Biogeochemistry (2012) 108:77–90
DOI 10.1007/s10533-011-9573-3

Temperature sensitivity of greenhouse gas production in wetland soils of different vegetation

K. S. Inglett · P. W. Inglett · K. R. Reddy · T. Z. Osborne

Received: 3 May 2010 / Accepted: 10 January 2011 / Published online: 29 January 2011

Abstract Organic matter decomposition regulates rates of carbon loss (CO_2 and CH_4) in wetlands and has implications for carbon sequestration in the context of changing global temperature. Here we determined the influence of temperature and vegetation type on both aerobic and anaerobic decomposition of organic matter in subtropical wetland soils. As in many other studies, increased temperature resulted in higher rates of respiration and methanogenesis under both aerobic and anaerobic conditions, and the positive effect of temperature depended on vegetation (source of carbon substrate to soil). Under anaerobic incubations, the proportion of gaseous C (CO_2 and CH_4) lost as CH_4 increased with temperature indicating a greater sensitivity of methanogenesis to temperature. This was further supported by a wider range of Q_{10} values (1.4–3.6) for methane production as compared with anaerobic CO_2 (1.3–2.5) or aerobic CO_2 (1.4–2.1) production. The increasing strength of positive linear correlation between CO_2:CH_4 ratio and the soil organic matter ligno-cellulose index at higher temperature indicated that the temperature sensitivity of methanogenesis was likely the result of increased C availability at higher temperature. This information adds to our basic understanding of decomposition in warmer subtropical and tropical wetland systems and has implications for C models in wetlands with different vegetation types.

Keywords Decomposition · Subtropical · Q_{10} · Methane · CO_2

K. S. Inglett (✉) · P. W. Inglett · K. R. Reddy · T. Z. Osborne
Soil and Water Science Department, University of Florida, 106 Newell Hall, P O Box 110510-0510, Gainesville, FL 32606, USA
e-mail: Kanika@ufl.edu

Introduction

The ability of wetlands to act as carbon (C) sinks is greatly influenced by rates of soil organic matter (SOM) decomposition and resultant losses of carbon dioxide (CO_2) and methane (CH_4) (McLatchey and Reddy 1998; DeBusk and Reddy 1998). Because natural wetlands also represent about 23–40% of the annual CH_4 emissions (Fung et al. 1991; Hein et al. 1997) studies of SOM decomposition in this area have become particularly important due to the environmental focus on greenhouse gas emissions. For these reasons, knowledge of the factors affecting wetland soil decomposition and gaseous C production is critical to understanding and predicting global climate change.

Production of CO_2 and CH_4 depends on interaction between several factors including soil characteristics (soil type, porosity, soil pH, electron acceptors), environmental conditions (temperature, water levels, plant cover), and plant properties contributing to

organic matter quantity and quality (biomass production, lignin content, C:N etc.) (Reviewed by Reddy and DeLaune 2008). Of these factors, it is widely known that litter quality (C:N ratio, lignin content, lignin:N ratio) significantly affects organic matter decomposition in wetlands, (Debusk and Reddy, 2005; Bridgham et al. 1998 and reviewed by Cadisch and Giller 1997), thus making litter quality a useful predictor of CO_2 production. It is also widely accepted that vegetation type/SOM quality influences CH_4 production. Many studies have assessed the importance of vegetation type from the supply (quantity) of C (Whiting and Chanton, 1993), while others have noted differences in C limitation through substrate additions (Bridgham and Richardson 1992; Klinger et al. 1994; Morrissey and Livingston 1992; Valentine et al. 1994). Vegetation type is often used as a surrogate for C quality (e.g., McKenzie et al. 1998; Smemo and Yavitt 2006; Rooney-Varga et al. 2007), and some studies have linked differences in methanogenesis to the quality of SOM (e.g., lignin or carbohydrate content) (Yavitt et al. 1997; Shaver et al. 2006).

Temperature is another well documented factor influencing SOM decomposition and respiration (Fierer et al. 2005). Similarly, rates of methanogenesis have been shown to vary according to manipulated (lab studies) and in situ temperatures (i.e. seasonal patterns) (reviewed by Segers 1998). With regard to decomposition, temperature sensitivity is well characterized in terms of Q_{10} factor that describes the change in reaction rate with an increase of 10°C in temperature. Wetland methane production has been documented with Q_{10} values ranging from 1.7 to 28 (Segers 1998). Although there have been studies documenting seasonal effects on C mineralization in wetlands, only a few studies have investigated the relationships between temperature and soil organic C quality in wetlands (Fissore et al. 2009). Therefore, despite our understanding of vegetation (OM quality) and temperature effects on greenhouse gas emissions, there is still much that is unknown about the interactive effects of temperature and SOM quality (Bergman et al. 2000).

Much of our lack of understanding surrounds the availability of C at different temperatures. For example, increased CO_2 and CH_4 production at higher temperatures is hypothesized to primarily occur through stimulation of microbial enzyme activities involved in breakdown of complex polymeric C compounds and enhanced bioavailability of dissolved organic compounds (Zak et al. 1999; Freeman et al. 2004). It has also been demonstrated that increased methane production at higher temperatures comes as a result of shifts in C availability affecting the dominant pathways of methane formation (acetoclastic versus hydrogenotrophic methanogenesis) (Chin and Conrad 1995; Hines et al. 2008). These findings suggest that C availability may explain not only differences in decomposition of SOM of different vegetation types, but also the differential response of different soils to temperature. Presumably, more labile C would respond faster (be more available) under elevated temperatures, however the literature shows widely differing results. For example, in studies of terrestrial soil C, increased CO_2 production at higher temperatures has been associated with sensitivity of labile soil C pools (Liski et al. 2000; Rey and Jarvis 2006), recalcitrant pools (Leifeld and Fuhrer 2005), or with no specific soil C pool (Conen et al. 2006) (reviewed by Bardgett et al. 2008).

Most studies of temperature affects on decomposition and methanogenesis have primarily focused on northern systems where the greatest increases in temperature and greenhouse gas emissions are likely to affect potential climate change feedback (Scanlon and Moore 2000; Freeman et al. 1995; Knoblauch et al. 2008). In contrast, limited data are available on tropical and subtropical wetland systems, despite the fact that they provide a model system to study the interactive effects of temperature and substrate quality because of their high variability (Bartlett and Harriss 1993). Tropical/subtropical wetlands (20° N–30° S) occupy almost 30% of the global wetland area (1.6×10^{12} m^2, Matthews and Fung 1987), 11% of the global peatland area (0.4×10^{12} m^2, Page et al. 2010) and account for an average of 55.7% of global wetland methane emissions (derived using data summarized in Mitra et al. 2005).

In the context of global warming, several studies have examined aerobic and anaerobic production of CO_2 and CH_4 from SOM of different vegetation types as they respond to changes in temperature (Wickland and Neff 2008; Raich and Schlesinger 1992; Freeman et al. 1995). The balance of CO_2 versus CH_4 production is critical due to the higher global warming potential of methane which is $\sim$25 times (100-year

period, IPCC 2007) and ~33 times (with the direct and indirect aerosol effect) greater than CO_2 (Shindell et al. 2009). The majority of these have been conducted in forests, and northern and temperate wetlands (Scanlon and Moore 2000; Freeman et al. 1995; Knoblauch et al. 2008), and there is comparatively little information on subtropical and tropical systems (Corstanje and Reddy 2004; Cao et al. 1998).

