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An Integrative Model for Soil Biogeochemistry and Methane Processes. II: Warming and Elevated CO₂ Effects on Peatland CH₄ Emissions

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Comments

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Fenghui Yuan and Yihui Wang contributed equally to this manuscript.

Key Points:

- Warming and elevated CO₂ stimulate peatland CH₄ emissions through different mechanisms
- The stimulating impact of warming is primarily through stimulation of microbial processes
- The stimulating impact of elevated CO₂ is primarily through enhanced substrate availability by increased photosynthesis

Supporting Information:

Supporting Information may be found in the online version of this article.

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An Integrative Model for Soil Biogeochemistry and Methane Processes. II: Warming and Elevated CO₂ Effects on Peatland CH₄ Emissions

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Abstract Peatlands are one of the largest natural sources for atmospheric methane (CH₄), a potent greenhouse gas. Climate warming and elevated atmospheric carbon dioxide (CO₂) are two important environmental factors that have been confirmed to stimulate peatland CH₄ emissions; however, the mechanisms underlying enhanced emissions remain elusive. A data-model integration approach was applied to understand the CH₄ processes in a northern temperate peatland under a gradient of warming and doubled atmospheric CO₂ concentration. We found that warming and elevated CO₂ stimulated CH₄ emissions through different mechanisms. Warming initially stimulated but then suppressed vegetative productivity while stimulating soil organic matter (SOM) mineralization and dissolved organic carbon (DOC) fermentation, which led to higher acetate production and enhanced acetoclastic and hydrogenotrophic methanogenesis. Warming also enhanced surface CH₄ emissions, which combined with warming-caused decreases in CH₄ solubility led to slightly lower dissolved CH₄ concentrations through the soil profiles. Elevated CO₂ enhanced ecosystem productivity and SOM mineralization, resulting in higher DOC and acetate concentrations. Higher DOC and acetate concentrations increased acetoclastic and hydrogenotrophic methanogenesis and led to higher dissolved CH₄ concentrations and CH₄ emissions. Both warming and elevated CO₂ had minor impacts on CH₄ oxidation. A meta-analysis of warming and elevated CO₂ impacts on carbon cycling in wetlands agreed well with a majority of the modeled mechanisms. This mechanistic understanding of the stimulating impacts of warming and elevated CO₂ on peatland CH₄ emissions enhances our predictability on the climate-ecosystem feedback.

Plain Language Summary Peatlands are one of the largest natural sources for a potential greenhouse gas—methane. In this study, we took use of a number of field observational data to parameterize a microbial model before applying the model to understand the methane processes in a northern temperate peatland under a gradient of warming and doubled atmospheric carbon dioxide concentration. We found that warming and elevated carbon dioxide stimulated methane emissions through different mechanisms. Warming initially stimulated but then suppressed vegetative productivity while stimulating soil organic matter mineralization and dissolved organic carbon fermentation, which led to higher acetate production and enhanced methane production. Elevated carbon dioxide enhanced ecosystem productivity and soil organic carbon decomposition, resulting in higher dissolved organic carbon and acetate concentrations, which stimulate methane production. Both warming and elevated carbon dioxide had small impacts on methane oxidation. The modeling results are consistent with a global data synthesis. This mechanistic understanding of the stimulating impacts of warming and elevated carbon dioxide on peatland methane emissions enhances our ability to predict the interactions between the climate system and the terrestrial ecosystems.

1. Introduction

Methane (CH₄) is a potent greenhouse gas which has 28 times global warming potential of CO₂ on a 100-years time frame (IPCC, 2013). Further, rising atmospheric CH₄ concentration has contributed to 20%–25% of

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climate warming since the Industrial Revolution (Stocker et al., 2013). Natural wetlands cover only 5%–8% of the total land area but serve a critical role in regulating climate. For example, natural wetlands contribute more than 15% of global terrestrial net primary productivity (NPP) (Schlesinger & Bernhardt, 2013) and, due to relatively low decomposition (Mitsch & Gosselink, 2007), northern peatlands store up to 50% of global soil organic carbon storage (Gorham, 1991; Nichols & Peteet, 2019; Tarnocai et al., 2009). Meanwhile, natural wetland contributes more than 30% of total global CH₄ emission (Jackson et al., 2020), with northern peatlands contributing about 5% (Frolking et al., 2006; Kirschke et al., 2013; Nazaries et al., 2013). Given the high organic carbon (C) storage and complicated thermal and hydrological processes that regulate CH₄ cycling in peatlands (Gill et al., 2017; Teh et al., 2011; Updegraff et al., 2001), it is imperative to understand the impacts of various environmental changes on CH₄ cycling in order to improve the predictions of CH₄ in peatlands.

Warming is projected to stimulate CH₄ emissions in wetlands. However, the complexity of microbial-mediated and vegetation-mediated processes that regulate CH₄ cycling in peatlands makes a mechanistic explanation of the impacts of warming challenging (Shindell et al., 2004). Under waterlogged condition, rising temperature enhances methanogenesis that leads to higher CH₄ emissions (Bardgett et al., 2008; Christensen et al., 2003). In addition, warming directly enhances photosynthesis and thus likely leads to greater plant-derived carbon input, the primary substrate for fermentation that produces acetate and H₂ to drive methanogenesis (Wu et al., 2011; Yin et al., 2013). Warming also increases C availability in peatlands through enhanced soil organic matter (SOM) decomposition, which leads to greater methanogenesis (Cao et al., 1996; Wickland et al., 2006). However, the magnitude and mechanisms of warming effects on CH₄ emissions vary dramatically due to various microbial responses to different warming intensities (Bridgman et al., 2013). Methanogens and methanotrophs with distinct temperature sensitivities show uneven feedbacks to temperature changes (Conrad, 1995, 1996), leading to large variations in CH₄ production and consumption.

Elevated atmospheric CO₂ (eCO₂) stimulates peatland CH₄ emissions by enhancing vegetation productivity that leads to more substrates for methanogenesis (Dijkstra et al., 2010). Previous studies reported that eCO₂ concentration promoted photosynthesis by stimulating Rubisco carboxylation capacity and RuBP regeneration rate, especially for C3 plants (Stirling et al., 1997), therefore increasing the substrate availability for methanogenesis (Megonigal & Schlesinger, 1997; Silvola et al., 2003). Higher substrate concentrations likely stimulate methanogenesis, but the underlying mechanisms remain unclear (Bridgman et al., 2013).

To develop a full mechanistic understanding of peatland CH₄ flux in response to multiple environmental changes, it is critically important to investigate the mechanisms of CH₄ cycling under concurrent warming and eCO₂ treatments. Ecosystem models are a powerful tool to disentangle the impacts of multiple environmental factors on CH₄ cycling (Xu et al., 2016), and a number of ecosystem models have been used to investigate CH₄ cycling under the warming and eCO₂ treatments. For example, Zhuang et al. (2004) used the Terrestrial Ecosystem Model (TEM) model to estimate CH₄ emissions from Arctic tundra ecosystems in response to climate change. Xu et al. applied the Dynamic Land Ecosystem Model (DLEM) model to interpret the response of CH₄ fluxes to multiple environmental factors from different ecosystems across North America (Xu, 2010; Xu et al., 2010), and in China (Xu & Tian, 2012). More recently, Xu et al. (2015) developed a microbial functional group-based CH₄ module, and the module has been incorporated into the Community Land Model (CLM) 4.5 and is being incorporated into the Energy Exascale Earth System (E3SM) land model (ELM). The module can provide mechanistic understanding into how warming and eCO₂ affect peatland CH₄ emissions (Ricciuto et al., 2021; Xu et al., 2015).

In this study, we reported on the simulating effects of warming and eCO₂ on CH₄ cycling in a northern Minnesota peatland under various warming and eCO₂ scenarios by using the ELM-SPRUCED model, a version of ELM designed for this experiment (Ricciuto et al., 2021; Shi et al., 2015, 2021). As the second in a series of two modeling papers, we expanded upon the model description provided by Ricciuto et al. (2021) and explored the warming and eCO₂ impacts on CH₄ cycling and further compared the simulated processes against observational data obtained from a global meta-analysis. Uncertainty analyses associated with the simulated CH₄ fluxes under the different treatments are reported as well. We address two questions: (1) how do different levels of warming and doubled atmospheric CO₂ affect CH₄ processes in peatlands, and

(2) what are the mechanisms contributing to the warming and eCO₂ impacts on CH₄ flux in the Minnesota peatland?

