



Testing the stability of carbon pools stored in tussock sedge meadows



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ABSTRACT

Tussocks formed by *Carex stricta* are a relatively large carbon (C) pool in sedge meadows, but the stability of organic matter in these ecosystems is not well understood. We initiated year-long incubation experiments (22.5 °C) to evaluate the CO₂ and CH₄ production potentials of sedge meadow substrates under field moist and inundated treatments from five sites in the Upper Midwest, USA (4 reference, 1 restored). C mineralization potentials decreased with depth (tussocks > underlying soil), and were positively correlated with macro-organic matter content and negatively with lignin. Across sites, C stored in tussocks and soil at the restoration was the least stable, suggesting that the restoration of C-storage function may take decades. Mineralization potentials were similar between field moist and inundated treatments, but inundation resulted in higher methane production, accounting for 24–51% of total carbon mineralized from tussocks. In the field however, *C. stricta* tussocks emitted less methane ($393 \pm 76 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) than tussock interspaces ($1362 \pm 371 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) early in the growing season; we suggest that tussock tops oxidized methane produced from deeper anoxic horizons. Our results highlight the importance of considering how microtopography modulates greenhouse gas flux from wetlands and suggests that the C stored in the older, more decomposed *C. stricta* tussock sedge meadow substrates (both within and between sites) is relatively stable.

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1. Introduction

The flux of carbon (C) from terrestrial soils to the atmosphere is an order of magnitude greater than C emitted by burning fossil fuels (Raich et al., 2002); therefore, insight into the stability of soil C pools in different ecosystems is integral to our understanding of climate change. Wetlands, especially peatlands, store a substantial fraction of global soil C (~20–33%; Batjes, 1996; Gorham, 1991), despite covering only ~5% of terrestrial land surface (Matthews and Fung, 1987). With climate change, ~25% of peatland C stocks are predicted to become vulnerable to decomposition this century, which could result in soil C losses two to three times greater than those from mineral soils (Davidson and Janssens, 2006). Therefore, understanding the mechanisms that protect wetland soil C is integral to predicting the response of wetlands to climate change and potential feedbacks to climate.

Waterlogged conditions promote the accumulation of C in wetlands by limiting decomposition more than net primary

production, but anaerobic environments also promote the production of methane (Bridgman et al., 2006), which has a global warming potential (GWP) 23 times that of CO₂ (Solomon et al., 2007). Despite methane's high GWP, (Jungkunst and Fieldler, 2007) review of organic matter decomposition from hydromorphic soils suggested that anaerobic decomposition (CH₄ production) has lower potential feedbacks to the climate than aerobic soil decomposition (CO₂ production). But they indicated that data on how different plants modulate CH₄ and CO₂ production under changing water tables are needed, as species with diverse growth forms modify ecosystem processes differently (Chapin, 2003). For example, plants that form organic tussocks dominate a range of wetland systems globally (Chapin et al., 1979; Nishikawa, 1990), but little is known about how different moisture regimes might affect the stability of C stored in tussocks.

Carex stricta is a dominant species in herbaceous wetlands throughout eastern North America (USDA-NRCS, 2009) that forms tussocks above the soil surface in response to inundated conditions (Lawrence and Zedler, 2011). The species is a desirable restoration target because its tussocks increase microtopography (Werner and Zedler, 2002), plant diversity (Peach and Zedler, 2006), and accumulate C rapidly (Lawrence and Zedler, 2011). Additionally, in relatively undisturbed sedge meadows in southern Wisconsin, *C. stricta* tussocks are composed of ~95% organic matter and

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store up to 1700 gC/m² (Lawrence and Zedler, 2013). Although the capacity of wetlands to sequester C in soil is increasingly a motivating force for restoration, the C that restored wetlands sequester may initially be less stable than reference sites, and they may also be methane sources. For example, in the soils of young constructed marshes (<20 years), Craft et al. (2003) found more labile organic compounds and less recalcitrant organic matter (e.g., less lignin) than reference salt marshes. Glatzel et al. (2004) observed high CO₂ and CH₄ production potentials in surface peats from restored Canadian peatlands because these newly formed substrates were more bio-available to the microbial community than deeper, more decomposed peat. Because data are lacking to evaluate whether wetland restoration will increase net radiative forcing globally (Bridgman et al., 2006), more research on C mineralization potentials of restored wetlands is necessary.

Several mechanisms could influence the stability of organic matter in tussocks and sedge meadow soils. C in the saturated zones persists presumably because it is environmentally protected by anaerobic conditions. The high organic content of *C. stricta* tussocks could enhance water holding capacity, allowing the capillary fringe to extend above the water table (Hunt et al., 1999) and maintain a reduced internal tussock environment. However, tussocks are typically above standing water, and estimates of tussock moisture indicate that they are aerobic at least during a portion of the growing season (Lawrence et al., 2013). Tussock components could also be chemically recalcitrant to decomposition (e.g., high lignin), though Lawrence and Zedler (2013) concluded that micro-environment (i.e., fluctuating temperature and moisture) rather than tissue chemistry restricted leaf litter decay rates on tops of tussocks in this study system.

Using year-long incubations in a growth chamber, we evaluated the stability of C stored in *C. stricta* tussocks and in sedge meadow soil. Specifically, we investigated the effect of depth (tussock top, tussock base, and tussock soil), donor site (4 reference sites, 1 restored), and moisture level (field moist vs. inundated) on CO₂ and CH₄ production. We considered C mineralization potentials to reflect microbial utilization of the most labile and abundant substrates; substrates with greater C mineralization potentials were considered less stable. To relate C mineralization rates to substrate quality, we characterized their lignin content, C:N ratios, and macro-organic matter content (biomass >2 mm). We also compared methane pools and field flux rates from tussocks and tussock interspaces at a reference site to provide context for our laboratory work.

C is generally more labile in surface horizons due to inputs of fresh plant material (Turetsky, 2004; Updegraff et al., 1995). Because the tops of *C. stricta* tussocks were less decomposed (i.e., less % duff per tussock dry mass; Lawrence and Zedler, 2013) and had higher root turnover rates than tussock bases (Lawrence et al., 2013), we expected C mineralization to decrease with depth (tussock tops > tussock bases > tussock soil). Similarly, we hypothesized that young tussocks from the restored site would be less stable than tussocks from reference sites, and that macro-organic matter content would be positively correlated to C mineralization potentials. High lignin content is commonly associated with slow decomposition rates (Melillo et al., 1982; Aerts, 1997; Hobbie, 2008); thus we expected C mineralization potentials to be negatively associated with this parameter. In the field, it is feasible that tussocks above the water table could oxidize CH₄ produced in lower horizons, as methanotrophs in aerobic surface soils can oxidize CH₄ as it diffuses toward the surface from anoxic depths (Segers, 1998). Therefore, we predicted that CH₄ concentration would be greater with depth and that CH₄ flux would be less from tussocks than tussock interspaces.

2. Material and methods

2.1. Study sites

We sampled tussocks and soils from four reference *C. stricta*-dominated (>75% cover) sedge meadows (Ref 1–4) in southern Wisconsin for comparison with a restored tussock meadow in northeastern Illinois, which was the only known restored tussock meadow in the region. The Upper Midwest has largely been converted into agriculture or urban uses, but we had access to three relatively undisturbed remnant sites (Ref 1–3). Reference sites 1 and 2 were located within the Cherokee Marsh complex in Dane County, WI (Ref 1: 16 T 0308528 E, 4782344 N; Ref 2: 16 T 0309614 E, 4782736 N), had thick peat surface layers (1–2 m) and were predominantly ground water fed. Reference site 3 was located in Clover Valley Fen State Natural Area, Walworth County, WI (16 T 0360508 E, 4738365 N), had ~40 cm of surface peat, and appeared to be groundwater fed. Reference site 4 was located within Curtis Prairie at the University of Wisconsin Arboretum, Dane County, WI (16 T 0302237 E, 4768005 N), had silt-loam surface soils, was historically grazed but not plowed, and is currently subject to sediment and nutrient rich storm water run-off (Stiles et al., 2008). We compared Ref 1–4 with the restoration, which was part of the Des Plaines River Wetland Mitigation Bank in Lake County, IL (0360508 E, 4738365 N), and was restored from a degraded wooded floodplain. After removing trees and accumulated sediment, the restoration was planted with *C. stricta* plugs into sandy loam soils on 30-cm centers between 1994 and 1997 (Jerry Curran, Wetlands Research Inc., Personal communication). The *C. stricta* tussocks we sampled in 2009 had a maximum age of ~15 years.