In this study, we investigated how SOM decomposition responds to temperature under aerobic and anaerobic conditions in a freshwater, subtropical wetland, and how the temperature response relates to SOM quality. In this study, we determined the influence of temperature on CO_2 and CH_4 production in peat soils from wetlands dominated by different emergent (*Typha domingensis*, *Cladium jamaicense,* *Eleocharis interstincta* and *Panicum hemitomon.*), woody (*Salix caroliniana*), and floating-leaved (*Nymphaea odorata*) vegetation.

Methods

Site description

For this study we sampled soils from a subtropical fresh water marsh, the Blue Cypress Marsh Conservation Area (BCMCA), located in Central Florida in the headwater region of the St. Johns River (Fig. 1). The annual temperature for this site ranges from 10 to 29°C (Ipsilantis and Sylvia 2007) and the annual mean precipitation is 1.19 m $year^{-1}$ for the past decade (St Johns River water Management District,

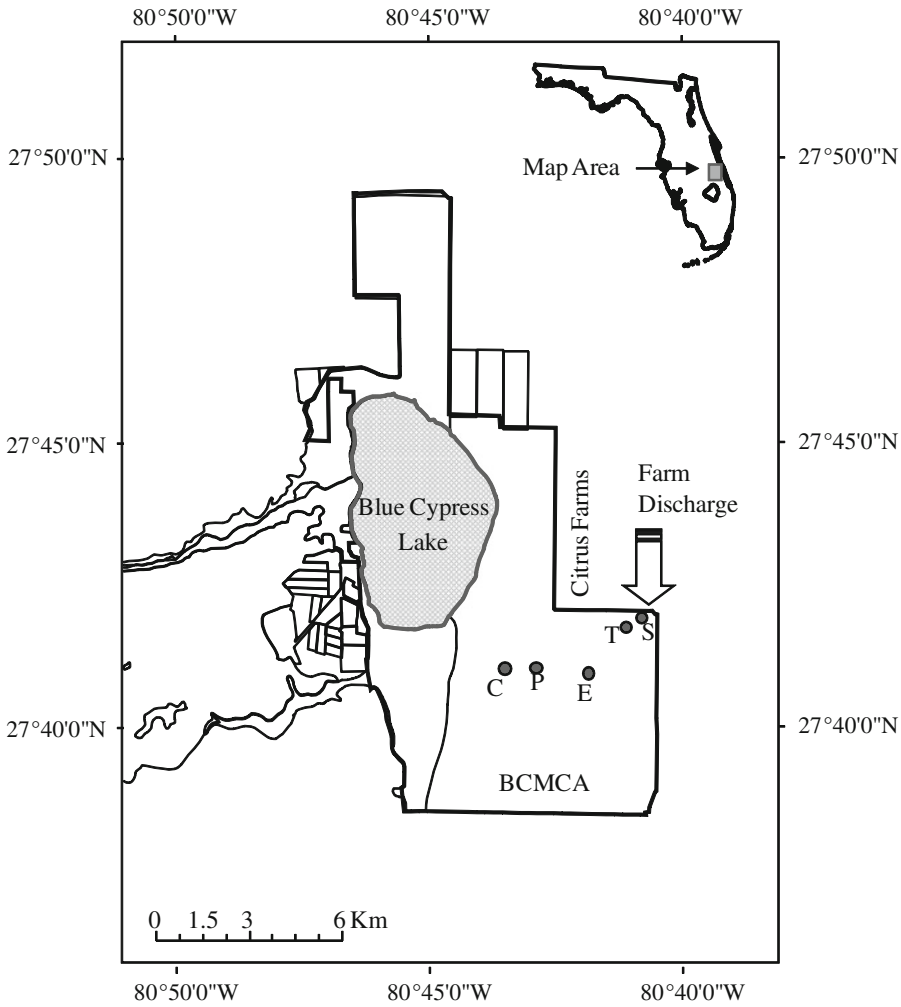

Fig. 1 Sampling sites in Blue Cypress Marsh Conservation Area. *Gray dots* represent the sampling regions with different dominating vegetations, C (*Cladium*), P (*Panicum*), E (*Nymphaea* and *Eleocharis*), T (*Typha*), and S (*Salix*). *Back arrows* represent the water flow; *Gray arrow* represents the historic flow

2010). Historically, this marsh received nutrient inflows in the form of farm discharge from the surrounding agricultural lands in the northeast region (Fig. 1). The inflows were diverted away from the marsh approximately two decades ago (Corstanje and Reddy 2004).

Dominant vegetation communities in this region include *Typha* (*Typha domingensis)*, *Salix* (*Salix caroliniana), Eleocharis* (*Eleocharis interstincta* with some *Nymphaea odorata), Cladium* (*Cladium jamaicense)* and *Panicum* (*Panicum hemitomon).* Soils in the Blue Cypress Marsh area are Histosols classified as Terra Ceia muck (Taxonomic class: euic, hyperthermic Typic Haplosaprists) with a SOM composition reflecting dominant vegetation communities. The soils are consistently flooded with infrequent draw downs occurring during the dry season (November-late April) (Seo 2002).

Soil sampling

Surface soil samples (0–10 cm) from stands of five different dominant vegetation communities (as mentioned above) were collected by inserting a 10 cm diameter soil auger in the soils and removing cores from depth of up to 60 cm. Three soil cores were removed from each site and they were sectioned every 10 cm and the top section was used in this study. Upon collection, soil samples were transported on ice to the Wetland Biogeochemistry Laboratory at the University of Florida in Gainesville. Sampled cores were stored at 4°C for no more than 48 h before processing. We acknowledge that storage at low temperatures can affect the biogeochemical processes (Arnold et al. 2008). However, our storage conditions are not dramatically different from the annual low temperature experienced at this site (10°C) (Ipsilantis and Sylvia, 2007) and we measured linear rates of gaseous C production throughout the experiment suggesting that this temperature or length of storage did not adversely affect microbial populations or result in alteration of the available organic carbon pool.

Soil organic matter characterization

Soil samples were analyzed for soil pH, total carbon, total nitrogen, and total phosphorus. Soil pH was measured by equilibrating soils with deionized water (2:1). For nutrient soil analyses, soil samples were dried and homogenized after removal of any visible plant material. Total C and N concentrations were determined with a Carlo-Erba NA-1500 CNS analyzer (Haak-Buchler Instruments, Saddlebrook NJ), while TP was determined by using the method of Andersen (1976) that involved combustion at 550°C, acidic (HCl) extraction of the ash, followed by analysis of P by ascorbic acid colorimetric method (Method 365.4, USEPA 1993). Soil organic matter was estimated by loss on ignition by heating the soils at 550°C for 5 h.

SOM quality was characterized by partitioning soil C into four fractions defined as soluble soil constituents (lipids, waxes, proteins, etc.), hemicellulose, α-cellulose, and lignin. These fractions were quantified by a modified sequential fiber extraction method (Ankom Technology, Fairport, NY) (Goering and Van Soest 1970; Rowland and Roberts 1994). All fiber fractions were then normalized for ash content and are hence expressed as percent of SOM.

