



Gradual drying of permafrost peat decreases carbon dioxide in drier peat plateaus but not in wetter fens and bogs

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Abstract. Permafrost thawing of northern peatlands can cause local collapse of peat plateaus into much wetter thermokarst bogs and fens, dominated by *Sphagnum* mosses and graminoids, respectively. However, permafrost thaw can also improve landscape drainage and thus lead to regional drying of peatlands. How gradual drying of these thawing permafrost peatlands affects the subsequent microbial production of carbon dioxide (CO₂) and nitrous oxide (N₂O) is uncertain because of landscape heterogeneity in moisture, peat quality, and vegetation. Here, we collected near-surface peat samples (5-20 cm) from Alberta, Canada, across transects representing a thaw gradient from peat plateaus to a fen or bog. We incubated the samples for two weeks at either field moisture conditions or under gradual drying, which reduced moisture by ~80%. Only the fen sites, which had high moisture and % total N, produced N₂O (0.06–6.7 µg N₂O-N g⁻¹ dry peat) but were unaffected by the drying treatments. Peat CO₂ production was greatest from the fen and the youngest stage of the thermokarst bog despite having the most water-saturated field conditions, likely reflecting their more labile plant inputs and, thus more decomposable peat. We found that CO₂ respiration was enhanced by drying in relatively wet sites like the fens and young bog but was suppressed by drying in relatively drier peat plateaus. Further, gradual drying increased ¹³C-CO₂ respiration, suggesting a possible shift to more decomposed, older C being lost with peat drying. Our study thus suggests that future peat CO₂ and N₂O production from peatlands will depend on whether peat plateaus thaw into fens or bogs and on their diverging responses of peat respiration to more moisture-limited conditions.

1 Introduction

Permafrost peatlands are a crucial reservoir of carbon (C), storing around 185 Pg of C (Hugelius et al., 2020). In Canada, 37% of peatlands remain perennially frozen, below a seasonal thawing active layer (Tarnocai et al., 2011), but are increasingly vulnerable to thaw due to climate change. Following the thaw of permafrost-affected peatlands, the hydrology of the landscape changes, potentially shifting the peat C balance and perturbing the climate system (Varner et al., 2022). As northern permafrost thaws, degradation features develop, including thaw lakes and increased active layer thickness



(Swindles et al., 2015). In response, some areas in the landscape can become water-saturated with ice melt and higher seasonal water tables (Rydin and Jeglum, 2013). However, drier conditions may also occur with thaw depending on the season or position in the landscape (Boike et al., 2016; Lawrence et al., 2015). For example, temperature-driven increases in evapotranspiration are expected to impart drier conditions on the surface layer of bogs and fens, especially in the summer, and faster drainage may occur with higher hydraulic conductivity following the thaw of underlying ground ice (Lee et al., 2014).

The degree to which permafrost thaw amplifies the release of microbial-produced greenhouse gases (GHGs) into the atmosphere, exacerbating the global greenhouse effect, will partly depend on whether peat becomes wetter or drier (Kane et al., 2013). Carbon dioxide (CO₂) is the dominant respired gas under drier, aerobic conditions, whereas methane, with a comparatively shorter residence time but higher global warming potential, is more prevalent under wetter, anaerobic conditions (Schädel et al., 2016). If a water-saturated ecosystem experiences drying, an increase in more efficient, aerobic microbial metabolism with subsequently higher CO₂ production is expected, but this assumes the microbial community will not become C- or moisture-limited. Recent studies have also demonstrated hot spots of permafrost nitrous oxide (N₂O) production with fluctuations between aerobic and anaerobic moisture conditions, challenging past assumptions that permafrost soils lose a negligible amount of nitrogen (N) to N₂O (Ramm et al., 2022; Voigt et al., 2020). Under wetter conditions, N₂O is primarily produced during incomplete denitrification of nitrate. However, anoxic, water-saturated conditions can also inhibit nitrification (and thus nitrate availability), and reduction of N₂O to N₂ can be favoured. With drier or more intermediate moisture conditions, N₂O can be produced via nitrification, so it is possible that a drier permafrost environment can induce N₂O production through enhanced nitrification (Gil et al., 2017).

In heterogenous permafrost environments, where limitations to microbial metabolism can be site-specific, GHG responses to warming or availability of C, nutrients, or O₂ is not necessarily similar across the landscape, as previously demonstrated in numerous lab incubations (Laurent et al., 2023; Schädel et al., 2014; Treat et al., 2013). However, to our knowledge, no study has isolated the effect of gradual drying, often an overlooked result of permafrost thaw, on GHG production across landscape features that vary in their moisture and C and N availability. We conducted an incubation to determine the relationship between experimental short-term gradual drying and the magnitude of CO₂ and N₂O gas production across a northern peatland thaw gradient and how drying affects the CO₂ isotopic signatures. We interpreted these isotopic signatures as a signal of the C source respired under drier conditions. Methane was not measured since experimental conditions were not anoxic, required for methanogenesis. We expected that 1) gradual drying will increase CO₂ and N₂O production in wetter fens and bogs compared to drier peat plateaus that could become C-limited more rapidly and 2) a decrease in moisture conditions will increase the enrichment of ¹³C-CO₂, possibly reflecting the metabolism of less decomposed peat.



