Feedback responses of soil greenhouse gas emissions to climate change are modulated by soil characteristics in dryland ecosystems

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ABSTRACT

Understanding feedback responses of greenhouse gas (GHG) emissions to future climate projections is critical for the effective development of mitigation and adaptation strategies. It is proposed that effects of elevated carbon dioxide (CO_2) and temperature can have differential effects on GHG fluxes but the magnitude and direction of such impact is not fully known, especially in dryland ecosystems, which are typically water and nutrient limited. We examined individual and interactive impacts of elevated CO_2 (400 ppm vs. 600 ppm) and elevated temperature (ambient vs. $+3\ °C$ increase) treatments on GHG fluxes, in three Australian dryland soils. Firstly, we quantified the individual and interactive effects of elevated CO_2 and temperature on CO_2, methane (CH_4) and nitrous oxide (N_2O) fluxes and the corresponding soil net global warming potential (GWP). Secondly, biotic and abiotic drivers of GHG emissions were identified by exploring the relationship between CO_2, CH_4 and N_2O fluxes with the abundance of bacteria, methanotrophs and N_2O-reducing bacteria as well as soil abiotic characteristics. Our results show that soil CO_2 emissions and CH_4 uptake respond mainly to elevated temperature in all dryland soils tested, with interactive treatment effects showing a less than additive trend on soil net GWP. Nitrous oxide emissions responded less to climate change treatments, and these were site-specific. Soil site characteristics were the main determinant of all GHG emissions; however, the abundance of total bacteria and N_2O-reducing bacteria significantly explained CO_2 and N_2O fluxes, respectively. This study shows that dryland soils respond to climate change with an offset under interactive climate treatments. Our findings suggest that future studies on GHG feedback responses should explicitly consider both biotic and abiotic soil characteristics in order to provide a better mechanistic understanding for the development of future mitigation strategies.

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1. Introduction

Increased atmospheric concentrations of CO_2, CH_4 and N_2O emissions are responsible for current global warming by substantially increasing the greenhouse gas (GHG) effect (IPCC, 2013). Increasing atmospheric CO_2 concentrations in particular, are the largest contributing factor to climate change since the industrial revolution (IPCC, 2013). Furthermore, global temperatures are predicted to increase by between 1.2 and 4.8 °C by the end of the 21st century (IPCC, 2013), with the direction and magnitude of terrestrial GHG responses (feedback responses) to current changing climate not fully known. Thus, GHG feedback responses could further accelerate (positive feedback response) or decelerate (negative feedback response) under elevated CO_2 and temperature (Singh et al., 2010). Additionally, interactive effects of elevated CO_2 and temperature are of great importance because these changes will occur simultaneously, with single-factor responses likely to overestimate GHGs feedback responses (Larsen et al., 2011; Brown et al., 2012).

Large areas of Australia are typified by nutrient-poor soils that support aboveground vegetation adapted to low nutrient availability. Many are classified as drylands, with about 70–85% of Australia classified as arid or dry (Orians and Milewski, 2007). Globally, drylands cover approximately 41% of the Earth's surface (Millennium Ecosystem Assessment, 2005) and are predicted to increase by 10% under future climates (Feng and Fu, 2013). Moreover, climate change experiments suggest that ecosystem

responses may be constrained over the long-term by nutrient availability, due to a progressive loss of the available nutrient pool in the soil (Luo et al., 2004; Luo, 2007). The underlying environmental impacts to ecosystem responses as well as land degradation, poverty and biodiversity (Reynolds et al., 2007) makes it important to study nutrient poor ecosystem dynamics, both in the short-term and long-term, under future climate change scenarios, to better understand how these extremely vulnerable ecosystems respond in terms of GHG feedback responses.

Terrestrial ecosystems are important sources and sinks of potent GHGs, such as CO_2, CH_4 and N_2O (Friedlingstein et al., 2006; IPCC, 2013). All of these GHGs are mainly produced and consumed through biological processes (Rastogi et al., 2002; Singh et al., 2010), including photosynthesis and soil respiration in the case of CO_2. Similarly, methanogenesis and methanotrophy are the microbial processes responsible for the production and consumption of CH_4, respectively. The methanogenesis process is mainly carried out by methanogenic archaea and methanotrophy, an aerobic process dominant in upland soils, is performed mainly by methanotrophic bacteria (Le Mer and Roger, 2001). Nitrification and denitrification processes are responsible for N_2O emissions in soils, particularly aerobic nitrification-mediated pathways (nitrifier nitrification and/or nitrifier denitrification), facilitated by ammonia-oxidizing archaea (AOA) and ammonia-oxidizing bacteria (AOB) (Baggs, 2011). Anaerobic denitrification can also generate N_2O as an intermediate or as an end product of the anaerobic respiratory pathway by reducing nitrate (NO_3^-) or nitrite (NO_2^-) (Baggs, 2011), but also consume N_2O in soil via the activity of N_2O-reducing microorganisms (Jones et al., 2014).

