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Carbon quality and nutrient status drive the temperature sensitivity of organic matter decomposition in subtropical peat soils

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Abstract Estimates of gaseous carbon (C) fluxes in wetlands are heavily based on temperature. However, isolating specific effects of temperature on anaerobic C processing from other controls (C quality and nutrients) has proven difficult. Here, we test the hypothesis that temperature sensitivity of soil organic matter (SOM) decomposition is more influenced by C quality than nutrient availability in subtropical freshwater, sawgrass (*Cladium jamaicense)*-based peats. Carbon age (characterized by depth: 0–10 and 10–20 cm) was used as a surrogate of C quality while two sites were selected with contrasting levels of nutrient (P) availability. In anaerobic laboratory incubations temperature was increased in 5 °C steps to assess the proportion of C available at a given temperature (i.e. thermo-labile C) as productions of gaseous (CO_2 and CH_4) and dissolved organic C (DOC) fractions. Thermo-labile C increased 3.1–3.6 times from 15 °C to 30 °C in all soils. Disproportionate increase in the production of gaseous forms versus DOC as well as CH_4:CO_2 was observed with warming. Observed Q_{10} values followed the trend of CH_4 ($\sim$14) $\gg$ CO_2 ($\sim$2.5) > DOC ($\sim$1.7) and temperature sensitivity was more dependent on C quality than nutrient availability over the entire temperature range. Spectral analysis indicated more bio-available DOC production at higher temperature. Regression analysis also indicated that C quality primarily influenced SOM decomposition at lower temperature, while at higher temperature nutrient limitation dominantly controlled SOM decomposition. These findings confirm the role of C quality in temperature sensitivity of warm peat soils, but also indicate an increased importance of nutrient limitation at higher temperature.

Keywords Organic matter decomposition · Peat · Greenhouse gas · Respiration · Methane · Dissolved organic carbon · Temperature sensitivity · Carbon quality · Nutrient availability

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Introduction

Wetlands are a globally important soil carbon (C) reservoir, accounting for about one-third of the total pool of soil C in the world (Bridgham et al. 1995; Mitsch and Gosselink 2007). In addition to being C sinks, wetlands are also the single largest source of methane (CH_4) (Matthews and Fung 1987; Bergamaschi et al. 2007; Bloom et al. 2010), but the size of this source remains highly uncertain. Biogeochemical

processes of anaerobic systems are known to be susceptible to temperature fluctuations (Gorham 1991; Melton et al. 2013), therefore, the C cycle in wetlands is also believed to be climate sensitive and is a critical component of the global climate system. Despite this understanding, the interaction of temperature and anaerobic C cycling remain poorly represented in ecosystem and climate models (Sulman et al. 2009).

There is a growing consensus that temperature accelerates the rates of soil organic matter (SOM) decomposition (Kirschbaum 1995; Davidson and Janssens, 2006; Conant et al. 2011), thus, a positive feedback of soil ecosystem to increasing temperature may accelerate the loss of C stocks of peats under future climate conditions. Wetlands are vulnerable to losing stored C to the atmosphere as carbon dioxide (CO_2) and CH_4 (Yavitt et al. 2005; Mitsch et al. 2010), and dissolved organic C (DOC) to receiving waters (Freeman et al. 2001; Moore and Dalva 2001). Despite this understanding, there is still high uncertainty in current C fluxes within wetland components (Bridgham et al. 2006) and in its variation across different scales (Li et al. 2007). In particular, there is high uncertainty in C emissions from tropical wetlands, where spatial coverage fluctuates seasonally, fluxes vary significantly across wetland types, and systems remain poorly studied, especially related to microbial and enzymatic processes that drive biogeochemical cycles, compared to those of temperate counterparts (Strack 2008).

Tropical wetlands emit nearly 60% of the total CH_4 from all natural wetlands combined (Megonigal et al. 2005); therefore, studies of SOM decomposition in warmer tropical or subtropical wetlands are particularly important. In warmer systems, it is generally assumed that temperature is not a dominant influence on anaerobic C processing. However, recent discoveries suggested that temperature not only affects the total C released from subtropical peatlands, but also the form of C released with higher CH_4 production at higher temperatures (Inglett et al. 2012).

The mechanisms underlying the temperature sensitivity of SOM decomposition are still a matter of debate. It is known that C quality is an important factor regulating CO_2 and CH_4 production where CH_4 production has been found to be more sensitive to recalcitrance of C compounds than is CO_2 (Bridgham et al. 1996). Higher CH_4 emission has been reported from soils with higher labile C fraction (Yavitt and Lang 1990; Waldrop et al. 2010), and recalcitrant C fraction (Paré and Bedard-Haughn 2013). Inglett et al. (2012) demonstrated that vegetation type and associated differences in SOM quality play an important role in the temperature sensitivity of SOM decomposition in subtropical peats, while other studies using C age (or depth) as a surrogate for C quality (Lomander et al. 1998; Fang et al. 2005; Jinbo et al. 2006; Karhu et al. 2010) have reported that deep soils (i.e. older SOM) were more temperature sensitive due to their relatively high recalcitrance. Increased SOM decomposition at higher temperatures has been reported with higher sensitivity of labile C fraction (Liski et al. 2000; Rey and Jarvis 2006), recalcitrant C fraction (Leifeld and Fuhrer 2005; Hartley et al. 2008), or with no specific soil C fraction (Giardina and Ryan 2000; Conen et al. 2006). Furthermore, Inglett et al. (2012) observed conflicting relationships between temperature sensitivity of peat soil decomposition and two measures of C quality, namely the ligno-cellulose index (LCI) and β (derived labile C).

Complicating the effect of C quality on temperature sensitivity of decomposition is the effect of nutrients on decomposition (Billings and Ballantyne 2013). It is widely accepted that nutrient availability is one of the dominant controls on decomposition in terrestrial (Wardle 1998; Hobbie and Vitousek 2000; Torn et al. 2005) and wetland (DeBusk and Reddy 1998, 2005; White and Reddy 2000; Newman et al. 2001; Neff and Hooper 2002; Penton and Newman 2007) ecosystems. Despite this, the effect of nutrients (e.g., N or P supply) on the temperature sensitivity of SOM decomposition is largely unknown, and the simultaneous assessment of temperature effects on CO_2, CH_4, and DOC production rates in soils of differing C quality and nutrient availability has not been reported yet. Uncertainty in this area results from the difficulty of distinguishing the intrinsic temperature sensitivity of a given process from its apparent sensitivity realized under natural conditions.

