

Fire History and Long-Term Carbon Accumulation in Hemi-boreal Peatlands

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ABSTRACT

Fire can play an important role in peatlands by modifying plant communities and carbon (C) stocks. However, baseline disturbance data on peatland fire history are lacking in the hemi-boreal region. We sampled 29 peatlands in northern Michigan, Wisconsin, and Minnesota and used peat core records, radiocarbon dating, and infrared spectrometry to identify and date past fire events in 4 major hemi-boreal peatland ecotypes including open poor fens, treed poor fens, forested poor fens, and forested rich fens. In this region all types of poor fens had widely variable fire frequencies between sites. The poor fens experienced 2.1 fires per thousand years, or once every 476 years, on average, while the rich fens experienced almost no fire. Overall C stocks ranged from 10.1 to 263.3 kg C m⁻² with a mean of 94.6 and median of

90.5 kg C m⁻². The long-term apparent rate of carbon accumulation (LARCA) varied between 10–45 g m⁻² y⁻¹ with an average of 28 g m⁻² y⁻¹. We found a significant negative relationship between fire frequency and LARCA. Our research indicates that fire frequency is not consistent across peatland types and increases in fire frequency will likely diminish peat C stocks. These findings provide a historical context for management decisions concerning wildland fires and their consequences for ecosystem C storage in hemi-boreal peatlands.

Key words: long-term apparent rate of carbon accumulation; LARCA; radiocarbon; disturbance; carbon cycle; histosol; wildfire; infrared spectrometry.

HIGHLIGHTS

- We analyzed the fire history of 29 peatlands in hemi-boreal North America
- Poor fens had a fire return interval of 476 years, rich fens had almost no fire
- Poor fens exhibited a negative relationship between LARCA and fire frequency

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Author Contributions DMU, ESK, and RAC conceived and designed the study and edited the paper. DMU performed the research, analyzed the data, and wrote the paper. KAH provided technical expertise, analyzed data, and edited the paper.

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INTRODUCTION

Fire is a significant ecological driver in many peatland types (Turetsky and St. Louis 2006). Fire influences hydrology through consumption of peat layers, reducing depth to the water table and driving changes in vegetation community composition (Benscoter and Vitt 2008; Sillasoo and others 2011; Benscoter and others 2015; Rowe and others 2017). While much has been done to understand how fire disturbances reset ecological trajectories in upland boreal forests (Johnson 1992; Johnstone and others 2010, 2016; Baltzer and others 2021), our understanding of how changes in fire frequency affect peatland structure and function is incipient (Loisel and others 2021). Fire has been shown to enhance microtopographic heterogeneity in peatlands (Benscoter and others 2015), which in turn enhances ecological diversity by maintaining niches for various *Sphagnum* species, among other mosses, sedges, shrubs, and trees. Collectively, these changes in ecosystem properties with fire frequency and time since fire have strong controls over the persistence of peatland soils (Wieder and others 2009; Kolka and others 2016).

Changes in fire frequency in peatland ecosystems exert considerable control over many ecosystem processes, which ultimately govern peatland soil C storage (Turetsky and others 2002, 2015; Loisel and others 2021). This is an important consideration because peatlands serve as long-term carbon (C) sinks, containing vast amounts of C, between 545 to 1055 Pg C globally (Nichols and Peteet 2019). Peat fires can, in extreme hydrological conditions, burn meters deep into organic soils but boreal peatlands typically burn up to 13 cm, releasing $\sim 3.3\text{--}3.6 \text{ kg C m}^{-2}$ of C (Turetsky and others 2011; Dieleman and others 2020; Walker and others 2020a). This has at least a transient negative impact on C storage which is incurred by each fire, so determining fire frequency is important for understanding the C sink strength of peatlands.

The long-term apparent rate of carbon accumulation (LARCA) in peatlands generally ranges from 0 to $60 \text{ g C m}^{-2} \text{ y}^{-1}$ (Clymo and others 1998; Pitkänen and others 1999; Loisel and others 2014), but is typically around $20 \text{ g C m}^{-2} \text{ y}^{-1}$ (Kolka and others 2018). Pitkänen and others noted a positive relationship between the spacing of char layers (implicitly related to fire frequency) and LARCA in Finland (Pitkänen and others 1999), a pattern which was also shown in a discontinuous permafrost region in Northwest Territories, Canada (Robinson and Moore 2000). Together, these findings agree with research in upland boreal sys-

tems suggesting that an increased fire return interval reduces long-term C accumulation (Bond-Lamberty and others 2007; Walker and others 2019), but to our knowledge this has not been examined in the hemi-boreal peatlands of North America.