Microbial communities are known to have a crucial role in soil nutrient cycling (Harris, 2009). Previous studies have shown that microbial communities are strongly impacted by environmental factors such as nutrient availability, pH and increasing nitrogen (N) deposition (Pennanen et al., 1999; Rousk et al., 2010; Fierer et al., 2012), with Koorem et al. (2014) showing that soil nutrient content is also capable of shaping microbial abundances in soil. Furthermore, under climate change treatments, microbial communities have been shown to respond differently across soils with different nutrient conditions, directly affecting soil respiration rates (Karhu et al., 2014). This suggests that soil nutrient availability may have an important role in shaping belowground functioning. Soil abiotic properties, particularly substrate availability (mineral N and labile carbon (C)), but also soil temperature, moisture, pH and gas diffusivity are capable of directly or indirectly impacting GHG emissions (Dalal and Allen, 2008).

Meta-analyses on the effect of elevated CO_2 and elevated temperature have become more common, further assisting in the understanding of ecosystem GHG responses. Soil CO_2 emissions have been reported to increase under elevated CO_2 and temperature (Cox et al., 2000; Piao et al., 2009; Adair et al., 2011). Previous studies have also shown that elevated CO_2 enhanced N_2O emissions from upland soils and CH_4 emissions from wetlands and rice fields (van Groenigen et al., 2011; Dijkstra et al., 2012) while in an upland grassland soil the net CH_4 and N_2O sink has been reported to decrease under elevated CO_2 and temperature (Dijkstra et al., 2013). However, the interactive effects of CO_2 and temperature can offset the individual effects by changing the environmental conditions for microbial activity. For example, elevated CO_2 can increase soil moisture levels due to increasing water use efficiency by plants whereas warming can directly reduce soil moisture content by evaporation (Morgan et al., 2011). This can lead to a less than additive impact of interactive climate effects on GHG emissions in comparison to individual effects. None of the previous studies have evaluated the response of functional microbial communities as key drivers of GHG emissions, rather exclusively focusing on environmental parameters as possible explanations for changes in GHG fluxes. Due to the complexity of the C cycle, and the numerous microorganisms involved, process rates rather than functional microbial groups are more frequently targeted. In the case of CH_4, a few studies have considered climate change effects on methanotrophs (Horz et al., 2005; Mohanty et al., 2007). Nonetheless, there are few studies that have investigated the effects of elevated CO_2 and temperature on N_2O emissions together with N_2O-related communities (Regan et al., 2011; Cantarel et al., 2012). Given the central role of microbes in GHG fluxes, studies linking (functional) microbial communities under future climate change scenarios are needed to better estimate future GHG feedback responses and develop effective mitigation and adaptation strategies.

This study aimed at quantifying the magnitude and direction of CO_2, CH_4 and N_2O emissions under elevated CO_2 (400 ppm vs. 600 ppm) and elevated temperature (ambient vs. +3 °C increase) treatments and their interactive effects, from three Australian dryland soils with low nutrient availability. We also aimed to identify the key environmental drivers (microbial and/or abiotic) of GHG emissions. In addressing these aims we hypothesised that climate change treatments would indirectly impact CO_2, CH_4 and N_2O emissions due to changes in soil moisture. Individual elevated CO_2 treatment indirectly increases soil moisture, whereas individual elevated temperature treatment directly decreases soil moisture. These indirect or direct effects of predicted climate change would change microbial activity and, hence alter GHG emissions. However, interactive treatments would offset individual treatment effects due to the antagonistic effect on soil moisture.

2. Materials and methods

2.1. Sampling sites, collection of soil monoliths, experimental design and climate-controlled growth chamber conditions

Three dryland field sites were selected based on low nutrient status; two (Rosemary [R] and Camerons [C]) located at the University of New England's Newholme farm near Armidale, NSW (S30°25′20.87″, E151°39′21.67″) and one (Driftway [D]) in Richmond, NSW (S33°37′11.3″, E150°44′12.4″). Both R and C soil sites, classified as Yellow Chromosols, have a history of removal of native *Eucalyptus* woodland. In particular, R soil represents ungrazed and unimproved open canopy woodland and C soil represents semi-improved (occurrence of fertilisation and/or legume inoculum more than two decades ago) open grazed woodland (Wilson et al., 2007). D soil is classified as Chromosol within the Clarendon Formation and occurs in native *Eucalyptus* woodland. Soil sites are characterized by a precipitation/evapotranspiration ratios of 0.5 and 0.6 for R/C and D soils, respectively, and thus classified as dry sub-humid ecosystems under the UNEP classification (Millennium Ecosystem Assessment, 2005). Full soil characteristics and climate description can be found in Hu et al. (2016).

At each site, 24 soil monoliths of 22 L were collected in March 2012 as described previously (Hu et al., 2016) and transported to climate-controlled growth chambers (Biochambers, Manitoba, Canada) facilities at Western Sydney University whereby they were incubated under controlled CO_2 concentrations, temperature and humidity for a duration of nine months. The experiment included a full factorial design, with three different soil sites (R, C and D) and four climate treatment combinations: ambient CO_2 × ambient temperature (aCaT), elevated CO_2 × ambient temperature (eCaT), ambient CO_2 × elevated temperature (aCeT) and elevated CO_2 × elevated temperature (eCeT). Ambient CO_2 corresponded to 400 ppm and elevated CO_2 to 600 ppm. Elevated temperature corresponded to +3 °C of ambient temperatures from monthly averages (20.3−29.4/7.1−16.8 °C day/night). Six monoliths from