We conducted this study to assess temperature sensitivity of organic matter decomposition in relation to C age (a surrogate for C quality) and nutrient loading in subtropical wetlands using sawgrass (*Cladium jamaicense*)-based freshwater peats of the Florida Everglades. We hypothesized that C quality (as characterized by age of SOM) would have a greater effect on temperature sensitivity of SOM decomposition than nutrient level and that the quality of mineralized C would change as a function of

temperature. The specific objectives of this experiment were to: (i) determine temperature sensitivity of C mineralization pathways and the quantity of mineralized C (thermo-labile C) in peats of contrasting nutrient (P)-level and C quality (surface vs. deep soil or young vs. old SOM), (ii) compare the influence of C quality and nutrient (P)-level on temperature sensitivity of SOM decomposition at low and high temperature ranges, and (iii) determine the changes in C quality/availability as a function of temperature.

Materials and methods

Site description and sample collection

Soil samples were collected from two locations in Water Conservation Area 2A (WCA-2A) in the northern Everglades (Fig. S1). Historically this peatland received elevated nutrient inflows from the Everglades Agricultural Area (EAA) to the north. A distinct P enrichment gradient in soil was notable between the high-nutrient inflow site and the low-nutrient interior marsh of the WCA-2A (Craft and Richardson 1993; DeBusk et al. 2001). Having a single vegetation type (*Cladium jamaicense*) helped us to eliminate potentially confounding effects associated with different types of peat as evidenced by uniform isotopic signature (Inglett and Reddy 2006) and consistent C:N ratio (Table 1) as well as similar hydrology (all *Cladium* ridge) among all soil samples. Six intact soil cores (0–20 cm) were collected on 13 March, 2012 from two sites along P-gradient using PVC tubes (10 cm id). Soil cores were sectioned in the field in 10 cm increments, with the top section treated as surface (0–10 cm) soil while the bottom section as subsurface (10–20 cm) soil here. Thus, we have used C age characterized by young (surface soil) and old (subsurface soil) SOM as a surrogate for C quality and sites with nutrient loadings as an indicator of contrasting nutrient levels (or status).

Upon collection, the soil samples were transported to the Wetland Biogeochemistry Laboratory, University of Florida and stored at 20 °C in dark for up to 24 h before they were prepared for analyses. Our storage temperature was close to the in-situ soil temperature (15–17 °C) in the field so that the temperature or length of storage did not shift microbial structure and existing enzymes which can result in the alteration of the available substrate pool (Turner and Romero 2009). Large detrital pieces and fine roots were removed from the soil samples manually and the samples were gently homogenized avoiding disturbance to microbial

Table 1 Biogeochemical characterization of soil organic matter (SOM) in a subtropical peat based ecosystem ($n = 3$, mean ± SE)

Parameters	Surface soil		Subsurface soil	
	High P site	Low P site	High P site	Low P site
pH	7.8 (0.4)^{a}	7.6 (0.4)^{a}	7.7 (0.5)^{a}	7.4 (0.3)^{a}
Total C (g kg^{-1})	424 (2)^{ab}	436 (6)^{a}	404 (10)^{a}	438 (5)^{a}
Total N (g kg^{-1})	29 (2)^{a}	33 (3)^{a}	35 (5)^{a}	41 (3)^{a}
Total P (mg kg^{-1})	807 (52)^{a}	391 (33)^{c}	533 (46)^{b}	254 (28)^{d}
C:N	14.6 (0.8)^{a}	13.4 (1.2)^{a}	11.9 (1.5)^{a}	10.8 (0.1)^{a}
N:P	36.4 (2.6)^{a}	84.6 (7.6)^{ab}	66.4 (9.6)^{b}	160.1 (7.8)^{c}
LOI (%)	93.2 (1.2)^{a}	92.2 (1.5)^{a}	91.9 (2.2)^{a}	95.4 (1.1)^{a}
$\delta^{13}C$	−26.8 (0.4)^{a}	−26.8 (0.1)^{ab}	−27.78 (0.01)^{b}	−27.5 (0.05)^{b}
Microbial biomass C (g kg^{-1})	9.5 (0.1)^{a}	9.1 (0.4)^{ab}	8.7 (0.2)^{ab}	7.8 (0.3)^{b}
Microbial biomass N (mg kg^{-1})	1183 (41)^{a}	739 (18)^{c}	964 (27)^{b}	513 (38)^{d}
Microbial biomass P (mg kg^{-1})	377 (8)^{a}	168 (8)^{c}	308 (11)^{b}	82 (14)^{d}
Salt-extractable C (mg kg^{-1})	986 (14)^{a}	872 (55)^{a}	708 (42)^{b}	627 (104)^{b}
Cold water-extractable C (mg kg^{-1})	420 (23)^{a}	355 (25)^{ab}	312 (25)^{bc}	265 (27)^{c}
Hot water-extractable C (mg kg^{-1})	3815 (377)^{a}	2621 (316)^{ab}	3689 (86)^{bc}	2178 (157)^{c}

The numbers represent averages of three samples with standard error (se) of mean in the parenthesis. Levels not connected by same letter are significantly different (α=0.05)

functions and alteration of their microsite distribution (Teh and Silver 2006). Care was taken during sample collection, storage, and processing to ensure minimum exposure of the soil samples to oxygenated air. Field moist (saturated) soils were used in anaerobic microcosm experiments as well as for determination of soil pH, microbial biomass carbon (MBC), nitrogen (MBN), and phosphorus (MBP) and labile organic C (LOC) content. Subsamples of all soils were dried at 70 °C for 72 h and ground using a mortar and pestle for analysis of total nutrients.

Biogeochemical measurements

Soil pH was determined in DDI water using a 2:1 soil:water ratio after the equilibration of soil suspension at 25 °C for 1 h on a mechanical shaker. SOM was estimated by loss on ignition (LOI) by heating the soils at 550 °C for 5 h (Nelson and Sommers 1996). Total C and N were determined using method 3010 (USEPA 1993) on a Carlo-Erba NA-1500 CNS analyzer (Haak-Buchler Instruments, Saddlebrook, NJ). Stable C isotopic ratios ($\delta^{13}C$) were determined using a Finnigan MAT Delta Plus^{XL} isotopic ratio mass spectrometer (Finnigan Corp., San Jose, CA) (Inglett and Reddy 2006). Total P was measured by ashing method of Andersen (1976) involving combustion at 550 °C followed by hydrochloric acid extraction of the ash and analysis of P by ascorbic acid colorimetric method (Method 365.4, USEPA 1993).