2. Methodology

2.1. Field Experiment

Our study was occurred in an ombrotrophic peatland with a perched water table that has little groundwater influence, located in a black spruce-*Sphagnum* spp. bog in northern Minnesota, USA (Hanson et al., 2016). The site is S1-Bog in the USDA Forest Service's Marcell Experimental Forest (MEF) (Kolka et al., 2011), which is set up for the Spruce and Peatland Responses Under Changing Environment (SPRUCE) experiment. The SPRUCE experiment was conducted to assess the response of northern peatland ecosystems to warming (five warming levels: ambient, +2.25, +4.50, +6.75, and +9.00°C) and eCO₂ concentration (800 ppm(v) in the atmosphere versus ambient CO₂) with long-term manipulations (Hanson et al., 2016, 2017). More detailed information for the experiment and the field site can be found in Hanson et al. (2017, 2020).

2.2. Model Description

We applied the ELM-SPRUCE model to simulate peatland biogeochemistry, focusing on CH₄ and CO₂ fluxes. The ELM-SPRUCE model was originally developed upon the default CLM4.5 (Oleson et al., 2013) and then modified to better simulate peatland hydrology and vegetation at the SPRUCE site (Shi et al., 2015). The improvements included (a) model representation of microtopography including hummocks and hollows (Shi et al., 2015), (b) an improved hydrology module (Shi et al., 2015), (c) a new moss plant functional type (Shi et al., 2021), and (d) an improved CH₄ module (Ricciuto et al., 2021; Wang et al., 2019; Xu et al., 2015). This new module represents CH₄ production and consumption in association with the existing decomposition subroutines in CLM4.5 (Thornton & Rosenbloom, 2005; Thornton & Zimmermann et al., 2007). Added processes associated with the CH₄ module include dissolved organic carbon (DOC) fermentation, hydrogenotrophic methanogenesis, acetoclastic methanogenesis, aerobic methanotrophy, anaerobic methanotrophy, and hydrogen (H₂) production (Ricciuto et al., 2021). The simulated surface CH₄ flux is the sum of diffusion, ebullition, and plant aerenchyma-mediated transport (Ricciuto et al., 2021; Wang et al., 2019; Xu et al., 2015). The CH₄ concentration is the difference between methanogenesis and methanotrophy; both processes are simulated as a function of microbial biomass, microbial growth efficiency, temperature, soil pH, and oxygen availability (Wang et al., 2019; Xu et al., 2015). Another improvement is the horizontal flow of water and associated biogeochemical variables between hummock and hollow columns. The vertical diffusion of DOC, acetate, CO₂, and CH₄ follows Fick's law along the concentration gradient (Ricciuto et al., 2021).

Model development and evaluation for the SPRUCE bog site are fully described in Ricciuto et al. (2021). Specifically, the formulation is listed in supplementary online materials of Ricciuto et al. (2021). The model predicted CH₄ flux in the SPRUCE bog site well when compared to several independent observational data sets ($R^2 = 0.33$ with land surface CH₄ flux; $R^2 = 0.58$ with the chamber-derived CH₄ flux), as well as vertical distribution of DOC ($R^2 = 0.97$) and acetate ($R^2 = 0.59$). However, the model showed high variability and lower accuracy in CH₄ concentrations in deeper soils (Ricciuto et al., 2021).

2.3. Model Implementation

The implementation of model simulation included three stages. The first two stages, accelerated decomposition (ad) spin-up and final spin-up, follow the same strategy as CLM4.5 (Oleson et al., 2013; Thornton & Rosenbloom, 2005). The ad-spin-up simulation of 1,200 years allowed the system to accumulate C to reach equilibrium state in an accelerated mode. A 50-years final spin-up subsequently allowed the system to operate with normal decomposition parameters before the transient run. The third phase was the transient run that is, for model application. After the final spin-up, the initial sizes of soil C/nitrogen(N) pools were adjusted based on the measured soil C and N content along soil profiles at the SPRUCE site (Ricciuto et al., 2021). Specifically, the C and N pools in each layer was proportionally adjusted so that the total C and N density in each layer equaled the observational data. Six independent manipulative experimental

simulations from 2015 to 2019 were then conducted to examine how CH₄ emissions respond to warming or eCO₂. The six manipulative simulations included one control scenario (ambient), four warming scenarios (+2.25, +4.50, +6.75, and +9.00°C above ambient under ambient CO₂, respectively), and one eCO₂ scenario (800 ppm CO₂ concentration under ambient temperature, 410 ppm above the ambient CO₂ concentration). Twelve variables were chosen for investigating the warming and eCO₂ impacts by comparing manipulated treatments with the ambient scenario. They are NPP, SOM mineralization, concentrations of DOC, acetate, CO₂ and CH₄ through the soil profile, acetoclastic, and hydrogenotrophic methanogenesis, rates of CH₄ transport via plants, diffusion and ebullition, and surface CH₄ flux. These variables were selected to represent the direct and indirect controls on CH₄ flux by biological, soil, and microbial mechanisms. The cumulative effects of warming and eCO₂ departure from the control scenario on each variable are reported.

2.4. Data Sources

The initial atmospheric forcing data (from 2011 to 2017) used in the model were obtained by the SPRUCE team and gap-filled as necessary (Ricciuto et al., 2021). For all simulations, we repeatedly cycled the 7-years forcing data, including: hourly temperature, precipitation, specific humidity, solar radiation, wind speed, pressure, and longwave radiation. Historical atmospheric CO₂ and N deposition data were from the nearest neighbor grid cell of a globally gridded historical atmospheric CO₂ data set (Oleson et al., 2013). The five model experiments from 2015 to 2019 were set up by adding the constant values of temperature (+2.25, +4.50, +6.75, and +9.00°C) and CO₂ (+410 ppm) to the original data of air temperature and atmospheric CO₂ concentration from 2014. Four plant functional types (PFTs) were defined as evergreen needle-leaf forest-boreal (25%), deciduous needle-leaf forest-boreal (25%), shrub (25%), and *Sphagnum* moss (25%). These PFTs were assumed to remain unchanged over the study period. Soil properties data were obtained from the SPRUCE project (<https://mnspruce.ornl.gov/>).

2.5. Uncertainty Analysis

A Monte Carlo approach was used to evaluate the uncertainty of the ELM_SPRUCE model. This approach is based on Bayesian statistics, and its main characteristic is that all model uncertainties are quantified in terms of probabilities, and these uncertainties can be determined by a large ensemble of model simulations with different parameter settings. The Latin hypercube sampling method, which can effectively represent the uncertainties caused by parameters with a manageable ensemble of model simulations, was applied to obtain different combinations of parameters following our previous studies (Xu, 2010; Xu et al., 2015; Wang et al., 2019).

In this study, a total of 100 model simulations were set up to represent the variations of 10 key parameters. All parameters used for the uncertainty analysis varied within a range of ±30% of their optimal values (Table 1). The 20% has been used in our previous studies (Wang et al., 2019; Xu et al., 2015), but in this study, we quantified a greater uncertainty in the parameters. These 10 key parameters are directly relevant to photosynthesis, soil carbon cycling, and microbial activities. Specifically, *flnr* represents the fraction of leaf N in the Rubisco enzyme, which controls the plant photosynthetic production by calculating the maximum rate of carboxylation at 25°C (*Vcmax25*); *froz_q10*, *K_s4*, and *k_dom* control the temperature dependence and decomposition rate of DOC. The variables *m_dAceProdACmax* and *m_dACMinQ10* determine acetate production, through controlling the maximum rate of acetate production and temperature sensitivity of DOC decomposition. Methane production from acetate and H₂ is governed by the growth and production efficiency of acetoclastic methanogens and hydrogenotrophic methanogens, as *m_dYAceMethanogens*, *m_dGrowRAceMethanogens*, and *m_dH2ProdAcemax*, respectively. The *m_dKCH4OxidCH4* represents the half-saturation efficiency for CH₄ concentration in computing CH₄ oxidation. Model simulations with each parameter ensemble were produced for six manipulative experiments, covering the period of 2015–2019.