2 Material and Methods

65 2.1. Study Site

The Lutose peatland study site (59.5°N, 117.2°W) is in Alberta, Canada, within the discontinuous permafrost zone (Heffernan et al., 2020). In this region, permafrost peatlands, with 2–6 m deep peat deposits, cover ~40% of the landscape (Vitt et al., 2000). We studied two transects, from a peat plateau to a bog and from a peat plateau to a fen (Fig. 1). These transects represent a space-for-time permafrost thaw gradient with distinct landscape features developing across thaw stages (Heffernan et al., 2020). For the bog transect, these features include a permafrost peat plateau, a young bog (~30 years since thaw), and a mature bog (~200 years since thaw). The peat plateau has an active layer thickness of ~70 cm, and its surface is raised 1–2 m above the adjacent thermokarst bogs and fens, and has relatively dry surface conditions that deepen with seasonal thaw (Table S1). The young bog (<5 – 10 m wide) is adjacent to the actively thawing area of the peat plateau and has a high growing season water table just below the peat surface. The mature bog, located >10 – 20 m from the thawing plateau edge, is drier with a lower growing season water table than the young bog (Table S1).

Similarly, in the fen transect, three thaw stages are represented: a permafrost peat plateau, a fen center, and a fen edge. Like the young bog, the fen edge is located where the plateau surface has collapsed. The water table is level with the surface and the peat surface is likely under anaerobic conditions (Heffernan et al., 2024). The fen center also has a high water table but has accumulated new peat material. The fen's relatively wetter conditions and higher pH (Table S1) result from its additional upstream water sources. In October 2019, we collected four separate peat samples from 5–20 cm at each transect point for a total of 24 cores. Cores were immediately stored on ice, shipped to McGill University, Quebec, and kept at -20 °C until the incubation.

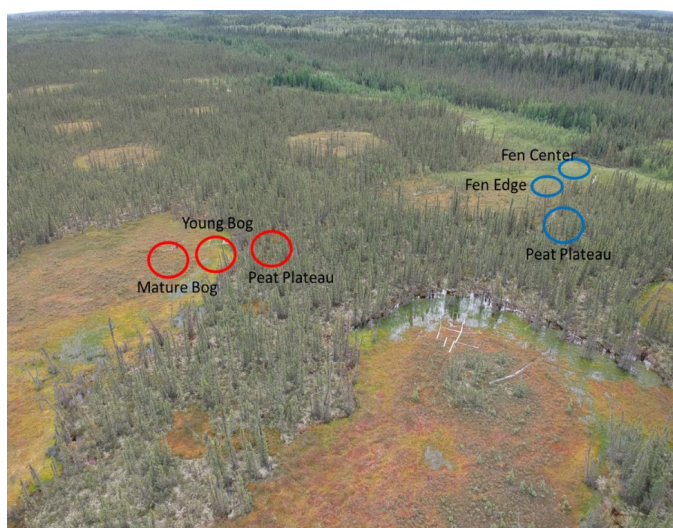


Figure 1. The Lutose peatland study site (Alberta, Canada) and the studied bog and fen transects with sample locations indicated by blue (fen) and red (bog) circles.



2.2 Incubation Design for Gradual Drying Experiment

We incubated the thawed (at 4 °C) peat samples from the four replicated cores collected within each transect site: Mature Bog (MB), Young Bog (YB), Peat Plateau 1 (PP1), and Fen Center (FC), Fen Edge (FE), and Peat Plateau 2 (PP2). For each sample, the sample core was homogenized and then 0.52–4.84 g of dry peat was weighed into a sterile specimen cup and placed in 1 L sealed mason jars with a septum gas sampling port. To create gradual drying conditions for our drying treatment, half of the incubations contained 150 g of calcium sulfate Drierite (>98% CaSO₄, <2% CoCl₂; 10-20 mesh) outside of the specimen cup that held the peat sample. This approach allowed us to slowly reduce peat moisture content without opening the incubation jars to maintain experimental headspace concentrations. Control incubations at field moisture conditions were maintained similarly but without the Drierite. In addition, we applied the same incubation treatments to a subset of samples to monitor changes in peat moisture during the incubation. We incubated the samples in the dark at 20 °C for two weeks, maintaining the incubation jar seal throughout the 2-week period. Frequent CO₂ measurements ensured the jars were maintained below a 3% CO₂ threshold of high headspace gas concentrations.

2.3 Gas Sampling and Peat Moisture

We sampled headspace CO₂ and N₂O at the following hourly time points during the two-week incubation: 0, 6, 24, 48, 96, 168, 240, and 336 h. At each time, 12 mL of gas was sampled with a syringe and stored in evacuated 9 mL vials. The second subset of incubating samples was massed for gravimetric water content at those same time points to produce a peat moisture curve over the incubation period. In addition, at times 0 and 336 h (i.e., the beginning and end of the incubation), we collected 20 mL of gas for isotope analysis stored in evacuated 12 mL vials.

2.4 Total and Isotopic Emission Quantification

We analysed total CO₂ and N₂O by gas chromatography (Shimadzu GC-2014, Shimadzu Scientific Instruments, Columbia, United States). For δ¹³C-CO₂, we analysed three analytical replicates of 20 mL gas on a Picarro G2201-i Carbon Isotope Analyzer connected to a sample introduction module. We calibrated the instrument using three internal CO₂ gas standards (-15.6‰, -28.5‰, and -43.2‰) (Stix et al., 2017).