Microcosm experiments

To prepare the soil microcosms, soil samples were homogenized using a glass stirring rod to break up bulk macro aggregate structure. Since destruction of the soil structure has been known to disrupt microbial community structure and alter microsite distribution resulting in disturbed microbial functions (Teh and Silver 2006) extreme care was taken to ensure minimal/no disturbance the microaggregate structures. Approximately 10 grams of homogenized soils from each of the cores was placed in 60 ml glass serum bottles. Three replicates of each vegetation/soil type were measured at each of three temperatures (10°C ± 1°C, 20°C ± 1°C, and 30°C ± 1°C) to approximate the annual temperature range (Ipsilantis and Sylvia 2007). For aerobic incubations, soil moisture content was adjusted to 65–75% of saturation content. Bottles were weighed periodically to ensure that the moisture content remained constant during the course of the study. On sampling days (every 2 days), aerobic bottles were capped with gray butyl stoppers and aluminum crimps (Wheaton, Millville, NJ) briefly for a few hours to allow accumulation of headspace CO_2 for gas sampling. Anaerobic microcosms were prepared in a similar manner except that soil and water were added as

1:2 ratio to mimic flooded conditions. Bottles were sealed, crimped, and purged with N_2 gas to create anaerobic conditions in the headspace. Unlike the aerobic microcosms, the incubation bottles remained capped throughout the experiment. Gas sampling (CO_2 and CH_4) was conducted for four consecutive weeks at 3 day intervals. Soil-free controls were included with every set of microcosm to account for background concentrations of CO_2 and CH_4, which were negligible, compared to that produced from soil.

Carbon dioxide and methane measurements

Measurements of CO_2 and CH_4 were conducted using a Shimadzu 8A gas chromatograph (GC) (Shimadzu Scientific Instruments Inc., Columbia, MD) fitted with a thermal conductivity detector (TCD) and a flame ionization detector (FID) respectively. Calibration curves for both gases were prepared using standard gas mixtures (Scotty Specialty Gases, Plumsteadville, PA).

Determination of Q_{10}

Responses of biological systems to temperature are often expressed as a Q_{10} function. By definition Q_{10} is a factor by which rate of respiration differs for a temperature range of 10°C where $Q_{10} = (k_2/k_1)^{[10/(T_2-T_1)]}$ and k_1 and k_2 are respiration rates at two observed temperatures T_1 and T_2 (Fissore et al. 2009; Winkler et al. 1996). The respiration rates at any given temperature were calculated as the linear slopes obtained by repeated measures of CO_2 and CH_4 during the period of incubation.

We also used another model described by Fierer et al. (2006) and Lloyd and Taylor (1994) where the following equation (line) describes the relationship between temperature-respiration

$$y_t = Be^{kT}$$

where y_t is the respiration at given temperature (μg CO_2–C g^{-1} soil h^{-1}), B is a parameter of exponential fit describing the y intercept, k is the rate constant described by the slope, and T is the temperature (°C). The parameter B is used as an index of relative C quality and it provides an estimate of soil organic C bioavailability from soils incubated under controlled conditions.

Statistical analyses

All statistical analyses were performed using JMP version 5.1 (Cary, NC, USA). The CO_2 and CH_4 production were analyzed as zero-order kinetic reactions and estimated as the coefficient of simple linear regression. Net CO_2 and CH_4 production data were log transformed prior to data analysis. Differences between vegetation types and temperature were tested with a two-way ANOVA. Multiple comparisons were conducted by using Tukey–Kramer test. Correlation analyses were used to determine relationships between microbial responses (CO_2 and CH_4) and soil characteristics (vegetation types, nutrient).

Results

With the exception of the high P content of the *Salix* soils and the high N content of the *Panicum* soils, the nutrient content of soils used in this study did not differ appreciably (Table 1). In contrast, the composition of SOM from different vegetation types varied significantly (Table 1). *Typha* soils had the highest soluble C content (16%), while *Salix* soils contained the least (5%). The acid-soluble C fraction ranged from 30 to 50% of dry weight with higher amounts in *Eleocharis* and *Typha* soils. Lignin content in *Cladium*, *Panicum* and *Salix* soils was found to be more than 50% of the dry weight in contrast to the *Eleocharis* and *Typha* soils where lignin comprised less than 50% of the soil dry weight. The lignocellulose index (ratio of lignin to the sum of lignin and cellulose, LCI) has been used as a measure of SOM quality (Melillo et al. 1989; DeBusk and Reddy 1998). In this study, the highest LCI was observed in *Cladium* soils (0.8) while *Typha* and *Eleocharis* soils had the lowest (0.3 and 0.4, respectively) LCI.

Soils obtained from different vegetation communities showed significant differences in CO_2 and CH_4 production rates (Table 2). In aerobic incubations, *Panicum* soils had overall higher rates of CO_2 production as compared to other soils, while the lowest rates were found in *Cladium* soils ($p < 0.05$). In contrast, under anaerobic conditions, *Eleocharis* soils showed the highest rates of CO_2 production with *Cladium* and *Typha* producing the least ($p < 0.01$). Similarly, *Eleocharis* and *Cladium* soils, showed the

Table 1 Biogeochemical parameters and plant compositional analyses of soil organic matter

	pH	TN (g kg^{-1})	TC (g kg^{-1})	LOI (%)	TP (mg kg^{-1})	Lignin (%)	Cellulose (%)	Labile (%)	C:N
Cladium	5.6	28.7 ± 0.5^{c}	469 ± 2^{ab}	93.5 ± 1.0^{ab}	533 ± 26^{b}	61.7 ± 4^{a}	30.7 ± 4^{b}	7.0 ± 1^{bc}	$16.3. \pm 0.3^{a}$
Eleocharis	5.4	33.6 ± 0.7^{b}	478 ± 5^{ab}	94.6 ± 0.4^{a}	562 ± 17^{b}	39.3 ± 6^{b}	50.7 ± 2^{a}	11.3 ± 2^{b}	14.3 ± 0.2^{b}
Panicum	5.8	36.9 ± 0.7^{a}	468 ± 3^{ab}	93.8 ± 0.2^{ab}	558 ± 91^{b}	58.3 ± 5^{a}	33.7 ± 3^{b}	8.0 ± 1^{bc}	12.7 ± 0.2^{c}
Salix	5.9	29.3 ± 1.2^{c}	480 ± 12^{a}	93.3 ± 0.6^{b}	809 ± 16^{a}	55.3 ± 4^{a}	40 ± 6^{b}	5.0 ± 2^{c}	$16. 4 \pm 0.0^{a}$
Typha	5.8	28 ± 0.5^{c}	463 ± 5^{b}	93.3 ± 0.2^{ab}	617 ± 36^{b}	28 ± 5^{b}	55.7 ± 3^{a}	16.0 ± 1^{a}	16.5 ± 0.2^{a}

Superscript letters represent the significant ($\alpha = 0.5$) differences between the soil types for each parameter measured

Table 2 Carbon dioxide and methane production rates (with standard deviations) from soils organic matter of different vegetation types

	Cladium	*Eleocharis*	*Panicum*	*Salix*	*Typha*
Aerobic CO_2 (μg C-g^{-1} dw d^{-1})					
10°C	78 ± 8^{b}	105 ± 19^{ab}	119 ± 5^{a}	108 ± 13^{ab}	78 ± 6^{b}
20°C	132 ± 14^{bc}	182 ± 28^{a}	171 ± 6^{ab}	167 ± 26^{ab}	109 ± 5^{c}
30°C	238 ± 14	269 ± 49	285 ± 30	243 ± 30	329 ± 64
Anaerobic CO_2 (μg C-g^{-1} dw d^{-1})					
10°C	16.2 ± 2.2	17.6 ± 2.0	15.7 ± 3.1	14.5 ± 0.5	13.7 ± 0.4
20°C	14.2 ± 3.6^{b}	26.3 ± 2.7^{a}	20.4 ± 4.2^{ab}	20.6 ± 2.1^{ab}	20.2 ± 2.7^{ab}
30°C	38.4 ± 6.3^{b}	$78.2 \pm 22.4a$	49.2 ± 15.2^{ab}	54.1 ± 2.3^{ab}	36.3 ± 6.0^{b}
CH_4 (μg C-g^{-1} dw d^{-1})					
10°C	3.6 ± 1.1^{c}	6.5 ± 1.5^{a}	4.0 ± 0.2^{bc}	6.1 ± 0.8^{ab}	4.0 ± 0.5^{bc}
20°C	4.0 ± 1.4^{c}	14.7 ± 2.6^{a}	5.9 ± 2.7^{bc}	9.0 ± 1.6^{b}	6.7 ± 1.6^{bc}
30°C	14.1 ± 3.0^{b}	54.3 ± 15.7^{a}	23.5 ± 10.4^{b}	31.8 ± 1.0^{ab}	34.6 ± 13.7^{ab}

Superscript letters represent the significant ($\alpha = 0.5$) differences between the soil types at each temperature

Superscript letters represent the significant differences ($\alpha = 0.5$)

highest and lowest rates of CH_4 production, respectively (Table 2). Two-way ANOVA showed that both vegetation and temperature significantly influenced CO_2 (aerobic and anaerobic) and CH_4 production (Table 3). Stronger effect of vegetation was evident on methane production when compared with that on CO_2 production.