2.6. A Meta-Analysis of Warming and eCO₂ Impacts on CH₄ Cycling

We compared our simulation results to experimental results from the SPRUCE site to evaluate the ELM-SPRUCE model at the site scale. Results of NPP and CH₄ flux were retrieved from Hanson et al. (2020), and results of CH₄ production were from Hopple et al. (2020). Moreover, we evaluated the broader applicability

Table 1
Key Parameters and Their Optimized Values and Uncertainty Ranges Used for the ELM_SPRUCE Model

Parameter	Description	Unit	Value	Standard deviation
Flnr	Fraction of leaf N in the Rubisco enzyme	(g N Rubisco g N leaf ⁻¹)	0.2	0.0306
froz_q10	Q ₁₀ for soil respiration rates	Unitless	1.5	0.2296
k_s4	Decomposition rate constant of soil organic carbon pool	Unitless	0.0001	1.53E-05
k_dom	Decomposition rate constant of dissolved organic matter	Unitless	0.007	0.0011
m_dAceProdACmax	Maximum rate of acetate production from available carbon	mmol m ⁻³ h ⁻¹	0.0000024	3.67E-07
m_dACMinQ10	Temperature sensitivity of available carbon fermentation	Unitless	3	0.4592
m_dGrowRAceMethanogens	Growth rate of acetoclastic methanogens	d ⁻¹	0.008	0.0012
m_dH2ProdAcemax	Maximum reaction rate of conversion of H ₂ and CO ₂ to acetate	mmol acetate g ⁻¹ h ⁻¹	0.00000005	7.65E-09
m_dYAceMethanogens	Growth efficiency of acetoclastic methanogens	mol C (mol acetate C) ⁻¹	0.2	0.0306
m_dKCH4OxidCH4	Half-saturation coefficient of CH ₄ oxidation for CH ₄ concentration	mmol L ⁻¹	1	0.1531

of our model by comparing model results to a meta-analysis of warming and eCO₂ manipulations in global wetlands. We searched in the Web of Science and Google Scholar with the keywords (“warming” or “rising temperature”) or (“elevated CO₂” or “rising CO₂” or “fumigation CO₂” or “CO₂ enrichment”) and (“CH₄” or “methane”) and (“wetland” or “peatland” or “bog” or “marsh” or “swamp” or “fen”). The search was completed in April 2019. Studies were only included if they (a) reported exact values or graphs for variables related to CH₄ processes from observations, (b) provided detailed information for the wetland types and treatment settings, and (c) were published in English. Fifteen warming studies and 20 eCO₂ studies met these criteria and were included in our meta-analysis (Table S1). Eight variables were chosen and extracted from these relevant publications; they are NPP, SOM, DOC, CH₄ production, CH₄ emission, and plant-mediated transport (CH₄-Plant), diffusion (CH₄-Diff), and ebullition (CH₄-Ebull). Among these observational studies, air temperature in the warming experiments was raised by 0.2–15°C, the ambient atmospheric CO₂ concentration was approximately 380 ppm(v), and the CO₂ concentration in the eCO₂ treatments fell within a range of 473–760 ppm(v). The experiments ran from 0.02 to 9 measurement years. Data from model simulations, experimental study, and the meta-analysis for both warming and eCO₂ were standardized to get percentage changes per unit (°C or 100 ppm(v)) for comparison.

3. Results

3.1. Effects of Warming and eCO₂ on NPP and SOM Mineralization

Net primary production and SOM mineralization showed similar seasonal patterns, reaching their maxima in summer and minima in winter seasons (Figures 1a and 1b). The warming and eCO₂ yielded different impacts on NPP and SOM mineralization (Figure 1). At the end of the study period, warming suppressed NPP while the eCO₂ greatly promoted NPP (Figures 1c and 1d). Warming greatly stimulated SOM mineralization with strongest effects at +9.00°C (Figure 1b), while eCO₂ stimulated SOM mineralization and the impacts increased over time, resulting in stimulation comparable with the warming effects under +2.25°C (Figure 1d).

The impacts of warming and eCO₂ showed large seasonal variations. In the warm season (primarily summer), both warming and eCO₂ accelerated photosynthesis activity more than plant respiration, thus stimulating NPP (Figures 1c and 1d). However, warming had a stronger suppression effect on NPP in the cold seasons (winter and early spring) than its promoting effects in the warm season, which led to a cumulative suppression of NPP during 5-years simulations. Elevated atmospheric CO₂ has positive but minimal impacts on NPP in cold seasons (Figure 1a). Additionally, the stimulating impact of warming on SOM mineralization was strongest in the warm season and relatively weak in the cold season (Figure 1b). The eCO₂ impact on SOM mineralization was constant throughout the year, without obvious seasonal variations (Figure 1d).

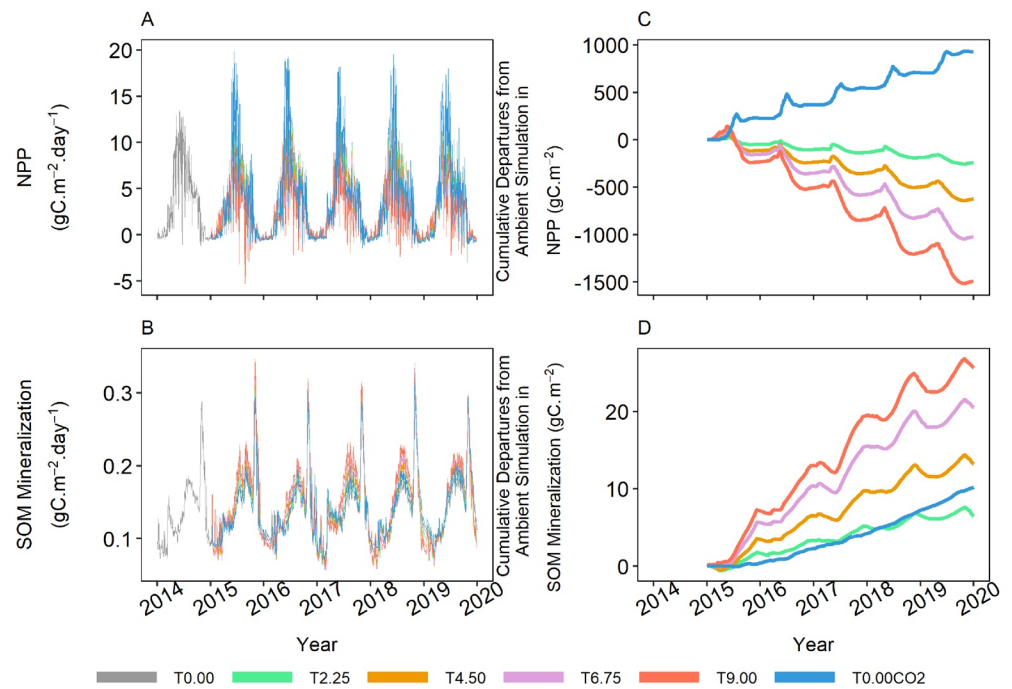


Figure 1. Time series of simulated net primary productivity (NPP) and soil organic matter (SOM) mineralization (at top 9 cm depth) under warming and elevated CO₂ concentration (eCO₂). (a, b) Simulated daily NPP and SOM mineralization under warming and eCO₂, and (c, d) cumulative departures of NPP and SOM mineralization from the ambient simulation (T0.00). Cumulative impacts are calculated as the cumulative difference between the treatment simulations and control simulations. The manipulation experiments (ambient temperature and CO₂ concentration, T0.00; +2.25°C warming, T2.25; +4.50°C warming, T4.50; +6.75°C warming, T6.75; +9.00°C warming, T9.90; elevated CO₂ concentration (+410 ppm) under ambient temperature, T0.00CO₂) began in 2015.

3.2. Effects of Warming and eCO₂ on Methanogenic Substrate Availability

The seasonal patterns of DOC, acetate, and CO₂ concentrations were slightly different. Soil CO₂ and DOC concentrations had similar seasonal patterns, low in warm seasons and high in cold seasons (Figures 2a and 2c). However, acetate concentrations showed more complex seasonal patterns, increasing in early spring, declining in summer, accumulating in fall, and depleting in winter (Figure 2b). The changes in acetate concentrations are the result of the net balance of DOC fermentation, acetogenesis, and acetoclastic methanogenesis. Overall, warming suppressed soil concentrations of DOC, acetate and CO₂, and the warming effects were stronger under higher warming scenarios (Figures 2d–2f). In contrast, eCO₂ increased DOC concentrations (Figure 2a).

