Wetlands (2020) 40:609–618
https://doi.org/10.1007/s13157-019-01203-5

WETLANDS AND CLIMATE CHANGE

# Impacts of Elevated Atmospheric $CO_2$ and Plant Species Composition on Methane Emissions from Subarctic Wetlands

Matthew J. Bridgman[1] · Barry H. Lomax[1] · Sofie Sjögersten[1]

Received: 20 June 2018 / Accepted: 15 July 2019 / Published online: 5 May 2020


## Abstract

Elevated atmospheric $CO_2$ may create greater methane ($CH_4$) emissions from subarctic wetlands. To date such ecosystem feedbacks remain poorly understood, particularly in relation to how different wetland plant species will control such feedbacks. In this study we exposed plant-peat mesocosms planted with four *Cyperaceae* species to 400 and 800 ppm atmospheric $CO_2$ concentrations and measured plant and peat properties as well as $CH_4$ fluxes. Above ground biomass for plants grown at 800 ppm $CO_2$ increased for *E. angustifolium*, *Eriophorum vaginatum* and *Carex brunnescens*, but the total biomass of *C. acuta* decreased relative to the ambient $CO_2$ treatment. The plant species and elevated $CO_2$ treatment affected both peat redox potential and pore water chemistry. There was no overall effect of the elevated $CO_2$ on $CH_4$ emissions, however, $CH_4$ emissions were related to above ground biomass and redox potential, both of which were significantly altered by elevated $CO_2$. Our study shows that species composition poses an important control on how wetland communities will respond to elevated $CO_2$ and that plant mediated changes of peat biogeochemical processes, in response to elevated $CO_2$ levels, may affect $CH_4$ emissions from subarctic wetlands, but any such responses will differ among species.

**Keywords** Methane · Subarctic · Wetland · Elevated $CO_2$ · Plant species

## Introduction

Northern peatlands store ca. half of global soil carbon (C), much of which is held in permafrost areas (Tarnocai et al. 2009). Arctic and sub-arctic peatlands are responding rapidly to climate warming, threatening their C storage capacity (IPCC 2013). In parallel with rising temperatures, atmospheric $CO_2$ levels have increased from pre-industrial levels of 280 ppm to 400 ppm with future atmospheric $CO_2$ concentrations predicted to increase to between 426 ppm (RCP 2.6) and 936 ppm (RCP 8.5) over the next century (IPCC 2013). These changes in climate and atmospheric $CO_2$ concentration may result in greater Net Primary Productivity (NPP) and decomposition rates which are both controls of greenhouse gas fluxes from ecosystems including wetlands (Curtis et al. 1989; Turetsky et al. 2014).

✉ Sofie Sjögersten
sofie.sjogersten@nottingham.ac.uk

[1] School of Biosciences, University of Nottingham, Sutton Bonington Campus, Loughborough LE12 5RD, UK

Wetlands release ca. 80% of methane ($CH_4$) emission from natural sources, equating to a third of overall global emissions (Kirschke et al. 2013) with the largest $CH_4$ atmospheric concentrations found north of 40° N (Steele et al. 1987). Indeed, the large area of wetlands at northern high latitudes are recognised as an important component of the global $CH_4$ budget (Moore and Knowles 1990; Bridgham et al. 2013; Turetsky et al. 2014). Wetland $CH_4$ emissions are determined by temperature, substrate and hydrology (Updegraff et al. 2001; Bridgham et al. 2013). In subarctic and arctic regions, these factors are strongly controlled by permafrost. Therefore future changes to permafrost are predicted to impact on $CH_4$ emissions from high latitude regions (Christensen et al. 2004; IPCC 2013). For example, waterlogging of peatland soils as a result of permafrost thaw will likely increase $CH_4$ emissions from arctic regions both in response to the anoxic conditions per se but also due to vegetation shifts from moss-lichen woody shrub tundra to wet sedge communities (Christensen et al. 2004; ACIA 2005; Bridgham et al. 2013).

Vegetation directly impacts $CH_4$ emissions from peatlands (Joabsson et al. 1999; Heilman and Carlton 2001; Öquist and Svensson 2002; Ström et al. 2005; Bhullar et al. 2013a, b). The main controls of $CH_4$ emissions in relation to vegetation

are; (i) release of labile organic compounds in to the root zone which increase $CH_4$ production; (ii) enhancing $CH_4$ oxidation due to root oxygen emissions in to the peat and; (iii) passive transport of $CH_4$ through plant tissues (Joabsson et al. 1999; Öquist and Svensson 2002). As most of the organic matter stored in arctic peatlands is recalcitrant and substrates for digestion by anaerobic bacteria are limiting (Bridgham et al. 2013; Sjogersten et al. 2016), input of labile photosynthates in the form of litter or root exudates are an important carbon source for methanogens (Torn and Chapin 1993; Ström et al. 2005). The diffusion of oxygen through aerenchyma from the atmosphere into the roots and leakage into the rhizosphere causes oxidation of $CH_4$ to $CO_2$ in the soil, substantially reducing net $CH_4$ emissions (Fritz et al. 2011). The quality and quantity of plant litter and root exudate as well as root $O_2$ inputs differs among wetland plant species, potentially creating species specific impacts on $CH_4$ fluxes (Updegraff et al. 1995; Ström et al. 2005). Plant mediated transport of $CH_4$ to the atmosphere can represent a major emission pathway but its contribution to net emissions varies among plant species as the rate of transport is strongly dependent on aerenchyma tissue (Kutzbach et al. 2004; Bhullar et al. 2013b). Indeed, while both *Eriphorumn* and *Carex* species can emit large amounts of $CH_4$ through their tissues the proportion of $CH_4$ emitted through plant tissues varies strongly among species (Bhullar et al. 2013b).

Elevated atmospheric $CO_2$ can influence wetland $CH_4$ production through its role in plant C assimilation and allocation. For example, greater root biomass in rice grown under elevated $CO_2$ concentration has substantially increased $CH_4$ emissions from paddy rice fields (Van Groenigen et al. 2011). Greater plant biomass and productivity in a range of wetland species in response to elevated $CO_2$ have resulted in increased $CH_4$ emissions from some wetland systems (Megonigal and Schlesinger 1997; Kao-Kniffin et al. 2011; Wang et al. 2013) while the growth of other species have not been affected resulting in no change in wetland $CH_4$ fluxes (Angel et al. 2012). Such contrasting responses may, in part, be controlled by the plant species composition of different wetlands as elevated atmospheric $CO_2$ concentrations influence plant activity including growth, photosynthetic rates and root exudate production, processes which also vary strongly among species (Lawlor and Mitchell 1991; Zak et al. 1993; Bellisario et al. 1999). These findings suggest that a more detailed understanding of how elevated $CO_2$ impact different plant species is required in order to tease apart the controls that govern plant mediated impacts on $CH_4$ emissions in response to elevated $CO_2$. It is likely that if elevated atmospheric $CO_2$ concentrations increase biomass, providing growth is not nutrient limited in the first place (Gordon et al. 2001), this will increase labile C inputs into the peat and potentially production of $CH_4$. However, greater plant biomass may also increase transport of $O_2$ to the rhizosphere and $CH_4$ to the atmosphere (Joabsson et al. 1999; Wolf et al. 2007; Laanbroek 2010). Taken together, the understanding of impacts of elevated $CO_2$ on arctic wetland $CH_4$ emissions is limited at both the ecosystem and species level, creating large uncertainties in model predictions of the role of elevated $CO_2$ on $CH_4$ feedback mechanisms (Ringeval et al. 2011).