Microbial biomass C and N (MBC and MBN) were determined by chloroform fumigation followed by 0.5 M K_2SO_4 extraction. Fumigated and non-fumigated extracts were filtered using Whatman 41 followed by determination of total dissolved organic C and N using a Shimadzu TOC analyzer and TKN digestion and colorimetric analysis, respectively (Sparling et al. 1990). Microbial biomass P (MBP) was determined by chloroform fumigation followed by 0.5 M $NaHCO_3$ extraction, persulfate digestion, and colorimetric analysis (Brookes et al. 1982). Microbial biomass C, N, and P was then calculated as the difference in concentration between the fumigated and the non-fumigated control. No extraction efficiency factor was used for MBP while, an extraction efficiency factor of 0.37 and 0.42 was used for MBC and MBN, respectively.

Labile OC (LOC) was characterized by three different extraction methods, namely cold-water extractable C (CWEC), hot-water extractable C (HWEC), and salt-extractable (0.5 M K_2SO_4) C (SEC) (Fang et al. 2005; Jinbo et al. 2006; Liu et al. 2006; Dodla et al. 2012). A sequential extraction process was used for the determination of CWEC and HWEC (Ghani et al. 2003). The CWEC and HWEC were determined by extraction with DDI water using a 1:10 soil:water ratio at 20 °C for 30 min and at 80 °C for 16 h, respectively, on an end-over-end shaker at 30 rpm followed by centrifugation for 20 min at 3500 rpm, filtered (0.2 µm filter) and analyzed in the same manner as for MBC. The non-fumigated K_2SO_4-extract C concentrations were reported as SEC. The CWEC fraction generally represents the hydrophilic fraction of C including carbohydrates, amino sugars, and low molecular weight organic acids (Fröberg et al. 2003). Likewise, SEC fractions are known to be positively associated with soluble carboxyl C compounds like organic acids and negatively associated with aromatic alkyl C compounds (Dodla et al. 2012). Carbonyl C (i.e. ketonic and aldehyde compounds), in addition to polysaccharides, also known to contribute to the HWEC fraction resulting from the ability of hot water to hydrolyze and cleave esters of various organic materials (Siskin and Katritzky 1991; Stange et al. 2001).

Anaerobic microcosms

Four replicates of twelve field samples were anaerobically incubated in 50 mL serum tubes by flooding 5 g dry weight equivalent of homogenized soils with 10 mL of N_2 purged distilled de-ionized (DDI) water (1:2 soil: water ratio). The serum tubes were sealed with butyl rubber stoppers, crimped with aluminum seals (Wheaton, Millville, NJ), and purged with ultrapure N_2 gas through a stopcock-septa assembly at the top for approximately 10 min. Four soil-free controls were included to account for background concentrations of different C fractions, which were negligible, compared to that produced from the soil.

The experiment was conducted by sequentially increasing incubation temperature by 5 °C at each step over a range of 15–30 °C to assess the proportion of C considered available at a given temperature (i.e. thermolabile C). In other words, we considered 15 °C as our control temperature and employed sequential warming in equal intervals such that our warmed temperatures are 5, 10, and 15 °C higher than the control condition. Duration of the whole experiment was around four months. It is important to note that the length of

incubations tended to decrease with each sequential warming treatment (i.e. length of incubations were 42, 30, 27, and 21 days for 15, 20, 25, and 30 °C temperatures, respectively) resulting from quicker adjustment (i.e. equilibration) of warming response of SOM decomposition with increasing temperature.

Production estimates of decomposition products were determined from these serum tubes by periodic sampling of headspace CO_2 and CH_4 (every third day), and DOC (every fifth-seventh day) in the water column. Linear rates of CO_2, CH_4, and DOC productions were obtained after cessation of the lag phase (~1–2 days for CO_2, and ~3–5 days for CH_4) using regression analysis applied to the linear portion of the cumulative concentrations of CO_2 and CH_4 over time. Gaseous C production rates from each temperature incubations were calculated from 12–15 points (~82–85% of observations at each step, $0.87 \geq R^2 \leq 0.96$, $p < 0.0001$), while DOC production rates were calculated from 3–4 points (~75–80% of observations at each step, $0.82 \geq R^2 \leq 0.91$, $p = 0.002$). We assumed all mineralized C passes through the dissolved phase, and thus use the term total dissolved organic C (TDOC) to represent the total OC decomposed (the sum of CO_2, CH_4, and DOC) measured at any given temperature. The amount of CO_2 and CH_4 in the dissolved phase was also calculated using Henry's law (Yaws and Yang 1992). During the experimental period, an equivalent amount of N_2 purged DDI water was replaced to compensate for the amount of DOC samples removed each time. We also monitored the pH of DOC on a weekly basis, which didn't change significantly over the course of the experiment resulting from flushing of the serum tubes with ultrapure N_2 after each step of temperature ramping.

CO_2 and CH_4 from the anaerobic microcosms were measured on 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 1% standard gas mixtures (Scotty Specialty Gases, Plumsteadville, PA). DOC samples were determined in a similar manner as for HWEC/CWEC.

Temperature sensitivity

Temperature sensitivity of any biological reaction can be estimated by determining Q_{10} function which is calculated as a value or factor in which a reaction rate is altered over a 10 °C temperature range. Q_{10} for C fractions (CO_2, CH_4, and DOC) were calculated using Eq. 1:

$$Q_{10} = e^{10k} \tag{1}$$

where k is derived from an exponential relationship (R^2 of the fit was always ≥0.90) between the SOM decomposition rate (expressed as production of DOC, CO_2, and CH_4) and temperature as follows:

$$Y = \beta * e^{kt} \tag{2}$$

where Y is the rate of production (at each temperature), β and k are derived values and t is the temperature (°C). The y-intercept of Eq. 2 (i.e. base respiration or β) can provide an index of the inherent lability of the C substrates undergoing decomposition such that a higher β value equates to the presence of more bioavailable C substrates while a lower β value indicates the prevalence of relatively recalcitrant C substrates (Fierer et al. 2005). Thus, the term β served as a derived C quality parameter in parallel to the water (CWEC and HWEC) and salt extracted C (SEC) fractions.

Spectral characteristics of DOC

DOC quality was determined using UV–Visible spectroscopic measurements, i.e. spectral slope analysis (Twardowski et al. 2004) and specific UV absorbance ($SUVA_{254}$). Spectral slope ratio (SR) was used as a proxy for the composition of DOC including fulvic acid to humic acid ratio, molecular weight (MW), and aromaticity (Spencer et al. 2010; Fichot and Benner 2012). Spectral slope (S) was calculated by fitting to an exponential function to the absorption spectrum over 275–295 and 350–400 nm range as follows:

$$a = 2.303A/la \tag{3}$$

$$a\lambda = a\lambda_{ref} e^{-S(\lambda - \lambda_{ref})} \tag{4}$$

where A = absorbance, a = absorption coefficient (m^{-1}), λ = wavelength (m), λ_{ref} = wavelength (m) and l = path length (m). SR was calculated as the ratio of 275–295 nm slope ($S_{275–295}$) to 350–400 nm slope ($S_{350–400}$) (Helms et al. 2008). These ranges of spectra were chosen based on the higher sensitivity of this region to changes in DOM

source and processing, and occurrence of lower errors due to higher absorption coefficients at shorter wavelengths (Spencer et al. 2007).

