field studies either show no effect or a positive effect (Pritchard, 2011).

Decreased precipitation and repeated wetting of soils reduce both bacterial and fungal biomass but fungal dominated food webs respond more readily to changing precipitation (Hawkes et al., 2011). Altered precipitation regulates the population of microbial grazers and bacterial-feeding nematodes are more sensitive to drought than fungal feeders (Landesman et al., 2011). Drier conditions can lead to changes at higher trophic levels due to bottom-up resource limitation as soil organisms appear to be more sensitive to dry conditions than to increased precipitation. Increased precipitation generally benefits detritivores and herbivores at the second trophic level.

**Climate change influence on multitrophic interactions involved in pathogen suppression**

Increased concentration of plant phenolics (Hartley et al., 2000; Percy et al., 2002) and tannins (McElrone et al., 2005) at high CO2 directly increases the resistance of plant tissue to pathogen invasion. Phenolics are antifungal compounds with a well-established role in defence against pathogens and herbivores, and flavonoids are involved in plant-pathogen signalling (Bednarek & Schulze-Lefert, 2009). These and other changes in host plants at high CO2 may affect survival, ecological/reproductive fitness and/or the severity of diseases caused by soil borne pathogens. Increased photosynthesis and water use efficiency raise tolerance of tomato.
roots to *Phytophthora parasitica* infection (Jwa & Walling, 2001); increased β-1, 3 glucanase reduce potato leaf necrosis due to *Phytophthora infestans* (Plessl et al., 2007); and production of the phytoalexin glyceollin increases resistance in soybean in response to an elicitor from *Phytophthora sojae* (Braga et al., 2006). The concentration of Glucosinolate can increase under elevated CO₂ (Schonhof et al., 2007), but how this increase impacts on pathogens, other soil microbes and their multitrophic interactions has not been addressed.

Altered rhizodeposition and root exudates under elevated CO₂ boost the frequency of iron-chelating *Pseudomonas* spp. (Tarnawski et al., 2006) and rhizosphere populations of other microbes associated with pathogen suppression. These and other rhizosphere bacteria, collectively known as plant growth promoting bacteria, stimulate plant growth by producing growth-promoting hormones, alleviating biotic and abiotic stresses and imparting ISR to plants (Har doseim et al., 2011). Populations of some plant growth promoting bacteria such as *Pseudomonas* and *Actinobacteria* are selectively enriched by certain host plants under CO₂ enrichment (Compant et al., 2010). Nevertheless, the overall impact on pathogen suppression is difficult to predict due to a lack of understanding of important interacting factors. For instance, the biomass of *Fusarium pseudograminearum* increases per unit of plant tissue at high CO₂ increasing the amount of inoculum (Melloy et al., 2010). Potentially this may balance the effects of increased populations of suppressive microbes. But this cereal pathogen has low saprophytic fitness and can be rapidly eliminated from organic matter by other microbes including fungi (Pereyra et al., 2004) and nematodes (Wolfarth et al., 2011).

The resistance to *Fusarium subglutinans* increases in pineapple under raised temperatures (Matos et al., 2000), but the influence is species-specific (Chakraborty & Newton, 2011; Eastburn et al., 2011). High temperature reduces resistance against *Phytophthora infestans* in potato (Mizubuti & Fry, 1998), against *Fusarium oxysporum* f. sp. *ciceris* in chickpea (Landa et al., 2006) and against two bacterial pathogens in pepper, but resistance remains unchanged against two fungal pathogens in pepper (Shin & Yun, 2010).

Crop plants now grow in areas where soil and climate are very different to their centres of origin. Often pathogens have migrated with their host, expanding their range. This trend is likely to continue with rising temperature as cropping areas shift pole-ward. Warming will expand the geographical range of *Phytophthora cinnamomi* (Bergot et al., 2004; Desprez-Loustau et al., 2007); increase the risk of severe *Phytophthora infestans* epidemics (Hannukkala et al., 2007) and the number of *Meloidogyne incognita* generations (Ghini et al., 2008). At least in the short term, habitat fragmentation is likely to uncouple above and belowground multitrophic interactions, which control the biological suppression of soil borne pathogens.