The effects of warming and eCO₂ on cumulative differences in concentrations of DOC, acetate and CO₂ varied interannually (Figures 2d–2f). Under the eCO₂ treatment, the concentrations of DOC and acetate increased relatively consistently while soil CO₂ concentrations slightly increased in first 3 years and then slightly decreased at the end of five years due to enhanced DOC at the beginning and strong enhancement of hydrogenotrophic methanogenesis (Figures 2d–2f; Table S2). With warming, DOC concentrations showed a smooth decreasing trend over time (Figure 2d). However, after four years of warming treatment, the warming effects on soil CO₂ concentrations tended to weaken, whereas its effects on acetate concentrations strengthened (Figures 2e and 2f). Additionally, soil acetate concentrations were slightly increased by warming at the start of simulations then decreased (Figure 2e).

3.3. Effects of Warming and eCO₂ on CH₄ Production

Both acetoclastic and hydrogenotrophic methanogenesis showed similar seasonal patterns, increasing in warm seasons while decreasing in cold seasons (Figures 3a and 3b). Additionally, acetoclastic methanogenesis was generally more than 10-fold faster than hydrogenotrophic methanogenesis in all six simulations

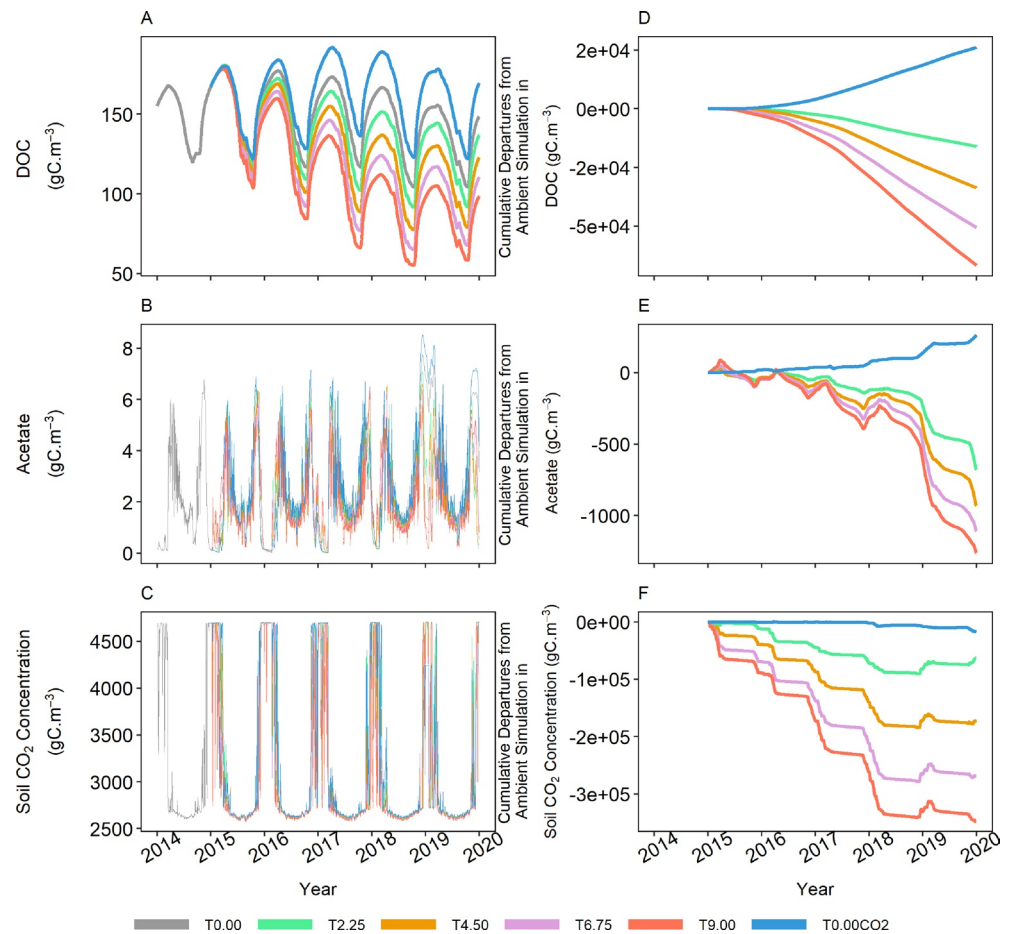


Figure 2. Time series of simulated dissolved organic carbon (DOC), acetate, and soil CO₂ concentration (at top 9 cm depth) under warming and elevated CO₂ concentration (eCO₂). (a–c) Simulated daily concentrations of DOC, acetate, and soil CO₂ under warming and eCO₂, and (d–f) cumulative impacts of warming and eCO₂ on concentrations of DOC, acetate, and soil CO₂ departure from the ambient simulation (T0.00). Descriptions of manipulation experiments and cumulative impact calculation are same as Figure 1.

(Figures 3a and 3b). Warming and eCO₂ stimulated acetoclastic and hydrogenotrophic methanogenesis, but with different magnitudes (Figures 3d and 3e). Methanogenesis increased in concert with greater warming (Figures 3d and 3e). After 5-year of warming, acetoclastic methanogenesis increased by 6.7 (5.4–8.0)%, 12.5 (10.1–14.9)%, 21.0 (16.9–25.1)%, and 28.0 (22.6–33.4)% for +2.25, +4.50, +6.75, and +9.00°C, respectively. Comparatively, warming increased hydrogenotrophic methanogenesis by 30.1 (24.3–35.9)%, 29.5 (23.8–35.2)%, 49.2 (39.7–58.7)%, and 56.8 (45.8–67.8)% along the ascending warming gradient. The stimulatory effects of eCO₂ on methanogenesis were less than warming effects at the start of simulations, but they intensified over time (Figures 3d and 3e). At the end of simulations, eCO₂ stimulated acetoclastic methanogenesis by 12.7 (10.2–15.2)% and hydrogenotrophic methanogenesis by 46.9 (37.8–56.0)%.

3.4. Effects of Warming and eCO₂ on CH₄ Transport and Emission, and Soil CH₄ Concentrations

Surface CH₄ emissions via plants, diffusion, and ebullition showed similar seasonal patterns, rising in warm seasons while decreasing in cold seasons (Figures 4a–4c). Both warming and eCO₂ enhanced all three pathways of CH₄ transport (Figures 4e–4g). Overall, greater warming led to greater transport, but warming effects tended to weaken in the last 2 years of simulation for ebullition and plant-mediated transport (Figures 4e–4g). At the end of simulations, warming by +2.25, +4.50, +6.75, and +9.00°C increased transport by 0.9 (0.7–1.1), 2.2 (1.8–2.6), 4.9 (4.0–5.8), and 6.9 (5.6–8.2) g C m⁻² via plants, by 1.6 (1.3–1.9), 3.1 (2.5–3.7),