Additionally, $SUVA_{254}$ was measured by following USEPA Method 415.3 (Potter and Wimsatt 2005). $SUVA_{254}$ values (L mg C^{-1} m^{-1}) were determined by dividing the absorption coefficient at $\lambda = 254$ nm by the DOC concentration. $SUVA_{254}$ is also widely used as a proxy for DOC aromaticity (Weishaar et al. 2003).

Statistical analysis

The experiment was carried out as a split–split plot design, with nutrient level (i.e. site) as the whole plot factor, C age (i.e. depth) as the split plot factor, and temperature as the split–split plot factor (SAS 9.3, SAS Institute, Cary, NC, USA). We fitted a linear mixed model using PROC GLIMMIX, where treatment (nutrient level, C age, and temperature) effects were fixed and error terms for whole plot, split plot, and split–split plot were random. Repeated measurements were taken on the same soil samples over four temperature levels and the residual errors across the temperature levels were grouped by nutrient level (or site) with an auto-regressive (AR-1) covariance structure. Tukey's multiple comparison procedure, as well as the corresponding letter grouping method, were used to separate the treatment means. Regressions were conducted using PROC PHREG procedure. All statistical analyses were done at 5% significance level ($\alpha = 0.05$).

Because temperature is a variable in the calculation of Q_{10}, redundancy analyses (RDA) were performed using R, version 3.0.1 (R Development Core Team, 2013) to determine which of the explanatory variables (nutrient level/status and C age/C quality) has more influence on Q_{10} of decomposition products. In this analysis, the projection of a point onto a line for the response variables (Q_{10} of CO_2, CH_4, and DOC) at right angle approximates the value of the corresponding variable of the observations, while the angles between lines of response variables and lines of explanatory variables (from centroid positions) represent a two-dimensional approximation of correlations.

Results

The biogeochemical characteristics of the wetland soils used in this study varied among samples collected from different sites and depths (Table 1). The pH of the soils was slightly alkaline ranging from 7.4 ± 0.3 in subsurface soil from low P site to 7.8 ± 0.4 in surface soil from high P site. Total C and N, and soil organic matter (estimated by LOI) values did not differ appreciably among the soils used in this study. The C:N ratios and $\delta^{13}C$ values were also not significantly different among all soil samples, which indicated that initial SOM has the same source (i.e. *Cladium* peat) while the difference in P-concentration was identified from the range of N:P ratios. The surface soil of high P site exhibited significantly higher MBC (9.5 ± 0.1 g kg^{-1}) compared to that in the subsurface soil of low P site (7.8 ± 0.3 g kg^{-1}) while MBN and MBP were significantly different among the four soil types ($p < 0.05$).

Total P ($p < 0.05$, Table 1) and $NaHCO_3$ extractable P ($p < 0.05$, data not shown) were significantly higher in soils from high P sites than low P sites. In contrast, there appeared to be a general trend in that the LOC parameters (SEC, CWEC, and HWEC) in the surface soil layers of these wetland sites were significantly higher than subsurface layers ($p < 0.05$, Table 1). Interestingly, independent metrics of C quality parameters, i.e. measured (extraction-based LOC) and derived (β) C quality parameters for SOM as well as DOC quality parameters (SR and SUVA), used in this study were found to correlate with each other (Table S1), where SEC, HWEC, β, and initial DOC quality parameters (measured at 15 °C) related more closely to each other ($0.86 \geq R^2 \leq 0.97$) than with HWEC ($0.44 \geq R^2 \leq 0.54$). Additionally, significant (but negative) correlations were observed between SR and $SUVA_{254}$ ($R^2 = 0.73$, $p < 0.0001$) values measured over the entire temperature spectra.

Analysis of variance (ANOVA) indicated that main effects of nutrient level (or status), C age (i.e. depth), and temperature were significant on the decomposition products (CO_2, CH_4, and DOC) at 5% ($\alpha = 0.05$) significance level (Table 2). However, stronger effect of C age ($p < 0.0001$) and temperature ($p < 0.0001$) were evident on gaseous and dissolved C fractions when compared with that of nutrient level ($p < 0.05$). These findings suggested an interactive role of C age and temperature for CO_2 ($p < 0.0001$), CH_4 ($p < 0.0001$), and DOC ($p < 0.01$) production.

The release of C increased with the sequential increase of temperature in all soils (Table S2, Fig. 1). We used the term thermo-labile C here to quantify the

Table 2 Effect of nutrient level, C age, and temperature on CO_2, CH_4, and DOC production rate as determined from microcosm experiment

Parameters	CO_2	CH_4	DOC
Nutrient level	*	*	*
C age	***	***	***
Temperature	***	***	***
Nutrient level*C age	NS	*	*
Nutrient level*temperature	**	NS	NS
C age*temperature	***	***	**
Nutrient level*C age*temperature	NS	NS	NS

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.0001$, *NS* not significant

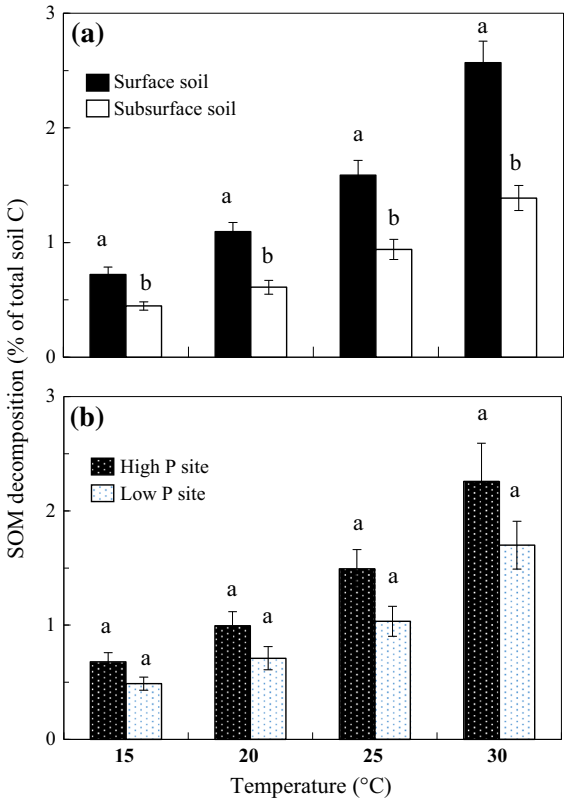

Fig. 1 Percent of total soil C lost (as DOC, CO_2 & CH_4) in **a** surface and subsurface soil versus **b** high P and low P site at different temperatures (thermo-labile C) ($n = 3$, mean ± SE)

fraction of C i.e. labile/available at a particular temperature. On average, as a percentage of total soil C, thermo-labile C increased from 0.72% to 2.57% and 0.45% to 1.39% in surface and subsurface soil, respectively over 15–30 °C temperature range (Fig. 1a). Likewise, thermo-labile C also increased from 0.68% to 2.26% and 0.49% to 1.70% in high P and low P soil, respectively (Fig. 1b). As a percentage of total soil C, production of thermo-labile C was significantly different between surface and subsurface soil ($p < 0.05$) at four temperature levels but no difference was observed between High P and Low P sites(Fig. 1a,b).