The literature on the effect of drought (McElrone et al., 2003; Cotty & Jaime-Garcia, 2007), flooding (Barta & Schmitthenner, 1986) and rainfall (Bowers et al., 1990) on plant pathogens show species-specific responses. A meta-analysis indicates that insect and pathogen feeding behaviour, plant parts affected and the severity of water stress are important factors that determine the impacts of changing precipitation on pathogens (Jactel et al., 2012).

Realistic impact assessment requires the combined influence of changing temperature, soil moisture and CO₂ on pathogen suppressiveness. As pasteurisation removes some forms of soil suppressiveness, pathogen suppression may be eliminated by small rises in soil temperature (Bormann & Becker, 2007; Bent et al., 2008). Under experimental conditions, *Gaeumannomyces graminis var. tritici*, survives in cool dry soils but a moist soil > 30 °C eliminates the pathogen within 3 months (Wong, 1984). However, these findings may not apply directly to field soils which are buffered from the effect of rising temperatures. Suppression of the potato common scab pathogen in cold and wet soil by volatile secondary metabolic gases from *Pseudomonas*, *Bacillus* and *Streptomycetes* becomes ineffective in hot and dry soils (Sturz et al., 2004). Other interactions in the rhizosphere will be favoured under rising temperatures. Strains of plant growth promoting bacteria including rhizobia that grow better at high temperature will dominate under warming to alleviate temperature and drought stress (Compant et al., 2010). Plants such as sunflower growing under drought stress may select strains of *Achromobacter* that offer higher growth promotion under drought (Forchetti et al., 2007).

**Climate change influence on multitrophic interactions involved in plant stress tolerance**

Elevated CO₂ can boost populations of mycorrhizal fungi and selectively enrich species or strains efficient at acquiring mineral nutrients (Pritchard, 2011). Increased levels of plant phenolics at high CO₂ boost mycorrhizal spore germination and colonisation, and certain flavonoids boost hyphal branching in AM (Scervino et al., 2007). This may increase nutrient and water uptake, overall fitness and health of plants to potentially increase their stress tolerance. However, these benefits will depend on the dynamics of fine root turnover rate, and the equilibrium between soil mineral nutrients and carbon fixation by plants (Pritchard, 2011).
Colonisation by some endophytic fungi can increase at elevated CO$_2$ leading to changes in biomass and chemical composition of plants, including alkaloid, protein and carbohydrate levels (Newsham, 2011). Elevated CO$_2$ increased colonisation of *Lolium arundinaceum* by *Neotyphodium coenophialum* but decreased concentrations of ergovaline and loline alkaloids (Brosi et al., 2011). However, endophytes have failed to improve plant function at elevated CO$_2$ in some studies (Alberton et al., 2010).

Warming generally increases root colonization and hyphal length by AM but findings are varied on EM from limited studies (Compant et al., 2010). Warming increases mycorrhizal colonization by directly stimulating fungal growth and indirectly by stimulating plant growth to accelerate the rate of transfer of plant photosynthates to the symbiont (Hawkes et al., 2008). Mycorrhizal response to warming is modulated by the duration of warming (Simard & Austin, 2010), and the acclimatization of the symbiotic community over time (Deslippe et al., 2011). Warming alters the structure of mycorrhizal networks (Hawkes et al., 2008; Deslippe et al., 2011). Larger EM networks under warming may explain the expansion and dominance of *Betula nana* in the Arctic plant community (Clemmensen et al., 2006).

Drought generally reduces mycorrhizal colonisation but the response is species-specific and EM may be more severely affected than AM. This can influence the competition between AM-shrubs and EM-trees. Mycorrhizae can make its host drought tolerant by improving water uptake by roots, tolerance of lower xylem pressure, greater lateral root formation, and osmotic adjustment to avoid dehydration (Compant et al., 2010).