2.2. Sample collection and preparation

At each site in November 2008, we established a 20 × 20-m grid and randomly selected four, 1-m² plots for collection of tussock and sedge meadow soil substrate. Within each plot we identified the tallest tussock, divided it into longitudinal quarters, and randomly selected one for harvest with a fine-toothed pull saw. Below the harvested tussock monolith, we collected a 5-cm diameter soil core to 20 cm (tussock soil = TS). To compare the stability of surface vs. deeper peat, we also collected peat from 80 to 100 cm (tussock deep soil = TDS) below tussocks at Ref 1 and 2. In addition, surface soil samples (0–20 cm) from the tussock interspace (TI) were collected from the restoration to compare how C inputs from *C. stricta* influence the stability of soil C. At reference sites, average height and basal perimeter of the tussocks we collected were 21.9 cm (±1.0) and 66.0 cm (±5.7), respectively. Because there were fewer tall tussocks at the restoration, we identified candidate tussocks (>10 cm) from four, 4-m² plots. These tussocks averaged 13.2 cm (±0.5) in height, with a basal perimeter of 51.6 cm (±4.3). We sampled more intensively at Ref 3 in order to compare the relative stability of C stored in tall vs. short tussocks. From five 1-m² plots, we collected a monolith from the tallest (height: 25.4 cm ± 1.7; basal perimeter: 92.8 cm ± 15.6) and shortest (height: 13 cm ± 2.2; basal perimeter: 42.2 cm ± 3.1) tussocks. All material was transported back to the lab and stored in plastic bags at 4 °C until further processing.

In the laboratory, we cut tall tussocks (>10 cm) into two strata because they appeared vertically stratified. We cut tussock monoliths 10 cm from their base into (0 to 10 cm = tussock base = TB; >10 cm = tussock top = TT). We subsampled all tussock substrates, including the short tussocks (S) from Ref 3, by cutting out the central four centimeters, and then subdivided it into four approximately 4 × 4 × 4-cm cubes. We mixed peat/soil substrates (TS, TDS, and TI) by hand and selected four ~50-g subsamples. From each site-substrate combination, we randomly assigned two subsamples to test C mineralization potential (field moist or inundated moisture

treatments), one was used to determine gravimetric water content and subsequently %C, %N, and lignin content, and one was dissected to quantify the proportion of macro-organic matter.

2.3. C mineralization potential

To facilitate moisture manipulation, we placed samples in plastic, 125-mL cups and then set them inside 934-mL glass incubation chambers (mason jars). We randomly placed sample jars in a dark growth chamber set at 22.5 °C which approximates the maximum temperature of tussock tops from Ref 1 during the 2009 and 2010 growing season (Lawrence et al., 2013). Thus, the mineralization rates we measured likely represent maximum field values and are considered mineralization “potentials.” To increase humidity and reduce evaporation rates, we added water to the bottom of the jars and placed lids on top of jar mouths. However, to prevent inhibition between gas sampling events, we offset the lids by ~1 cm to create “vented” jars.

To test how moisture status influenced C mineralization potentials, we subjected replicates from each site and substrate to inundated or field moist conditions ($n=4-5$). Inundated samples were completely submerged with de-ionized water throughout the experiment. Because the water holding capacities of organic and mineral substrate types were divergent, we used the average water content of organic ($75.8\% \pm 1.2$) and mineral ($31.9\% \pm 2.1$) substrates across sites as the baseline for “field moist” conditions. Mineral substrates included Ref 4-TS, Restor-TS, and Restor-TI; all other substrates were considered organic. We maintained field moist treatments within 10% of the target value; samples were weighed weekly and water was added as necessary.

We used the methods outlined by Robertson et al. (1999) to quantify potential C availability to the microbial community. Prior to gas sampling, we flushed incubation jars with humidified air and then sealed them with canning-jar lids fitted with rubber septa. To estimate CO₂ and CH₄ production rates, we sampled the headspace with a syringe immediately after sealing and at 3 h. We determined this sampling design to be appropriate based on preliminary gas production curves from samples measured at 0, 3, 6, 12, and 24 h after sealing. We stored gas samples in evacuated vials until analysis by gas chromatography with a flame ionization detector (Shimadzu GC-14B, Shimadzu Analytical and Measuring Instruments Division, Kyoto, Japan). Rates of CO₂ and CH₄ production were calculated from gas concentration differences between 3 h gas-sampling periods. Similar to Updegraff et al. (1995), Bridgham et al. (1998), Craft et al. (2003) and others, we report C production rates as the proportion of C mineralized per total sample C (i.e., milligrams of C mineralized per gram of total substrate C) in order to compare soils with divergent physical characteristics. Due to differences in soil bulk density and C content, relationships among substrates would change if mineralization were on a mass or volume basis (Updegraff et al., 1995). Expressing C mineralization per g C represents a turnover rate of the C pool and thus is a measure of the lability of that pool, whereas expressing it on a mass or volume basis would be a measure of soil C availability (Bridgham et al., 1998).

We conducted two incubation experiments to explore the C mineralization potential of *C. stricta*-dominated sedge meadows. Our first experiment (“Phase 1”) involved 11 sampling dates with material from one site (Ref 3), using two moisture treatments (field moist vs. inundated) and four substrates: short tussocks (S; $n=4$), tall-tussock tops (TT; $n=4$), tall-tussock bases (TB; $n=4$) plus the underlying peat (TS; $n=5$), for a total of 34 samples. We began incubating these samples on January 7, 2009, and estimated gas production on day 7, 17, 30, 64, 94, 125, 162, 222, 253, 317 and 385 of the experiment. Our second experiment tested C mineralization potential among four sites, two moisture levels, three substrates

(plus TDS at Ref 1 and 2, and TI at Restor). We initiated “Phase 2” on April 16, 2009, incubating substrate from Ref 1 and 2 (TT, TB, TS, and TDS), Ref 4 (TT, TB, and TS), and Restor (TT, TB, TS, and TI). We sampled gas production on days 14, 35, 98, 172, 250 and 364 of this experiment. We tested four replicates from each site, substrate, and moisture level treatment combination, except for Ref 2: TDS-inundated, where we only had three replicates. Together, we incubated 119 samples during Phase 2.

2.4. Substrate quality

After drying samples to assess their water content, we ground them in a Wiley mill (1-mm² mesh) to homogenize the substrate. A sub-sample of ground material ($n=4$ for each site and substrate) was analyzed for C and N content on a Flash EA 1112 C-N elemental analyzer (CE Instruments, Wigan, UK). To estimate lignin content, we sent ground material ($n=2$ for each site and substrate) to the University of Wisconsin-Soil and Plant Analysis Laboratory, Marshfield, WI, for analysis of acid-detergent lignin (%ADL).

We also quantified the proportion of macro-organic matter composing sedge meadow substrate from Phase 2 subsamples and used it as an index of fresh plant input. For tussock samples, we hand-sorted biomass >2 mm (i.e., roots, rhizomes, and basal leaf structures), and for non-tussock substrates (TS, TDS, and TI), we washed subsamples over a 2-mm mesh screen. Biomass was dried (48 h at 60 °C), weighed, and analyzed for organic matter content by loss on ignition (Carter, 1993) to estimate the ash-free dry weight of macro-organic matter.