Methanogenesis was the most temperature sensitive process ($Q_{10} \sim 14$), followed by respiration ($Q_{10} \sim 2.5$), and least for DOC ($Q_{10} \sim 1.7$) (Table 3). Correspondence of higher Q_{10} values with lower β (derived labile parameter) confirmed that recalcitrant C was more temperature sensitive. Most of the variation in Q_{10} of decomposition products was explained by the C age (or depth) and associated C quality, as shown on the first RDA axis (Fig. 2); where the subsurface soil (i.e. old SOM) had the strongest effect overall as indicated by the small angles between lines of response variables (i.e. Q_{10} of CO_2, CH_4, and DOC) and line of the explanatory variable subsurface soil (if drawn from its centroid position).

CO_2–C and CH_4–C increased as a percentage of TDOC while the proportion of DOC decreased with temperature in all soils (Fig. 3a–f). Higher temperature also affected the form of C released, favoring methanogenesis disproportionately relative to CO_2-respiration (Fig. 4a). The differences between surface and subsurface soil were more evident at higher temperatures (e.g., 25 and 30 °C, $p < 0.05$). In contrast, there were no significant differences in the proportions of C forms in TDOC between High P and Low P soils.

Overall, surface soil from both sites exhibited significantly higher spectral slope ratio i.e. SR (275–295 nm slope to 350–400 nm slope) and significantly lower $SUVA_{254}$ compared to that in subsurface soil at all temperatures. While, SR showed an increasing trend with the corresponding increase in temperature in all soils (Fig. 4b), $SUVA_{254}$ values showed a declining trend with warming (Fig. 4c). In surface layer soils, slope ratios increased from 0.86, 0.77 at 15 °C to 1.06, 1.45 at 30 °C in high P and low P site, respectively. In subsurface soil layers, slope ratios increased from 0.50 and 0.46 at 15 °C to 0.68 and 0.62 at 30 °C in high P and low P sites, respectively. On the other hand, $SUVA_{254}$ decreased from 3.20, 3.53 at 15 °C to 2.17, 2.42 at 30 °C in surface soils from high P and low P site, respectively. In subsurface soil layers, $SUVA_{254}$ decreased from 3.93,

Table 3 Temperature sensitivity (Q_{10}) and β value of different C fractions (n = 3, mean ± SE)

C fractions	Surface soil				Subsurface soil			
	High P site		Low P site		High P site		Low P site	
	Q_{10}	β	Q_{10}	β	Q_{10}	β	Q_{10}	β
CO_2	2.3 (0.4)	20.1 (1.7)	2.3 (0.2)	16.7 (1.4)	2.4 (0.3)	10.8 (1.3)	3.1 (0.4)	2.6 (0.2)
CH_4	13 (1.7)	0.010 (0.002)	13.2 (1.8)	0.003 (0.0005)	14.9 (2.1)	0.007 (0.0004)	14.9 (1.7)	0.007 (0.0003)
DOC	1.6 (0.1)	40.8 (3.4)	1.7 (0.3)	32.5 (3.1)	1.8 (0.2)	25.1 (1.9)	1.9 (0.3)	12.6 (1.1)
TDOC	1.6 (0.1)	41.2 (3.7)	1.7 (0.3)	33.1 (3.3)	1.8 (0.3)	25.6 (2.2)	1.8 (0.3)	13.0 (1.6)

TDOC represents total dissolved organic C (i.e. sum of CO_2, CH_4, and DOC production)

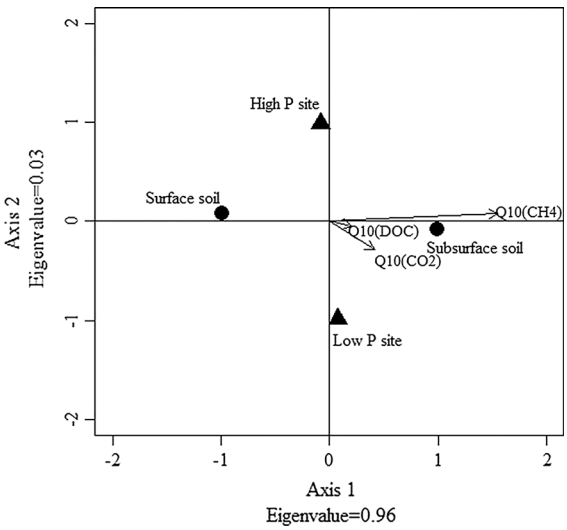

Fig. 2 Biplot of redundancy analysis (RDA) for Q_{10} of decomposition products with nutrient level and C age. *Triangles* and *circles* represent the centroid positions of the nutrient level factor and C age factor, respectively

4.26 at 15 °C to 3.01, 3.31 at 30 °C in soils from high P and low P site, respectively.

To explore the influence of C quality and nutrient (N and P) supply, stepwise multiple regression models were developed (forward process) for the rates of SOM decomposition products. At 15 °C, the importance of C quality parameters (SEC, CWEC, and HWEC) on the production of CO_2, CH_4, and DOC was evident. While, regression results at 30 °C consistently identified nutrients (i.e. C:P, $NaHCO_3$ extractable P, and K_2SO_4 extractable N) as dominant variables explaining SOM mineralization rates (Table 4). Multiple regression results for 20 °C were similar to the 15 °C models while those for 25 °C had similar response to that of the 30 °C models (data not shown).

Discussion

Many wetland studies have evaluated the effect of temperature (Gorham 1991; Moore 2001; Mitsch et al. 2013; Melton et al. 2013), C quality (Moore and Knowles 1990; Bridgham and Richardson 1992; Karhu et al. 2010; Inglett et al. 2012), and nutrients (Davis 1991; Craft and Richardson 1993; DeBusk and Reddy 2003) on SOM decomposition. In contrast, relatively few studies have evaluated the interactive effect of C quality and temperature (Hartley and Ineson 2008; Inglett et al. 2012), and to our knowledge, no studies have compared the relative interaction of temperature with C quality and nutrient availability on all decomposition products (i.e. CO_2, CH_4, and DOC) in wetlands. In this study, we used peat soils from a single vegetation type (*Cladium jamaicense*) to allow better separation of the effects of C quality (characterized by C age), nutrient availability, temperature, and their interactions on anaerobic C processing (Bridgham et al. 1996).