Arctic and sub-arctic peatlands are currently responding rapidly to climate warming, which has resulted in expansions of graminoid-dominated flooded areas (Prater et al. 2007; Åkerman and Johansson 2008). Such changes in the vegetation has lead to large increases in $CH_4$ emissions (Christensen et al. 2004; Hodgkins et al. 2014). In subarctic and arctic wetlands, graminoids (e.g. *Eriophorum* sp. and *Carex* sp.) are known to directly impact $CH_4$ emissions both by transport of $CH_4$ from the rhizosphere to the atmosphere (Bhullar et al. 2013b; Turetsky et al. 2014) and by impacting $CH_4$ production and oxidation in the rhizosphere (Ström et al. 2005; Koelbener et al. 2010; Fritz et al. 2011; Ström et al. 2012). However, these effects are species specific (Christensen et al. 2004; Ström et al. 2005; Prater et al. 2007; Hodgkins et al. 2014). To explore how variation in graminoid species composition and elevated atmospheric $CO_2$ impacts $CH_4$ emissions we established a controlled environment experiment exposing peat mesocosms planted with either *C. acuta*, *C. brunnescens*, *E. vaginatum* or *E. angustifolium* to elevated $CO_2$ and measured how this affected plant growth, peat physicochemical properties and $CH_4$ fluxes. This experiment was used to test the hypothesis that: Elevated atmospheric $CO_2$ will increase productivity of *Carex* and *Eriophorum* species and subsequently stimulate $CH_4$ emissions due to increased root inputs of labile substrates for methanogens, with the largest effect of elevated $CO_2$ on $CH_4$ emissions found in peats planted with *C. acuta* (the highest biomass species).

## Methods

### Site Description

The study site is a subarctic peatland located on the southern edge of Lake Torneträsk in Northern Sweden (68° 21′ 30.96“ N 18° 46’ 56.064” E). The mean annual precipitation is 310 mm, more than 40% of this occurs during summer. Mean annual temperature is 0.7 °C, with a July average of 11 °C (1913–2000 average, Kohler et al. 2006). The site is a palsa mire complex, a common peatland type in the region. The area is made up of two distinct communities of vegetation (Sjogersten et al. 2016). The raised, mesic area is dominated by dwarf shrubs (*Betula nana*, *Empetrum nigrum* and *Vaccinium uliginosum*). The active layer depth in these hummocks is 30 ± 0.9 cm in summer. In the flooded areas there are three dominant Cyperaceae species: *C. acuta*, *E. angustifolium* and *E. vaginatum* as well as the less common

*C. brunnescens* (Nilsson 1991; Mossberg and Stenberg 2008). On average, ($n = 5$) *C. acuta* grew in locations with an active layer depth of 119 ± 21 cm below the peat surface, *E. angustifolium* at 122 ± 12 cm and *E. vaginatum* and *C. brunnescens* at 95 ± 21 cm. The water level depth in the flooded areas varied, averaging +34 ± 7 cm where *C. acuta* was found, + 30 ± 3 cm for *E. angustifolium* and + 15 ± 2 cm for *E. vaginatum* and *C. brunnescens*, note that positive values means that the peat surface was submerged. The peat pH at 5 cm depth was 4.3 ± 0.04; with conductivity of 66 ± 30.8 μS; extractable $PO_4^{3-}$ of 3.9 ± 1 μg $g^{-1}$ and extractable $NH_4^+$ of 0.12 ± 0.02 μg $g^{-1}$. Peat pH and conductivity was determined following mixing peat with DI water in a 1:2 ratio by volume and analysis on a dual pH and conductivity analyser. Extractable $PO_4^{3-}$ and $NH_4^+$ was determined using standard colourimetrically methods following a $K_2SO_4$ extraction of 5 g of fresh weight soil.

## Experimental Design and Analysis

### Growth Room Experiments

Growth room experiments were established using two walk-in growth rooms (Unigrow, UK) which had fixed atmospheric $CO_2$ concentrations of 400 ppm and 800 ppm. Mesocosms planted with either *C. acuta*, *C. brunnescens, E. angustifolium* or *E. vaginatum* were established with peat and plant material collected from the field site. The degree of replication per treatment was; $n = 10$ for *C. acuta* and *E. vaginatum*, $n = 6$ for *E. augustifolium*, and n = 5 for *C. brunnescens*, this resulted in a total number of 42 mesocosms. Peat samples were collected as several 20 × 20 × 20 cm blocks taken ca. 30 cm below the peat surface from submerged areas free of vegetation with a water table depth of ca. 30 cm. The recovered plant and soil samples were transported, separated and transplanted into separate water-tight one litre pots ensuring good contact between plant roots and the peat. Care was taken that peat did not dry out prior to the experiment started, however, some oxygenation of the peat will have occurred. For *C. acuta*, *C. brunnescens, E. angustifolium* individual shoots were transplanted in to the peat while *E. vaginatum* was planted as small tussocks reflecting the plants growth form in the field. As the starting biomass differed among pots the mesocosms were grouped as pairs according to biomass and then randomly allocated to a $CO_2$ treatment. The volume of peat in the pots were ca. one litre, water levels were adjusted (using tap water) to 2–3 cm above the peat surface throughout the experiment. This water level is shallower than those in the field but where used to reduce ebullition and bubble formation on the inside edges of the mesocosm which were deemed to be a risk associated with using deeper water levels. The conditions used in the growth chambers was a day length of 16 h, day/night temperature was 21/15 °C, reflecting the conditions found at the sites during warm summers to stimulate growth and microbial activity. The relatively high temperatures compared to the average air temperature during the field sampling period of 13.3 °C. Daytime light levels were constant at 400 μmol $m^{-2}$ $s^{-1}$ and day/night humidity was 65/75%. The mesocosms were equilibrated for ca. 1 month before the measurements started to allow the system to settle from the disturbance and any remaining oxygen to be used up so that the experiment took place under anoxic conditions.