2.5. CH₄ field flux and pools

To relate laboratory results to field dynamics, we compared CH₄ flux between tussocks and unvegetated tussock interspaces using in situ closed-cover chambers during the 2009 growing season. We conducted this work at Ref 2 due to ease of access. Within the same 20 × 20-m grid we used to collect incubation substrate, we randomly established five paired plots a week prior to the first sampling event during June 2009. In each plot we identified a 20–22 cm tall tussock and surrounded it with a static chamber (plastic, 26.5-L Leticia bucket with the base removed). Within 20 cm of each tussock plot, we placed an identical chamber in the tussock interspace. All chambers were installed ~10 cm into the peat in order to maintain a gas-tight seal. During sample collection, tall vegetation was gathered within the chamber to account for plant transport, as clipping vegetation can accelerate methane transport to the atmosphere through cut stems (Dingemans et al., 2011). Chambers were capped with lids fitted with a rubber stopper that was connected to 2 m of Tygon tubing (1 mm internal diameter) and fitted with a 3-way stopcock. A needle inserted into septa in the chamber lid equilibrated air pressure in the chamber with atmospheric pressure. A 30 mL syringe was used to mix air in the headspace (3×) and draw a 15 mL sample. We collected gas samples at 0, 15, 30, and 45 min after lid placement, and transferred them to evacuated vials for transport to the lab where they were analyzed for CH₄. Flux rates were calculated as the slope of the CH₄ concentration over time. We collected gas samples between 0730 and 1000 h once during June, July, September, and October 2009; water table depth, soil and air temperature were also measured.

We also estimated peat CH₄ pools at Ref 2 using methods similar to Smemo and Yavitt (2006). We installed 2-mm (internal diameter) stainless steel wells to 5-, 10-, and 15-cm depths in tussocks (~20-cm tall) and in their adjacent interspaces ($n=4$). We connected the wells to Tygon tubing and used a 30-mL syringe to flush and then extract porewater or air (if not saturated) in July and September, 2009. Methane was stripped from porewater by vigorously shaking the syringe for 5 min. The gas was then transferred

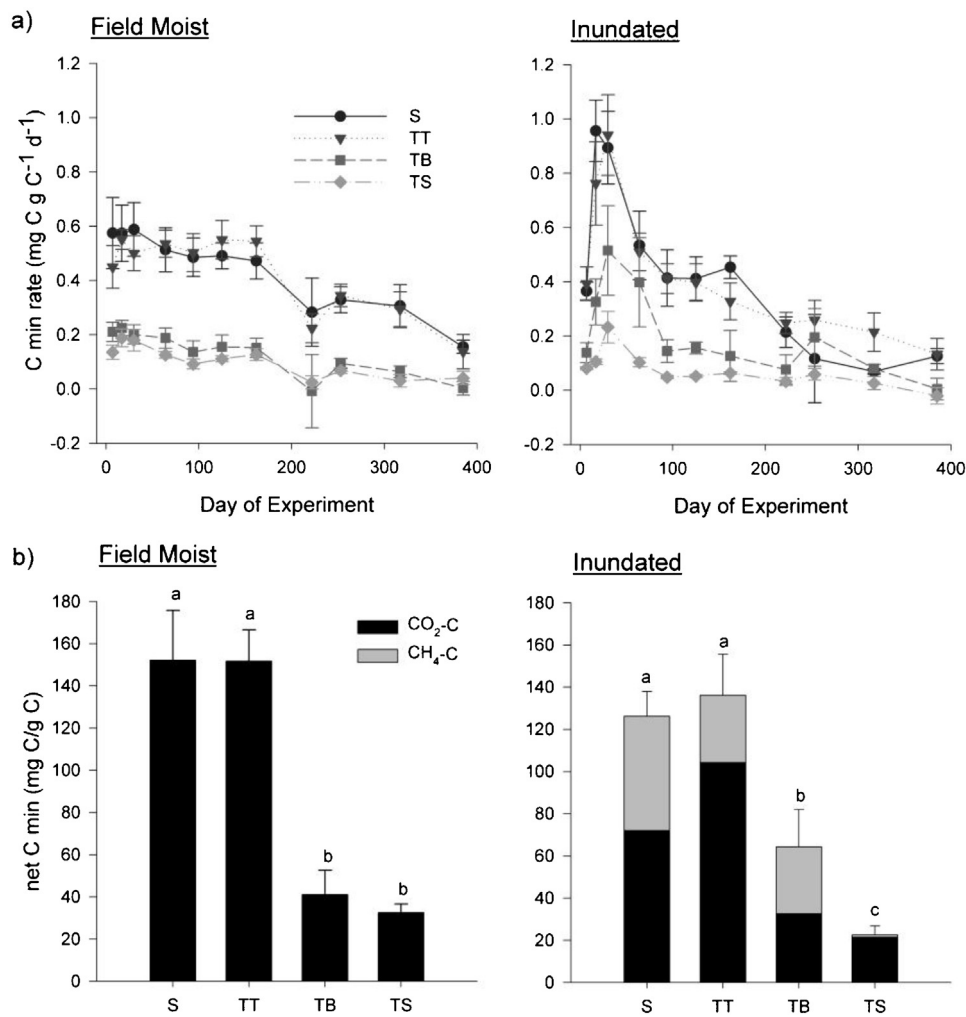


Fig. 1. (a) Comparison of mean (± 1 SE) C mineralization (C min) rates during phase I among four substrates (S = short tussock, TT = tall tussock, TB = tussock base, TS = tussock soil) under field moist and inundated treatment conditions ($n=4-5$). (b) Net C min among substrates and moisture treatments during the 385 day experiment ($n=4-5$). Substrates with the same letter did not differ significantly based on Tukey HSD pair-wise comparisons conducted on transformed data ($\alpha=0.05$).

to an evacuated vial and transported to the lab for CH_4 analysis. To estimate moisture content of tussock tops and unvegetated interspaces, we collected volumetric soil moisture measurements to 6-cm depth with a hand-held Dynamax Thetaprobe (Delta-T Devices, Cambridge, England).

2.6. Statistical analysis

To estimate the net amount of C mineralized during our incubation experiments, we extrapolated the CO_2 and CH_4 production rates to the midpoints between sampling events and estimated the area under their curves. We added the amounts of C mineralized as CO_2 and CH_4 and report it as net C min. We used linear mixed effect models to test for C mineralization differences among substrates, moisture treatments, and sites. We accounted for possible correlations between substrates from the same plots (e.g., TT, TB, TS from plot 1) by considering “plot” to be a random effect. All other factors were considered fixed. For comparisons across sites, we compared net C min for the three substrates that we tested at all sites (TT, TB, and TS). We tested for linear relationships between net C min with %ADL, and % macro-organic matter using linear regression. We used analysis of variance (ANOVA) to compare methane flux between sampling months and microhabitats, and also to compare methane concentrations with depth and microhabitat. We made

post hoc pair-wise comparisons among significant treatment levels with Tukey HSD ($\alpha < 0.05$). Response variables were transformed when necessary to promote homoscedasticity. All statistical analyses were conducted using R 10.2.1 (R Development Core Team, 2009).

3. Results

3.1. Phase 1-comparison of tussock substrates and moisture levels

C mineralization rates generally decreased throughout the experiment (Fig. 1a). When inundated however, C mineralization rates peaked after about two weeks and then declined (Fig. 1a). The net amount of C mineralized during the 385-day experiment differed among sedge meadow substrates ($p < 0.0001$; Fig. 1b). Generally, substrate from short tussocks and tall tussock tops had similarly high C mineralization rates compared to bases of tall tussocks and their underlying soil (Fig. 1). While field moist and inundated treatments had similar net C min ($p = 0.53$), methane production contributed 5 to 43% to net C min under inundated conditions, but less than 1% under field moist conditions (Fig. 1b). When inundated, tussock substrates (S, TT, and TB) produced significantly more methane than the underlying soil ($p < 0.001$).