The δ¹³C of the input C source in the headspace gas was calculated with the following mixing model:

$$\delta^{13}C_{input} = \frac{\delta^{13}C_{final} - (\delta^{13}C_{lab\ air} * Fraction\ lab\ air)}{1 - Fraction\ lab\ air}$$

The *fraction of lab air* was calculated by dividing the CO₂ concentration at time 0 by that at the time of sampling.



To ensure the $\delta^{13}\text{C}$ - CO_2 of the headspace gas was not an artifact of the Drierite, we ran another two-week incubation
115 with Drierite and without peat, and a control with no Drierite or peat. To simulate the high CO_2 concentrations experienced
in the original incubations due to peat respiration, we added 60 mL of 5% CO_2 gas to the unevacuated Drierite and control
jars. Samples from the start and end of the 336 hours were analyzed on the Picarro Carbon Isotope Analyzer. We found that
the Drierite had no significant effect on the ^{13}C isotope composition (mean δ -16.8) compared to the control (mean δ -17.14)
($p=0.07$), or on the Drierite test CO_2 concentrations (mean 1589 ppm) compared to the mean 1523 ppm for the control (p =
120 0.31). Thus, we ruled out the possibility that changes in incubation $\delta^{13}\text{C}$ or CO_2 ppm values were an artifact of the drying
agent.

2.5 Peat Chemistry and Isotopic Composition

We measured 1M KCl-extractable nitrate and ammonium colorimetrically on all peat samples immediately before and after
the incubations. Ammonium and nitrate concentrations in KCl extracts were determined colorimetrically on a 96-well
125 spectrometer (BioTek Synergy Microplate Reader, Santa Clara, CA, USA) with the wavelength set at 650 and 540 nm
respectively. We measured peat $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, total carbon (TC), and total nitrogen (TN) on ground oven-dried peat at the
Geotop Stable Isotope Laboratory at the Université du Québec à Montréal using an Elementar Vario MicroCube Elemental
Analyzer and, for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, coupled with a Micromass model Isoprime 100 isotope ratio mass spectrometer. Results are
expressed as $\delta^{13}\text{C}$ values in ‰ vs. VPDB (Vienna Pee Dee Belemnite) and as $\delta^{15}\text{N}$ in ‰ vs. AIR (Coplen, 2011).

130 2.6 Statistical Analyses

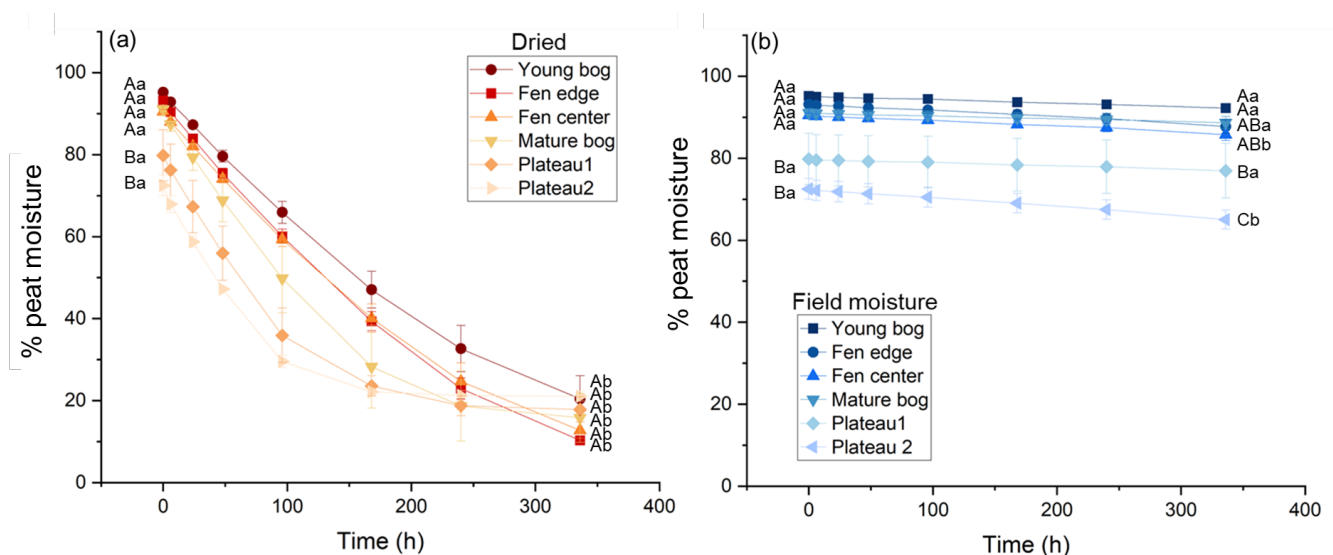
Means and standard errors were calculated in Matlab and field cores within each transect point were treated as replicates
($n=4$). Data was checked to ensure homogeneity and normalcy. To test the influence of landscape feature and drying on
cumulative gas concentrations, $\delta^{13}\text{C}$ - CO_2 , peat C:N, and moisture content, we performed 2-way ANOVA tests, using
landscape position and moisture treatment as fixed effects in RStudio (v4.3.2). To compare changes in peat moisture and
135 CO_2 and N_2O production over time and between moisture treatments, a two-way repeated measures ANOVA was performed
within each landscape feature, using the Greenhouse-Geisser test for significant effect. Moisture and time were treated as
factors and peat core/incubation jar was the subject of repeated measures. We determined mean differences with Tukey's
tests. Lastly, we examined the relationships between changes in peat moisture with drying and CO_2 production based on the
 r^2 and linear fit ANOVA p -value from linear regressions. Significance is reported at $\alpha=0.05$.