Warming generally favours endophytic colonisation that protects the host plant from abiotic stress. The influence of elevated CO$_2$, warming and precipitation on *Lolium arundinaceum–Neotyphodium coenophialum* interaction has revealed complex but interesting findings (Brosi et al., 2011). Contrary to previous studies, endophytic colonisation was not affected by warming or precipitation. Warming increased loline concentrations by 28% but had no effect on ergovaline. The two alkaloids influence two different groups of grazers with very different ecological and economic significance. Consumption of ergovaline containing plant materials causes ‘tall fescue toxicosis’ in livestock, with symptoms of poor weight gain, reduced fertility and lactation, and gangrene (Panaccione et al., 2001). Loline alkaloids, on the other hand, have insecticidal properties making their host plant tolerant to insect and nematode attack (Yule et al., 2011). By enhancing the insecticidal property of tall fescue pastures without increasing their detrimental effect on livestock grazing, climate change may have an overall beneficial effect.

### Conclusions and recommendations

Summarising the influence of climate change on soil multitrophic interactions is a daunting task due to an overall paucity of knowledge and a lack of clarity on the ecological networks that constitute these interactions. The scant literature is fragmented along disciplinary lines, often reporting inconsistent findings that are context and scale-dependent. We have argued for the differentiation of soil multitrophic interactions along functional and spatial domains as a framework to synthesise cross-disciplinary knowledge. Distinct from litter mediated interactions in detritosphere or elsewhere in the soil, the proposed ‘pathogen suppression’ and ‘stress tolerance’ interactions operate in the rhizosphere. While partitioning soil multitrophic interactions into functional domains will improve understanding, these networks must be mechanistically linked to reproduce all functionalities of the overall soil food web.

A review of the literature suggests that climate change will influence the relative importance, frequency and composition of functional groups, their trophic interactions and processes controlling these interactions. The key influences of elevated CO$_2$ and temperature, and changed precipitation are summarised for the three networks of multitrophic interactions (Table 2).

Soil microbial resources offer great promise in improving tolerance of plants to biotic and abiotic stresses (Mazzola, 2010; Pritchard, 2011), but amendments to enhance nutrient availability, disease suppressiveness or biological control of pests and pathogens often give inconsistent results (Juroszek & Von Tiedemann, 2011). Climate change will increase uncertainty by giving rise to novel interactions and by uncoupling above and belowground multitrophic interactions (Van Der Putten, 2009). Even without climate change considerations, improved understanding of soil multitrophic interactions will have definite scientific and practical benefits in managing soil biota.

Improved understanding of soil multitrophic interactions is a prerequisite to predicting how a changing climate will influence these interactions to impact on the delivery of vital ecosystem services. A lack of clarity on soil multitrophic interactions has obscured important processes such as the sequestration of carbon in soil and its release from organic matter and feedback to global climate systems despite much research. There is a risk of multiplying ignorance without a clear framework and well-formulated research questions. We propose four major lines of enquiry.

**Improved understanding of soil multitrophic interactions**

Additional baseline information on specific soil multitrophic interactions has to be the foundation for any
improved understanding. Empirical and modelling approaches will be equally important in balancing roles and links between the functional domains and multitrophic interaction networks. The lack of understanding of soil multitrophic interaction multiplies with increasing spatial and temporal scales. One approach will be to use a combination of process and organism-oriented models with the flexibility to incorporate new properties that become evident only at a higher spatial/trophic level.

**Linking biodiversity to function**

The use of molecular tools has greatly expanded knowledge of soil microbial biodiversity but its role in multitrophic interactions is yet to be addressed. A large biodiversity by itself is not enough for soil resilience. The functional potential of soil biota has to be optimally expressed under climate change and determining thresholds for important interactions between functional groups will be essential. Other characteristics that determine soil resilience and sustainability, and how these are influenced by climate change will be important to understand the buffering and inherent adaptive capacity of soils.

**Influence of combinations of climatic factors on multitrophic interactions**

Most studies have mainly dealt with the influence of single climatic factors such as elevated temperature and/or CO₂ on specific interactions at lower trophic levels over short to medium time periods. A multi-factorial approach (Singh *et al.*, 2010) based on realistic field studies using temperature and CO₂ gradients to mimic gradual climate change (Chakraborty *et al.*, 2008) will avoid overestimation of community response to abrupt rise in CO₂ (Klironomos *et al.*, 2005). These studies are necessary to identify processes that will be significantly altered and to develop options to maintain ecosystem services. New research must also address how multitrophic interactions will cope with increased frequency and magnitude of extreme events.