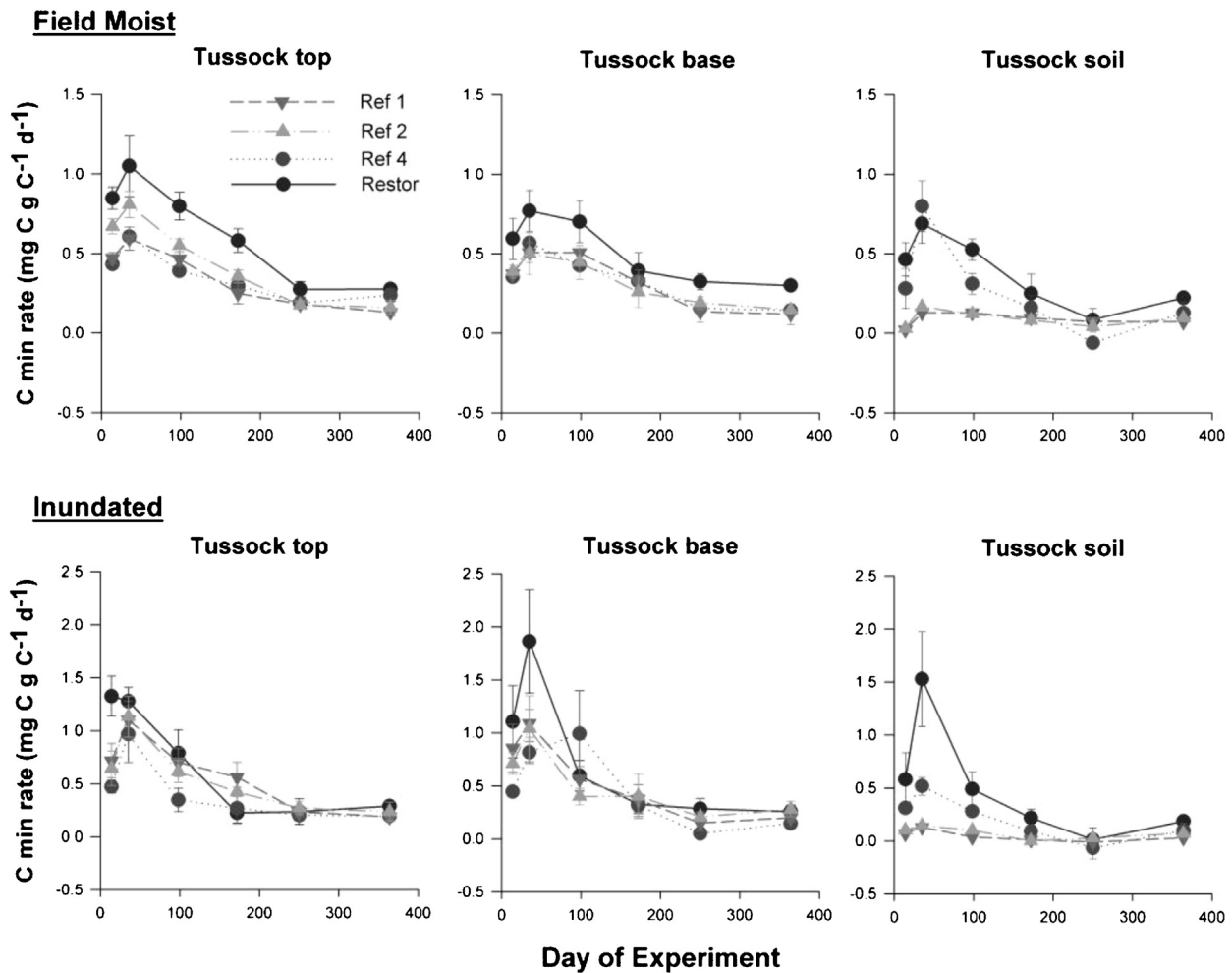


Fig. 2. Comparison of C mineralization rates ($\text{CO}_2\text{-C} + \text{CH}_4\text{-C}$) among four sites, field moist and inundated treatments, and three *C. stricta* sedge meadow substrates during phase 2 (mean \pm 1 SE; $n = 4$).

3.2. Phase 2-comparison of sites, substrates, and moisture levels

C mineralization rates peaked on day 35 of the experiment then decreased and tended to plateau after about 200 days (Fig. 2). Differential C mineralization rates among sites and substrates resulted in differences in the total amount of C that mineralized over the course of the 364-day experiment ($p < 0.0001$; Fig. 3). Similar amounts of C were mineralized from the two moisture treatments ($p = 0.49$; Fig. 3), but a considerable quantity of the C mineralized was produced as CH_4 (up to 54%) when inundated.

Across sites, we generally observed reduced C mineralization with depth. Tussock tops mineralized more C than tussock soil ($p < 0.001$), but unlike our findings during phase 1, tussock bases had mineralization rates more similar to tussock tops than tussock soil ($p < 0.001$). At Ref 1 and 2, deep soil substrates (TDS) mineralized less C than surface soil under field moist conditions ($p < 0.01$), but when inundated, these substrates mineralized similar amounts of C (Fig. 3). When inundated, tussock substrates across sites produced significantly more CH_4 than the underlying soil ($p < 0.01$) and accounted for a large percentage of the total amount of C mineralized (30–54%).

Restoration substrate mineralized C more rapidly than reference sites when averaged across moisture levels and substrates ($p < 0.01$). Tussock tops from the restoration mineralized more C than those from Ref 1 or 4 ($p < 0.001$), but tussock bases mineralized similar amounts of C across sites ($p > 0.1$). The soil underlying

tussocks at the restoration mineralized more C than all the reference sites ($p < 0.001$). Within the restoration, we observed similar net C min between moisture treatments, but differential responses among substrates; tussock interspace samples mineralized less C than the other three substrates ($p = 0.001$). A large proportion (~34%) of C mineralized in the form of CH_4 from restoration tussock substrates, but in contrast to the reference sites, the soil underlying tussocks at the restoration also had high CH_4 production when inundated (Fig. 3).

3.3. Substrate quality

Percent C, N, as well as C:N ratios varied among sites and substrates ($p < 0.01$; Table 1). In general, %C, and C:N ratios declined with depth, but %N did not vary predictably with depth. Tussocks had higher %C and C:N ratios than the underlying soil, especially at sites with mineral soils (Ref 4, Restor). Undisturbed reference sites (Ref 1–3), especially Ref 1, tended to have greater %ADL (acid-detergent lignin) than Ref 4 and the restoration. At Ref 1–3, %ADL tended to increase with depth, though the opposite trend was apparent at Ref 4 and the restoration. Sites had similar % macro-organic matter content ($p = 0.09$), but it was consistently greater in tussocks than in sedge meadow soil ($p < 0.01$). Averaged across sites, tussock tops, bases and underlying soil had $56.5 \pm 6.9\%$, $35.7 \pm 7.4\%$, and $3.9 \pm 0.9\%$ macro-organic matter respectively.