140 3 Results and Discussion

3.1 Initial and Final Peat Moisture

At the beginning of the incubation, peat moisture ranged from 73–95%. Initial field moisture was lowest in the peat plateaus compared to the fen and bogs ($p < 0.001$) (Fig. 2), consistent with other studies from this field site (Heffernan et al., 2024, 2024). In the treatments maintained at field moisture conditions, changes in peat moisture during the two-week period were minimal (Fig. 2b). In the gradual drying treatment, peat moisture declined consistently over time across all the landscape features, except for the peat plateaus which stopped losing moisture at the end of the first week (168 h). Following two weeks of drying, peat moisture was between 10–21%, representing a 71–89% moisture reduction, and was similar across landscape features ($p = 0.301$).



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Figure 2. Mean peat moisture over incubation time for each landscape feature under gradual drying (a) or maintained at field moisture conditions (b). More color saturation indicates higher *in situ* moisture. Uppercase letters that are different within each panel indicate a significant difference across landscape features for initial and final moisture. Lowercase letters that are different within each panel indicate a significant difference between initial and final moisture within a landscape feature.

155 Error bars are standard error around the mean, $n=4$.

3.2 Landscape Feature Effects on CO₂ and N₂O

We observed that the YB, followed by the FC and FE, produced the most total CO₂-C over the two-week incubation (9.06–14.4 mg g⁻¹ dry weight) across moisture treatments (Fig. 3a; Fig. S1). We suspect this higher CO₂ production reflects

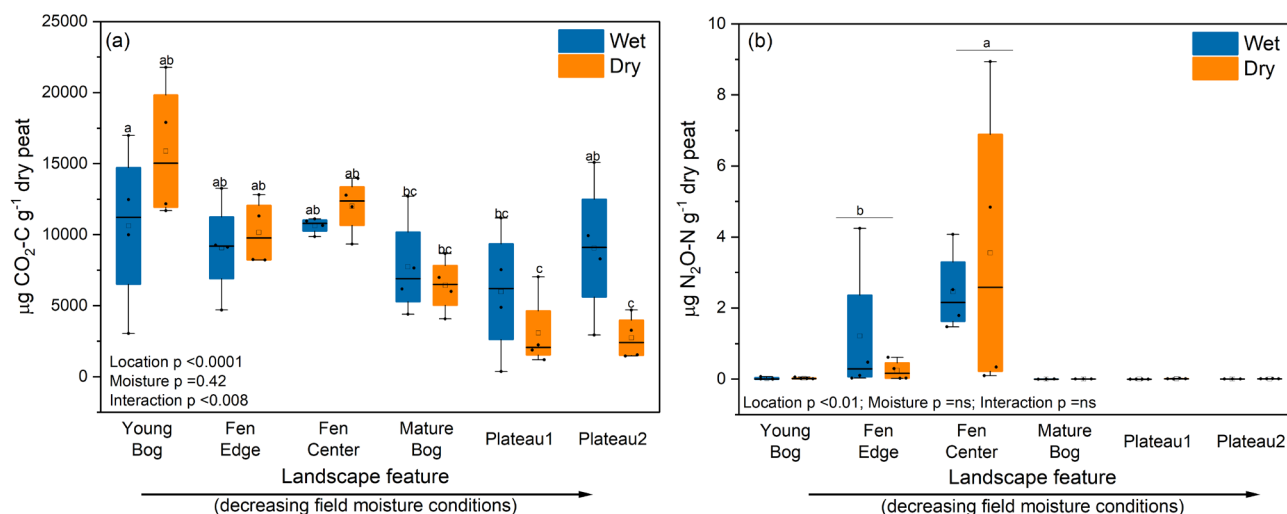


160 the more labile plant inputs in the fen and young bog, and thus more decomposable peat (Table S1) that can support elevated microbial respiration, despite the potential for lower oxygen availability under the field moisture conditions.

We only detected N₂O emissions from the fen center and fen edge, and these were highly variable (0.03–8.3 μg N₂O-N g⁻¹ dry peat h⁻¹), with no effect of drying (Fig. 3b; Fig. S2). This is in contrast to a recent review that showed lower N₂O production in wetland permafrost compared to upland permafrost sites (e.g. peat plateaus), which they attributed to a combination of inhibited nitrification and more complete denitrification to N₂ (Voigt et al., 2020). However, in our sites, initial nitrate concentrations indicate nitrification potential and we do not expect that our incubations were either water-saturated or N-limited enough to cause complete denitrification during the incubation. While the sedge-dominated fens had similar concentrations of inorganic N concentrations to the bogs, they had the lowest C:N (<25) and the highest %TN (Table S1). This may contribute to rapid N cycling and thus higher N₂O production during the incubation, whereas the *sphagnum*-dominated bogs are potentially more N-limited based on the observed higher C:N and more depleted ¹⁵N (Klemmedtsson et al., 2005; Liao et al., 2021). The peat plateaus and bogs at the same study site were previously found to be N₂O sinks (e.g. consumption of N₂O to N₂) *in situ* where anaerobic conditions occur (Schulze et al., 2023). Our observed N₂O emissions from the fen center are considerably elevated for this region, and within the range of many temperate fertilized ecosystems (Elberling et al., 2010). These results further support the emerging evidence that permafrost ecosystems have N₂O hotspots that should be accounted for in estimating the global warming potential of GHG production.