**Evolutionary ecology of multitrophic interactions in a changing climate**

Soil microbial communities can rapidly adapt to elevated CO₂ (Allison *et al.*, 2010), temperature (Compant *et al.*, 2010) and raised fecundity at high CO₂ can accelerate micro-evolution (Chakraborty & Datta, 2003). But evolutionary ecology is not often considered for soil organisms (Hassall *et al.*, 2006). Multitrophic interactions are an important driver of selection processes for organisms and functional groups to alter their ability to adapt to a changing climate, and/or new geographical range (Van Der Putten *et al.*, 2010). New long-term research on climate change mediated evolution of microbial communities and their multitrophic interactions, with or without habitat fragmentation, will be essential.

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**Table 2  A summary of observed and potential influence of climate change on soil multitrophic interactions (MI)**

<table>
<thead>
<tr>
<th>Soil MI</th>
<th>Elevated CO₂</th>
<th>Elevated temperature and changed precipitation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil food web</td>
<td>Increased litter and roots with altered quality</td>
<td>Increased fungal and nematode population</td>
</tr>
<tr>
<td></td>
<td>Potentially delay litter decomposition and nutrient cycling</td>
<td>Increased mineralisation</td>
</tr>
<tr>
<td></td>
<td>Potential fungal domination of soil food web</td>
<td>Fungi dominated food webs respond more readily to moisture changes</td>
</tr>
<tr>
<td></td>
<td>Stimulation of N₂-fixing bacteria</td>
<td>Drier conditions influence trophic interactions due to bottom-up resource limitation</td>
</tr>
<tr>
<td></td>
<td>Inconsistent findings on multitrophic interactions</td>
<td></td>
</tr>
<tr>
<td>Pathogen suppression</td>
<td>Increased resistance to fungal pathogens due to rising secondary metabolites</td>
<td>Enhanced mycorrhizal growth</td>
</tr>
<tr>
<td></td>
<td>Growth stimulation and changed mycorrhizal community</td>
<td>Pole-ward shift of plants and their pathogens from changed climate suitability</td>
</tr>
<tr>
<td></td>
<td>Improved plant health from increased activity of plant growth promoting bacteria</td>
<td>Necrotrophic pathogens becoming more damaging if plants are stressed in the new environment</td>
</tr>
<tr>
<td></td>
<td>Pathogen suppression determined by the balance between increased pathogen inoculum and population of suppressive microbes</td>
<td>Uncoupling of above and below ground links due to habitat fragmentation</td>
</tr>
<tr>
<td></td>
<td>Drier conditions influence trophic interactions</td>
<td>Altered effectiveness of disease resistance genes</td>
</tr>
<tr>
<td>Plant stress tolerance</td>
<td>Boosted population and diversity of mycorrhizae and enrichment of species efficient at nutrient acquisition</td>
<td>Improved stress tolerance from increased mycorrhizal colonisation</td>
</tr>
<tr>
<td></td>
<td>Boosted phosphorous and nitrogen nutrition of plants</td>
<td>Potentially increased biotic and abiotic stress tolerance in combination with high CO₂</td>
</tr>
<tr>
<td></td>
<td>Increased stress tolerance and plant defence against herbivore and pathogen</td>
<td></td>
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<tr>
<td></td>
<td>Potentially improved stress tolerance from increased alkaloid production by endophytes</td>
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</tbody>
</table>

Acknowledgements

This review stems from an invited presentation by the senior author at the 6th IOBC working group meeting on multitrophic interactions in soil held in Cordoba, Spain during 4-7 April 2011. We acknowledge the numerous discussions with colleagues in forming opinions expressed in this review. Some of the findings come from research by graduate students including Peter Wilson, Femi Akinsanmi, Rhynann Westcott and Paul Melloy and technical assistance from Ross Perrott. Co-investment in research from the Cooperative Research Centre for National Plant Biosecurity, CSIRO Plant Industry and the Grains Research and Development Corporation is gratefully acknowledged.

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