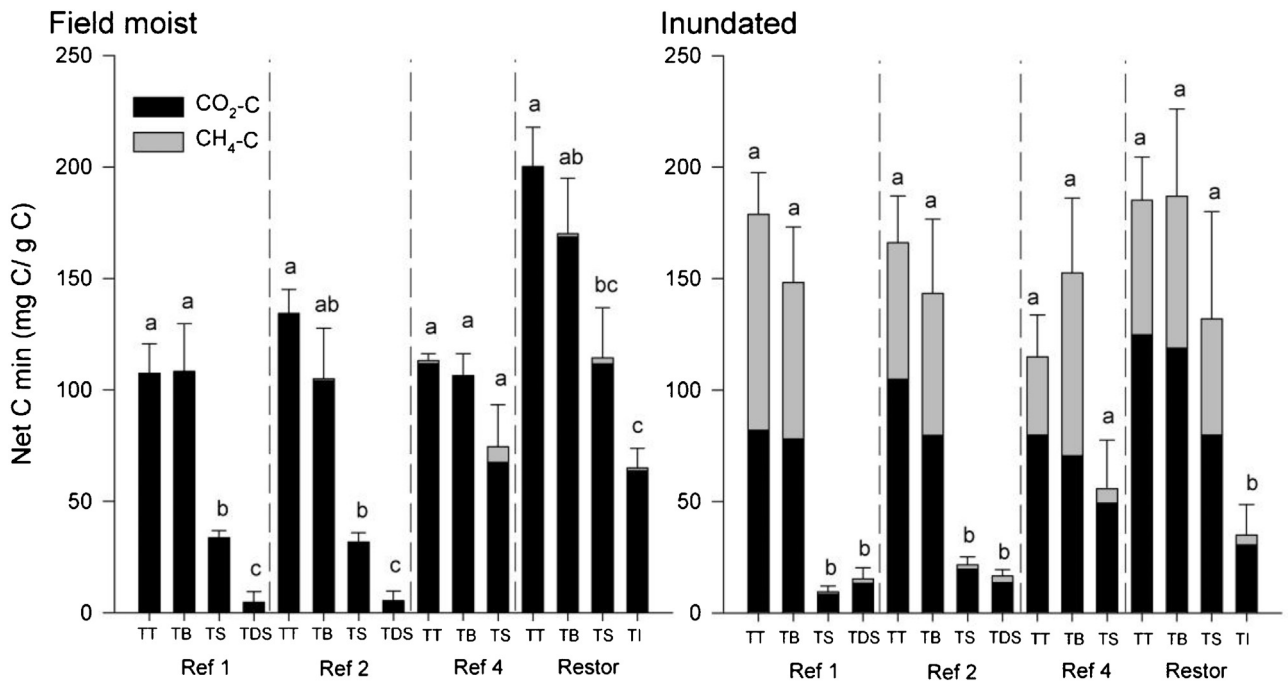


Fig. 3. Comparison of net C mineralized (mean + 1 SE) during the year-long experiment (Phase 2) between moisture treatments, sites, and substrates. Mean contribution of C from CO₂ (black) and CH₄ (gray) are indicated. Substrate codes: TT = tussock top, TB = tussock base, TS = tussock soil, TDS = tussock deep soil, TI = tussock interspace. Substrates within sites with the same letter had similar net C min based on Tukey HSD pair-wise comparisons conducted on transformed data ($\alpha = 0.05$).

Using linear models to compare net C min with %ADL and % macro-organic matter, we observed lower C mineralization in substrates with higher %ADL ($p < 0.01$; Fig. 4a) under field moist and inundated treatments, whereas net C min was positively correlated with % macro-organic matter ($p < 0.01$; Fig. 4c).

3.4. Methane field flux and pools

Methane flux estimates varied over several orders of magnitude from a maximum flux rate of $2470 \text{ mg m}^{-2} \text{ d}^{-1}$ to a net consumption rate of $-220 \text{ mg m}^{-2} \text{ d}^{-1}$. Flux rates were spatially and

Table 1

Sedge meadow substrate quality parameters (%C, %N, C:N: mean \pm 1 SE ($n = 4$); %ADL: range ($n = 2$); % macro-organic matter: mean \pm 1 SE ($n = 3-4$)). Substrate codes: TT = tussock top, TB = tussock base, TS = tussock soil, TDS = tussock deep soil, TI = tussock interspace. Substrates within sites sharing a common letter did not differ from one another after Tukey HSD pair-wise comparisons.

| | Substrate | Ref 1 | Ref 2 | Ref 3 | Ref 4 | Restor |
|------------------------|-----------|------------------------------|------------------------------|------------------------------|------------------------------|------------------------------|
| C% | TT | 47.1 \pm 0.2 ^a | 47.5 \pm 0.2 ^a | 43.6 \pm 0.7 ^a | 40.9 \pm 1.0 ^a | 26.4 \pm 4.2 ^a |
| | TB | 45.0 \pm 1.1 ^{ab} | 46.1 \pm 0.3 ^{ac} | 39.9 \pm 2.7 ^a | 10.1 \pm 0.8 ^b | 23.6 \pm 5.7 ^a |
| | TS | 42.2 \pm 0.5 ^{bc} | 41.1 \pm 0.7 ^b | 31.9 \pm 2.8 ^b | 3.8 \pm 0.8 ^c | 3.5 \pm 0.3 ^b |
| | TDS | 42.4 \pm 1.2 ^c | 42.4 \pm 1.2 ^{bc} | — | — | — |
| | TI | — | — | — | — | 4.8 \pm 0.6 ^b |
| | | | | | | |
| N% | TT | 2.1 \pm 0.2 ^a | 1.6 \pm 0.3 ^a | 2.1 \pm 0.1 ^a | 1.5 \pm 0.1 ^a | 1.2 \pm 0.2 ^a |
| | TB | 2.6 \pm 0.1 ^{ab} | 2.2 \pm 0.2 ^{ab} | 2.3 \pm 0.1 ^a | 0.7 \pm 0.0 ^b | 1.1 \pm 0.2 ^a |
| | TS | 3.3 \pm 0.1 ^b | 3.0 \pm 0.1 ^c | 2.8 \pm 0.2 ^a | 0.3 \pm 0.1 ^b | 0.3 \pm 0.0 ^b |
| | TDS | 2.4 \pm 0.0 ^a | 2.8 \pm 0.1 ^{bc} | — | — | — |
| | TI | — | — | — | — | 0.4 \pm 0.1 ^b |
| | | | | | | |
| C:N | TT | 23.5 \pm 2.3 ^a | 30.9 \pm 4.8 ^a | 21.0 \pm 0.6 ^a | 26.8 \pm 1.2 ^a | 21.4 \pm 1.6 ^a |
| | TB | 17.5 \pm 1.1 ^b | 21.1 \pm 1.7 ^{ab} | 17.3 \pm 1.3 ^{ab} | 14.3 \pm 0.9 ^b | 21.4 \pm 2.6 ^a |
| | TS | 12.9 \pm 0.3 ^b | 13.5 \pm 0.4 ^b | 11.5 \pm 0.2 ^b | 10.7 \pm 0.6 ^c | 12.6 \pm 0.7 ^b |
| | TDS | 16.2 \pm 0.3 ^b | 15.3 \pm 0.5 ^b | — | — | — |
| | TI | — | — | — | — | 14.7 \pm 2.6 ^{ab} |
| | | | | | | |
| % ADL | TT | 54.5–55.0 | 17.3–25.1 | 25.0–25.1 | 13.6–16.2 | 12.2–18.7 |
| | TB | 26.4–52.9 | 21.0–30.0 | 15.5–36.6 | 4.4–5.9 | 4.7–14.7 |
| | TS | 61.0–61.7 | 29.8–43.3 | 23.2–43.2 | 3.8–9.7 | 3.3–17.8 |
| | TDS | 53.0–74.8 | 45.8–60.0 | — | — | — |
| | TI | — | — | — | — | 2.2–5.6 |
| | | | | | | |
| % macro-organic matter | TT | 65.3 \pm 9.4 ^a | 67.0 \pm 8.3 ^a | NA | 60.8 \pm 10.3 ^a | 34.9 \pm 11.1 ^a |
| | TB | 42 \pm 10.8 ^a | 51.2 \pm 7.3 ^a | NA | 4.7 \pm 1.5 ^b | 44.8 \pm 15.8 ^a |
| | TS | 5.5 \pm 0.4 ^b | 7.1 \pm 0.8 ^b | NA | 0.6 \pm 0.1 ^c | 2.6 \pm 1.7 ^b |
| | TDS | 0.0 \pm 0.0 ^c | 0.0 \pm 0.0 ^c | — | — | — |
| | TI | — | — | — | — | 4.9 \pm 2.4 ^b |
| | | | | | | |

