5-12-2020

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A. M. Hopple
R. M. Wilson
M. Kolton
Cassandra A. Zalman
J. P. Chanton

See next page for additional authors

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This article was originally published in *Nature Communications* in 2020. https://doi.org/10.1038/s41467-020-16311-8

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Authors
A. M. Hopple, R. M. Wilson, M. Kolton, Cassandra A. Zalman, J. P. Chanton, J. Kostka, P. J. Hanson, Jason K. Keller, and S. D. Bridgham
Massive peatland carbon banks vulnerable to rising temperatures

A. M. Hopple1,2,3,7✉, R. M. Wilson4,7, M. Kolton5, C. A. Zalman2, J. P. Chanton4, J. Kostka5, P. J. Hanson6, J. K. Keller2 & S. D. Bridgham1

Peatlands contain one-third of the world’s soil carbon (C). If destabilized, decomposition of this vast C bank could accelerate climate warming; however, the likelihood of this outcome remains unknown. Here, we examine peatland C stability through five years of whole-ecosystem warming and two years of elevated atmospheric carbon dioxide concentrations (eCO2). Warming exponentially increased methane (CH4) emissions and enhanced CH4 production rates throughout the entire soil profile; although surface CH4 production rates remain much greater than those at depth. Additionally, older deeper C sources played a larger role in decomposition following prolonged warming. Most troubling, decreases in CO2:CH4 ratios in gas production, porewater concentrations, and emissions, indicate that the peatland is becoming more methanogenic with warming. We observed limited evidence of eCO2 effects. Our results suggest that ecosystem responses are largely driven by surface peat, but that the vast C bank at depth in peatlands is responsive to prolonged warming.
peatland soils represent a major global carbon (C) stock that is sensitive to climate change. Increases in temperature and atmospheric carbon dioxide (CO₂) concentrations, along with corresponding changes in hydromorphy, have the potential to stimulate the return of stored soil C to the atmosphere as CO₂ and/or methane (CH₄)⁶⁻⁷, amplifying the drivers of climate change. However, prior soil-warming experiments have primarily focused on surface responses to warming and long-term data from manipulative field studies remain scarce⁸⁻¹⁰. Therefore, the fate of peatland catotelm C under future climate conditions remains largely unknown.

The SPRUCE project alleviates this knowledge gap with an in-situ, manipulative experiment that addresses climate-driven questions on an ecosystem scale over the span of a decade. Located in an ombrotrophic peatland in northern Minnesota, USA (S1 Bog)¹², this study uses a regression-based experimental design that warms the vegetation and peatland soil profile to a depth of 3 m within ten, 12-m-diameter enclosures to five target temperature differentials (+0 to +9 °C above ambient), with duplicate enclosures subjected to ambient and ~500 p.p.m.v. above ambient atmospheric CO₂ concentrations (eCO₂; Supplementary Fig. 1a). Capturing comprehensive peatland responses to climate change requires the use of active surface and deep-soil warming because deep-soil temperatures will naturally increase in concert with rising annual air temperatures. Based on current greenhouse gas emission rates, forcing estimates in line or greater than the RCP 8.5 scenario are likely to occur. This will result in 2.6–4.8 °C increases in global mean surface temperatures by 2100¹⁷, with Minnesota experiencing 4.07–4.14 °C increases in annual air temperature. However, both models and observations indicate that northern boreal forests and tundra will continue to be exposed to greater warming than most other terrestrial biomes. This is largely due to positive feedback effects related to decreases in surface heat flux from increasing sea ice and shorter periods of winter snow cover. The effects of temperature increases are further compounded by the heightened frequency of extreme heat events which are expected to expose peatlands to acute heat stress, exceeding the conditions for which vegetation is currently adapted. Thus, under a globally averaged projection of +4 °C warming by the end of this century, boreal regions may experience temperature increases up to 8.3 ± 1.9 °C¹⁹,²⁰; thus, the +9 °C treatment implemented in this study represents an upper limit on what can be expected under the most extreme scenarios. In addition, implementing warming treatments at a range of temperatures allows for the exploration of ecosystem-wide response surface thresholds and nonlinear curve response fitting.