175 3.3 Effects of Drying on CO₂ Production

We observed an effect of gradual drying on cumulative CO₂ production within each site, though it did not consistently impart a negative or positive forcing on CO₂ production. Rather, drying reduced CO₂ in the peat plateaus but marginally increased total CO₂ production for the YB, FC, and FE sites (Fig. 3a) (interaction p < 0.008).





180 **Figure 3.** Cumulative CO₂ (a) and N₂O (b) production by moisture treatment and landscape feature ordered from high to low *in situ* peat moisture. Wet treatments were incubated at field moisture conditions, and dry treatments were incubated under gradual drying. ANOVA p-values are shown for each factor and their interaction. Horizontal lines show the median (n=4) and boxes show the 25th and 75th percentiles. Means that do not share a same letter are significantly different.

185 Further supporting this site-dependent effect of drying on CO₂ production, a decrease in % peat moisture was strongly negatively correlated with increasing CO₂ and the strength of this relationship was strongest in the wettest sites ($r^2 > 0.8$), declining as *in situ* moisture also declined (Fig. 4). We also found a strong, positive correlation between field moisture and the difference in cumulative CO₂ emissions between treatments at the same site (Fig. 4). At initial peat moisture above 90%, gradual drying increased cumulative CO₂ emissions— conversely, below 90%, drying decreased cumulative CO₂. This suggests that a threshold exists for optimum peat moisture that affects the trajectory of microbial respiration responses to

190 short-term gradual drying.

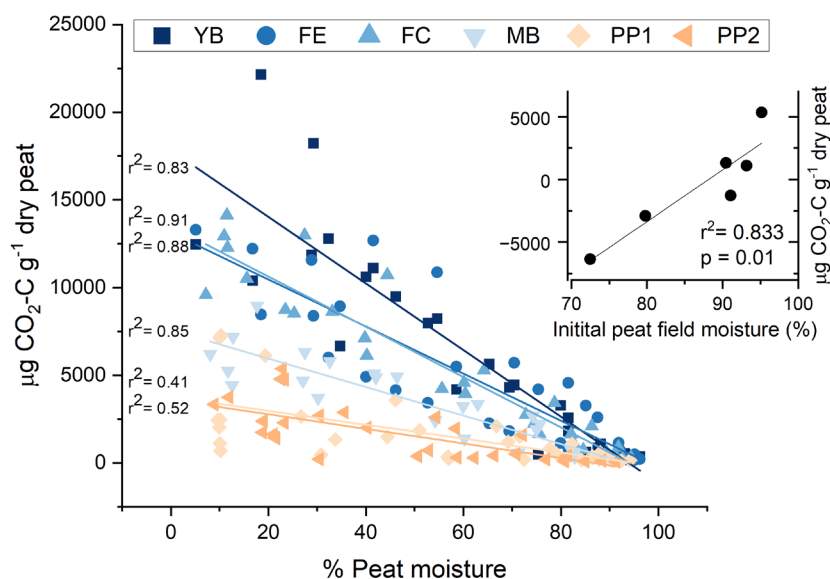


Figure 4. Linear regression of CO₂ production and peat moisture. Points are individual peat samples measured at 8 time periods while exposed to drying for 2 weeks. Landscape features are indicated by different colors and symbols in order of sites with the wettest to driest *in situ* field moisture conditions: young bog (YB), fen edge (FE), fen center (FC), mature bog (MB), peat plateau 1 (PP1), and peat plateau 2 (PP2). The inset is a regression of the mean initial peat field moisture and the absolute change in total CO₂-C after 2 weeks of gradual drying.

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The site differences in total CO₂ production reflect what was observed in CO₂ production over time where, as the *in situ* peat moisture of the landscape feature became progressively drier, a negative impact of drying on CO₂ production emerged

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(Fig. S3), occurring relatively early (within the first week) in the peat plateaus ($p < 0.005$). Generally, CO_2 production increased linearly over time, regardless of the moisture treatment (Fig. S3). The PP2 (fen transect) was the exception, where after 1.5 weeks we no longer observed significant increases in net CO_2 production.

Our short-term experimental drying would allow for increased aerobic respiration in initially inundated or near-saturated environments, like the YB and FE. However, all our landscape features had similar moisture after drying. Thus, the wetter features (YB, FE) that responded positively to drying were likely influenced by other microbial metabolic drivers that coincide with moisture. For example, more microbial available C is more likely to accumulate in wetter sites than in the drier peat plateaus, where aerobic metabolism would be less constrained, reducing readily available C supply (Treat et al., 2014). Drying the peat plateaus may have thus suppressed CO_2 production because C became limited faster than at the wetter sites. Thus, it was not necessarily moisture conditions during the incubation driving our opposing responses, but rather the initial moisture conditions and covarying factors such as C availability and reactivity specific to each landscape feature.

Some studies suggest that drier, more oxic permafrost peatlands contribute more to the positive carbon-climate feedback effect than anoxic soils because of the higher rates of CO_2 production (Schädel et al., 2016; Schuur et al., 2015; but see Knoblauch et al., 2018). Our data suggest it is more nuanced than this where, all else being equal, lower moisture by itself may reduce CO_2 in less degraded peat plateaus. At the same time, due to enhanced evapotranspiration, the edges of bogs and fens which form with thaw and the collapse of peat plateaus, are expected to experience drying first, which our results imply may increase CO_2 emissions from those sites. While we cannot account for the influence of vegetation or anoxic conditions that could enhance methane production, the potential outflux of C associated with hydrological changes may thus initially only be amplified from surface peat within permafrost collapse features, and not from more stable permafrost plateaus.