Two types of head space chamber were used for the gas sampling. A taller chamber (15 cm diameter × 100 cm height, 17.7 l volume) was used for the mesocosms with *C. acuta* and *E. angustifolium* and a smaller chamber (15 cm diameter × 25 cm height, 4.4 l volume) was used for the shorter *E. vaginatum* and *C. brunnescens*.

To define individual plant-mediated methane-controlling mechanisms over the experimental period, $CH_4$ flux, redox, and plant extension growth measurements were measured fortnightly during daytime conditions. These measurements were taken at five time points over a 10 week period between January and April 2015. Methane fluxes were determined using static headspace chambers (Denmead 2008) with samples collected over 20 min. Air in the chambers was circulated using small computer fans. The air samples were stored in 12 ml exetainers (Labco, Lampeter, UK). $CH_4$ concentrations were determined by gas chromatography (GC-2014, Shimadzu UK LTD, Milton Keynes, UK) using a single injection system with a 1 mL sample loop that passed the gas sample using $H_2$ as carrier, the flow rate was 30 ml $min^{-1}$. The oven temperature was 40 °C and the column was a molecular sieve, the injector temperature was 80 °C. Flame ionization (detector temperature was 250 °C) detectors were used to measure $CH_4$. The analytical error was ca. 5%. Methane fluxes were calculated using the ideal gas law (e.g. Mangalassery et al. 2014) and were expressed as both per unit area and peat dry weight.

Peat redox potential was measured in three points in each pot using a redox probe (General Purpose ORP Electrode, Van London Phoenix, Randburg, South Africa) connected to a millivolt pH meter. To assess plant growth, three leaves of each individual plant were labelled and extension growth recorded. At the end of the experiment, pore-water samples were extracted from each mesocosm using rhizon samplers (Rhizosphere Research Products, Wageningen, Netherlands). In the soil solution we determined the E4:E6 ratio, which is an indices of the humification capacity of dissolved organic carbon in the solution, using a spectrophotometer (Cecil CE1011 1000 series) set at 465 nm and 665 nm (Worrall et al. 2002). TOC-TN analysis (Shimadzu TOC-V CPH; TNM-1) was used to measure the total dissolved organic carbon (TOC) and total dissolved nitrogen (TN) content of the water with the ratio of TOC:TN reflecting the lability of carbon in the pore water (Kokfelt et al. 2009). Above and below ground

biomass of plant samples was separated, roots were picked from the peat using tweezers and then washed. The biomass samples and the remaining peat were dried at 60 °C for 72 h then weighed to calculate total above and below ground biomass and peat dry weight.

### Data Analysis

Data analysis was carried out using GenStat (15th Edition). Treatment effects on plant extension growth and biomass production, pore water chemistry and $CH_4$ fluxes was assessed using linear mixed models. In the model we used the $CO_2$ treatment, species treatment and time as fixed factors while individual mesocosms were used as the random factor. Statistics reported are the *F*-value, which is the ratio for between group variance and within group variance, numerator (i.e. fixed) degrees of freedom and denominator (i.e. residual) degrees of freedom, the *P* value indicating significance when <0.05. When required, data were transformed to meet the normality assumption. Linear regression was used to determine relationships between variables (e.g. $CH_4$ fluxes, biomass, pore water chemistry).

## Results

Extension growth differed among species with the greatest extension growth found for *C. acuta* (species effect: $F_{3,\ 53} = 11.32$, $P < 0.001$), the growth rates of the other three species was in the same range (e.g. 24 ± 2, 12 ± 2.8, 13 ± 2.6, 11 ± 2.0 mm week$^{-1}$, respectively for *C. acuta, C. brunnescens, E. angustifolium, E. vaginatum* at the start of the experiment). The elevated $CO_2$ treatment caused a significant overall reduction in extension growth ($CO_2$ treatment effect: $F_{1,\ 53} = 12.11$; $P < 0.001$; Fig. 1) with a particularly strong negative impact for *C. acuta*. At the end of the experiment, above ground biomass differed significantly among species with the lowest biomass found for *C. brunnescens* ($F_{3,52} = 8.34$, $P < 0.001$; Fig. 2a). The elevated atmospheric $CO_2$ levels tended to increase above ground biomass in *E. angustifolium*, *E. vaginatum* and *C. brunnescens* but decreased above ground biomass in *C. acuta* (near significant species × $CO_2$ treatment interaction: $F_{1,52} = 3.58$, $P = 0.064$; Fig. 2a). Below ground biomass differed among species (Fig. 2b; $F_{3,52} = 8.31$, $P < 0.001$); furthermore the $CO_2$ treatment affected belowground biomass differently among the four species (species × $CO_2$ treatment interaction: $F_{3,52} = 2.58$, $P = 0.063$) as below ground biomass declined in the elevated $CO_2$ treatment relative to ambient $CO_2$ for *E. angustifolium* and *C. acuta*. As a result of the contrasting above and below ground biomass responses among species to the $CO_2$ treatment, the response of the shoot:root ratios to elevated $CO_2$ differed among the species (Fig. 2c; species × $CO_2$ treatment interaction: $F_{3,52} = 6.45$, $P < 0.001$). Specifically the shoot:root ratio increased for all species apart from *C. brunnescens*.

The plant species treatment strongly affected $CH_4$ fluxes with the greatest emissions from *E. angustifolium* and the lowest emissions from *C. brunnescens* (Fig. 3; $F_{3,\ 52} = 5.57$, $P = 0.002$). In contrast, the $CO_2$ treatment did not affect the $CH_4$ fluxes ($F_{3,\ 52} = 0.79$, $P = 0.39$).

The $CO_2$ and species treatment affected soil properties. Specifically, redox potential was consistantly lower in the 800 ppm treatment ($F_{1,\ 53} = 3.39$, $P = 0.07$, Fig. 4). Redox also differed among the plant species treatments ($F_{3,\ 53} = 27.01$, $P < 0.001$) with the two *Carex* species having the highest redox potentials. The redox potential was negatively related to above ground plant biomass (Fig. 5a; $F_{1,\ 7} = 4.27$, $P = 0.08$). The elevated $CO_2$ treatment had a contrasting effect on total dissolved organic carbon (TOC) for the different plant species ((species × $CO_2$ treatment interaction, $F_{3,\ 52} = 2.82$, $P = 0.048$), Fig. 6a). Specifically, *E. vaginatum* and *C. acuta* differed in their response to elevated $CO_2$, with pore water in the 800 ppm treatment exhibiting 0.9 mg L$^{-1}$ more organic carbon in *E. vaginatum* but 1.5 mg L$^{-1}$ less in *C. acuta* when compared to ambient $CO_2$ conditions. In contrast, TOC levels for *E. angustifolium* and *C. brunnescens* were not affected by the $CO_2$ treatment.