All soils showed higher rates of CO_2 and CH_4 production at elevated temperatures, however, the level of response varied with soil type and incubation temperature (Table 2). At 10°C, *Panicum* showed significantly higher aerobic CO_2 production than *Cladium* and *Typha*, while at 20°C, *Eleocharis* showed higher aerobic CO_2 production than *Cladium* and *Typha*, and at 30°C, there were no significant differences in aerobic CO_2 production between the soil types. For anaerobic incubations, there were no differences in CO_2 production rates of the soil types at 10°C, while at 20 and 30°C, *Eleocharis* consistently showed higher rates than *Cladium*. Similarly, *Eleocharis* exhibited the highest, and *Cladium* the lowest rates of CH_4 production at all temperatures (Table 2).

Table 3 Effect of vegetation type and temperature on C respiration and methane production in soils

Source	DF	*F*-values		
		Aerobic	Anaerobic	
		CO_2	CO_2	CH_4
Vegetation	4	3.3*	7.9**	10.6***
Temperature	2	167.8***	95.6***	84.8***
Vegetation * Temperature	8	3.9*	3.8*	4.3*

* $p < 0.01$

** $p < 0.001$

*** $p < 0.0001$

Overall, rates of anaerobic CO_2 production were 7% of that observed in the aerobic conditions, whereas the average rate of total anaerobic C loss ($CO_2 + CH_4$) from the soils was 13% of that observed in aerobic conditions. There was also an overall significant positive correlation between of anaerobic CO_2 and CH_4 production rates ($r^2 = 0.87$, $p < 0.0001$) which was strongest at 30°C ($r^2 = 0.67$, $p = 0.0002$) and 20°C ($r^2 = 0.60$, $p = 0.0006$), but was absent at 10°C. For specific soil types, the ratio of anaerobically produced CO_2:CH_4 declined with increasing temperature in all soils, and ranged from 4.5 in *Cladium* soils at 10°C to 1.0 in *Typha* soils at 30°C (Fig. 2). The decline in this ratio with increasing temperature was greatest for *Typha* soils (decreasing from 3.4 at 10°C to 1.0 at 30°C), and was least for *Salix* soils (decreasing from 2.4 at 10°C to 1.7 at 30°C).

There was no correlation between C quality of any fractions of SOM and CO_2 production under both aerobic and anaerobic decomposition. In contrast, rates of methanogenesis were positively correlated with cellulose fractions ($r^2 = 0.38$, $p = 0.014$), and negatively correlated with both lignin ($r^2 = 0.33$, $p = 0.026$) and the LCI ($r^2 = 0.66$, $p = 0.05$). There was also a strong correlation ($r^2 = 0.69$, 30°C) between soil LCI and the ratio of anaerobic CO_2 and CH_4 production rates (Fig. 3). This trend also appeared to be influenced by temperature, with strength of the correlation being significant at 30°C ($r^2 = 0.69$, $p = <0.001$) and no correlation at lower temperatures of 20°C, ($r^2 = 0.15$) and 10°C ($r^2 = 0.11$). *Typha* soil (with the lowest LCI) resulted in the highest proportional methane production, followed by *Eleocharis*, *Salix*, *Panicum*, and lastly, *Cladium*.

Soil organic C quality was presented in two ways (a) LCI, (b) calculated *B* as in Fierer et al. (2005) and Lloyd and Taylor (1994). The relationship between respirable C (for aerobic and anaerobic CO_2 and CH_4) and Q_{10} (10–30°C) (Fig. 4) revealed that soils higher in methane production also showed higher Q_{10} values ($r^2 = 0.93$). A similar trend existed for

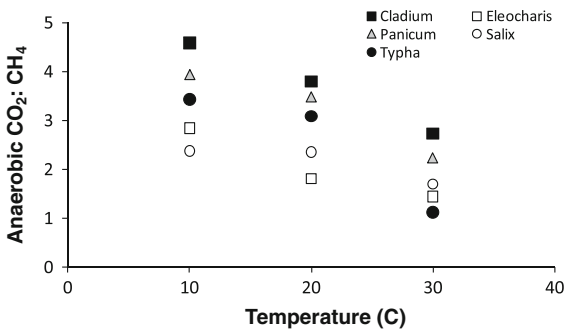

Fig. 2 Change in ratio of rates of anaerobic CO_2:CH_4 production from five soil types incubated at different temperatures

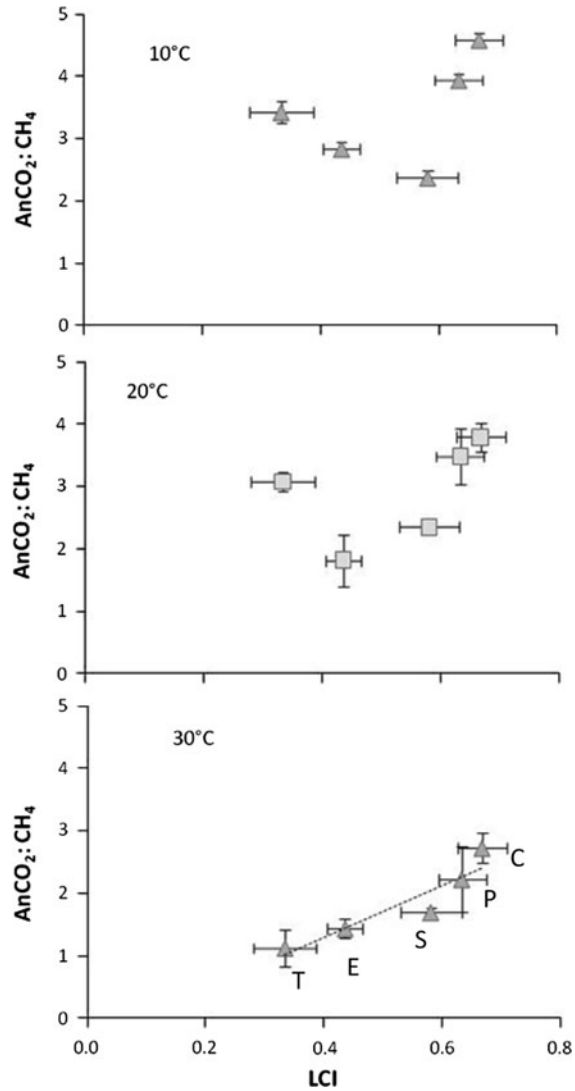

Fig. 3 Relationship between LCI and ratio of rates of anaerobic CO_2:CH_4 production at three temperatures (10°C, 20°C, and 30°C). *Black solid squares* represent the *Panicum* soils, *open circles* represent *Salix* soils; *closed circles* represent *Typha* soils; *gray squares* represent *Eleocharis* soils; and *open triangles* represent *Cladium* soils