3.3 Respired Peat $\delta^{13}\text{C-CO}_2$

We observed a consistent and significant drying-induced trend in $\delta^{13}\text{C-CO}_2$ (Fig. 5). Within each landscape feature, gradual drying produced cumulative CO_2 with relatively higher $\delta^{13}\text{C}$ than the field-moist peat, although differences in $\delta^{13}\text{C}$ for the peat plateaus were insignificant.

The substantially higher $\delta^{13}\text{C-CO}_2$ with drying implies that the C sources being respired change systematically in response to drying. One potential explanation is that, under drier conditions, decomposition shifts away from *sphagnum*-derived peat that can be relatively $\delta^{13}\text{C}$ -depleted due to its symbiosis with methanotrophs (Kip et al., 2010). However, the mechanism leading to a possible shift away from sphagnum decomposition towards other more enriched- ^{13}C sources is unclear.

More generally, $\delta^{13}\text{C-CO}_2$ enrichment could signal a shift towards respiration of more decomposed peat under drying. Typically, more decomposed C is expected to be enriched in ^{13}C (Agren et al., 1996) due to selective microbial respiration of ^{12}C . Under high moisture, especially near saturation, metabolism of highly decomposed peat may be energetically



unfavorable. Improved aeration of the dried peat would lead to more oxidizing conditions, allowing for the mineralization of more decomposed C with greater $\delta^{13}\text{C}$ enrichment (Alewell et al., 2011). This might explain why we see less isotopic differentiation in the peat plateaus where initial moisture was less limiting to aerobic decomposition. Previous studies have also shown that older, more degraded peat experienced greater degradation under reduced peat moisture conditions (Hardie et al., 2011). Overall, the isotopic data imply that changes in CO_2 production with drying are likely associated with a shift from decomposition of fresh plant-derived substrates, including *sphagnum*, to more degraded peat. Future incubations involving ^{14}C measurements could indicate whether this also entails a shift to the decomposition of older peat C pools.

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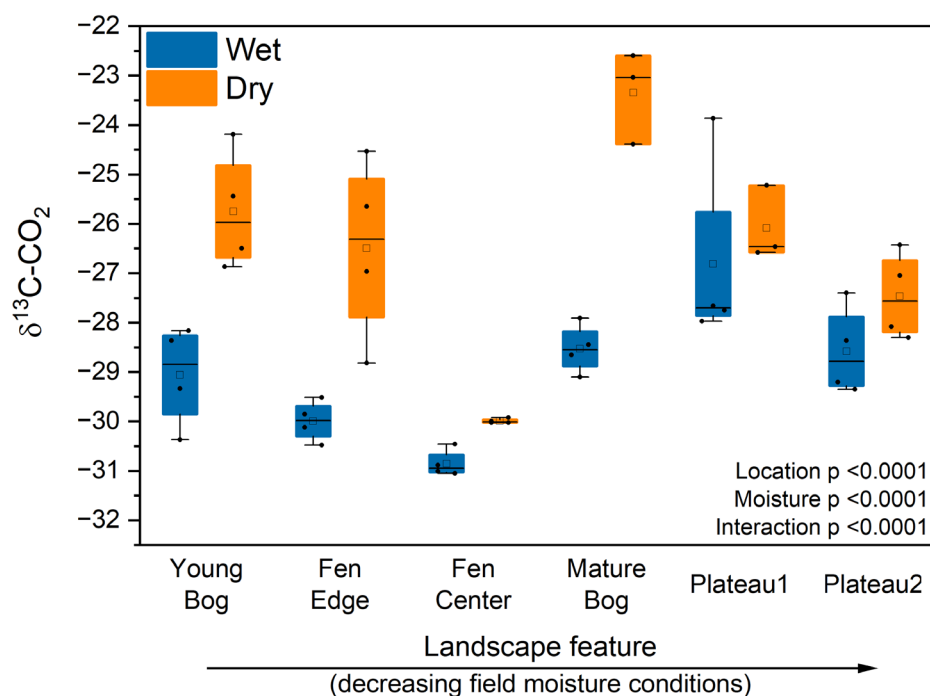


Figure 5. Cumulative $\delta^{13}\text{C-CO}_2$ by landscape feature and moisture treatment. Landscape features are ordered from high to low average *in situ* peat moisture. Wet moisture treatments were incubated at field moisture conditions and dry moisture treatments were incubated under gradual drying. Horizontal lines show the median ($n=4$) and boxes show the 25th and 75th percentiles. Means that do not share a same letter are significantly different.

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4 Conclusion

As permafrost thaws, changes to hydrologic conditions and atmospheric temperatures lead to moisture loss from peat in some circumstances, influencing microbial CO_2 and N_2O production. We establish the importance of initial peat moisture on



250 the effect that short-term gradual drying imparts on cumulative CO₂ emissions. Respiration is enhanced by drying in
relatively wet sites and depressed by drying in relatively dry sites. Thus, as some permafrost systems undergo drying
following thaw, the CO₂ response and subsequent loss of peat C may depend on antecedent moisture conditions, whereas
N₂O emissions may be largely controlled by total N availability. Furthermore, gradual drying increased the ¹³C respiration,
suggesting a shift to more decomposed, potentially older C mineralized with peat drying, implying the loss of previously
255 stable peat C reservoirs.