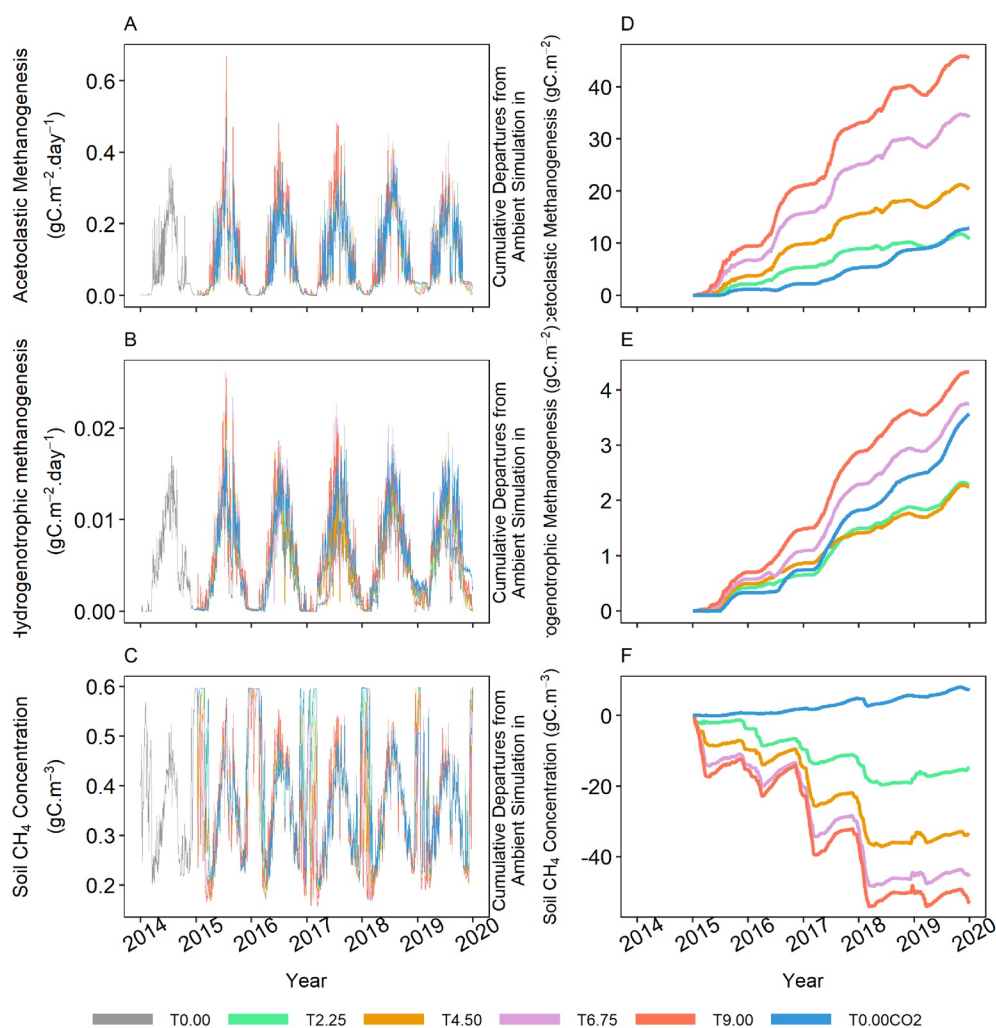


Figure 3. Time series of simulated acetoclastic methanogenesis, hydrogenotrophic methanogenesis, and soil CH₄ concentration (at top 9 cm depth) under warming and elevated CO₂ concentration (eCO₂). (a, b) Simulated daily acetoclastic methanogenesis, hydrogenotrophic methanogenesis, and soil CH₄ concentration under warming and eCO₂, and (c, d) cumulative impacts of warming and eCO₂ on acetoclastic methanogenesis, hydrogenotrophic methanogenesis, and soil CH₄ concentration departure from the ambient simulation (T0.00). Descriptions of manipulation experiments and cumulative impact calculation are same as Figure 1.

5.0 (4.0–6.0), and 6.5 (5.2–7.8) g C m⁻² via diffusion, and by 4.4 (3.6–5.2), 7.2 (5.8–8.6), 10.0 (8.1–11.9), and 12.6 (10.2–15.0) g C m⁻² via ebullition for treatments, respectively.

The eCO₂ effects on plant-mediated transport rapidly intensified and increased it by 6.1 (4.9–7.3) g C m⁻² at the end of simulations, which was greater than warming effects of all but the +9.0°C treatment (Figure 4e). Positive effects of eCO₂ on diffusion were always lower than warming effects, and an additional 0.8 (0.6–1.0) g C m⁻² of CH₄ fluxes were transported via diffusion at the end of simulations (Figure 4f). The eCO₂ effects on ebullition were generally lower than warming effects (Figure 4g). After 5-years simulations, an additional 3.8 (3.1–4.5) g C m⁻² of CH₄ fluxes were transported to the atmosphere via ebullition.

Overall, CH₄ emission exhibited a similar seasonal dynamic across the six simulations, high in warm seasons and low in cold seasons (Figure 4d), which corresponded to the seasonal patterns of CH₄ transport. CH₄ emissions were enhanced by warming and eCO₂ but with different magnitudes (Figure 4h). Greater emission occurred with greater warming but this effect weakened at the end of the simulations (Figure 4h). The positive effects of eCO₂ were initially comparable to warming effects at +2.25°C (Figure 4h). However,

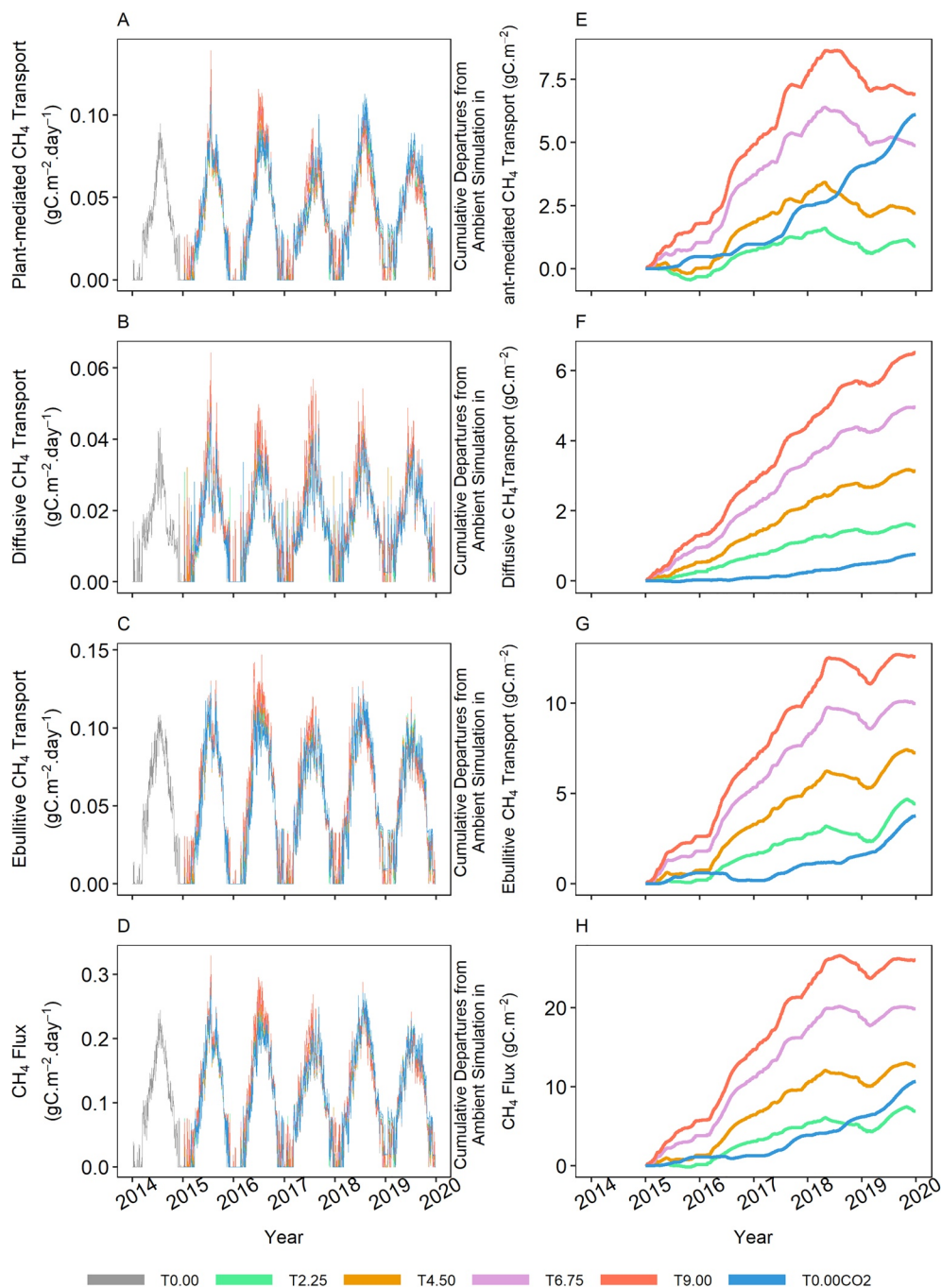


Figure 4. Time series of simulated plant-mediated CH₄ transport, diffusive CH₄ transport, ebullitive CH₄ transport, and CH₄ flux under warming and elevated CO₂ concentration (eCO₂). (a–d) Simulated daily plant-mediated CH₄ transport, diffusive CH₄ transport, ebullitive CH₄ transport, and CH₄ flux under warming and eCO₂, and (e–g) cumulative impacts of warming and eCO₂ on plant-mediated CH₄ transport, diffusive CH₄ transport, ebullitive CH₄ transport, and CH₄ flux departure from the ambient simulation (T0.00). Descriptions of manipulation experiments and cumulative impact calculation are same as Figure 1.

since eCO₂ effects intensified over time, they exceeded warming effects at +2.25°C by the end of the simulation with an increase of 10.6 (8.6–12.6) g C m⁻² (Figure 4h).