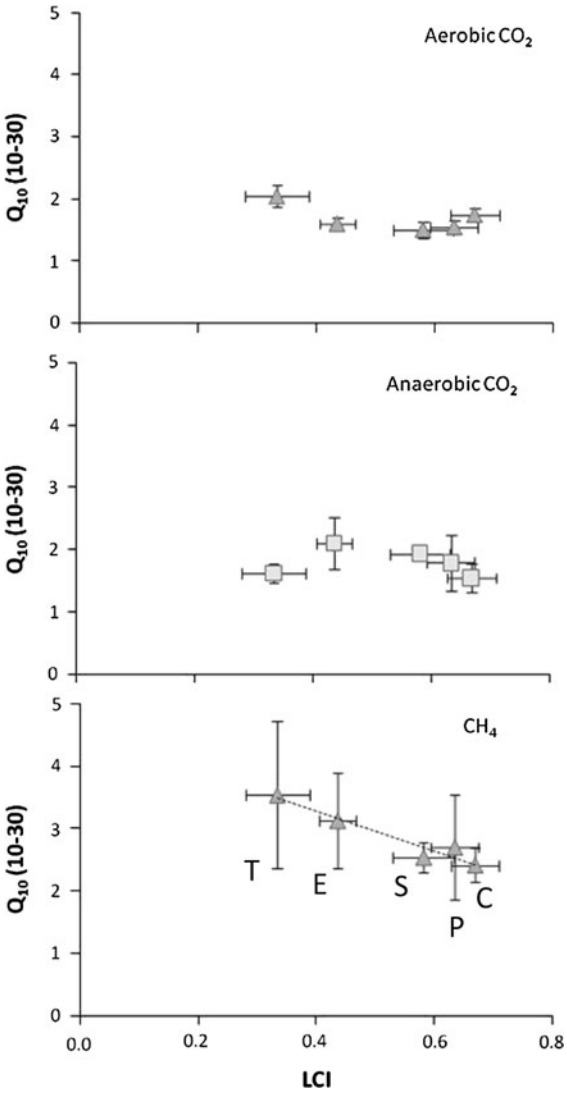

Fig. 4 Relationship between LCI and Q_{10} values (10–30°C) for aerobic and anaerobic CO_2 and CH_4 for all 5 soil types. *Black solid squares* represent the *Panicum* soils, *open circles* represent *Salix* soils; *closed circles* represent *Typha* soils; *gray squares* represent *Eleocharis* soils; and *open triangles* represent *Cladium* soils

anaerobic CO_2, but was not observed for aerobic CO_2. On relating the C quality (B) with Q_{10}, a reverse relationship was observed indicating higher Q_{10} values for soils with lower C quality for all three measured parameters aerobic CO_2, anaerobic CO_2 and CH_4 (Fig. 5).

Calculated Q_{10} values for temperatures between 10 and 30°C ranged from 1.5 to 2.1, 1.5 to 2.1, and 2.4 to 3.5 for the production of aerobic CO_2, anaerobic CO_2

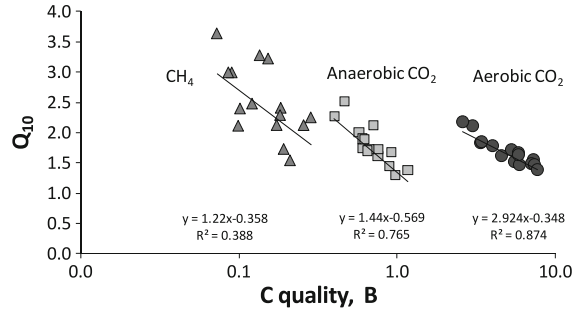

Fig. 5 Relationship between Q_{10} (10–30°C) and the C quality (calculated *B* value) for (aerobic CO_2, anaerobic CO_2 and CH_4. The C quality is presented on a logarithmic scale

and CH_4, respectively (Table 4). For aerobic CO_2 production, the effect of temperature was similar when considering the 10–20°C and 20–30°C ranges separately; however, much higher Q_{10} values were observed at the 20–30°C range for both anaerobic CO_2 (1.8 times higher) and CH_4 production (2.6 times higher) (Table 4). Most of the soil types showed similar results for Q_{10}, but in the high temperature range, *Typha* soils had higher Q_{10} values than the other soil types for aerobic CO_2 and CH_4 production, and correspondingly lower Q_{10} values for anaerobic CO_2.

Discussion

Results of our study showed that rates of respiration and methanogenesis in soils are influenced by soil carbon quality regulated by different vegetation types. These observations are in agreement with the results reported in literature (Bridgham and Richardson 1992; Raich and Schlesinger 1992; Bergman et al. 2000; McKenzie et al. 1998). In this study, higher rates of CO_2 and CH_4 production were found in *Typha* and *Eleocharis* soils.

Studies on the effect of temperature on SOM decomposition are not conclusive and show considerable variability depending on composition of soil organic matter, mineral content, redox status, and temperature (Fang and Moncrieff 2001; Reichstein et al. 2005). For example, Fang and Moncrieff (2001) showed an exponential increase in soil respiration rate with temperature under laboratory conditions with intact soil cores with varying moisture conditions. However, Reichstein et al. (2005) did not find

Table 4 Q_{10} values for aerobic and anaerobic decomposition of SOM from different vegetation types

	Respiration						Methanogenesis		
	Aerobic			Anaerobic			Anaerobic		
	10–20°C	20–30°C	10–30°C	10–20°C	20–30°C	10–30°C	10–20°C	20–30°C	10–30°C
Cladium	1.69	1.81	1.75	0.90	2.76	1.55	1.20	3.63	2.41
Eleocharis	1.74	1.48	1.60	1.50	2.98	2.11	2.41	3.86	3.13
Panicum	1.43	1.67	1.54	1.30	2.61	1.79	1.50	3.90	2.70
Salix	1.56	1.46	1.50	1.43	2.64	1.93	1.46	3.62	2.54
Typha	1.40	3.04	2.05	1.47	1.84	1.62	1.67	5.42	3.55

any direct evidence of 'temperature sensitivity on soil respiration' being influenced by soil moisture, soil horizon and incubation time. This conclusion was based on their study of intact soil cores incubated under controlled lab conditions designed to minimize the confounding effects of multiple factors such as radiation, soil water availability and vegetation production. They were unable to conclude if the rate constant for the temperature sensitivity for organic and mineral soil layer C should be different.

Hogg et al. (1992) reported no change in soil respiration under flooded conditions at elevated temperatures and concluded that the decomposition process was inhibited due to the lack of oxygen. In this study, the effect of elevated temperature on SOM decomposition was evident as increased rates of CO_2 and CH_4 production in both aerobic and anaerobic conditions (Tables 2 and 4). Rates of aerobic respiration in this study were approximately three times higher than anaerobic respiration and were close to that observed in other peat soils (Moore and Dalva 1997; Wright and Reddy 2001). Rates of CH_4 production were approximately 1.2 times lower than that of anaerobic CO_2 production rates, and were higher than those reported for northern peatlands (Phelps and Zeikus 1985; Bridgham and Richardson 1992) and similar to those reported for tropical and subtropical systems (King et al. 1981; Wright and Reddy 2001; Corstanje and Reddy 2004; Grand and Gaidos 2010).