Author Contribution

AS helped conceive the experimental approach, was the primary person conducting the experiment, lab and data analyses,
wrote the first draft of the manuscript, and contributed to subsequent drafts; CMK helped conceive the experimental
260 approach, and contributed to funding, data interpretations, and writing of all subsequent drafts; MSB helped design the
experimental approach, conducted some of the experiment, and contributed to the writing; DO and CS collected the samples
and data of the field sites, and contributed to the developed of the experiment and writing; RM contributed to the developed
of the ideas for the experiment, laboratory analyses, and writing; PMJD contributed to funding, conceiving the experimental
approach, data interpretations, and writing of all subsequent drafts.

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Data Availability

All relevant data to this study can be accessed at from “Data collected from Lutose, Alberta surface peat permafrost
samples”, <https://doi.org/10.5683/SP3/J6YIEJ>, Borealis, V2.

270 Supplemental Material

The supplemental material related to this article is available online at: Xxxxxx

Conflict of Interest

The authors have no conflict of interest related to this research to declare.

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References

- Ågren, G.I., Bosatta, E. and Balesdent, J., 1996. Isotope discrimination during decomposition of organic matter: a theoretical analysis. *Soil Science Society of America Journal*, 60(4), pp.1121-1126.
- 285
- Alewell, C., Giesler, R., Klaminder, J., Leifeld, J. and Rollog, M., 2011. Stable carbon isotopes as indicators for environmental change in peatlands. *Biogeosciences*, 8(7), pp.1769-1778.
- Boike, J., Grau, T., Heim, B., Günther, F., Langer, M., Muster, S., Gouttevin, I. and Lange, S., 2016. Satellite-derived changes in the permafrost landscape of central Yakutia, 2000–2011: Wetting, drying, and fires. *Global and Planetary Change*, 139, pp.116-127.
- 290
- Bush, E. and Lemmen, D.S., editors. 2019. *Canada's Changing Climate Report*; Government of Canada, Ottawa, ON. <https://doi.org/10.4095/314614>.
- 295
- Coplen, T.B., 2011. Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results. *Rapid communications in mass spectrometry*, 25(17), pp.2538-2560.
- Elberling, B., Christiansen, H.H. and Hansen, B.U., 2010. High nitrous oxide production from thawing permafrost. *Nature Geoscience*, 3(5), pp.332-335.
- 300
- Gil, J., Pérez, T., Boering, K., Martikainen, P.J. and Biasi, C., 2017. Mechanisms responsible for high N₂O emissions from subarctic permafrost peatlands studied via stable isotope techniques. *Global Biogeochemical Cycles*, 31(1), pp.172-189.
- 305
- Hardie, S.M.L., Garnett, M.H., Fallick, A.E., Rowland, A.P., Ostle, N.J. and Flowers, T.H., 2011. Abiotic drivers and their interactive effect on the flux and carbon isotope (¹⁴C and ^δ¹³C) composition of peat-respired CO₂. *Soil Biology and Biochemistry*, 43(12), pp.2432-2440.
- Heffernan, L., Estop-Aragónés, C., Knorr, K.H., Talbot, J. and Olefeldt, D., 2020. Long-term impacts of permafrost thaw on carbon storage in peatlands: Deep losses offset by surficial accumulation. *Journal of Geophysical Research: Biogeosciences*, 125(3), p.e2019JG005501.
- 310



- Heffernan, L., Estop-Aragonés, C., Kuhn, M.A., Holger-Knorr, K. and Olefeldt, D., 2024. Changing climatic controls on the greenhouse gas balance of thermokarst bogs during succession after permafrost thaw. *Global Change Biology*, 30(7), p.e17388.
- 315
- Hugelius, G., Loisel, J., Chadburn, S., Jackson, R.B., Jones, M., MacDonald, G., Marushchak, M., Olefeldt, D., Packalen, M., Siewert, M.B. and Treat, C., 2020. Large stocks of peatland carbon and nitrogen are vulnerable to permafrost thaw. *Proceedings of the National Academy of Sciences*, 117(34), pp.20438-20446.
- 320
- Kane, E.S., Chivers, M.R., Turetsky, M.R., Treat, C.C., Petersen, D.G., Waldrop, M., Harden, J.W. and McGuire, A.D., 2013. Response of anaerobic carbon cycling to water table manipulation in an Alaskan rich fen. *Soil Biology and Biochemistry*, 58, pp.50-60.
- 325
- Kip, N., Van Winden, J.F., Pan, Y., Bodrossy, L., Reichart, G.J., Smolders, A.J., Jetten, M.S., Damsté, J.S.S. and Op den Camp, H.J., 2010. Global prevalence of methane oxidation by symbiotic bacteria in peat-moss ecosystems. *Nature Geoscience*, 3(9), pp.617-621.
- 330
- Klemetsson, L., von Arnold, K., Weslien, P., Gundersen, P., 2005. Soil CN ratio as a scalar parameter to predict nitrous oxide emissions. *Global Change Biology* 11, 1142–1147.
- Knoblauch, C., Beer, C., Liebner, S., Grigoriev, M.N. and Pfeiffer, E.M., 2018. Methane production as key to the greenhouse gas budget of thawing permafrost. *Nature Climate Change*, 8(4), pp.309-312.
- 335
- Lawrence, D.M., Koven, C.D., Swenson, S.C., Riley, W.J. and Slater, A.G., 2015. Permafrost thaw and resulting soil moisture changes regulate projected high-latitude CO₂ and CH₄ emissions. *Environmental Research Letters*, 10(9), p.094011.
- Laurent, M., Fuchs, M., Herbst, T., Runge, A., Liebner, S. and Treat, C.C., 2023. Relationships between greenhouse gas production and landscape position during short-term permafrost thaw under anaerobic conditions in the Lena Delta. *Biogeosciences*, 20(11), pp.2049-2064.
- 340
- Lee, H., Swenson, S.C., Slater, A.G. and Lawrence, D.M., 2014. Effects of excess ground ice on projections of permafrost in a warming climate. *Environmental Research Letters*, 9(12), p.124006.
- 345
- Liao K, Lai X, Zhu Q. Soil $\delta^{15}\text{N}$ is a better indicator of ecosystem nitrogen cycling than plant $\delta^{15}\text{N}$: A global meta-analysis. *Soil*. 2021 Oct 28;7(2):733-42.