Soil CH₄ concentrations had an obvious seasonal pattern but showed different responses to warming and eCO₂ (Figures 3c and 3f). CH₄ concentrations exhibited large seasonal variations with a “W” curve trend

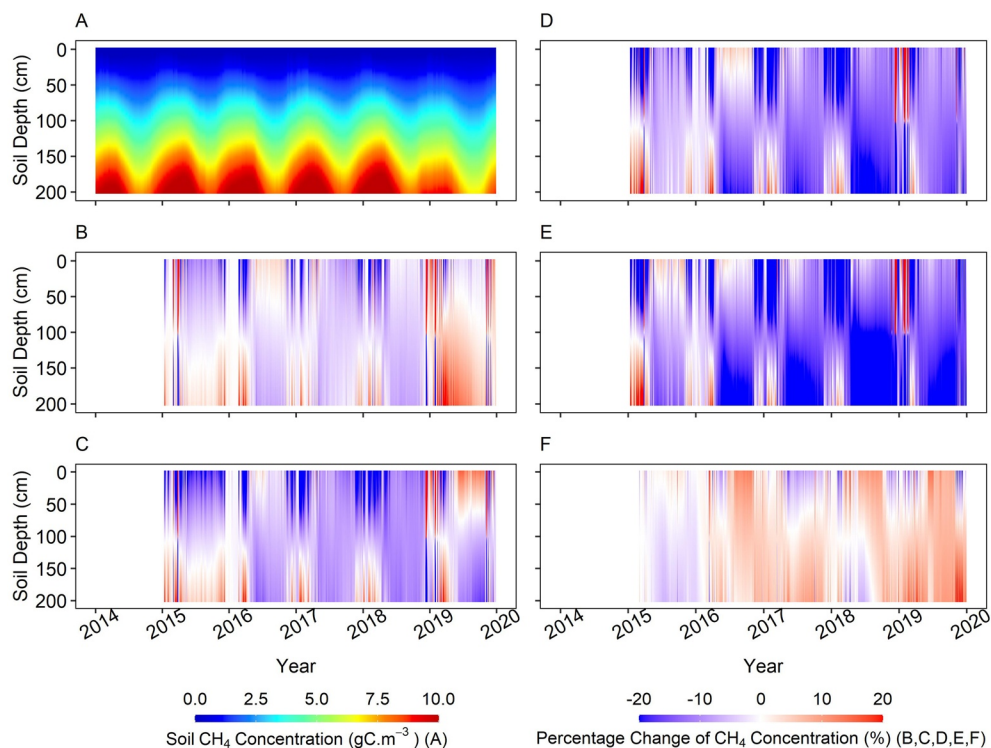


Figure 5. Simulated soil CH₄ concentration along 0–200 cm soil profile under warming and elevated CO₂ concentration (eCO₂). (a) Simulated soil CH₄ concentration in soil profiles under the ambient simulation (T0.00), and (b–f) percentage changes of soil CH₄ concentration under warming (+2.25°C, +4.50°C, +6.75°C, and +9.00°C) and eCO₂ (+410 ppm) compared with T0.00.

in each year (Figure 3c). At the beginning of a year, soil CH₄ concentrations declined, then increased to their maximum in late summer which corresponded with the strong CH₄ production (Figure 3c). In winter, CH₄ accumulated in soils until the next year (Figure 3c). CH₄ accumulated under eCO₂, whereas CH₄ was consumed and transported to the atmosphere under warming (Figure 3f). Additionally, warming effects on CH₄ concentrations tended to decrease after 2 year of simulations (Figure 3f).

The vertical distribution of CH₄ concentrations along soil profiles showed a seasonality and were consistent with rates of methanogenesis (Figure 5a). Soil CH₄ concentrations were higher in deeper soil layers and increased in warm seasons but decreased in cold seasons (Figure 5a). The suppression effects of warming and promotion effects of eCO₂ tended to intensify over time (Figures 5b–5f). Effects of warming and eCO₂ on CH₄ concentrations were usually opposite between the top and bottom soil layers (Figures 4b–4f). At the end of simulations, warming increased CH₄ concentration in deep soils, but it still suppressed the CH₄ concentrations in shallow layers (Figures 5b–5e). eCO₂ slightly suppressed CH₄ concentrations at the beginning of simulations, but promoted the accumulation of CH₄ concentrations, especially in deep soils, at the end of simulations (Figure 5f).

3.5. A Mechanistic Framework of Warming and eCO₂ Impacts on CH₄ Cycling

Based on our model output and the compiled experimental results, a mechanistic framework was developed to summarize all mechanisms of warming and eCO₂ impacts on CH₄ cycling (Figure 6). Under warming scenarios, NPP initially increased but then declined over time. In concert with rising SOM mineralization, soil carbon storage tended to decline slightly, while warming-induced decomposition led to lower DOC. Higher DOC fermentation led to a small increase in acetate initially followed by a decline after a few months. Meanwhile, soil CO₂ concentrations decreased. Despite warming stimulating both acetoclastic and hydrogenotrophic methanogenesis, soil CH₄ concentrations declined due to warming-induced lower CH₄ solubility and high CH₄ transport from the soil.

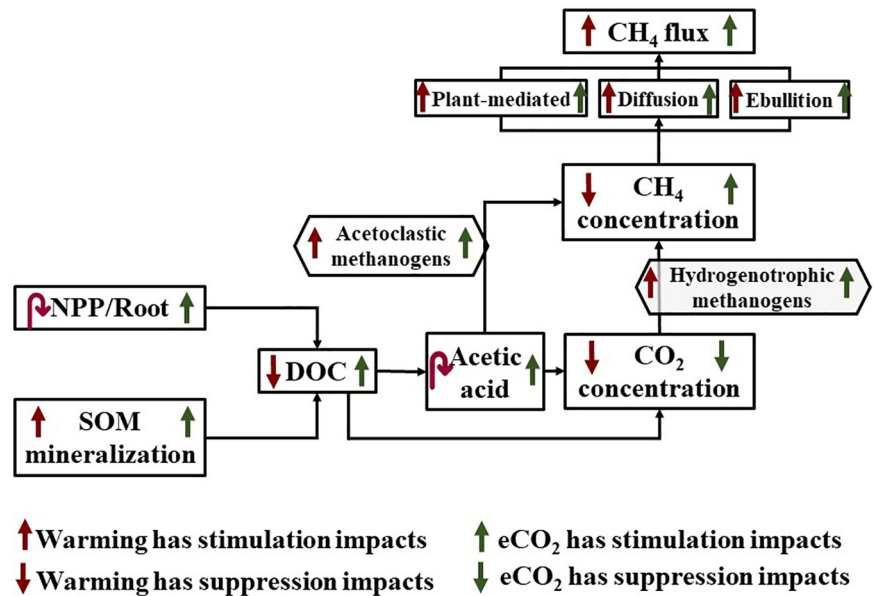


Figure 6. Diagram showing the mechanisms for warming and elevated CO₂ impacts on CH₄ processes (NPP: net primary production; SOM: soil organic matter; DOC: dissolved organic carbon). Black arrows represent CH₄ processes, while red and green arrows represent the impacts of warming and elevated CO₂. Regular upward or downward arrows represent the positive or negative effects under treatments, respectively. Curved downward arrows mean the impacts of treatments are positive, then negative.

Different from the mechanism of warming effects on CH₄ processes, eCO₂ enhanced NPP and SOM mineralization, subsequently increasing soil DOC and acetate concentrations. Although soil CO₂ concentrations decreased under eCO₂, soil CH₄ concentrations went up primarily as a result of increasing acetoclastic and hydrogenotrophic methanogenesis and higher acetate availability. This increased dissolved CH₄ also contributed to a larger CH₄ emissions.