Total dissolved nitrogen (TN) (Fig. 6b) was not significantly influenced by treatment or species effects. The TOC:TN ratio differed among species and was highest in *E. vaginatum* ($F_{3,\ 52} = 7.91$, $P < 0.001$, Fig. 6c) out of the planted treatments but was not affected by the $CO_2$ treatment. Pore water in the two species of *Carex* display the highest E4:E6 ratio (i.e. relatively more low molecular weight compounds) ($F_{3,\ 52} = 6.05$, $P = 0.001$, Fig. 6d) but again there was no significant difference between the $CO_2$ treatments.

Although the $CH_4$ fluxes were not directly related to plant biomass, redox potential, which was influenced by the above ground biomass, was negatively related to $CH_4$ fluxes (Fig. 5b; $F_{1,\ 7} = 5.75$, $P = 0.05$). In contrast, the pore water chemistry was not related to the $CH_4$ fluxes.

## Discussion

The increase in above ground biomass for three of the four study species in response to the elevated $CO_2$ treatment (Fig. 2a) supported the hypothesis, which predicted greater biomass production under high $CO_2$ conditions. The different responses of above ground biomass of the study species to increased $CO_2$ concentrations (Fig. 2a) suggest that wetland plant species will respond in contrasting ways to rising $CO_2$ concentrations. Previous studies support the notion of species specific responses to elevated $CO_2$. For example, following two years of experimental $CO_2$ treatments (ambient +340 ppm) different biomass responses was reported for

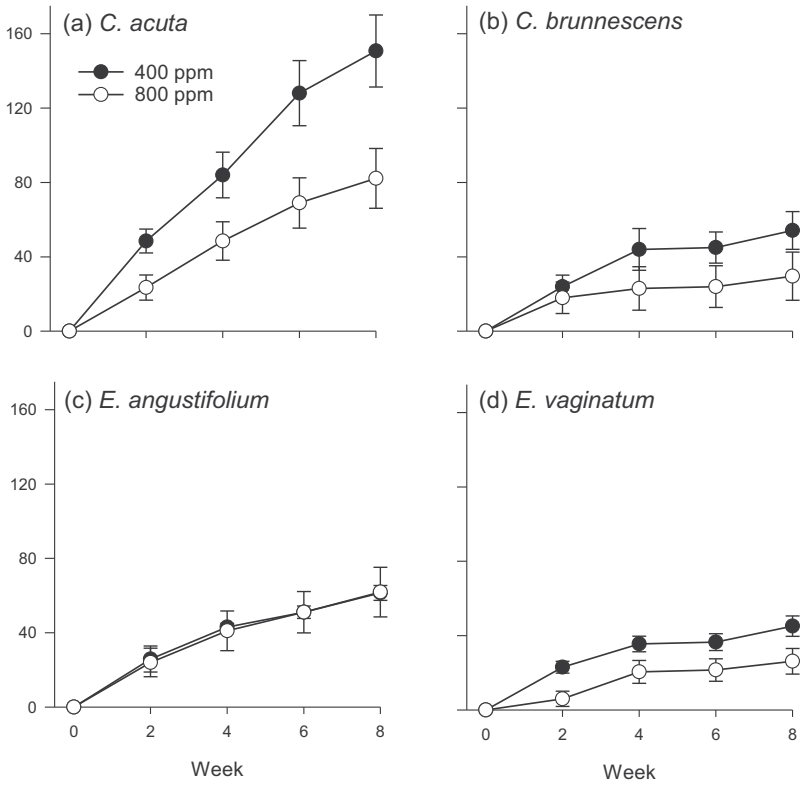


**Fig. 1** Cumulative growth of **a** *C. acuta*, **b** *C. brunnescens*, **c** *E. angustifolium*, and **d** *E.vaginatum* over the cause of the experiment. Mean and standard error of the mean are shown

*Schoenoplectus americanus* and *Spartina patens* in a salt marsh ecosystem (Langley et al. 2013). This was also the case for above ground biomass of *Typha* species (*T. angustifolia, T. glauca* and *T. latifolia*) exposed to 350–390 (control) to 550–600 ppm (treatment) $CO_2$ (Sullivan et al. 2010). The lower extension growth under elevated $CO_2$ indicates that greater above ground biomass is likely due to increased tillering and number of leaves. However, of the *Typha* species investigated by Sullivan et al. (2010), all increased their below ground biomass in response to the elevated $CO_2$ treatment. This differs to our study in which above ground biomass of *E. angustifolium, E. vaginatum* and *C. brunnescens* was higher in the elevated $CO_2$ treatment while below ground biomass only increased for two of the study species (*E.vaginatum* and *C. brunnescens* (Fig. 2b)). No below ground responses for *Schoenoplectus americanus* and *Spartina patens* was also reported by Langley et al. (2013) after two years exposure to elevated $CO_2$. Species specific responses to atmospheric $CO_2$ are well known, with fundamental differences in stomatal numbers and size being observed (Woodward et al. 2002; Lomax et al. 2014), which can then influence physiology and ultimately impact on biomass.

This study has demonstrated that different plant species control the amount and quality of substrate found in the pore water, with elevated atmospheric $CO_2$ influencing TOC concentrations in planted treatments (Fig. 6a), largely reflecting trends in biomass (Fig. 2). This correlates with data from temperate salt marshes exposed to elevated $CO_2$ (Marsh et al. 2005; Keller et al. 2009). In addition, the trend of lower root biomass, lower TOC and TN concentrations and lower $CH_4$ emissions in the 800 ppm *C. acuta* treatment suggests a link among these parameters. Indeed, contrasting above/below ground carbon allocation and quantity and quality of root exudates (e.g. Ström et al. 2005; Koelbener et al. 2010; Ström et al. 2012) may drive some of the species specific responses to elevated $CO_2$ and the subsequent impact on $CH_4$ emissions. The contrasting porewater chemistry with regard to the E4:E6 and TOC:TN ratios (Fig. 6 c and d) suggests that species composition alters rhizospheric organic matter inputs, likely due to differences in the concentration and lability of root exudates, with implications for $CH_4$ fluxes (King et al. 2002; Ström et al. 2005; Dorodnikov et al. 2011). Furthermore, root exudates have been found to enhance degradation of older recalcitrant soil organic matter which may further increase substrate availability for $CH_4$ production (Basiliko et al. 2012). The study was too short to measure how elevated $CO_2$ may alter litter chemistry, however, larger biomass as a result of elevated $CO_2$ (namely in *C. brunnescens* and *E. vaginatum,* Fig. 2) is likely to increase inputs from freshly produced litter which may also increase $CH_4$ production (Curtis et al. 1990).