Whole-ecosystem warming (WEW) was initiated in August 2015, following 14 months of deep-peat heating (DPH). During the DPH phase of this experiment, deep-soil temperature targets were successfully maintained throughout the year; however, the lack of air warming resulted in muted surface warming. After the introduction of air warming, target temperature differentials were attained from the atmosphere to peat depths of at least 2 m. Finally, eCO₂ was introduced in a subset of the enclosures in June 2016 (Supplementary Fig. 1b).

Here, we present four years of data (2015–2018) that expand upon early results from the SPRUCE experiment by exploring the response of peatland CH₄ cycling through 5 years of warming and 2 years of eCO₂. We continue to observe exponential increases in surface CH₄ emissions and although surface CH₄ production rates remain much greater than those at depth, rates of CH₄ production are now positively responding to increasing temperatures throughout the entire soil profile. In addition, while CH₄ was produced primarily from decomposition of modern surface photosynthate prior to warming, radiocarbon analyses indicate that older deeper C sources are playing a larger role following prolonged warming. Most troubling, we observe decreases in the ratios of CO₂:CH₄ in gas production, porewater concentrations, and emissions, providing three lines of independent evidence that the peatland is becoming more methanogenic with warming. Finally, while we observed limited evidence of any eCO₂ effect to date, it remains to be seen whether this treatment will eventually modify the observed temperature effects via future ecological cascades. Our current results suggest that ecosystem responses remain largely driven by surface peat, but that following a relatively short lag, the vast C bank at depth in peatlands is responsive to warming.

Results and discussion

Ecosystem responses to prolonged WEW and eCO₂. During WEW, increasing temperatures stimulated CH₄ production rates.
throughout the peat profile (30–200 cm below the hollow surface; \( p \leq 0.05 \); Fig. 1), as well as CO₂ production rates of deep peat (≥75 cm; \( p < 0.01 \); Supplementary Fig. 2) in anaerobic laboratory incubations at in-situ temperatures. This contrasts with earlier results which showed no temperature effect on CH₄ and CO₂ production in catotelm peat (≥50 cm) following 14 months of DPH\(^{22}\). It is possible that this lag period may be longer under natural conditions where the soil profiles warm from the top down.

A positive temperature response at depth does not in and of itself indicate enhanced decomposition of ~8000–10,000-year-old soil C. However, comparisons of the radiocarbon (¹⁴C) content of dissolved inorganic carbon (DIC = CO₂) and CH₄ (decomposition products) with those of DOC and solid peat (decomposition sources) allowed us to discern whether the organic matter fueling heterotrophic decomposition was recent photosynthate (DOC) or ancient peat\(^{23-26}\). While CH₄ ¹⁴C analyses were not conducted at every depth and timepoint, multiple studies have shown that the ¹⁴C contents of CO₂ and CH₄ are tightly coupled\(^{23}\) (Supplementary Fig. 3). Previous research has shown that almost all heterotrophic decomposition in deep peat (up to 2 m) at S1 Bog was driven by relatively young, surface-derived DOC prior to WEW\(^{22,26}\). However, during WEW, porewater DIC, and presumably CH₄, appear older (¹⁴C depleted) in the warmest enclosures when compared to the decomposition products of ambient temperature plots (Fig. 2). While the ¹⁴C signatures in the warmest treatment plots remain much younger than that of solid peat\(^{22}\), this does suggest that older peat C has begun to play a larger role in decomposition at depth following warming; however, the decomposition of older C at depth took years to be observed.