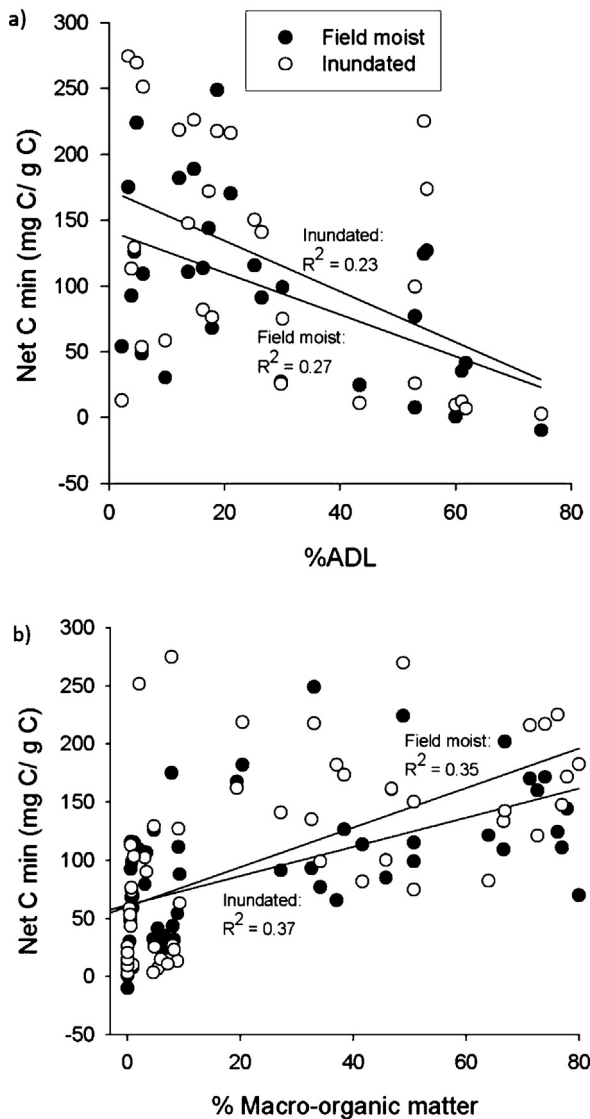


Fig. 4. (a) Net C mineralization (C min) was negatively associated with lignin (%ADL) concentration ($n=29$), and positively correlated with (b) % macro-organic matter ($n=56$) under field moist and inundated treatments.

temporally variable. In June, when 8 to 10 cm of water inundated the site, methane flux rates from interspaces were significantly larger than from tussocks ($p=0.02$; Fig. 5). In contrast, we observed no differences between tussocks and interspaces during July and September when water levels were 10–25 cm below the soil surface ($p>0.1$), but methane flux was similarly low among plots in October when water was standing 8–10 cm above the soil surface ($p>0.1$).

We observed low methane concentration in tussocks during our July and September sampling events (mean: 6.2 ± 1.3 ppm) with no difference among depths ($p>0.5$; Fig. 5). Volumetric soil moisture was lower in tussocks when we sampled in July and September ($31.8 \pm 2.7\%$, $33.3 \pm 1.9\%$, respectively), compared to interspaces (July: $61.3 \pm 2.7\%$, Sept: $58.6 \pm 3.4\%$). Methane concentration in interspaces tended to decrease with depth. In July, we observed significantly higher methane concentrations at 25-cm depth compared to 5-cm depth ($p=0.04$; Fig. 5).

4. Discussion

Our work highlights the importance of microtopography as an important driver of C dynamics in wetlands. Though *C. stricta*

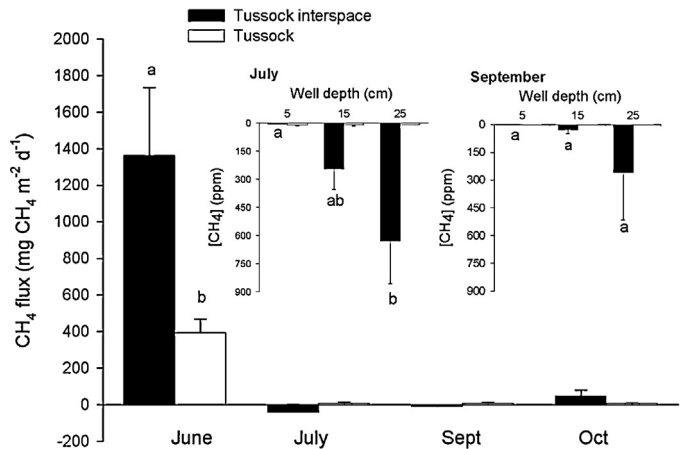


Fig. 5. Comparison of methane flux (mean \pm 1 SE) from tussock interspaces (black) and tussocks (white) at Ref 2 during the 2009 growing season ($n=5$). Inset graphs are methane concentration (ppm; mean \pm 1 SE) of pore air or water samples collected from wells in July and September 20, 2010 ($n=4$).

tussocks store a large proportion of C in Upper-Midwestern sedge meadows (Lawrence and Zedler, 2013), we observed tussock C to be more labile than the underlying soil. During laboratory incubation, anaerobic conditions did not stabilize the organic matter stored in tussocks, as tussocks produced a considerable amount of methane when inundated. However, consideration of growth form in the field is imperative, as the topographic heterogeneity supported by *C. stricta* tussocks mitigated methane flux to the atmosphere during our field study.

4.1. C mineralization

C mineralization potentials serve as an index of C stability and potential for C storage within ecosystems; we used the net C mineralized throughout our year-long incubation experiments as an index of C stability for comparison among sites, sedge meadow substrates, and moisture treatments, though we also observed changes in mineralization rates over time. After peak C production within the first month of incubation, C mineralization rates declined and tended to stabilize after about 200 days. We attribute the initial lags in peak C mineralization rates observed in almost all substrate and site combinations to the decomposition of roots that were severed during sampling (de Graaff et al., 2013; Kane et al., 2013). In inundated treatments where lag peaks were more pronounced, another possibility is that initial inundation promoted the production of organic acids, which might favor methanogens and result in high initial methane production (J. Yavitt, personal communication).

Similar to other wetland studies (Blodau et al., 2004; Scanlon and Moore, 2000; Updegraff et al., 1995; Waddington et al., 2001), we observed decreased C mineralization with depth, with tussocks mineralizing C quicker than the underlying surface soil, which in turn mineralized more quickly than deep peat. The high macro-organic matter content of tussocks, along with root exudates and C compounds leached from senesced leaves, likely supply the microbial community with an abundant source of labile C, resulting in high mineralization rates. Our results are similar to those of Michaelson and Ping (2003), who compared the CO₂ production potentials of 88 Arctic soil profiles using field moist incubation at -2°C . In the two *Eriophorum vaginatum* tussock profiles they sampled, they observed relatively high respiration rates from tussock surface organic layers (two of the highest rates they observed across profiles), and reduced respiration in lower horizons. In addition to more labile surface materials, the spatially explicit adaptation of

soil microbial communities to vertical tussock heterogeneity might play a role in the C dynamics of tussock-dominated wetlands.

4.2. Restoring C dynamics

Labile C inputs from young *C. stricta* plants appear to fuel high microbial respiration, as sedge meadow substrate from the restored site had greater C mineralization potentials than reference sites. Radiocarbon age estimates suggest that restored site tussocks were most likely ~50 years younger than reference site tussocks (Lawrence and Zedler, 2013). Thus, the relatively young, fresh plant material at the restored site appeared to support higher heterotrophic respiration than reference sites. Craft et al. (2003) also observed greater C mineralization in recently restored (<15 years) salt marshes and suggested that these soils had more labile organic compounds and less recalcitrant materials than reference marshes. Also, we observed greater C mineralization potentials from soil underlying tussocks than interspaces at the restored site, supporting the idea that labile *C. stricta* inputs promote microbial metabolism. Likewise, Michaelson and Ping (2003) observed greater CO₂ production from *Eriophorum* tussock cores than interspace samples.

Although our results indicate that C sequestered in young *C. stricta* tussocks and sedge meadow soil at the 15-year-old restoration was less stable than that at reference sites, we were limited by the paucity of restored tussock sedge meadows in the region. Other studies suggest that soil C properties may take decades or centuries to reach reference wetland levels (Ballantine and Schneider, 2009; Hossler and Bouchard, 2010), though the trajectory of restored wetlands are dependent on restoration methods, site management, climate, topography, and historical conditions (Zedler and Calloway, 1999). Because *C. stricta* has bundles several ecosystem services (i.e., microtopography, biodiversity, and C storage; Lawrence and Zedler, 2013), we recommend planting it in created and restored wetlands throughout its range to test the effects of various soils and hydroperiods on tussock formation, C sequestration, and C stability.