4. Discussion

4.1. Comparison With the Compiled Warming and eCO₂ Impacts on CH₄ Processes

Our simulations agreed with the global meta-analysis and observations in the SPRUCE project, although the observational data generally had larger variations in treatment impacts on NPP, SOM mineralization, DOC concentration, and CH₄ fluxes (Figure 7), which could be caused by large uncertainties associated across-site differences and experimental design. SPRUCE observations also showed that tree growth and moss cover were being suppressed by warming (Norby et al., 2019), and by water-table level declines with enhanced ET under the warming treatments (Hanson et al., 2020; McPartland et al., 2019; Norby et al., 2019). The SPRUCE field experiments found that eCO₂ enhanced NPP for all species, while warming stimulated tree NPP but suppressed moss NPP. In the model, NPP was suppressed by warming and increased by eCO₂ in our simulations (Figure 7). This discrepancy could be caused by the constant plant community over the model simulations. In addition, experimental results showed an exponential increase in CH₄ production and emissions in surface soil layers (25 cm depth) under warming but minor response of CH₄ production and emissions to eCO₂ (Hopple et al., 2020; Wilson et al., 2016), which were partially in agreement with our simulation results.

Compared with the global meta-analysis, our model simulations were consistent with the positive effects of eCO₂, but had a slightly different pattern for warming treatments. The global meta-analysis found that warming stimulated all CH₄ processes; however, model results indicated that NPP and DOC were suppressed at the SPRUCE site (Figure 7). This discrepancy may result from differences in techniques and durations in incubation and field experiments. Studies for the global meta-analysis usually had short-term observational data, with most lasting a few months (Saarnio et al., 1998; Wolf et al., 2007), whereas our

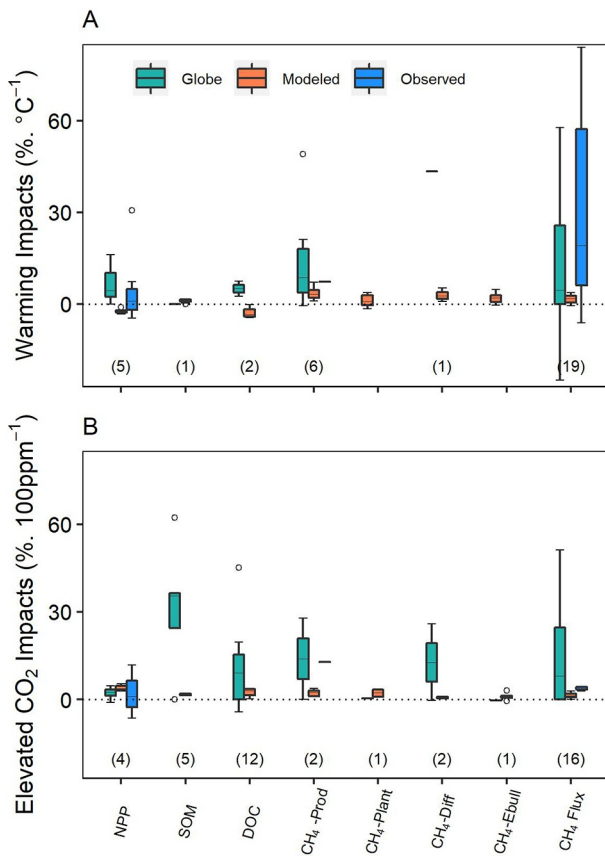


Figure 7. Responses of selected variables (NPP: net primary production; SOM: soil organic matter; DOC: dissolved organic carbon; CH₄-Prod: CH₄ Production; CH₄-Plant: CH₄ fluxes via plants; CH₄-Diff: CH₄ fluxes via diffusion; CH₄-Ebull: and CH₄ fluxes via ebullition) under (a) warming and (b) elevated CO₂ (eCO₂) based on the global meta-analysis, model simulations and observations from SPRUCE studies. Modeled impacts of warming and eCO₂ on selected variables are calculated by the differences between the experimental and controlled simulations in each year during 2015–2019. All data were standardized to the percentage changes per unit under warming and eCO₂. In boxplots, lower and upper bars represent the 25th and 75th percentiles, respectively; the upper and lower whiskers extend to the highest/lowest value within 1.5 times the interquartile range; the horizontal lines within boxes represent the median values, and outlier dots represent data beyond the end of the whiskers. The (value) above the x axis for each variable is the number of observed data points. Four observed data points are out of the ranges.

simulations for warming effects lasted five years. A meta-analysis found that warming with open-top chambers caused NPP reduction while the greenhouse and infrared heater approaches stimulated NPP (Lu et al., 2013); the same study also reported that <5 years warming might suppress NPP while >5 years warming stimulated NPP regardless of warming techniques (Lu et al., 2013). Different warming intensities could cause distinct responses of plant communities and SOM decomposition (Weltzin et al., 2000). Due to the difficulties in measuring CH₄ transport, few data were retrieved for the global synthesis, but they were generally consistent with our simulations that warming and eCO₂ enhance CH₄ transport (Figures 7a and 7b).

4.2. Different Mechanisms of Warming and eCO₂ Impacts on CH₄ Cycling

Both warming and eCO₂ stimulated CH₄ emission but with different mechanisms. Warming affected photosynthesis and resource partitioning (Mäkiranta et al., 2018), but these impact varied among plant species and functional types (Updegraff et al., 1995; Weltzin et al., 2000), due to variations in their photosynthetic rates and different physiological responses to warming (Mäkiranta et al., 2018; Riutta et al., 2007). Based on our model results, a negative response of NPP under different warming scenarios occurred in the black spruce bog; this suppression further led to declining SOM accumulation, consistent with some field experiments for SOM loss under warming (Megonigal & Schlesinger, 1997; Yavitt et al., 1997). The declining DOC under warming can be explained by the warming-induced DOC fermentation. Soil microbial activities were stimulated by warming, resulting in a rise of acetate from DOC decomposition in the first year, but acetate began to decrease in the following years in parallel with a reduction in DOC, in agreement with Hoppel et al. (2020).

Warming led to stronger methanogenesis and more CH₄ production but lower CH₄ concentrations in soils, which is due to the warming-enhanced CH₄ emissions. Both acetoclastic and hydrogenotrophic methanogenesis were enhanced under warming scenarios even with the limited supply of substrates for methanogenesis, indicating that warmer temperature rather than substrate availability primarily controls the activities of methanogenesis (Walker et al., 2018). Moreover, a few studies suggested changes in the composition and biomass of microbial communities due to warming mainly accounted for variations in CH₄ emissions (Megonigal & Schlesinger, 1997; Yavitt et al., 1987). Warming may also affect CH₄ emissions by decreasing the abundance of methanogens even with community composition remaining unchanged (Peltoniemi et al., 2016; Turetsky et al., 2008). Furthermore, a diminishing strength of warming effects

on CH₄ dynamics over time was shown in this study, consistent with a previous experiment (Mäkiranta et al., 2018; Walker et al., 2018). Additionally, warming could facilitate soil CH₄ transport to the atmosphere via diffusion and ebullition (Askaer et al., 2011), which is similar to this study and another modeling study at the SPRUCE bog site (Ma et al., 2017). The increased aerenchyma-mediated CH₄ transport was found in first year when warming stimulated NPP but declined as warming suppressed NPP.

The mechanism of eCO₂ enhancing peatland CH₄ emissions was different from that of warming, which is consistent with previous studies (Turetsky et al., 2008; Xu et al., 2010; Yvon-Durocher et al., 2011). The major difference was that eCO₂ increased NPP, soil DOC, and acetate while warming suppressed them. Previous studies showed that eCO₂ promoted plant carbon pools in various wetland ecosystems (Liu et al., 2018) because of the increased photosynthetic rates (Lin et al., 2017). On the contrary, warming can cause a