Calculation of Q_{10} (10–30°C) revealed that anaerobic processes responded more to increased temperature than aerobic respiration with Q_{10} values ranging from 1.4 to 2.2 for aerobic CO_2, 1.3–2.5 for anaerobic CO_2 and 1.5–3.6 for methane (Table 4). Higher Q_{10} for anaerobic processes have been documented in other studies, with our values falling in the ranges reported for CO_2 (1–16; Moore and Dalva 1993; McKenzie et al. 1998) and CH_4 (1.8–28; Segers 1998). We further found that higher value of Q_{10} of anaerobic processes occurred mostly at the higher temperature range (20–30°C) indicating that most of the overall temperature sensitivity occurred at progressively higher temperatures (Table 4).

The ratio of CO_2:CH_4 production declined with increasing temperature and was largely the result of a disproportionate increase in CH_4 production at higher temperatures (Table 2, Fig. 2). The observed decrease in the CO_2:CH_4 ratio at higher temperatures was also dependent on soil type with *Typha* and *Eleocharis* soils showing the greatest increase in CH_4 production at 30°C (Table 2). The strong correlation between CO_2:CH_4 and LCI at the highest temperature (Fig. 3) appeared to indicate that the increase in methane at high temperature was associated with soil quality, where soils with low LCI (higher C quality) showed lower CO_2:CH_4 ratios (or higher CH_4 production). It also suggests that below 30°C other factors besides LCI become more influential in regulating CO_2:CH_4.

Production of CH_4 in soils is dependent on low redox conditions, carbon substrate (acetate, CO_2/H_2), presence of other electron acceptors, and the presence of active methanogenic communities. High Q_{10} values for this process have been explained as a result of temperature effects on microbial fermentation rates (Valentine et al. 1994). Higher microbial enzyme activities, as a result of increased temperature, influence microbial fermentation and associated byproducts. Methanogens utilize some of these fermentation products (acetate, hydrogen and other methyl compounds, and therefore, the methane production depends on the quality and the amount of C substrate bioavailable. Changes in methane production rate have been attributed to alteration of

the C and electron flow (Chin and Conrad 1995). In fresh water systems, acetate and hydrogen are the most important methanogenic substrates (Yavitt and Lang 1990; Lovley and Klug 1983), and higher temperatures are known to favor hydrogenotrophic methanogens (Chin et al. 1999). Thus, the observed higher rates of CH_4 production in the *Typha* and *Eleocharis* soils of our study may have been due to higher availability of C substrates or a shift in the methanogenic community at high temperature.

In our study, the correlation of LCI with both CO_2:CH_4 (Fig. 3) and Q_{10} values for CH_4 production (Fig. 4) is consistent with the findings of Updegraff et al. (1995) and Valentine et al. (1994) which showed that higher Q_{10} values of methanogenesis were related to the soil substrate quality. Yavitt and Lang (1990) also reported higher CH_4 emissions from soils with higher labile C fractions and lower CH_4 production in SOM with more recalcitrant C fractions. Similarly, at the higher temperatures in this study, the positive correlation between CH_4 production and the soil cellulosic content and the corresponding negative correlation with lignin content indicated that the response of methanogenesis at high temperature was dependent upon the abundance of labile C.

Temperature sensitivity in decomposition of labile and recalcitrant C has been a widely discussed in the literature with no clear conclusions. Some studies have reported temperature sensitivity to be higher in recalcitrant material (Leifeld and Fuhrer 2005), labile material (Liski et al. 2000; Rey and Jarvis 2006), and some have found no difference in sensitivity between labile and recalcitrant materials (Conen et al. 2006). In terrestrial studies, Fierer et al. (2005) reported a steady increase in Q_{10} values during the decomposition of litter for 53 days, and concluded higher temperature sensitivity was exhibited by the more recalcitrant material.

In our study, varying temperature sensitivity (as Q_{10}) was noted in soils of various peat types, but the relationship depended on the metric used to gauge SOM quality. For example, using LCI as the index of C availability (Melillo et al. 1989), we observed a weak negative correlation between this parameter and the Q_{10} of aerobic CO_2 production, no correlation with the Q_{10} of anaerobic CO_2 production, and a significant strong negative correlation with the Q_{10} of CH_4 production rates (Fig. 4). The negative correlation between LCI and Q_{10} indicates that soils high in cellulose (low in lignin) are more responsive to changes in temperature. Such findings would agree with other studies finding that lignin is a highly recalcitrant compound under anaerobic conditions (e.g. Freeman et al. 2001).

In contrast to the more traditional LCI approach, when plotting our data similar to Fierer et al. (2005) and Lloyd and Taylor (1994), we also observed an association between substrate quality (as indicated by base respiration, B) and Q_{10} (Fig. 5). In these and other studies, Fierer et al. (2005) and Lloyd and Taylor (1994) used the y-intercept of the plot of respiration versus temperature as a term to describe SOM quality at $T = 0$. Fierer et al. (2005) demonstrated this concept by following decreases in B during short-term litter decomposition, and simultaneous increases in Q_{10} of respiration. Using this approach, we also observed an inverse relationship between Q_{10} and B, suggesting that higher quality SOM was less temperature sensitive than the lower quality (Fig. 5). This trend was observed for both respiration (aerobic and anaerobic) and methanogenesis implying that the relatively recalcitrant C is more responsive to temperature in all three conditions and pathways (aerobic CO_2, anaerobic CO_2 and CH_4).

There was no correlation between B and the cellulosic and lignin soil fractions indicating that the C quality represented by the B parameter was not consistent with that represented by LCI. Thus, it is difficult to interpret the difference between the two opposing relationships of Q_{10}'s for respiration and methanogenesis with B and LCI. In the case of aerobic respiration, there is evidence that more recalcitrant SOC is more sensitive to temperature (Bosatta and Agren (1999), ''carbon quality-temperature'' hypothesis) and B, is frequently used to describe this relationship (Fierer et al. 2006). Mean monthly temperature is stated as a factor related to increased SOM decomposition (resulting in lower organic matter quality), but all SOM used in our study came from the same warm, subtropical wetland. The warm conditions and increased decomposition may indeed explain the low range of Q_{10} under aerobic conditions. To our knowledge, this is the first attempt at relating B to anaerobic decomposition processes, but the similar result to aerobic respiration is noteworthy. The increased range of Q_{10} in anaerobic processes may be the result of increased stimulation of fermentation at high temperature (Larionova et al. 2008). Based on

our results, the soils with high Q_{10} also have lower B, however, they are also the soils high in cellulosic (and low lignin) C content (Fig. 5).

Cellulose is generally a good predictor of respiration in wetland soils (DeBusk and Reddy 1998) and Fierer et al. (2005) found a distinct trend between age of decomposition (which implies increasing lignin content), decreasing B, and increasing Q_{10}. In our study, the better statistical fit of the B term suggests there is a good utility in this approach in predicting temperature responses of various soils. However, because LCI is a measured parameter (while B is derived), it has a more interpretable meaning, especially in peat soils. One explanation for this could be that the SOM of our study is much older than that of the fresh litter decomposed for 53 days in the study of Fierer et al. (2005). High demand for C under aerobic conditions may drive the system to use more complex polymers, while in our study this observation was not noted in 4 weeks of incubation.

Another difference is that the utilization of C may vary in terrestrial versus wetland soils. In terrestrial soils, aerobic conditions mean that most of the labile C is decomposed and the total C produced reflects the abundance of recalcitrant SOM. However, in wetland soils, during anaerobic decomposition, the relatively labile soils (lower LCI) show higher C loss than the more recalcitrant soils because enzyme activity is limited by the anaerobic conditions. This may suggest that the relatively labile fraction of the soil may be a major source of methanogenesis substrates which are mostly byproducts of fermentation pathways.