As observed in other studies, we consistently found that temperature and C quality (i.e. C age) were the dominant factors controlling decomposition rate, while the effect of nutrient (P) level was always secondary to C quality, as evidenced by the ANOVA model (Table 2). The importance of C quality was also reflected in the strong association of C age (or soil depth) with Q_{10} of decomposition products (Fig. 2), as well as the differences between surface (i.e. young SOM) and deep (i.e. old SOM) soils in the proportional production of CO_2–C (Fig. 3a), CH_4–C (Fig. 3c), and DOC (Fig. 3e) (as % of TDOC) which was particularly evident at higher temperature.

Our observation of the high temperature dependence of production of the various C forms i.e. CO_2, CH_4, and DOC is another commonly reported finding

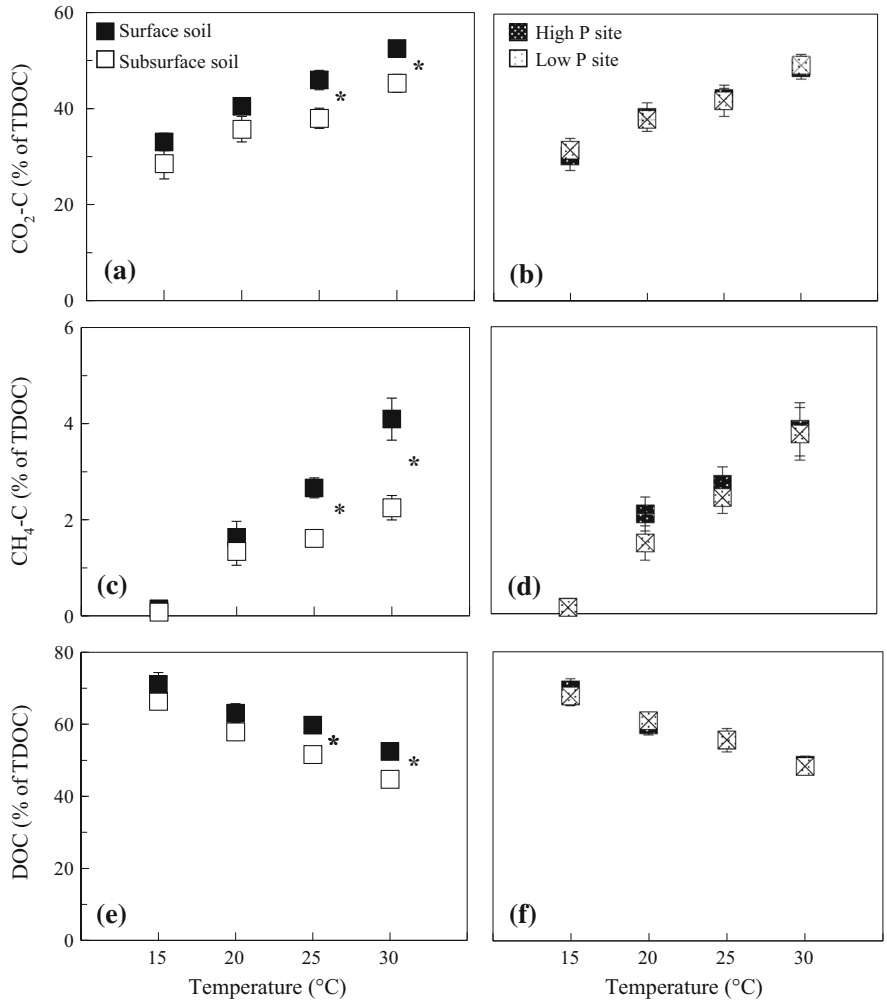

Fig. 3 Production of **a**, **b** CO_2, **c**, **d** CH_4, and **e**, **f** DOC as % of total C decomposed (TDOC) in surface and subsurface soil (left panel) versus high P and low P site (right panel) (n = 3, mean ± SE)

(Inglett et al. 2012; Taggart et al. 2012). Overall, production of thermo-labile C increased at higher temperature, where on average TDOC increased approximately 3 fold in all soils from 15 to 30 °C (Fig. 1). Similar amount of increase in the C pool sizes with warming have been reported previously by others (Macdonald et al. 1995; Zogg et al. 1997). Of the forms of these released C, the relative trend in temperature sensitivity (Q_{10}) followed the trend of $CH_4 \gg CO_2 > DOC$ (Table 3), which is also similar with that reported by others (Tsutsuki and Ponnamperuma 1987; Updegraff et al. 1995; Neff and Hooper 2002).

Patterns of C forms demonstrate more gaseous C production at higher temperature. For instance, production rates of gaseous C relative to DOC, i.e. (CO_2–C + CH_4–C):DOC ratios increased 1.8–2.3 times in all soils from 15 to 30 °C. Furthermore, the decreased proportion of CO_2–C:CH_4–C ratio implied increased C channeling through the methanogenic pathway at higher temperatures (Fig. 4a). Our measured Q_{10} of CO_2 production is in agreement with Waddington et al. (2001), however, our measured Q_{10} of CH_4 production observed in this study was comparatively higher than that reported by Van Hulzen et al. (1999) and Inglett et al. (2012) ($Q_{10} \sim$ 2–4), but comparable to Gujer and Zehnder (1983), Tsutsuki and Ponnamperuma (1987), Schütz et al. (1990), and Megonigal and Schlesinger (2002) ($Q_{10} \sim$ 7–16). Higher Q_{10} of CH_4 as compared to