Ramm, E., Liu, C., Ambus, P., Butterbach-Bahl, K., Hu, B., Martikainen, P.J., Marushchak, M.E., Mueller, C.W.,
Rennenberg, H., Schloter, M. and Siljanen, H.M., 2022. A review of the importance of mineral nitrogen cycling in the plant-
350 soil-microbe system of permafrost-affected soils—changing the paradigm. *Environmental Research Letters*, 17(1), p.013004.

Rydin, H., Jeglum, J.K. and Bennett, K.D., 2013. *The biology of peatlands*, 2e. OUP Oxford.

Schädel, C., Schuur, E. A. G., Bracho, R., Elberling, B., Knoblauch, C., Lee, H., Luo, Y., Shaver, G. R., and Turetsky, M.
355 R., 2014. Circumpolar assessment of permafrost C quality and its vulnerability over time using long-term incubation data,
Global Change Biology, 20 (2), pp.641–652.

Schädel, C., Bader, M.K.F., Schuur, E.A., Biasi, C., Bracho, R., Čapek, P., De Baets, S., Diáková, K., Ernakovich, J., Estop-
Aragones, C. and Graham, D.E., 2016. Potential carbon emissions dominated by carbon dioxide from thawed permafrost
360 soils. *Nature Climate Change*, 6(10), pp.950-953.

Schulze, C., Sonnentag, O., Voigt, C., Thompson, L., van Delden, L., Heffernan, L., Hernandez-Ramirez, G., Kuhn, M., Lin,
S. and Olefeldt, D., 2023. Nitrous oxide fluxes in permafrost peatlands remain negligible after wildfire and thermokarst
disturbance. *Journal of Geophysical Research: Biogeosciences*, 128(4), p.e2022JG007322.

365

Schuur, E.A., McGuire, A.D., Schädel, C., Grosse, G., Harden, J.W., Hayes, D.J., Hugelius, G.,
Koven, C.D., Kuhry, P., Lawrence, D.M. and Natali, S.M., 2015. Climate change and the permafrost carbon feedback.
Nature, 520(7546), pp.171-179.

370 Stix, J., Lucic, G. and Malowany, K., 2017. Near real-time field measurements of $\delta^{13}\text{C}$ in CO_2 from volcanoes. *Bulletin of
Volcanology*, 79, pp.1-10.

Swindles, G.T., Morris, P.J., Mullan, D., Watson, E.J., Turner, T.E., Roland, T.P., Amesbury, M.J., Kokfelt, U., Schoning,
K., Pratte, S. and Gallego-Sala, A., 2015. The long-term fate of permafrost peatlands under rapid climate warming. *Scientific
375 Reports*, 5(1), pp.17951.

Tarnocai, C., Kettles, I.M., and Lacelle, B., 2011. *Peatlands of Canada*; Geological Survey of Canada, Open File 6561; CD-
ROM. doi:10.495/288786



380 Treat, C.C., Wollheim, W.M., Varner, R.K., Grandy, A.S., Talbot, J. and Frolking, S., 2014. Temperature and peat type control CO₂ and CH₄ production in Alaskan permafrost peats. *Global Change Biology*, 20(8), pp.2674-2686.

Varner, R.K., Crill, P.M., Frolking, S., McCalley, C.K., Burke, S.A., Chanton, J.P., Holmes, M.E., Isogenie Project Coordinators, Saleska, S. and Palace, M.W., 2022. Permafrost thaw driven changes in hydrology and vegetation cover
385 increase trace gas emissions and climate forcing in Stordalen Mire from 1970 to 2014. *Philosophical Transactions of the Royal Society A*, 380(2215), p.20210022.

Vitt, D.H., Halsey, L.A., Bauer, I.E. and Campbell, C., 2000. Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. *Canadian Journal of Earth Sciences*, 37(5), pp.683-693.

390

Voigt, C., Marushchak, M.E., Abbott, B.W., Biasi, C., Elberling, B., Siciliano, S.D., Sonnentag, O., Stewart, K.J., Yang, Y. and Martikainen, P.J., 2020. Nitrous oxide emissions from permafrost-affected soils. *Nature Reviews Earth & Environment*, 1(8), pp.420-434.

395