The reduction in redox potential under the elevated $CO_2$ treatment (Fig. 4), together with the negative relationship between above ground biomass and soil redox potential (Fig. 5a), suggests that plant-mediated shifts in soil redox

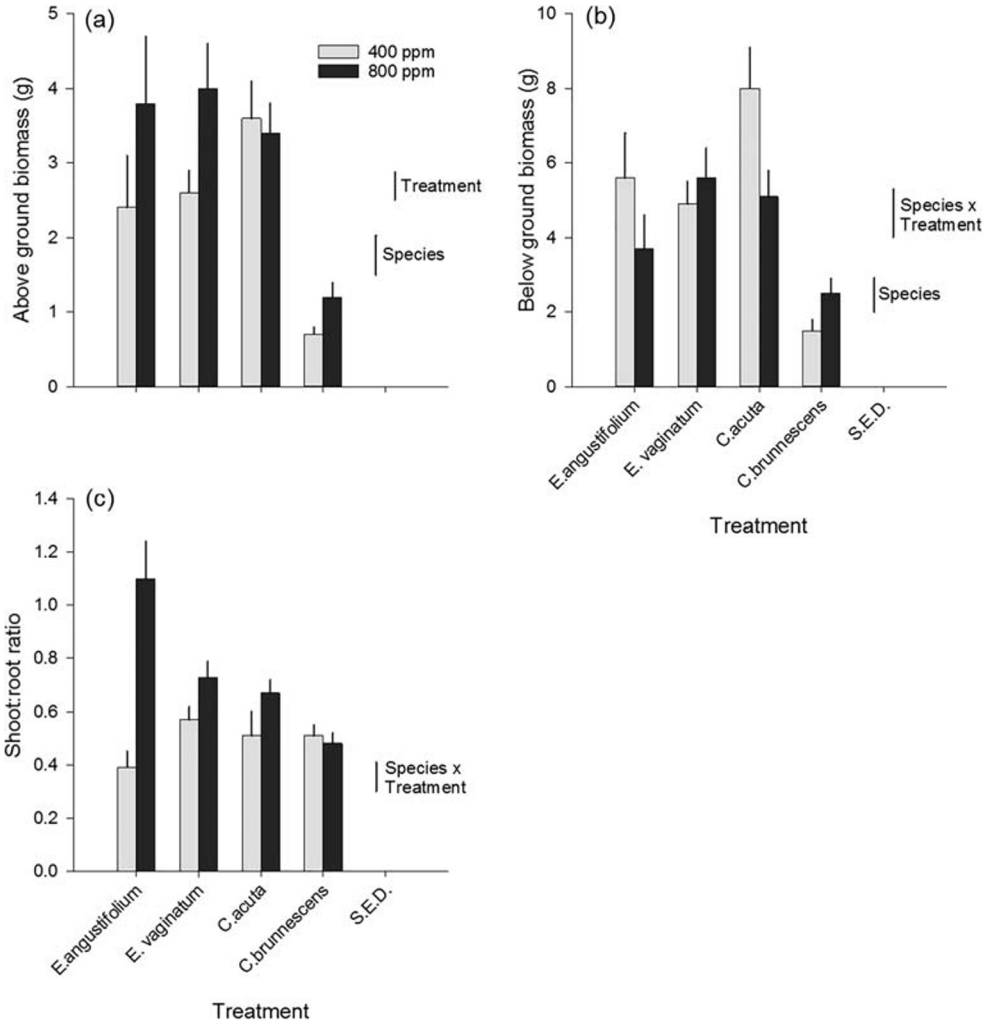


**Fig. 2** **a** Above, **b** below ground biomass and **c** shoot:root ratio for all *Cyperaceae* species at the 400 and 800 ppm atmospheric $CO_2$ treatments. Mean, standard errors of the mean and S.E.D.s for significant Species, $CO_2$ Treatment and Species×$CO_2$ Treatment effects are shown

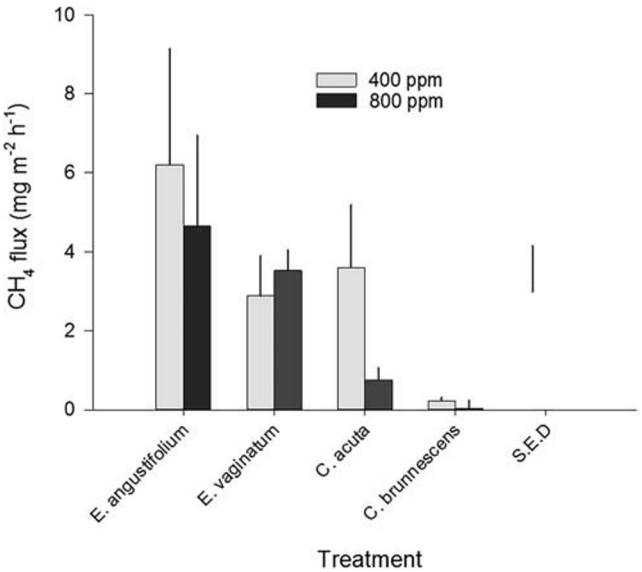


**Fig. 3** $CH_4$ fluxes across four plant species treatments and under 400 and 800 ppm atmospheric $CO_2$ treatments showing methane per unit area. Means across the experimental period, standard error of the means, and S.E.D for the significant $CO_2$ Treatment and Species effects are shown

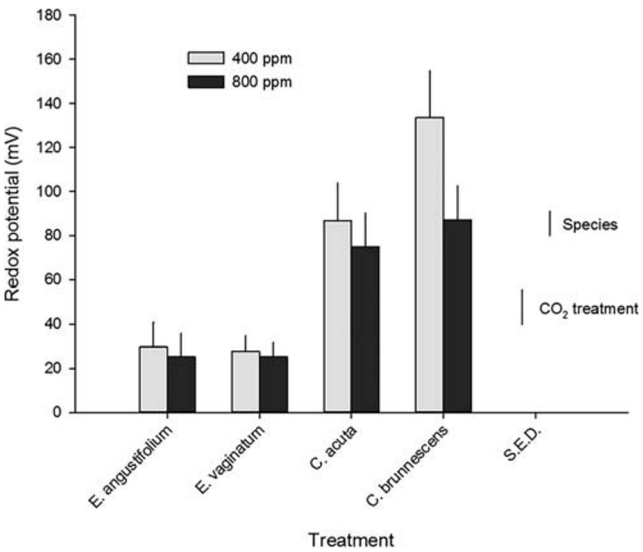


**Fig. 4** Mean redox potential with standard error of the mean for the four plant species treatments across 400 and 800 ppm atmospheric $CO_2$ treatments. S.E.D for the Species and $CO_2$ Treatment effects are shown in the figure