Ecological significance

Greenhouse gas emission is a function of production and flux processes. Vegetation type is already known to affect flux of greenhouse gases via transport through aerenchyma tissue (McNamara et al. 2008; Strom et al. 2005; Chanton et al. 1993; Schipper and Reddy 1994). Findings of this study further highlight the importance of vegetation type as a regulator of SOM quality and production of greenhouse gases through decomposition.

This study demonstrated that vegetation type (and associated differences in SOM quality) plays an important role in the temperature sensitivity of wetland decomposition processes similar to the conclusions reported by Strom et al. (2005). Peat from areas dominated by *Typha* and *Eleocharis* produced more CH_4 as compared to those dominated by *Cladium*, *Salix* and *Panicum*, implying that plant communities can directly influence methane production rates. This increased decomposition and methane production appeared to follow SOM quality where soils with more decomposable organic matter had higher gaseous C production.

Vegetation type and SOM quality were also factors affecting the response of soil respiration and methanogenesis to increased temperature. In particular, anaerobic decomposition of SOM leading to CH_4 production showed a higher response to increased temperature than aerobic processes. This finding has implications for understanding SOM decomposition in wetlands and modeling the potential for greenhouse gas production. Overall, elevation in temperatures appeared to shift SOM decomposition towards methanogenesis implying that increased temperatures may increase the methane production in wetland systems. This finding highlights the importance of vegetation type decomposition in warmer subtropical and tropical wetland regions, and it also has implications for understanding the response of temperate and northern systems to increasing temperatures due to climate change or seasonality.

Results from this study warrant further field studies to support these observations that with increasing temperature more C can be channeled to formation of CH_4 and that this response may be plant species specific. These findings are of significance in freshwater wetlands such as the Everglades, where large portions of the area are dominated with vegetation communities like *Typha* or in systems where vegetation shifts are occurring.

Acknowledgments This work was supported by funding from the St Johns River water management district, Palatka, Florida. We sincerely appreciate the critical reviews provided by the anonymous reviewers, which greatly improved the overall quality of our paper.

References

Andersen JM (1976) An ignition method for determination of total phosphorus in lake sediments. Water Res 10:329–331

Arnold J, Corre MD, Veldkamp E (2008) Cold storage and laboratory incubation of intact soil cores do not reflect in

situ nitrogen cycling rates of tropical forest soils. Soil Biol Biochem 40:2480–2483

Bardgett RD, Freeman C, Ostle NJ (2008) Microbial contributions to climate change through carbon cycle feedbacks. ISME J 2:805–814

Bartlett KB, Harriss RC (1993) Review and assessment of methane emissions from wetlands. Chemosphere 26: 261–320

Bergman I, Klarqvist M, Nilsson M (2000) Seasonal variation in rates of methane production from peat of various botanical origins: effects of temperature and substrate quality. FEMS Microbiol Ecol 33:181–189

Bosatta E, Agren GI (1999) Soil organic matter quality interpreted thermodynamically. Soil Biol Biochem 31: 1889–1891

Bridgham SD, Richardson CJ (1992) Mechanisms controlling soil respiration (CO_2 and CH_4) in southern peatlands. Soil Biol Biochem 24:1089–1099

Bridgham SD, Updegraff K, Pastor J (1998) Carbon, nitrogen, and phosphorus mineralization in northern wetlands. Ecology 79:1545–1561

Cadisch G, Giller KE (eds) (1997) Driven by nature. Plant litter quality and decomposition. CAB International, Wallingford, p 409

Cao MK, Gregson K, Marshall S (1998) Global methane emission from wetlands and its sensitivity to climate change. Atmos Environ 32:3293–3299

IPCC (Intergovernmental Panel on Climate Change) (2007) Climate change 2007: the physical science basis. In: Solomon S, Qin D, Manning M et al. (eds) Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, UK

Chanton JP, Whiting GJ, Happell JD, Gerard G (1993) Contrasting rates and diurnal patterns of methane emission from emergent aquatic macrophytes. Aquat Bot 46:111–128

Chin KJ, Conrad R (1995) Intermediary metabolism in methanogenic paddy soil and the influence of temperature. FEMS Microbiol Ecol 18:85–102

Chin KJ, Lukow T, Conrad R (1999) Effect of temperature on structure and function of the methanogenic archaeal community in an anoxic rice field soil. Appl Environ Microbiol 65:2341–2349

Conen F, Leifeld J, Seth B, Alewell C (2006) Warming mineralizes young and old soil carbon equally. Biogeosciences 3:515–519

Corstanje R, Reddy KR (2004) Response of biogeochemical indicators to a drawdown and subsequent reflood. J Environ Qual 33:2357–2366

DeBusk WF, Reddy KR (1998) Turnover of detrital organic carbon in a nutrient-impacted Everglades marsh. Soil Sci Soc Am J 62:1460–1468

Debusk WF, Reddy KR (2005) Litter decomposition and nutrient dynamics in a phosphorus enriched Everglades marsh. Biogeochemistry 75:217–240

Fang C, Moncrieff JB (2001) The dependence of soil CO_2 efflux on temperature. Soil Biol Biochem 33:155–165

Fierer N, Craine JM, Mclauchlan K, Schimel JP (2005) Litter quality and the temperature sensitivity of decomposition. Ecology 86:320–326

Fierer N, Colman BP, Schimel JP, Jackson RB (2006) Predicting the temperature dependence of microbial respiration in soil: a continental-scale analysis. Global Biogeochem Cycles 20:GB3026

Fissore C, Giardina CP, Kolka RK, Trettin CC (2009) Soil organic carbon quality in forested mineral wetlands at different mean annual temperature. Soil Biol Biochem 41:458–466

Freeman C, Liska G, Ostle NJ, Jones SE, Lock MA (1995) The use of fluorogenic substrates for measuring enzyme-activity in peatlands. Plant Soil 175:147–152

Freeman C, Evans CD, Monteith DT, Reynolds B, Fenner N (2001) Export of organic carbon from peat soils. Nature 412:785

Freeman C, Fenner N, Ostle NJ et al (2004) Export of dissolved organic carbon from peatlands under elevated carbon dioxide levels. Nature 430:195–198

Fung I, John J, Lerner J, Matthews E, Prather M, Steele LP, Fraser PJ (1991) 3-Dimensional model synthesis of the global methane cycle. J Geophys Res 96:13033–13065

Grand M, Gaidos E (2010) Methane emission from a tropical Wetland in Ka'au Crater, O'ahu. Hawai'I Pacific Sci 64:57–72

Hein R, Crutzen PJ, Heimann M (1997) An inverse modeling approach to investigate the global atmospheric methane cycle. Global Biogeochem Cycles 11:43–76

Hines ME, Duddleston KN, Rooney-Varga JN, Fields D, Chanton JP (2008) Uncoupling of acetate degradation from methane formation in Alaskan wetlands: connections to vegetation distribution. Global Biogeochem Cycles 22:2017

Hogg EH, Lieffers VJ, Wein RW (1992) Potential carbon losses from peat profiles—effects of temperature, drought cycles, and fire. Ecol Appl 2:298–306

Ipsilantis I, Sylvia DM (2007) Abundance of fungi and bacteria in a nutrient impacted Florida wetland. Appl Soil Ecol 35:272–280

King GM, Berman T, Wiebe WJ (1981) Methane formation in the acidic peats of Okefenokee Swamp, Georgia. Am Midl Nat 105:386–389