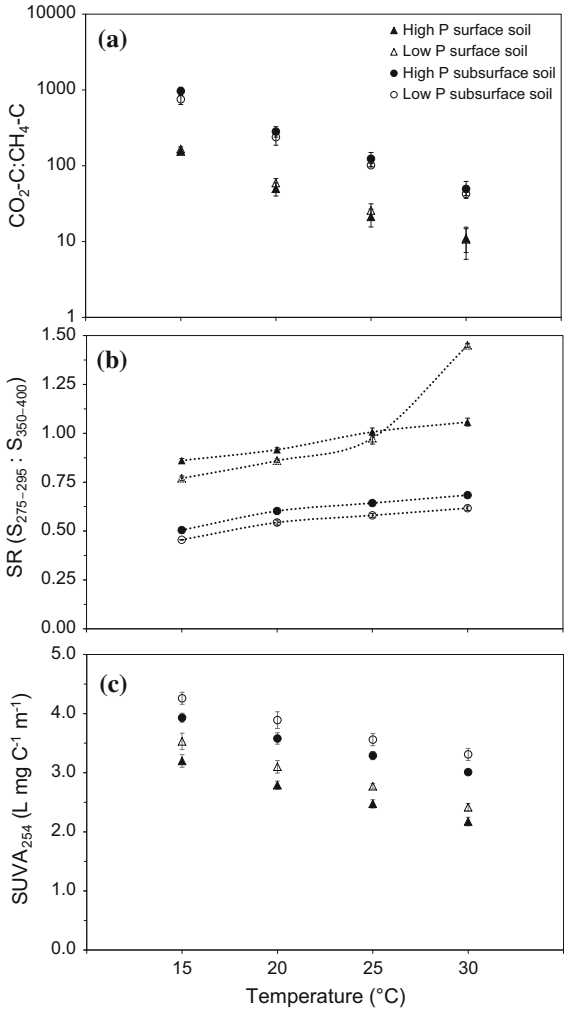

Fig. 4 Effect of temperature on **a** CO_2–C: CH_4–C ratio, **b** spectral slope ratios (SR) of DOC, and **c** Specific UV absorbance ($SUVA_{254}$) of DOC ($n = 3$, mean ± SE)

CO_2 in our system is not a function of electron acceptor competition of being reduced with warming as suggested by Segers (1998). Rather it is more likely the result of a cascading temperature effect on C flow where either fermenters are stimulated (Bridgham et al. 1995), or there is a simultaneous stimulation of fermenters and methanogens at higher temperature (Larionova et al. 2007).

Like some other studies, we also observed that old SOM (i.e. deep soil), here used as a surrogate of recalcitrant C, was more sensitive to elevated temperature (Table 3). It is generally believed that higher temperature allows more decomposition of refractory C through stimulation of enzyme reactions (Sinsabaugh and Linkins 1993; Bosatta and Ågren 1999; Fierer et al. 2005; Wagai et al. 2013; Liang et al. 2015). Additionally, inherent decomposability (β values) were strongly negatively correlated with Q_{10} of CO_2 ($P < 0.01$), CH_4 ($P = <0.01$), and DOC ($P < 0.05$), respectively (data not shown). Therefore, the warming-induced increase of C availability allowed greater flow through the methanogenic community, which was observed to be more pronounced with increasing organic matter recalcitrance.

Many biogeochemical reactions accelerate as temperature increases (Kadlec and Reddy 2001) and a number of mechanisms have been proposed to explain apparent increases in C availability with warming. Elevated temperature can stimulate C-decomposition via amplifying cellulose and chitin-degradation (Nie et al. 2013), chemical changes in conformation or C compound solubility (Davidson and Janssens 2006), or shifts in microbial community composition (Waldrop and Firestone 2004; Andrews et al. 2000). Also, isoenzymes of different temperature optima are maintained by both individual microorganisms (Hochachka and Somero 2002) and communities (Grzymski et al. 2008), and warming may increase production of enzymes with greater conformational stability and function (reviewed by Conant et al. 2011; Wallenstein et al. 2011).

In addition to biochemical processes, apparent temperature sensitivity of a reaction is also dependent on biophysical factors. For example, higher temperature can enhance dissolution and diffusion of C substrates to enzyme's active sites, thus increasing substrate availability to soil microbes (Xu and Saiers 2010; Davidson et al. 2012). Higher temperature could also favor desorption of SOM–humate complexes (Ten Hulscher and Cornelissen 1996; Davidson and Janssens 2006), which could accelerate SOM decomposition by reducing physical protection (Conant et al. 2011; Schmidt et al. 2011). Elevated temperatures may also lead to an increased solubilization of substrates like waxes and lipids from the membranes of the dead microorganisms (Davidson and Janssens 2006). For example, Dodla et al. (2012) and Wang and Wang (2007) demonstrated a primary effect of increased temperature on direct solubilization of C in terms of HWEC and CWEC. In our study, HWEC was 7–12 times greater than CWEC and there was a relatively weak correlation of HWEC with other

Table 4 Model parameters for stepwise multiple regression analysis of log transformed rates of CO_2, CH_4, and DOC production

Carbon fraction	Lower temperature incubation at 15 °C				Higher temperature incubation at 30 °C			
	Model R^2	Variables included	Estimate	SE	Model R^2	Variables included	Estimate	SE
CO_2	0.95	CWEC	14.02	5.13	0.92	C:P	−66.49	9.13
		SEC	18.38	3.71		$NaHCO_3$ Ex. P	23.02	5.13
		HWEC	9.36	2.28		K_2SO_4 Ex. N	1.18	0.06
		C:P	−1.32	1.88		HWEC	0.02	0.004
		$NaHCO_3$Ex. P	0.04	0.02		SEC	0.28	0.08
CH_4	0.98	CWEC	10.32	1.51	0.91	$NaHCO_3$ Ex. P	10.1	1.2
		SEC	8.02	2.06		C:P	−43.91	2.56
		$NaHCO_3$ Ex. P	0.001	0.00		K_2SO_4 Ex. N	1.6	0.1
		K_2SO_4 Ex. N	0.002	0.00		SEC	0.01	0.00
		C:P	−0.13	0.05		HWEC	0.03	0.01
DOC	0.96	CWEC	13.42	3.18	0.92	C:P	−98.65	16.05
		SEC	22.16	2.72		K_2SO_4 Ex. N	10.6	1.9

Units for extractale C (CWEC, SEC, HWEC), N (K2SO4 Ex. N), and P (NaHCO3Ex. P) were expressed as mg kg−1. Note that C:P ratio is an unitless quantity here

LOC fractions (SEC and CWEC) that mostly represent carboxyl-C containing compounds like polysaccharides (Table S2), suggesting that elevated temperature may also have increased C solubilization either by hydrolyzing ester linkages (Siskin and Katritzky 1991; Stange et al. 2001) or by desorption of occluded C compounds (Ghani et al. 2003; von Lüzow et al. 2007) in these soils.