It is imperative to express C evolution rates on a per gram of soil C basis when comparing sites with diverse soils, as C mineralization rates tend to correlate with soil organic C, which is typically lower in created than reference wetlands (Ballantine and Schneider, 2009; Craft et al., 2003). Our findings support the work of Craft et al. (2003), who found that C mineralization rates (per g of soil C) were higher for surface soils of constructed *Spartina* marshes than reference wetlands. Hossler and Bouchard (2010) compared C-based properties of created and natural freshwater marshes and reported higher C mineralization in natural than created sites when expressed per soil mass (because reference sites had higher soil C), and they interpret these data as evidence that created marshes functioned at levels lower than natural sites. However, when standardized by soil organic C content, there were no differences in mineralizable C between created and natural wetlands. This suggests that created and natural sites were functionally equivalent or similar in C dynamics. Hence, we recommend standardizing the indicators of C dynamics, careful interpretation of C mineralization potentials, and further study of the stability of C in restored and reference wetlands.

4.3. Substrate quality

Macro-organic matter percentage was strongly correlated to C mineralization potentials. Likewise, of the 39 measures of substrate quality in Minnesota peatlands used by Bridgham et al. (1998), indices of the physical degree of decomposition (i.e., fiber content, von Post decomposition) were the best predictors of C, N, and P mineralization. The high macro-organic matter content of tussocks,

along with root exudates and C compounds leached from senesced leaves, likely supply the microbial community with an abundant source of labile C. As labile C sources are utilized, more complex compounds such as lignin remain. As expected, we observed lower C mineralization in deeper sedge meadow substrate that tended to have greater lignin content.

Similar to Chapin et al.'s (1979) observations of *E. vaginatum* tussocks, C:N ratios of *C. stricta* declined from tussock tops to lower horizons, but our sedge meadow substrate had relatively low C:N ratios (ranging from 11 to 31), indicating that N was not limiting microbial mineralization (Taylor et al., 1989). Further, N was neither lost through denitrification (we observed negligible N₂O production), nor lost in leachate (as in incubation designs by Updegraff et al., 1994) and thus was presumably recycled by the microbial community within our incubation chambers.

4.4. Methane production potential

While reducing conditions prevalent in wetlands tend to reduce decomposition and lead to C accumulation in peatlands, a review by Blodau (2002) found aerobic–anaerobic ratios of CO₂ mineralization to range from 1 to 6 dependent on chemical controls and fluctuations in redox conditions. In our study, CO₂ mineralization ratios between field moist and inundated samples averaged ~2. However, we found no statistical difference in net C mineralization between moisture treatments, as tussock substrates had particularly high methane production when inundated. This contrasts with the findings of Bridgham et al. (1998), who incubated a range of Minnesotan wetland soil over a year. Net C mineralization rates from our field moist treatments were similar to their aerobic surface peat samples from (~150 mg C/g total soil C), but they observed considerably less methane production under anaerobic conditions (maximum ~5 mg CH₄-C/g total soil C) than our inundated treatments (maximum 96 mg CH₄-C/g soil C). Several possibilities might explain the relatively low CO₂ production under field moist conditions we observed. Periodic drying and rewetting of field moist samples during incubation may have caused microbial biomass to suffer osmotic stress and reduce their metabolism (Blodeau, 2002). Another possibility is that O₂ limitation may have slowed CO₂ production in the field moist treatment, as the O₂ supply via diffusion would be very slow in our incubation chambers.

When inundated, our tussock substrates had nearly a 1:1 ratio of CO₂:CH₄, which is indicative of methanogenic dominance of anaerobic microbial respiration (Sutton-Grier and Megonigal, 2011). To explain why *C. stricta* tussocks have such high potential for methane production, we suggest that the availability of labile organic matter is a major control. Many studies have observed greater methane production from surface peat samples compared to lower horizons (Blodau et al., 2004; Glatzel et al., 2004; Smemo and Yavitt, 2006). Segers (1998) suggests that root decay and root exudation promote methane production. Because *C. stricta* tussocks have high macro-organic matter content in addition to high root productivity and root turnover (up to 1.43 yr⁻¹; Lawrence et al., 2013), abundant labile C substrates should be available for methanogens. Potential methane production and pH are also positively correlated (Segers, 1998); Costello (1936) reported that *C. stricta* tussocks were consistently alkaline with pH values ranging between 7.2 and 8.1, which might further promote methane production from tussocks.

4.5. Methane flux in tussock meadows

Although *C. stricta* tussocks have the potential to produce considerable methane when inundated, long-term continuous inundation is unlikely in natural tussock meadows. The hydroperiods of native *C. stricta* sedge meadow are characterized by shallow standing water (5–15 cm) early in the growing season, followed

by late summer drawdown (Kurtz et al., 2007). Further, our estimates of methane field flux were greater from interspaces than tussocks when standing water was present early in the growing season. Methane flux is a result of methane production by methanogens under anoxic conditions and aerobic methane oxidation by methanotrophs (Segers, 1998). Because tussocks form in response to anoxic conditions to mitigate oxygen-poor conditions (Lawrence and Zedler, 2011), they typically protrude above the water surface. Therefore, they have the capacity to oxidize methane produced from underlying anoxic horizons – in essence acting as methane sponges. Our data support this mechanism, as we observed negligible methane flux in July and September when surface horizons were relatively dry and increasing methane concentration with depth, suggesting that methane produced below the water table was oxidized in aerobic surface horizons.

Our results have global relevance, as tussock-dominated ecosystems are a worldwide phenomenon. Large areas of tussock tundra are predicted to experience permafrost thaw with climate change, which will alter moisture regimes and methane fluxes. The general influence of tussocks on wetland methane emissions is unresolved, however. Corradi et al. (2005) found no difference in methane flux between *Carex appendiculata* tussocks and interspaces, and Frenzel and Rudolph (1998) and Tuittila et al. (2000) both observed higher methane emissions from *Eriophorum vaginatum* tussocks than from interspaces in the field. In a microcosm study, Johnson et al. (1996) also observed greater methane flux from *E. vaginatum* tussocks than from interspaces. It is unclear if tussocks formed by different species have distinct methane dynamics, or if study-specific environmental conditions (e.g., moisture, temperature) were responsible for the observed differences in methane flux. Recent work by Kao-Kniffen et al. (2010) suggested that plant growth form affects methane flux; they found tussock/clump-forming graminoids emitted more methane than clonal dominants and forbs, and of the ten species studied, *C. stricta* emitted the most methane. However, their 4-month greenhouse experiment was conducted on young seedlings or plugs, and not on mature tussocks, which might modulate methane dynamics as discussed above. Their work and that of Strom et al. (2005) suggest that different species emit methane in distinct ways, warranting further study of the methane dynamics of a range of tussock-forming species in the field.

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References

Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79, 439–449.

Ballantine, K., Schneider, R., 2009. Fifty-five years of soil development in restored freshwater depression wetlands. *Ecol. Appl.* 19, 1467–1480.

Batjes, N.H., 1996. Total carbon and nitrogen in the soils of the world. *Eur. J. Soil Sci.* 47, 151–163.

Blodau, C., 2002. Carbon cycling in peatlands – a review of processes and controls. *Environ. Rev.* 10, 111–134.

Blodau, C., Basiliko, N., Moore, T.R., 2004. Carbon turnover in peatland mesocosms exposed to different water table levels. *Biogeochemistry* 67, 331–351.

Bridgman, S.D., Updegraff, K., Pastor, J., 1998. Carbon, nitrogen, and phosphorus mineralization in northern wetlands. *Ecology* 79, 1545–1561.

Bridgman, S.D., Megonigal, J.P., Keller, J.K., Bliss, N.B., Trettin, C., 2006. The carbon balance of North American wetlands. *Wetlands* 26, 889–916.

Carter, M.R., 1993. *Soil Sampling and Methods of Analysis*. Lewis Publishers, Boca Raton, FL.

Chapin, F.S., 2003. Effects of plant traits on ecosystem and regional processes: a conceptual framework for predicting the consequences of global change. *Ann. Bot.* 91, 455–463.

Chapin, F.S., van Cleve, K., Chapin, M.C., 1979. Soil temperature and nutrient cycling in the tussock growth form of *Eriophorum vaginatum*. *J. Ecol.* 67, 169–189.