We initially hypothesized that this delayed response may be due to the slow growth of methanogens given the low thermodynamic yield of methanogenesis under in-situ conditions\(^{27,28}\). Yet, the abundance of methanogens in peat (using quantitative PCR of the mcrA gene) did neither change with temperature \(( p = 0.59; \text{Supplementary Fig. 4})\) nor with increased time exposed to warming \(( p = 0.58)\) during WEW. We hypothesize alternative microbial community attributes, likely physiological activity and/or composition, must be underlying observed increases in deep CH₄ production. For example, recent experiments suggest that the temperature optimum for S1 Bog methanogens is around 30 °C\(^{29}\). Thus, the warmer treatments likely stimulated methanogen activity as soil temperatures were closer to their thermal optimum. Furthermore, laboratory-based incubation experiments using S1 Bog peat linked increases in CH₄ production to rising temperatures, as well as shifting methanogen community composition\(^{24}\).

**Fig. 2 Radiocarbon measurements of decomposition products.** Depleted DI14C signatures (in ‰) from (a) three of the warmest enclosures (≥6.75 °C with ambient CO₂, ≥9 °C with elevated CO₂, and +9 °C with elevated CO₂) following 5 years of warming. Due to a possible effect of elevated CO₂ on DI14C signatures (see “Methods”), we also provide ¹⁴C depth profiles for the (b) +9 °C and (c) +6.75 enclosures without elevated atmospheric CO₂ concentrations during 5 years of warming. Symbols and colors denote individual samples collected within each experimental enclosure from 2014 to 2018. The 2014 data points were during deep-peat heating, prior to the initiation of whole-ecosystem warming. Shaded areas and dotted lines indicate the DI14C LOESS locally weighted polynomial regression smooth curves, 95% confidence intervals from one ambient temperature enclosure (pink shading), and one reference plot with no infrastructure (blue shading). Control samples were collected over the same time period. In (b), symbols and whiskers indicate averages ± 1 standard deviation of each year for samples collected from the +9 °C with ambient CO₂ enclosure. Three samples from each depth were collected in 2018 and plotted, but at some depths the standard deviation was much smaller than the symbols at this resolution. As a reference, the solid peat matrix has a ¹⁴C signature that ranges from −400 to −600‰ at depths below 100 cm\(^{5}\).
Emission CO2:CH4 ratios were stable during the first 2 years of warming (p < 0.01), with an even steeper decrease observed in 2018 (p < 0.001; Fig. 4c). While porewater concentration and emission measurements encompass both autotrophic and heterotrophic respiration, we found that the declining CO2:CH4 ratios in both the porewater and the emissions were caused by increasingly methanogenic heterotrophic soil respiration (rather than decreasing CO2 rates). Together, these three lines of independent evidence suggest that the ecosystem as a whole is becoming more methanogenic. This is troubling because CH4 is a potent greenhouse gas with 45 times the sustained-flux global warming potential of CO2 over a 100-year timeframe. Thus, even if warming stimulates plant biomass production and enhances soil C sequestration, these effects are unlikely to completely offset the climate forcing due to increased CH4 emissions.

It should be noted that we report the warming response of one bog and CH4 emissions and anaerobic C cycling have been shown to vary substantially among southern boreal habitats. Thus, the results described here do not necessarily reflect the expected or observed responses from other peatland habitats. Nonetheless, our conclusions have far-reaching implications for understanding ecosystem-atmosphere feedbacks that exist in systems experiencing climate change, highlighting the need for similar manipulative studies implemented across a diverse array of ecosystem types and biomes. Finally, as the SPRUCE experiment continues into the next decade, it remains to be seen whether the observed temperature effects will persist, diminish through acclimation of the ecosystem, or be further modified by the impacts of changes in water-table position and eCO2 on plant-community productivity and composition. However, our results indicate that the vast stores of C at depth in peatlands are vulnerable to rising temperatures, but that ecosystem responses remain largely driven by surface peat and, altogether, these responses have resulted in a more methanogenic peatland.