Klinger LF, Zimmerman PR, Greenberg JP, Heidt LE, Guenther AB (1994) Carbon trace gas fluxes along a successional gradient in the Hudson-Bay lowland. J Geophys Res 99:1469–1494

Knoblauch C, Zimmermann U, Blumenberg M, Michaelis W, Pfeiffer EM (2008) Methane turnover and temperature response of methane-oxidizing bacteria in permafrost-affected soils of northeast Siberia. Soil Biol Biochem 40:3004–3013

Larionova AA, Zolotareva BN, Yevdokimov IV, Sapronov DV, Kuzyakov YV, Buegger F (2008) The rates of organic matter renewal in gray forest soils and chernozems. Eur Soil Sci 41:1378–1386

Leifeld J, Fuhrer J (2005) The temperature response of CO_2 production from bulk soils and soil fractions is related to soil organic matter quality. Biogeochemistry 75:433–453

Liski J, Ilvesniemi H, Makela A, Westman CJ (2000) Temperature dependence of old soil organic matter. Ambio 29:56–57

Lloyd J, Taylor JA (1994) On the temperature-dependence of soil respiration. Func Ecol 8:315–323

Lovley DR, Klug MJ (1983) Sulfate reducers can out-compete methanogens at fresh-water sulfate concentrations. Appl Environ Microbiol 45:187–192

Matthews E, Fung I (1987) Methane emission from natural wetlands: global distribution, area and environmental characteristics of sources. Global Biogeochem Cycles 1:61–86

McKenzie C, Schiff S, Aravena R, Kelly C, St. Louis V (1998) Effect of temperature on production of CH_4 and CO_2 from Peat in a Natural and Flooded Boreal Forest Wetland. Clim Change 40:247–266

McLatchey GP, Reddy KR (1998) Regulation of organic matter decomposition and nutrient release in a wetland soil. J Environ Qual 27:1268–1274

McNamara NP, Plant T, Oakley S, Ostle NJ (2008) Gully hotspot contribution to landscape methane and carbon dioxide fluxes in a northern peatland. Sci Total Environ 404:354–360

Melillo JM, Aber JD, Linkins AE, Ricca A, Fry B, Nadelhoffer KJ (1989) Carbon and nitrogen dynamics along the decay continuum—plant litter to soil organic-matter. Plant Soil 115:189–198

Mitra S, Wassmann R, Vlek PLG (2005) An appraisal of global wetland area and its carbon stock. Curr Sci 88:25–34

Moore TR, Dalva M (1993) The influence of temperature and water table position on carbon dioxide and methane emissions from laboratory columns of peatland soils. J Soil Sci 44:651–664

Moore TR, Dalva M (1997) Methane and carbon dioxide exchange potentials of peat soils in aerobic and anaerobic laboratory incubations. Soil Biol Biochem 29:1157–1164

Morrissey LA, Livingston GP (1992) Methane emissions from Alaska Arctic tundra: an assessment of local spatial variability. J Geophy Res 97:16661–16670

Page SE, Rieley JO, Banks CJ (2010) Global and regional importance of the tropical peatland carbon pool. Global Change Biol. doi:10.1111/j.1365-2486.2010.02279.x

Phelps TJ, Zeikus JG (1985) Effect of fall turnover on terminal carbon metabolism in Lake Mendota sediments. Appl Environ Microbiol 50:1285–1291

Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44:81–99

Reddy R, DeLaune RD (2008) Biogeochemistry of wetlands: science and applications. Taylor and Francis group LLC, Boca Raton

Reichstein M, Subke J-A, Angeli AC, Tenhunen JD (2005) Does the temperature sensitivity of decomposition of soil organic matter depend upon water content, soil horizon, or incubation time? Global Change Biol 11:1754–1767

Rey A, Jarvis P (2006) Modelling the effect of temperature on carbon mineralization rates across a network of European forest sites (FORCAST). Global Change Biol 12:1894–1908

Rooney-Varga JN, Giewat MW, Duddleston KN, Chanton JP, Hines ME (2007) Links between archaeal community structure, vegetation type and methanogenic pathway in Alaskan peatlands. FEMS Microbiol Ecol 60:240–251

Rowland AP, Roberts JD (1994) Lignin and cellulose fractionation in decomposition studies using acid-detergent fiber methods. Commun Soil Sci Plant Anal 25:269–277

Scanlon D, Moore T (2000) Carbon dioxide production from peatland soil profiles: the influence of temperature, oxic/anoxic conditions and substrate. Soil Sci 165:153–160

Schipper LA, Reddy KR (1994) Methane production and emissions from four reclaimed and Pristine Wetlands of Southeastern United States. Soil Sci Soc Am J 58: 1270–1275

Segers R (1998) Methane production and methane consumption: a review of processes underlying wetland methane fluxes. Biogeochemistry 41:23–51

Seo M (2002) Influence of nutrients, vegetation types and seasonality on microbial activities of carbon in a subtropical wetland, Masters Thesis. University of Florida, Gainesville, FL

Shaver GR, Giblin AE, Nadelhoffer KJ, Thieler KK, Downs MR, Laundre JA, Rastetter EB (2006) Carbon turnover in Alaskan tundra soils: effects of organic matter quality, temperature, moisture and fertilizer. J Ecol 94:740–753

Shindell DT, Faluvegi G, Koch DM, Schmidt GA, Unger N, Bauer SE (2009) Improved attribution of climate forcing to emissions. Science 326:716–718

Smemo KA, Yavitt JB (2006) A multi-year perspective on methane cycling in a shallow peat fen in central New York State, USA. Wetlands 26:20–29

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

Teh YA, Silver WL (2006) Effects of soil structure destruction on methane production and carbon partitioning between methanogenic pathways in tropical rain forest soils. J Geophyl Res-Biogeo, 111, G01003, 1–8. doi:10.1029/2005JG000020

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

USEPA (1993) Methods for chemical analysis of water and wastes. Environmental Monitoring Support Lab, Cincinnati, OH

Valentine DW, Holland EA, Schimel DS (1994) Ecosystem and physiological controls over methane production in northern wetlands. J Geophys Res 99:1563–1571

Goering HK, Van Soest, PJ (1970). Forage fiber analysis (apparatus, reagents, procedures and some applications). In: Agriculture Handbook No. 379. Agriculture Research Service, United States Department of Agriculture, Washington, USA

Whiting GJ, Chanton JP (1993) Primary production control of methane emission from wetlands. Nature 364:794–795

Wickland KP, Neff JC (2008) Decomposition of soil organic matter from boreal black spruce forest: environmental and chemical controls. Biogeochemistry 87:29–47

Winkler JP, Cherry RS, Schlesinger WH (1996) The Q_{10} relationship of microbial respiration in a temperate forest soil. Soil Biol Biochem 28:1067–1072

Wright AL, Reddy KR (2001) Heterotrophic microbial activity in northern Everglades wetland soils. Soil Sci Soc Am J 65:1856–1864

Yavitt JB, Lang GE (1990) Methane production in contrasting wetland sites: response to organic-chemical components of peat and to sulfate reduction. Geomicrobiol J 8:27–46

Yavitt JB, Williams CJ, Wieder RK (1997) Production of methane and carbon dioxide in peatland ecosystems across North America: effects of temperature, aeration, and organic chemistry of peat. Geomicrobiol J 14:299–316

Zak DR, Holmes WE, MacDonald NW, Pregitzer KS (1999) Soil temperature, matric potential, and the kinetics of microbial respiration and nitrogen mineralization. Soil Sci Soc Am J 63:575–584