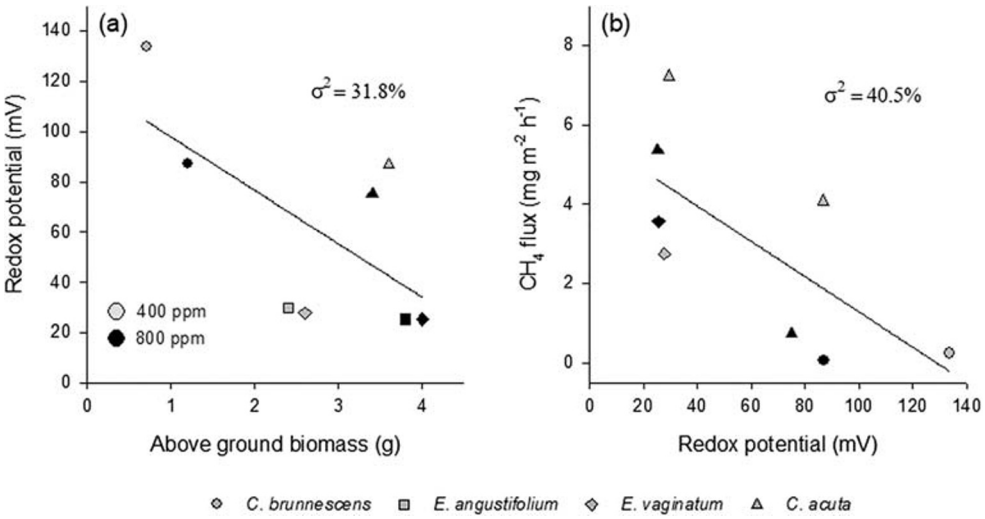


**Fig. 5** Relationship between **a** redox potential and above ground biomass and **b** $CH_4$ fluxes and redox potential. $CH_4$ fluxes and redox data are from the final sampling time point. Best fit linear regressions and % variance explained are shown

potential in response to elevated $CO_2$ may impact soil processes. As soil redox potential is a strong driver of $CH_4$ production and oxidation (Fritz et al. 2011) such changes may impact $CH_4$ fluxes. Effects of elevated $CO_2$ on soil redox potential were also demonstrated in mesocosms with *Phragmites australis* grown under ambient and elevated $CO_2$ (+330 ppm $CO_2$) (Mozdzer and Megonigal 2013). We speculate that the lowering of the redox potential is caused by greater release of

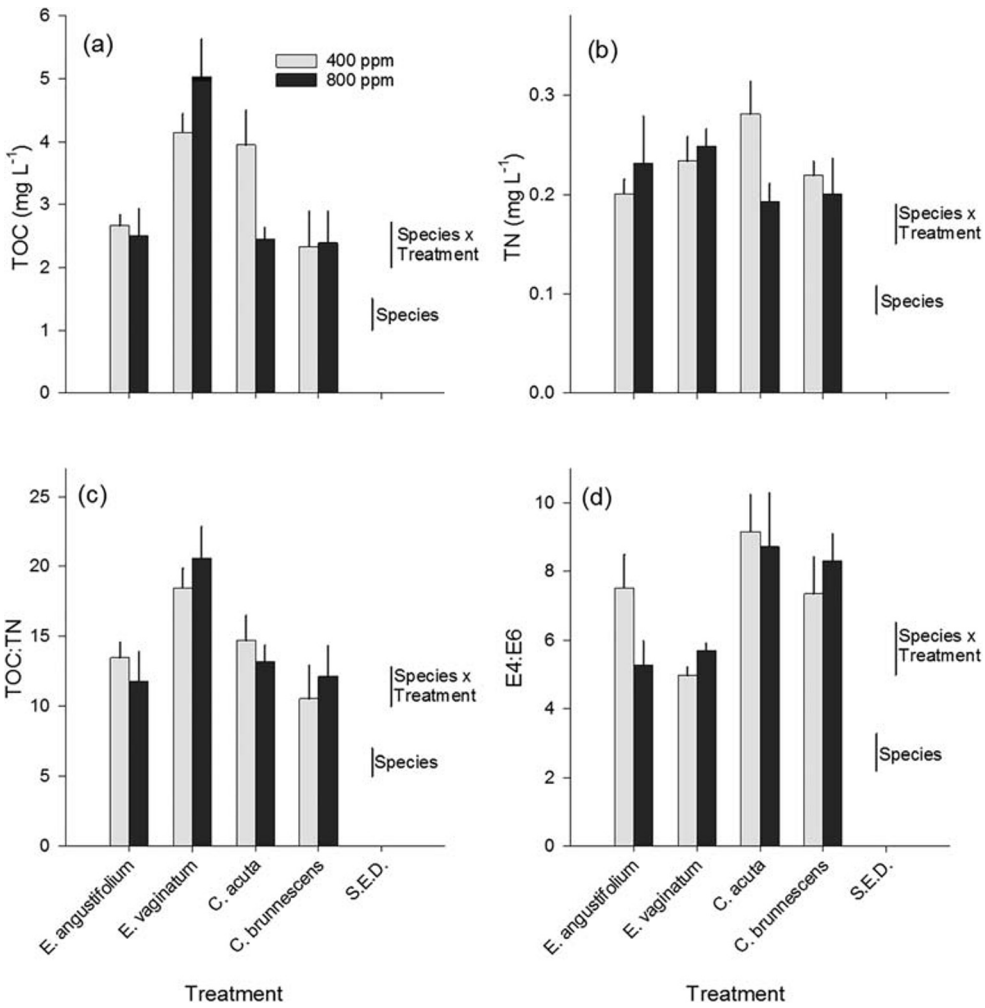


**Fig. 6** Means with standard error for (**a**) Total Organic Carbon (TOC); **b** Total Nitrogen (TN); **c** TOC:TN ratio and; **d** E4:E6 ratio in pore water samples for four Cyperaceae species under atmospheric $CO_2$ conditions of 400 and 800 ppm. S.E.D for the Species and Species × $CO_2$ Treatment effects are shown in the figure

organic material into the rhizosphere contributing to microbial respiration and depletion of electron donors (Yavitt and Seidman-Zager 2006; Laanbroek 2010). Our findings and those of Mozdzer and Megonigal (2013) contrast with those of Wolf et al. (2007) who demonstrated higher soil redox potentials in mesocosms planted with *Scirpus olneyi* due to greater root $O_2$ inputs reflecting greater root biomass in the elevated $CO_2$ treatment. The differing impact of plant species on the soil redox conditions, possibly in response to different levels of root exudation among species and/or differences in gas exchange via aerenchyma, suggests that plant species composition is a key control of the redox environment and by extension $CH_4$ production and oxidation (Bridgham et al. 2013).