Methods

Site description. The Spruce and Peatland Responses Under Changing Environments (SPRUCE) experimental site (http://mnspruce.ornl.gov/), S1 Bog, is an 8.1 ha peatland in north-central Minnesota, USA within the US Forest Service Marcell Experimental Forest (N 47°30.476′ W 93°27.162′). Since the 1960s, extensive scientific investigations have been done at this site and include in-depth descriptions of its physicochemical and biotic characteristics. This precipitation-fed, ombrotrophic bog has a perched water table with an average pH of 4.1 at the surface which increases with depth to roughly 5.1 at 2 m depth. The overstory vegetation is primarily dominated by Picea mariana (black spruce) and, secondarily by Larix laricina (larch), while the understory is composed of low ericaceous shrubs, such as Rhododendron groenlandicum (Labrador tea) and Chamaedaphne calyculata (leatherleaf), and herbaceous perennials, such as Maianthemum trifolium (three-leaved Solomon’s seal) and Eriophorum vaginatum (cotton grass). The bog surface is characterized by hummock and hollow microtopography, with a typical relief of 10 to 30 cm between the tops of the hummocks and the hollows. Sphagnum magellanicum generally colonizes the hummocks, while S. angustifolium and S. fallax cover the hollows. The beloground peat profile and geochemistry are described in ref. 34.
warming resulted in reduced temperature separation among treatments at the surface. After the introduction of air warming (which signaled the start of WEW), we attained 9°C temperature separation and differentials across treatment enclosures from the tops of the trees to peat depths of at least 2 m. Temperature differentials have largely been maintained throughout the WEW period, with some variation observed in surficial peat zones due to rain and snow events. Finally, eCO2 was introduced in a subset of the enclosures on 15 June 2016, completing the full set of experimental climatic manipulations planned by the SPRUCE project (Supplementary Fig. 1b). In these enclosures, ambient atmospheric CO2 concentrations were on average elevated by ~500 p.p.m.v. using pure CO2 from a fossil source (i.e., 14C-free CO2). The mixture of local ambient air (±0 to 9%) with pure CO2 yielded eCO2 chambers having typical values of ~520 to 540% on the Δ13C scale. Due to the compounding effect of the treatment, we include all 10 enclosures in most analyses and explicitly explore eCO2 in some cases.

CH4 and CO2 production. Following the same protocol that was used throughout the DPH experimental phase, intact soil cores were collected from multiple depths within each experimental enclosure to discern how rates of CH4 and CO2 production, as well as CO2:CH4 ratios, varied with climate treatment and depth. Sampling events were conducted 1–4 times per year during the growing season, and over the course of 4 years (2015–2018) throughout WEW. In 2015, soil cores were collected from 20 to 30, 50 to 75, 100 to 125, 125 to 150, and 175 to 200 cm depth increments (depth increments are denoted with the lower end of their ranges in figures). We used the same sampling protocol from 2016 to 2018, but collected soil cores at 40–50 cm instead of 125–150 cm to better capture variation in surficial peat horizons. All depths were measured relative to the surface of the hollows. To prevent compression of surface peat samples, a serrated knife was used to collect a 10 cm diameter core from the hollow surface to ~20 cm within the peat profile. A 5-cm diameter Russian core was subsequently used to extract the remaining samples up to 2 m deep. Soil cores were immediately flushed with nitrogen (N2) in the field to minimize exposure to aerobic conditions. In addition, porewater samples were anaerobically collected from within each enclosure using 1.25 cm diameter PVC piezometers installed at corresponding depth increments (25, 50, 75, 100, 150, and 200 cm below the hollow surface) and a peristaltic pump. Both soil and porewater samples were collected from piezometers permanently installed at 25, 50, 75, 100, 150, and 200 cm below the hollow surface within each experimental enclosure. The 1.25-cm diameter opening was parallel to the sampling depth with a screen covering to prevent solid intrusion. Piezometers were pumped out and allowed to passively refill for 24 h prior to sampling. Given the length of the piezometers and small cross-sectional area (1.25 cm diameter), little exchange with the atmosphere was expected over 24 h. A peristaltic pump and flexible sections of silicon tubing were used to collect porewater samples from piezometers, while surface water samples were collected using perforated stainless-steel tubes that were inserted into the peat to 10 cm or the top of the water table, whichever was shallowest.

Di-hydrogen samples were collected four times during the growing season in 2016. Immediately following collection, porewater was stored in pre-evacuated glass vials sealed with butyl stoppers, and phosphoric acid was added to each sample to preserve for shipment to the UO. At the UO, headspace samples were analyzed for H2 using a Peak Performer gas chromatograph with a reducing compound photometer. The level of detection for H2 was 1 ppm mL−1.

