Agriculture, Ecosystems and Environment 257 (2018) 165–174

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

An additive effect of elevated atmospheric CO_2 and rising temperature on methane emissions related to methanogenic community in rice paddies

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ARTICLE INFO

Keywords:
CH_4
Elevated CO_2
FACE
Global warming
Methanogenic archaea
Rice paddy

ABSTRACT

Both elevated atmospheric carbon dioxide (CO_2) and rising temperature can alter soil methane (CH_4) fluxes, leading to a feedback to climate change. However, predicting this feedback needs to understand the microbial mechanisms involved in CH_4 emissions driven by climate change. A 3-year field measurement of CH_4 fluxes from rice paddies was taken in 2012–2014 to examine their responses to elevated CO_2 (enriched up to 500 μmol mol^{-1}) and rising canopy air temperature (above ambient 1.5–2.0 °C) using a free-air CO_2 enrichment (FACE) system. Using real-time PCR and Illumina MiSeq sequencing of 16S rRNA genes, we measured the abundance and composition of methanogenic community in rhizosphere soil of rice paddies in 2014. Elevated CO_2 and rising temperature showed additive effects on CH_4 fluxes and methanogen abundances, where CH_4 fluxes were correlated with methanogen abundances. Elevated CO_2, rising temperature and their combination increased seasonal CH_4 emissions by 28–120%, 38–74% and 82–143%, respectively. Either elevated CO_2 or rising temperature did not significantly alter the diversity of methanogenic community, and methanogenic genera *Methanosaeta*, *Methanosarcina*, *Methanobacterium*, *Methanocella* and *Methanoregula* dominated in rhizosphere soils for all treatments. However, elevated CO_2 induced a shift from acetoclastic to hydrogenotrophic methanogens in their relative abundances. Rising temperature stimulated CH_4 emissions by increasing CH_4 production per individual predominant methanogen genus. Besides the enhancement of soil C substrates and rhizosphere methanogen abundances as previously reported, an additive effect of elevated CO_2 and canopy warming on CH_4 emissions is also associated with elevated CO_2-induced changes in the composition of methanogenic archaea and warming-stimulated the activity of methanogenic archaea in rice paddies.

1. Introduction

Atmospheric carbon dioxide (CO_2) and methane (CH_4) are the two major potent greenhouse gases (GHGs). Increasing concentrations of GHGs for 2011 relative to 1750 have contributed to an anthropogenic radiative forcing of 2.83 W m^{-2}, where CO_2 and CH_4 account for 1.68 W m^{-2} and 0.97 W m^{-2}, respectively (IPCC, 2013). As a consequence of continuing buildup of GHGs in the atmosphere, increases in global surface air temperature between the mid-21 st century and the reference period of 1986–2005 are projected to likely exceed 1.4 °C and 2.0 °C for RCP4.5 and RCP 8.5, respectively (IPCC, 2013). Both elevated atmospheric CO_2 and rising temperature can alter soil GHG fluxes, leading to a feedback to climate change (Frank et al., 2010; van Groenigen et al., 2011; Gaihre et al., 2014). Predicting this feedback needs to understand the mechanisms and processes involved in GHGs emission under climate change scenarios (Schimel and Gulledge, 1998; Conrad, 2007). However, the combined effects of elevated CO_2 and rising temperature on soil carbon and nitrogen biogeochemistry and soil GHGs emission remain poorly understood (Dijkstra et al., 2012; Liu et al., 2012; Yue et al., 2017).

Rice paddies play an important role in atmospheric GHGs budget, accounting for 10% of total anthropogenic CH_4 emissions or about 1.5%

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https://doi.org/10.1016/j.agee.2018.02.003
Received 8 January 2018; Received in revised form 31 January 2018; Accepted 1 February 2018
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of global gross GHGs emissions (FAOSTAT, 2014). While rice production responses to climate change are of great concern (Ainsworth and Long, 2005; Wang et al., 2015, 2016; Cai et al., 2016), recent attention has been increasingly directed towards the effects of climate change on CH_4 emissions from rice paddies to understand its feedback to climate change. By summarizing available field measurements, a meta-analysis synthesized that elevated atmospheric CO_2 incurred, on average, an increase of 43% in CH_4 emissions from rice paddies (van Groenigen et al., 2011). However, the magnitude of this effect varies widely with many other factors, such as soil property, water management regime, crop residue amendment, fertilizer application, rice cultivar and plant growth, and experimental method (Allen et al., 2003; Inubushi et al., 2003; Xu et al., 2004; Zheng et al., 2006; van Groenigen et al., 2011).

Numerous experiments have been carried out to examine the response of CH_4 emissions to elevated atmospheric CO_2 in controlled-environment chambers and in the field FACE (Free-Air-CO_2-Enrichment) systems (Ziska et al., 1998; Allen et al., 2003; Inubushi et al., 2003; Xu et al., 2004; Zheng et al., 2006; Tokida et al., 2010; Liu et al., 2012). The effects of increased soil temperature on CH_4 emissions from paddy soils are examined mostly in laboratory incubation experiments, while very few studies have concentrated on the effects of canopy air temperature on CH_4 emissions in the field (Allen et al., 2003; Gaihre et al., 2014). It is generally believed that CH_4 fluxes response to elevated CO_2 is more realistic under field FACE experiments than under phytotron or greenhouse conditions. Rice growth and yield responses to elevated CO_2 are less in field FACE experiments than in the controlled enclosure experiments (Ainsworth and Long, 2005; Wang et al., 2015; Cai et al., 2016), which would incur a difference in CH_4 fluxes response to elevated CO_2 between the two experiment methods.