In contrast to our hypothesis, which predicted increased $CH_4$ production in the elevated $CO_2$ treatment, there was no significant effect of the elevated $CO_2$ treatment on $CH_4$ fluxes (Fig. 3b). However, the negative relationship between above ground biomass and redox potential, and redox potential and $CH_4$ fluxes, demonstrates the important role of the vegetation as a control of redox and $CH_4$ fluxes (Fig. 5). Our lack of direct responses of $CH_4$ fluxes to elevated $CO_2$ contrasts with studies on *Taxodium distichum* and *Orontium aquaticum* mesocosms exposed to an experimental increase in $CO_2$ levels from 350 to 700 ppm (Vann and Megonigal 2003) and mesocosms planted with *Typha angustifolia* when $CO_2$ levels were increased from 380 to 700 ppm (Kao-Kniffin et al. 2011), where increased root growth under elevated $CO_2$ translated in to greater $CH_4$ emissions. However, limited or no impact of elevated $CO_2$ on $CH_4$ emissions was found in two sedge dominated salt marsh communities (Marsh et al. 2005) illustrating that $CH_4$ responses to elevated $CO_2$ may vary strongly among species and ecosystems depending on the physiological responses of the plant species to elevated $CO_2$. Furthermore, limited responses to elevated $CO_2$ by some species may be linked to nutrient limitation (Mozdzer and Megonigal 2013).

In conclusion, we have demonstrated that elevated atmospheric $CO_2$ increased above ground biomass production in *E. vaginatum, E. angustifolium* and *C. brunnescens* but not in *C. acuta*. Our study suggests links between plant biomass, soil redox potential and CH4 production but no direct impact of elevated $CO_2$ on $CH_4$ emissions. Our study demonstrates the importance for improved mechanistic understanding of how wetland plants species respond to elevated $CO_2$ before assumptions can be made with regard to impacts on elevated $CO_2$ on $CH_4$ emissions from wetlands.

**Acknowledgements** We are grateful to James Verran and John Corrie for laboratory for technical support. The project was funded by the University of Nottingham.



## References

ACIA (2004) Impacts of a warming arctic: Arctic climate impact assessment. ACIA Overview report. Cambridge University Press, Cambridge pp 140

Åkerman HJ, Johansson M (2008) Thawing permafrost and thicker active layers in sub-Arctic Sweden. Permafrost Periglac 19(3):279–292

Angel R, Kammann C, Claus P, Conrad R (2012) Effect of long-term free-air $CO_2$ enrichment on the diversity and activity of soil methanogens in a periodically waterlogged grassland. Soil Biology and Biochemistry 51:96–103

Basiliko N, Stewart H, Roulet NT, Moore TR (2012) Do root exudates enhance peat decomposition? Geomicrobiology Journal 29(4):374–378

Bellisario LM, Bubier JL, Moore TR, Chanton JP (1999) Controls on CH4 emissions from a northern peatland. Global Biogeochemical Cycles 13(1):81–91

Bhullar GS, Iravani M, Edwards PJ, Venterink HO (2013a) Methane transport and emissions from soil as affected by water table and vascular plants. BMC Ecology 13:32

Bhullar GS, Edwards PJ, Venterink HO (2013b) Variation in the plant-mediated methane transport and its importance for methane emission from intact wetland peat mesocosms. Plant Ecology, rts045

Bridgham SD, Cadillo-Quiroz H, Keller JK, Zhuang Q (2013) Methane emissions from wetlands: biogeochemical, microbial, and modeling perspectives from local to global scales. Global Change Biology 19(5):1325–1346

Christensen TR, Johansson T, Åkerman HJ, Mastepanov M, Malmer N, Friborg T, Svensson BH (2004) Thawing sub-arctic permafrost: Effects on vegetation and methane emissions. Geophysical Research Letters 31(4)

Curtis PS, Drake BG, Leadley PW, Arp WJ, Whigham DF (1989) Growth and senescence in plant communities exposed to elevated CO2 concentrations on an estuarine marsh. Oecologia 78(1):20–26

Curtis PS, Balduman LM, Drake BG, Whigham DF (1990) Elevated atmospheric $CO_2$ effects on belowground processes in C3 and C4 estuarine marsh communities. Ecology 2001-2006

Denmead (2008) Approaches to measuring fluxes of methane and nitrous oxide between land scapes and the atmosphere. Plant and Soil 309: 5–24

Dorodnikov M, Knorr KH, Kuzyakov Y, Wilmking M (2011) Plant-mediated $CH_4$ transport and contribution of photosynthates to methanogenesis at a boreal mire: a 14C pulse-labeling study. Biogeosciences 8(8):2365–2375

Fritz C, Pancotto VA, Elzenga J, Visser EJ, Grootjans AP, Pol A, Smolders AJ (2011) Zero methane emission bogs: extreme rhizosphere oxygenation by cushion plants in Patagonia. The New Phytologist 190(2):398–408

Gordon C, Wynn JM, Woodin SJ (2001) Impacts of increased nitrogen supply on high Arctic heath: the importance of bryophytes and phosphorus availability. New Phytologist 149(3):461–471

Heilman MA, Carlton RG (2001) Methane oxidation associated with submersed vascular macrophytes and its impact on plant diffusive methane flux. Biogeochemistry 52(2):207–224

Hodgkins SB, Tfaily MM, McCalley CK, Logan TA, Crill PM, Saleska SR, Rich VI, Chanton JP (2014) Changes in peat chemistry associated with permafrost thaw increase greenhouse gas production. Proceedings of the National Academy of Sciences of the United States of America 111(16):5819–5824

IPCC (2013) Climate Change 2013: The Physical Science Basis. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Cambridge University Press, Cambridge, pp 1535. https://doi.org/10.1017/CBO9781107415324

Joabsson A, Christensen T, Wallén B (1999) Vascular plant controls on methane emissions from northern peatforming wetlands. Trends Ecol Evol 14(10):385–388

Kao-Kniffin J, Freyre DS, Balser TC (2011) Increased methane emissions from an invasive wetland plant under elevated carbon dioxide levels. Applied Soil Ecology 48(3):309–312

Keller J, Wolf AA, Weisenhorn PB, Drake AEBG, Megonigal JP (2009) Elevated CO2 affects porewater chemistry in a brackish Marsh. Biogeochemistry 96:101–117. https://doi.org/10.1007/s10533-009-9347-3

King JY, Reeburgh WS, Thieler KK, Kling GW, Loya WM, Johnson LC, Nadelhoffer KJ (2002) Pulse-labelling studies of carbon cycling in Arctic tundra ecosystems: The contribution of photosynthates to methane emission. Global Biogeochemical Cycles 16(4):10-1–10-8

Kirschke S, Bousquet P, Ciais P, et al. (2013) Three decades of global methane sources and sinks. Nature Geoscience. https://doi.org/10.1038/ngeo1955

Koelbener A, Ström L, Edwards PJ, Venterink HO (2010) Plant species from mesotrophic wetlands cause relatively high methane emissions from peat soil. Plant and Soil 326(1–2):147–158

Kohler J, Brandt O, Johansson M, Callaghan T (2006) A long-term Arctic snow depth record from Abisko, northern Sweden, 1913–2004. Polar Research 25(2):91–113