Acetate samples were collected 1–4 times during the growing season in 2015, 2016, and 2017. Analysis of CH4 and CO2 concentrations and stable isotope composition (δ13C) on a ThermoFinnigan Delta V Isotope Ratio Mass Spectrometer using the headspace equilibration method with He. Each sample was analyzed twice, and the average results for each sample were recorded. Analytical precision was 0.2‰ for 13C.

Preparation of δ13C-DIC samples was done at FSU by He stripping and cryogenic purification, and the resultant pure CO2 was transferred to 6 mm tubes for Δ13C analysis at the National Ocean Sciences Accelerator Mass Spectrometry Facility. CO2 was prepared as graphite targets, and analyzed by accelerator mass spectrometry. Values are reported according to the Δ notation put forth in ref. 38. The Δ notation normalizes the radiocarbon content of a sample to a nominal δ13C value (−25‰) and the collection time. The scale is linear and starts at −1000‰ when a sample has essentially 0% modern carbon, which would represent petroleum residue. Analytical precision was 2‰ for 13C.

Fig. 4 CO2:CH4 production, porewater concentration, and emission ratios. Decreasing CO2:CH4 ratio temperature responses from peatland a depth-specific CO2 and CH4 production rates from anaerobic incubations, b depth-specific in-situ CO2 and CH4 porewater, and c surface CO2 and CH4 emissions following 5 years of warming. Emission measurements were collected 6–8 times per year during 2015–2018. Production measurements were made using peat samples collected from six depths during the same time period and anaerobically incubated within 1°C of in-situ temperatures. Porewater samples were collected from piezometers wells 3–4 times per year in 2016 and 2017. In (a) and (b), colors represent different sampling depths and in (c), colors represent different sampling years. Linear regressions with 95% confidence intervals are shown in black and gray, respectively. NS not significant.
Methanogen abundance. Following the same protocol that was used throughout the DPH experimental phase, soil cores were collected in parallel with CH4 and CO2 production measurements, 1–2 times per year during the growing season, from 20 to 30, 40 to 50, 75 to 100, 150 to 175-cm depth increments. Soil cores were immediately frozen on dry ice, shipped to the Georgia Institute of Technology (GT), and stored at −80°C until analysis. The total DNA was extracted from homogenized peat samples using the DNeasy PowerSoil Kit (Qiagen, formerly MoBio) and stored at −80°C.

Data sets pertaining to this study are in the online project archive at https://mnspruce.lbl.gov.

**Data availability**

Statistical analyses. General linear mixed-effect models were used to determine the effects of depth, temperature, and elevated CO2 concentrations on gas production (CH4 and CO2 production and CH4:CO2 ratios), porewater concentration (H2, acetate, CH4, and CO2 concentrations and CO2:CH4 ratios), microbial (methanogen abundance), and gas emission (CH4 and CO2 emissions and CO2:CH4 ratios) data sets. In all cases, enclosure was treated as a random effect, and all other predictor variables were analyzed as fixed effects. If significant differences among depths were detected (p < 0.05), pairwise comparisons using Tukey’s honest significant difference test (p < 0.05) were conducted. If not significantly different, depths were combined for linear regression analysis. In addition, stepwise multiple linear regression with Akaike Information Criterion (AIC) as the model selection condition was used to assess the ability of temperature, water-table position, and exposure to elevated CO2 conditions to predict peatland CH4 emissions. Data were tested for normality and log-transformed where the transformation resulted in an improvement in overall distribution. The above statistical analyses were completed using R 3.2.2 Statistical Software.

The LOESS (locally estimated scatterplot smoothing) regression for the radiocarbon plots was accomplished using a weighted least square and 2nd degree polynomial model via the smooth function in MATLAB 2017b (MathWorks, Inc.).

Received: 24 October 2019; Accepted: 17 April 2020; Published online: 12 May 2020

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