As a result of both biogeochemical and biophysical mechanisms, total C mineralized increases as well as the residual DOC pool (Table S1) with warming. However, at higher temperature, proportionally more DOC pool was made available for gaseous C production, suggesting much of this dissolved pool made available (i.e. of better quality) for microbial utilization at higher temperature. In support of this, we observed increases in slope ratio (SR) of DOC from 19–47% over the range of 15–30 °C, however, the increase was 19–26% for most of the soil, with an exceptionally higher increase for the low P surface soil at 30 °C (Fig. 4b). Additionally, we observed decreases in $SUVA_{254}$ from 22–32% over the range of 15–30 °C (Fig. 4c). Bianchi et al. (2013) observed strong positive correlations of $SUVA_{254}$ with dissolved lignin and humification index in a riverine study. Additionally, Osburn and Stedmon (2011) further indicated that absorption coefficients measured at 300 nm strongly predicted dissolved lignin concentrations in a marine ecosystem. These observations suggests warming induced increases in SR and decreases in $SUVA_{254}$ in our study may represent either degradation of complex phenolic compounds (Zhao 2012) or release of other water soluble, extracellular substances excreted by microorganisms resulting from cell death and lysis (i.e. freshly produced or less condensed aromatics of microbial origin) in DOC pool (Birdwell and Engel 2010; Tfaily et al. 2015).

Our observation of increased C bioavailability as a function of temperature is in contrast to many studies in terrestrial systems, where depletion of labile C substrates was identified as the key driver for reduced soil respiration in short-term laboratory incubation studies (Fang et al. 2005; Hartley et al. 2008; Tucker et al. 2013). Within this context, findings of some theoretical models (Kirschbaum, 2004; Eliasson et al., 2005; Knorr et al., 2005) also suggested that rates of microbial respiration will acclimate on a longer time scale resulting from a change in the composition of the remaining SOM pool after the C pools with shorter turnover times are preferentially lost. In our study, as C availability increased (both quantity and apparent quality) under warming, it is likely that C limitation of respiration was less at higher temperatures. Thus, nutrient availability could limit decomposition at higher temperature due to the stoichiometric control of microbial nutrient demand (Allison and Vitousek 2005; Geisseler and Horwath 2009; Sinsabaugh et al. 2009; Hernández and Hobbie 2010; Billings and

Ballantyne 2013). In support of this, stepwise multiple regressions demonstrated that at lower temperatures (15 and 20 °C), SOM decomposition was better predicted by C quality, while at higher temperatures (25 and 30 °C), decomposition became more influenced by nutrient parameters (Table 4).

The positive coefficients of $NaHCO_3$ extractable P and the large negative coefficients of C:P in models for the high temperature range were indicative of a potentially P-limited decomposition process, an observation which is not surprising, given the high degree of P-limitation in the Everglades (Craft and Richardson 1993; DeBusk et al. 2001). With regards to anaerobic methanogenic C cycling, studies have also reported that P availability directly limited fermentation and CH_4 production in low P Everglades soils (reviewed by Medvedeff et al. 2014). Secondary to P, N was also identified in the high-temperature multiple regression models. Although little studied, N has also received support as a limiting nutrient in the Everglades, either in activities of enzymes (Penton and Newman 2007), N_2 fixation (Inglett et al. 2004, Liao and Inglett 2014), or in peat dynamics (Inglett et al. 2011; Wozniak et al. 2012) across the Everglades landscape. The temperature-driven decoupling of the C-limited and nutrient-limited decomposition in our peat-based system is qualitatively similar to the observation in an anoxic marine system. Weston and Joye (2005) also reported a sudden change in the microbial C processing above 20 °C resulting from a variable temperature response of anaerobic microbial metabolisms in the marine sediment.

We acknowledge that our study used only a relative measure of temperature sensitivity (Q_{10}), and although Q_{10} is a widely used parameter, it could be biased if used over a larger temperature range as the measurement is itself temperature dependent (Lloyd and Taylor 1994; Hamdi et al. 2013). Additionally, we did not include the indirect effect of temperature mediated by the temperature-induced increase in diffusion of soluble substrates and C allocation to aboveground and belowground plant tissues which can alter substrate concentrations at enzyme's active site and thus confound the temperature effect on the apparent response of the soil microbial process (Davidson et al. 2006). While these extrinsic temperature effects are extremely important on an ecosystem scale response, it is beyond the scope of this paper, and our results highlight the interacting effect of temperature with C age and nutrient status when evaluating the intrinsic sensitivity of SOM decomposition in warmer wetlands.

Studies evaluating the sensitivity of SOM decomposition with sequential methods generally increase temperature over a very short duration, varying from few hours (Fang et al. 2005; Liu et al. 2006; Yuste et al. 2007) to few days (Koch et al. 2007). While these studies quantify the instantaneous effect of temperature on rates of C loss, longer term laboratory (Bradford et al. 2010; Tucker et al. 2013) and field (Oechel et al. 2000; Luo et al. 2001; Melillo et al. 2002) warming studies often report an attenuation of the immediate warming response with time resulting from either labile C limitation (Hartley et al. 2008), microbial physiological acclimation (Allison et al. 2010), or both (Bradford et al. 2008). To that end, our experiment accounted for not only the instantaneous warming response but also the gaseous C production rate after acclimation. Undoubtedly, an alteration of the initial microbial community structure may have contribute to the observed long-term warming response in our study (also see Bradford et al. 2010), but this longer incubation may be justified by the fact that, ultimately, it is the total amount of SOC loss (not the immediate response) that matters for assessing climate change feedbacks.

Conclusions

Our findings add to a growing body of evidence that the effect of temperature on SOM decomposition is highly interactive with C quality and, as in this study, nutrients. Overall, greater influence of C quality than nutrient availability on temperature sensitivity of dissolved and gaseous C (CO_2, CH_4) production evokes the need to better account for temperature effects on microbial physiological parameters (e.g. C use efficiency) in response to C and nutrients in anaerobic system models. Likewise differential C versus nutrient limitation on SOM decomposition with temperature suggests our observation of nutrient limited decomposition at higher temperatures more broadly applies to tropical ecosystems, given the fact that warmer systems already tend toward a more nutrient (especially P) limited condition than arctic/boreal systems (Fisher et al. 2012; Sistla and Schimel 2012). This indicates that anthropogenic

loading of nutrients would further stimulate C losses from tropical and subtropical wetlands in the future warmer world.

Our observation of increasing C quality at higher temperature ranges disagrees with studies in terrestrial systems where short-term attenuation of respiration results from labile C-limited conditions. Rather, in anaerobic wetland soils transient responses (acclimation) of anaerobic C processing may be more associated with adaptation of microbial and enzymatic processes due to microbial nutrient limitation. Based on the results of our multiple regression models, we have identified a need for incorporation of microbial nutrient demand and enzymes to existing physiology-based, C-only models (Allison et al. 2010; German et al. 2012; Sihi et al. 2016). Integration of these microbial parameters in next-generation climate models has been suggested (Schimel 2001; Allison and Martiny 2008; Todd-Brown et al. 2012; Cotrufo et al. 2013; Wieder et al. 2013), and if accomplished, climate-C feedback would be better predicted. Therefore, we believe our findings would be useful, in conjunction with other modeling approaches, for improved understanding of global (terrestrial and wetland) C stocks.

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