Kokfelt U, Rosén P, Schoning K, Christensen TR, Förster J, Karlsson J, Reuss N, Rundgren M, Callaghan TV, Jonasson C, Hammarlund D (2009) Ecosystem responses to increased precipitation and permafrost decay in subarctic Sweden inferred from peat and lake sediments. Global Biogeochemical Cycles 15(7):1652–1663

Kutzbach L, Wagner D, Pfeiffer E-V (2004) Effect of micro-relief and vegetation on methane emission from wet polygonal tundra, Lena delta, Morthern Siberia. Biogeochemistry 69:341–362

Laanbroek HJ (2010) Methane emission from natural wetlands: interplay between emergent macrophytes and soil microbial processes. A mini-review. Annals of Botany 105:141–153

Langley JA, Mozdzer TJ, Shepard KA, Hagerty SB, Megonigal JP (2013) Tidal marsh plant responses to elevated $CO_2$, nitrogen fertilization, and sea level rise. Global Change Biology 19(5):1495–1503

Lawlor DW, Mitchell RAC (1991) The effects of increasing $CO_2$ on crop photosynthesis and productivity: a review of field studies. Plant, Cell & Environment 14(8):807–818

Lomax BH, Hilton J, Bateman RM, Upchurch GR, Lake JA, Leitch IJ, Cromwell A, Knight CA (2014) Reconstructing relative genome size of vascular plants through geological time. The New Phytologist 201:636–644

Mangalassery S, Sjögersten S, Sparkes DL, Sturrock CJ, Craigon J, Mooney SJ (2014) To what extent can zero tillage lead to a reduction in greenhouse gas emissions from temperate soils? Scientific Reports 4

Marsh AS, Rasse DP, Drake BG, Megonigal JP (2005) Effect of elevated $CO_2$ on carbon pools and fluxes in a brackish marsh. Estuaries 28(5):694–704

Megonigal JP, Schlesinger WH (1997) Enhanced $CH_4$ emission from a wetland soil exposed to elevated CO2. Biogeochemistry 37(1):77–88

Moore TR, Knowles R (1990) Methane emissions from fen, bog and swamp peatlands in Quebec. Biogeochemistry 11(1):45–61

Mossberg B, Stenberg L (2008) Fjällflora. Sverige, Finaland, Norge and Svalbard. Wahlstrom & Widstrand, Värnamo

Mozdzer TJ, Megonigal JP (2013) Increased methane emissions by an introduced Phragmites australis lineage under global change. Wetlands 33(4):609–615

Nilsson Ö (1991) Nordisk fjällflora. Bonniers

Öquist MG, and Svensson, BH (2002) Vascular plants as regulators of methane emissions from a subarctic mire ecosystem. Journal of Geophysical Research-Atmospheres (1984–2012), 107(D21), ACL 10-1 – 10-10

Prater JL, Chanton JP, and Whiting GJ (2007) Variation in methane production pathways associated with permafrost decomposition in collapse scar bogs of Alberta, Canada. Global Biogeochemical Cycles 21(4)

Ringeval B, Friedlingstein P, Koven C, Ciais P, Noblet-Ducoudré ND, Decharme B, Cadule P (2011) Climate-CH 4 feedback from wetlands and its interaction with the climate-CO 2 feedback. Biogeosciences 8(8):2137–2157

Sjogersten S, Caul S, Daniell TJ, O'Sullivan OS, Stapleton CS, Titman JJ (2016) Organic matter chemistry controls greenhouse gas emissions from permafrost peatlands. Soil Biology and Biochemistry 98:42–53

Steele LP, Fraser PJ, Rasmussen RA, Khalil MAK, Conway TJ, Crawford AJ, Thoning KW (1987) The global distribution of methane in the troposphere. In Scientific Application of Baseline Observations of Atmospheric Composition (SABOAC), 417–463. Springer Netherlands

Ström L, Mastepanov M, Christensen TR (2005) Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. Biogeochemistry 75(1):65–82

Ström L, Tagesson T, Mastepanov M, Christensen TR (2012) Presence of *Eriophorum scheuchzeri* enhances substrate availability and methane emission in an Arctic wetland. Soil Biology and Biochemistry 45:61–70

Sullivan L, Wildova R, Goldberg D, Vogel C (2010) Growth of three cattail (Typha) taxa in response to elevated CO2. Plant Ecology 207(1):121–129

Tarnocai C, Canadell JG, Schuur EAG, Kuhry P, Mazhitova G, and Zimov S (2009) Soil organic carbon pools in the northern circumpolar permafrost region. Global Biogeochemical Cycles 23(2)

Torn MS, Chapin FS (1993) Environmental and biotic controls over methane flux from arctic tundra. Chemosphere 26(1):357–368

Turetsky M, Kotowska A, Bubier J et al (2014) A synthesis of methane emissions from 71 northern, temperate, and subtropical wetlands. Global Change Biology 20:2183–2197

Updegraff K, Pastor J, Bridgham SD, Johnston CA (1995) Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. Ecological Applications 5(1):151–163

Updegraff K, Bridgham SD, Pastor J, Weishampel P, Harth C (2001) Response of $CO_2$ and $CH_4$ emissions from peatlands to warming and water table manipulation. Ecological Applications 11(2):311–326

Van Groenigen KJ, Osenberg CW, Hungate BA (2011) Increased soil emissions of potent greenhouse gases under increased atmospheric CO2. Nature 475:214–216

Vann C, Megonigal JP (2003) Elevated $CO_2$ and water depth regulation of methane emissions: comparison of woody and non-woody wetland plant species. Biogeochemistry 63:117–134

Wang JM, Murphy JG, Geddes JA, Winsborough CL, Basiliko N, Thomas SC (2013) Methane fluxes measured by eddy covariance and static chamber techniques at a temperate forest in Central Ontario, Canada. Biogeosciences 10(6):4371–4382

Wolf AA, Drake BG, Erickson JE, Megonigal JP (2007) An oxygen-mediated positive feedback between elevated carbon dioxide and soil organic matter decomposition in a simulated anaerobic wetland. Global Change Biology 13(9):2036–2044

Woodward FI, Lake JA, Quick WP (2002) Stomatal development and $CO_2$: ecological consequences. The New Phytologist 153:477–484

Worrall F, Burt TP, Jaeban RY, Warburton J, Shedden R (2002) Release of dissolved organic carbon from upland peat. Hydrological Processes 16(17):3487–3504

Yavitt JB, Seidman-Zager M (2006) Methanogenic conditions in northern peat soils. Geomicrobiology Journal 23(2):119–127

Zak DR, Pregitzer KS, Curtis PS, Teeri JA, Fogel R, Randlett DL (1993) Elevated atmospheric CO2 and feedback between carbon and nitrogen cycles. Plant and Soil 151(1):105–117