To examine the combined effect of elevated CO_2 and rising temperature on CH_4 emissions, almost all FACE field experiments were designed with increased soil temperature (Tokida et al., 2010, 2011; Liu et al., 2012), while elevated CO_2 combined with rising air temperature was designed only in two studies, one in controlled-environment chambers (Allen et al., 2003) and the other one in open-top chambers (OTCs) (Ziska et al., 1998). The response of CH_4 emissions to rising soil temperature may differ with their response to rising canopy air temperature in rice paddies (Ziska et al., 1998; Allen et al., 2003; Liu et al., 2012; Gaihre et al., 2014). In rice paddies, flood water and soil temperature can track the controlled air temperature closely during the initial flooding and midseason drainage stages when there is little shading of the water surface by rice vegetation (Allen et al., 2003). During the late season with complete rice vegetative cover, soil temperature can hardly increase with canopy warming (Ziska et al., 1998; Gaihre et al., 2014; Liu et al., 2016a). Since elevated atmospheric CO_2 is accompanied by an increase in air temperature under future climate change, nevertheless, the experiments of elevated CO_2 combined with rising canopy air temperature deserve to be highlighted, particularly under field conditions.

The interactive effects of multiple global change factors on soil C and N biogeochemistry may be additive (i.e., not differing from the sum of their individual effects), non-additive synergistic or non-additive antagonistic (Dijkstra et al., 2012; Yue et al., 2017). By synthesizing available data, a meta-analysis concluded that the interactive effects of elevated CO_2 and rising temperature on soil C pools are generally additive (Yue et al., 2017). However, the interactive effects of elevated CO_2 and rising temperature on CH_4 emissions from rice paddies have been rarely examined and very few available studies have generated contradictory results (Dijkstra et al., 2012). A non-additive synergistic effect of elevated CO_2 and rising temperature on CH_4 emissions was found in controlled-environment chamber studies (Allen et al., 2003) or laboratory soil microcosms (Das and Adhya, 2012), while an additive effect of elevated CO_2 and rising soil/air temperature on CH_4 emissions was reported in field OTC/FACE studies (Ziska et al., 1998; Liu et al., 2012). Nevertheless, more field FACE studies under simulating atmospheric CO_2 enrichment combined with rising air temperature are highly needed to reconcile this debate.

Given that CH_4 is produced by methanogenic archaea in rice paddies, it is important to understand how methanogenic archaea abundance and community structure influences CH_4 production under climate change scenarios (Schimel and Gulledge, 1998; Conrad, 2007). Some studies showed that elevated atmospheric CO_2 and rising temperature can alter the soil, rhizosphere or root microbial community (Yue et al., 2007; Peng et al., 2008; Das and Adhya, 2012; Lu et al., 2015; Liu et al., 2016a), while their effects on the abundance and composition of methanogenic community were not significant in field FACE studies (Angel et al., 2012; Liu et al., 2012, 2016b). Nevertheless, insights into responses of methanogenic community to elevated CO_2 and rising temperature in rice paddies are remained poor (Alpana et al., 2017). In particular, rising canopy air temperature effects and the interactive effects with elevated CO_2 on methanogenic community have not been linked to CH_4 fluxes (Singh et al., 2010; Liu et al., 2016a; Alpana et al., 2017). Our FACE experiment under atmospheric CO_2 enrichment combined with rising air temperature would help to examine their combined effects on the methanogenic abundance and structure and the consequences for CH_4 production in rice paddies.

Here, we first presented field measurements of CH_4 flux from rice paddies under elevated CO_2 and rising canopy temperature in a FACE system over the 2012–2014 seasons. The FACE system under elevated atmospheric CO_2 (up to 550 μmol mol^{-1}) combined with rising canopy temperature (1.5–2.0 °C above ambient) has been established in rice paddies in southeast China since 2011. To understand methanogenic community linking to seasonal CH_4 flux responses to elevated CO_2 and rising temperature, the abundance and composition of methanogenic community were measured in rhizosphere soil of rice paddies over the 2014 rice-growing season. The main objective of this study is to examine the combined effect of elevated CO_2 and rising canopy temperature on CH_4 emissions related to methanogenic community in rice paddies. Specifically, we attempted to address the following concerns: (i) Whether the interactive effects of elevated CO_2 and rising air temperature on CH_4 emissions are additive, non-additive synergistic or non-additive antagonistic in rice paddies? (ii) How do combined elevated CO_2 and rising air temperature affect methanogenic community (abundance, composition and activity) in rice paddies? (iii) Whether CH_4 fluxes are related to methanogenic community over the rice-growing season under FACE systems?

2. Materials and methods

2.1. Experiment site

A field FACE experiment over the 2012–2014 rice seasons was carried out in rice paddies on the experimental farm of Nanjing Agricultural University, Changshu, Jiangsu province, China (31°30′N, 120°33′E). The field site is located in the center of the Tai Lake Plain region, where cropping regime is overwhelmingly dominated by an annual paddy rice-winter wheat rotation system. The region displays a typical monsoonal climate, where seasonal mean temperature was 22.0 °C in 2012, 27.0 °C in 2013 and 24.2 °C in 2014. Seasonal rainfall totaled 1045 mm in 2012, 680 mm in 2013 and 760 mm in 2014. Soil of the experimental site is classified as Gleyic Stagnic Anthrosol, which is developed from clayey lacustrine deposit and under paddy rice-wheat rotation cultivation for hundreds of years. Prior to the 2012 rice season, topsoil pH, bulk density, organic C and total N contents were 6.7 (1:2.5, water/soil, w/w), 1.20 g cm^{-3}, 15.0 g kg^{-1} and 1.6 g kg^{-1}, respectively.

2.2. Rice cultivation

All the experimental plots were in line with the local typical cultivation practices including rice cultivar, water and fertilization regimes in rice paddies in 2012–2014. Rice (*Oryza sativa* L. cv. Changyou 5)

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