Corradi, C., Kolle, O., Walter, K., Zimov, S.A., Schulze, E.D., 2005. Carbon dioxide and methane exchange of a north-east Siberian tussock tundra. *Global Change Biol.* 11, 1910–1925.

Costello, D.F., 1936. Tussock meadows in southeastern Wisconsin. *Bot. Gaz.* 97, 610–648.

Craft, C., Megonigal, P., Broome, S., Stevenson, J., Freese, R., Cornell, J., Zheng, L., Sacco, J., 2003. The pace of ecosystem development of constructed *Spartina alterniflora* marshes. *Ecol. Appl.* 13, 1417–1432.

Davidson, E.A., Janssens, I.A., 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature* 440, 165–173.

de Graaff, M., Six, J., Jastrow, J., Schadt, C., Wulfschlegel, S., 2013. Variation in root architecture among switchgrass cultivars impacts root decomposition rates. *Soil Bio. Biochem.* 58, 198–206.

Dingemans, B.J., Bakker, E.S., Bodelier, P.L., 2011. Aquatic herbivores facilitate the emission of methane from wetlands. *Ecology* 92, 1166–1173.

Frenzel, P., Rudolph, J., 1998. Methane emission from a wetland plant: the role of CH₄ oxidation in *Eriophorum*. *Plant Soil* 202, 27–32.

Glatzel, S., Basiliko, N., Moore, T., 2004. Carbon dioxide and methane production potentials of peats from natural, harvested and restored sites, eastern Quebec, Canada. *Wetlands* 24, 261–267.

Gorham, E., 1991. Northern peatlands: role in the carbon budget and probable responses to global warming. *Ecol. Appl.* 1, 182–195.

Hobbie, S.E., 2008. Nitrogen effects on decomposition: a five-year experiment in eight temperate sites. *Ecology* 89, 2633–2644.

Hossler, K., Bouchard, V., 2010. Soil development and establishment of carbon-based properties in created freshwater marshes. *Ecol. Appl.* 20, 539–553.

Hunt, R.J., Walker, J.F., Krabbenhoft, D.P., 1999. Characterizing hydrology and the importance of ground-water discharge in natural and constructed wetlands. *Wetlands* 19, 458–472.

Johnson, L.C., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J., Rastetter, E.R., Laundre, J.A., Murray, G.L., 1996. Effects of drainage and temperature on carbon balance of tussock tundra microcosms. *Oecologia* 108, 737–748.

Jungkunst, H.F., Fieldler, S., 2007. Latitudinal differentiated water table control of carbon dioxide methane and nitrous oxide fluxes from hydromorphic soils: feedbacks to climate change. *Global Change Biol.* 13, 2668–2683.

Kane, E.S., Chivers, M.R., Turetsky, M.R., Treat, C.C., Petersen, D.G., Waldrop, M., Harden, J.W., McGuire, A.D., 2013. Response of anaerobic carbon cycling to water table manipulation in an Alaskan rich fen. *Soil Biol. Biochem.* 28, 50–60.

Kao-Kniffen, J., Freyre, D.S., Balser, T.C., 2010. Methane dynamics across wetland plant species. *Aquat. Bot.* 93, 107–113.

Kurtz, A.M.D., Bahr, J.M., Carpenter, Q.J., Hunt, R.J., 2007. The importance of subsurface geology for water source and vegetation communities in Cherokee Marsh, Wisconsin. *Wetlands* 27, 189–202.

Lawrence, B., Fahey, T., Zedler, J.B., 2013. Root dynamics of *Carex stricta*-dominated tussock meadows. *Plant Soil* 364, 325–339.

Lawrence, B.A., Zedler, J.B., 2011. Formation of tussocks by sedges: effects of hydroperiod and nutrients. *Ecol. Appl.* 21, 1745–1759.

Lawrence, B.A., Zedler, J.B., 2013. Carbon storage by *Carex stricta* tussocks: a restorable ecosystem service? *Wetlands*, <http://dx.doi.org/10.1007/s13157-013-0405-1>.

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

Melillo, J.M., Aber, J.D., Muratore, J.M., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63, 621–626.

Michaelson, G.J., Ping, C.L., 2003. Soil organic carbon and CO₂ respiration at subzero temperature in soils of arctic Alaska. *J. Geophys. Res.* 108, 1–10.

Nishikawa, Y., 1990. Role of rhizomes in tussock formation by *Carex thunbergii* var. *appendiculata*. *Ecol. Res.* 5, 261–269.

Peach, M., Zedler, J.B., 2006. How tussocks structure sedge meadow vegetation. *Wetlands* 26, 322–335.

R Development Core Team, 2009. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria <http://www.R-project.org>

Raich, J.W., Potter, C.S., Bagawati, D., 2002. Interannual variability in global soil respiration, 1980–1994. *Global Change Biol.* 8, 800–812.

Robertson, G.P., Wedin, D., Groffman, P.M., Blair, J.M., Holland, E.A., Nadelhoffer, K.J., Harris, D., 1999. Soil carbon and nitrogen availability-nitrogen mineralization, nitrification, and soil respiration potentials. In: Robertson, G.P., Coleman, D.C., Bledsoe, C.S., Sollins, P. (Eds.), *Standard Soil Methods for Long-term Ecological Research*. Oxford University Press, New York, pp. 258–271.

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.

- Segers, R., 1998. Methane production and methane consumption: a review of processes underlying wetland methane fluxes. *Biogeochemistry* 41, 23–51.
- Smemo, K.A., Yavitt, J.B., 2006. A multi-year perspective on methane cycling in a shallow peat fen in central New York State, USA. *Wetlands* 26, 20–29.
- Solomon, S., Qin, D., Manning, M. (Eds.), 2007. IPCC Fourth Assessment Report – Climate Change 2007: The Physical Science Basis. Cambridge University Press, New York.
- Stiles, C.A., Bemis, B., Zedler, J.B., 2008. Evaluating edaphic conditions favoring reed canary grass invasion in a restored native prairie. *Ecol. Restor.* 26, 61–70.
- Strom, L., Mastepanov, M., Christensen, T.R., 2005. Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. *Biogeochemistry* 75, 65–82.
- Sutton-Grier, A.E., Megonigal, J.P., 2011. Plant species traits regulate methane production in freshwater wetland soils. *Soil Bio. Biochem.* 43, 413–420.
- Taylor, B.R., Parkinson, D., Parsons, W.F.J., 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70, 97–104.
- Tuittila, E.S., Komulainen, V.M., Vasander, H., Nykänen, H., Martikainen, P.J., Laine, J., 2000. Methane dynamics of a restored cut away peatland. *Global Change Biol.* 6, 569–581.
- Turetsky, M.R., 2004. Decomposition and organic matter quality in continental peatlands: the ghost of permafrost past. *Ecosystems* 7, 740–750.
- Updegraff, K., Bridgham, S.D., Pastor, J., Johnston, C.A., 1994. A method to determine long-term anaerobic carbon and nutrient mineralization in soils. In: Doran, J., Bezdicsek, D., Coleman, D. (Eds.), *Defining Soil Quality for a Sustainable Environment*. Soil Science Society of America, Madison, WI, USA.
- Updegraff, K., Pastor, J., Bridgham, S.D., Johnston, C.A., 1995. Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. *Ecol. Appl.* 5, 151–163.
- USDA-NRCS, 2009. The PLANTS Database. National Plant Data Center, Baton Rouge, LA, USA <http://plants.usda.gov> (06.03.09).
- Waddington, J.M., Rotenberg, P.A., Warren, F.J., 2001. Peat CO₂ production in a natural and cutover peatland: implications for restoration. *Biogeochemistry* 54, 115–130.
- Werner, K.J., Zedler, J.B., 2002. How sedge meadow soils, microtopography, and vegetation respond to sedimentation. *Wetlands* 22, 451–466.
- Zedler, J.B., Calloway, J.C., 1999. Tracking wetland restoration: do mitigation sites follow desired trajectories? *Restor. Ecol.* 7, 69–73.