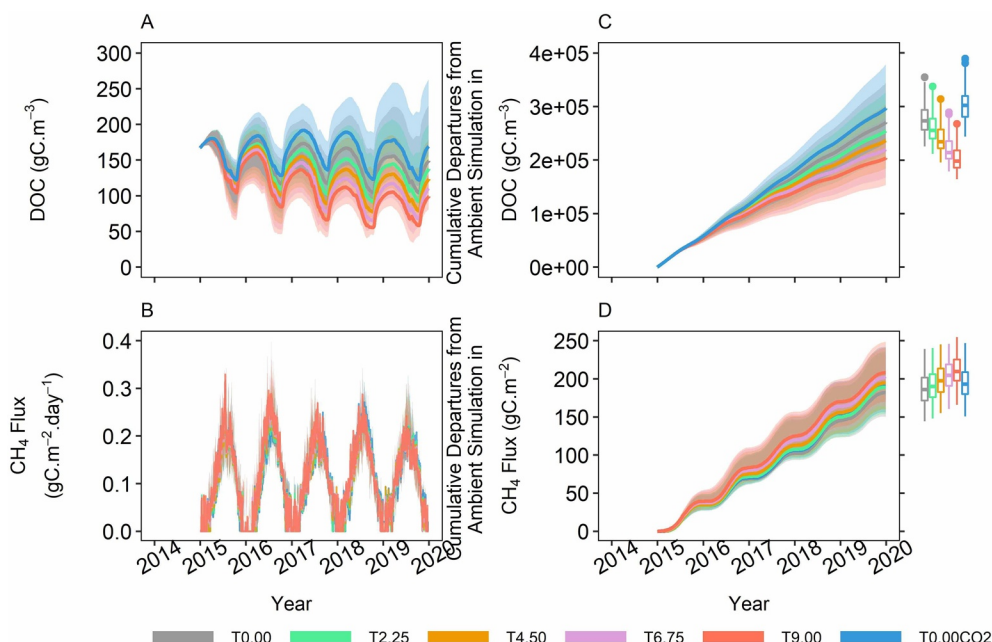


Figure 8. Uncertainty analysis for dissolved organic carbon (DOC) (at top 9 cm depth) and CH₄ flux under warming and elevated CO₂ concentration (eCO₂). Each assembled simulation based on 100 sets of combination of 10 parameters is shown with the mean (solid line) and the 5%–95% range (shading) across the distribution. Boxes and whiskers (mean, one standard deviation, minimum, and maximum) in figure c and d indicate the differences of DOC and CH₄ flux under warming and eCO₂ after 5-years simulations. Descriptions of manipulation experiments and cumulative impact calculation are same as Figure 1.

decline in plant growth and C accumulation in some natural wetlands (Sánchez-Carrillo et al., 2018), due to more C allocation to root exudation (Sánchez-Carrillo et al., 2018), which was not found in the present study. Our study simulated a higher SOM mineralization under eCO₂, which may be caused by priming effect on SOM decomposition induced by higher root exudates (Ross et al., 2004; Van Groenigen et al., 2014), consistent with field measurements at the SPRUCE site (Hopple et al., 2020; Wilson et al., 2016).

Beside the increased substrate availability for methanogenesis, eCO₂ may stimulate microbial activities for CH₄ production (Conrad, 2002) and inhibit CH₄ oxidation (Bodelier & Laanbroek, 2004; Hutchin et al., 1995; Ineson et al., 1998) by reducing soil N availability that may partially release the N suppression on methanotrophs (Xu et al., 2004; Zhang et al., 2020). The simulated stimulating impacts of eCO₂ on CH₄ emission is partially due to greater aerenchyma in plant tissues that promotes CH₄ transport (Bellisario et al., 1999; Megonigal & Schlesinger, 1997). Moreover, we found that most CH₄ processes appeared to respond progressively under eCO₂, much slower than responses to warming, indicating the importance of long-term eCO₂ treatment.

4.3. Uncertainty Analysis

The uncertainty analysis based on 100 sets of 10 key parameters under each warming and eCO₂ scenario indicated that the uncertainties of CH₄ processes grow in concert with the treatment duration (Figure 8). The uncertainty of DOC reached 28.4% at the end of simulations due to the cumulative effects of warming and eCO₂ on soil C pools. The uncertainty of surface CH₄ flux (19.3%) was smaller than that of DOC after 5-years simulations. Furthermore, there was no significant difference in uncertainties among different warming or eCO₂ scenarios, indicating larger uncertainties in both DOC and CH₄ flux defined in the ELM_SPRUCE model than changes in air temperature and eCO₂ concentrations. Additionally, the uncertainties of simulated CH₄ flux were mainly determined by the process of methanogenesis, inferring the importance of accurately simulating substrate and SOM mineralization for better predicting CH₄ cycling. In summary, the

model parameter-caused uncertainties are relatively well constrained and did not change our conclusions about simulated CH₄ cycle in responses to warming and eCO₂.

4.4. Future Work

This study explored the different mechanisms of warming and eCO₂ effects on CH₄ cycling in S1 Bog, Minnesota. We identified five limitations of the present study that will be addressed in future work. First, the magnitudes and mechanisms of CH₄ cycling responses to warming and eCO₂ could change among different peatland types and at different spatial scales due to the complexity of wetland ecosystems (Zalman et al., 2018). Thus, it is necessary to verify the mechanistic framework built in our study at different spatial and temporal scales. Second, microbial acclimation is a key feature of microbial responses to environmental changes, and this is also true for methanogens (Conrad, 1995, 1996). In our current model, we did not include microbial physiological changes in responses to warming. Rather, the current model only considers the changes in substrate for methanogenesis under warming and eCO₂. The modeled CH₄ production might be overestimated without the mechanisms of microbial acclimation, although temperature acclimation of CH₄ production and microbial CO₂ respiration has not occurred to date at SPRUCE (Hopple et al., 2020). Third, wetland ecosystems are characterized by their unique soil hydrological and thermal conditions, which brings large uncertainties and variabilities in CH₄ cycling, which requires further mechanistic investigations (Zalman et al., 2018). Although the hydrology module in the ELM_SPRUCE model has already been improved with hummock-hollow microtopography in previous studies (Shi et al., 2015), it is unknown how local and regional soil hydrology will change under future warming and eCO₂. Such long-term climate change might impact the trajectory of experimental observations provided by SPRUCE through extended changes in vegetation productivity and composition, and extended modification of peatland biogeochemical cycles.

Fourth, prior studies suggested soil N availability in wetlands is a critical factor impacting the CH₄ cycle as it might stimulate methanogenesis (Haveroen et al., 2005) and suppress methanotrophy (Bender & Conrad, 1994). The current simulation indicates increased N availability with warming (Malhotra et al., 2020) and decreased N availability with eCO₂. Nevertheless, the effects of N availability on CH₄ flux need further investigation and validation with observations. Fifth, as the SPRUCE field experiments are still operating (whole ecosystem warming began in 2015) and new observational data are becoming available (operations are expected to continue through 2025), additional information on longer-term effects of warming and eCO₂ on peatland CH₄ cycling will be available for future evaluation. For example, large changes in plant community composition have been observed at SPRUCE under warming, particularly the increasing cover in shrubs and concomitant loss of *Sphagnum* moss and forbs, which could have large ramifications for CH₄ dynamics. It should be noted that the present modeling results are not intended to provide a realistic prediction of the CH₄ flux under warming and eCO₂ conditions, but rather, are to be used to develop a mechanistic understanding of CH₄ processes under warming and eCO₂ (Figure 6). Through such insights a better understanding of the mechanisms of ecosystem behavior in the changing environments can be obtained. Although the present modeling study is relatively consistent with early treatment effects of the SPRUCE project, new empirical findings show sustained C loss as CH₄ with persistent warming (Hopple et al., 2020). Therefore, further model integration with future results from SPRUCE is urgently needed to better understand long-term CH₄ cycling under warming and eCO₂.

5. Conclusions

With a data-model integration approach, we found that warming and elevated CO₂ stimulated CH₄ emissions in a temperate peatland with different mechanisms. The differences are expressed primarily through soil biogeochemistry, controlled by plant net primary production and DOC and acetate availability, which further affects both the acetoclastic and hydrogenotrophic methanogenesis pathways. In summary, the stimulating effects of warming on CH₄ emissions are primarily determined by the temperature responses of microbial activities, while elevated CO₂ concentration stimulated CH₄ emissions primarily via the enhanced availability of substrate for methanogenesis.

The different mechanisms of warming and eCO₂ on surface CH₄ emissions underscore the importance of representing biogeochemical mechanisms for better simulating and predicting C₄ cycling in Earth system

models. With the growing recognition of the CH₄ contribution to climate change (Saunio et al., 2016), it is critical to mechanistically simulate CH₄ cycling under multiple environmental changes. In particular, warming might cause alteration of soil water content and water-table depth in the field (Waddington et al., 2015), which affect the impacts of warming and elevated CO₂ on CH₄ cycling. Future mechanistic investigations of peatland biogeochemistry in association with hydrological feedbacks will assist global-scale CH₄ estimation, improving predictability of CH₄ cycling and climate mitigation.

Data Availability Statement

Model code used in these simulations is available on the GitHub repository at <http://doi.org/10.5281/zenodo.3733924>. Model simulation output used in this analysis is can be accessed at <https://doi.org/10.25581/spruce.082/1638024>.

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