Few studies in boreal or hemi-boreal regions have quantitatively estimated peatland fire frequency, often finding wide ranges even within the same soil profile. Within North America, a few studies suggest a wide range between 0 and 13 fires per thousand years (ka^{-1}) (Kuhry 1994; Wieder and Vitt 2010), with large variation across ecoregions (Walker and others 2020b). Studies in Finnish peatlands have also produced wide ranges from $2.3\text{--}33.3 \text{ fires ka}^{-1}$ (Pitkänen and others 2001), $1.7\text{--}10 \text{ fires ka}^{-1}$ (Pitkänen and others 1999), and a narrower estimate of $11.9\text{--}12.5 \text{ fires ka}^{-1}$ (Tolonen 1985). The use of upland proxies, dendrochronological records from uplands adjacent to or even within peatland complexes, can provide another perspective on peatland fire regimes, hopefully capturing higher frequency, lower severity fires. Two studies that are particularly informative on this topic focus on a northern Michigan peatland complex (Drobyshev and others 2008) and on the hemi-boreal Great Lakes region (USA), which was in coordination with the present study sites (Sutheimer and others 2021). Drobyshev and others estimate long-term fire frequencies from $30.6\text{--}87.0 \text{ fires ka}^{-1}$ depending on landform (Drobyshev and others 2008). Sutheimer and others estimate fire frequencies between $37.0 \text{ fires ka}^{-1}$ in the central Upper Peninsula of Michigan and $142.9 \text{ fires ka}^{-1}$ in Northern Wisconsin (Sutheimer and others 2021). Both studies employed dendrochronological techniques in wetland-adjacent ecosystems to estimate fire return intervals. However, as Kasin and others conclude, “dendrochronological and charcoal-based approaches complement each other, and cannot substitute one for another” (Kasin and others 2013). Direct dendrochronology is not possible in peatlands due to a lack of fire-resistant trees, and paleo-ecological microscopy is typically limited to 1–3 cores owing to the effort required by the method (Tolonen 1985; Markgraf and Huber 2010; Sillasoo and others 2011; Marcisz and others 2015; Pérez-Obiol and others 2016), with some notable exceptions (Kasin and others 2013), limiting the extent and quality of our collective understanding of peatland fire. As such, high-quality, peatland-specific measurements of fire history are still needed to compliment other approaches and improve our overall grasp of peatland fire ecology.

There are several types of peatlands present in the hemi-boreal zone, each of which, due to differences in hydrology, vegetation, or other factors, could have distinct fire regimes and C accumulation rates. Our goal was to quantify the fire regimes of some of the most numerous hemi-boreal peatland ecotypes: poor fens and rich conifer swamps. Specifically, we hypothesized that, (1) the forested rich fens would experience significantly lower wildfire frequency than other peatland ecotypes, due to a fire-resistant overstory, relative lack of understory, and consistent water table. (2) LARCA would be negatively related to fire frequency, as indicated by Pitkänen and others (1999) because of the consumption of sequestered C during combustion, and (3) that LARCA would be higher in poor fens than rich fens overall (Robinson and Moore 1999), due to relatively lower decomposition rate in poor fens compared to rich fens, though LARCA may be curtailed by fire.

METHODS

Sample Locations

We analyzed 29 soil cores from peatlands across the Upper Peninsula of Michigan, northern Wisconsin, and northern Minnesota (Figure 1). The boreal zone of North America is typically considered to reach its southernmost extent along the north shore of Lake Superior, with a hemi-boreal zone that encompasses the Upper Peninsula, a small part of northern Wisconsin, and much of northern Minnesota (Langor and others 2014). Our sampling locations were all within this hemi-boreal zone. All

sites also fell within the Northern Lakes and Forests (III) Ecoregion as defined by the US EPA (U.S. Environmental Protection Agency 2013). This ecoregion is described as “humid continental, marked by warm summers and severe winters, with no pronounced dry season,” with a mean annual temperature ranging from ~ 2 °C to ~ 6 °C, and mean annual precipitation ranging from 500 to 960 mm (Wiken and others 2011).

The hemi-boreal peatlands that we sampled were all fens. Both the poor fens and forested rich fens sampled are peat bearing and groundwater fed. These fen ecotypes are common and may be isolated, coastal, or part of large upland-peatland complexes (Bourgeau-Chavez and others 2017). The poor fens are dominated by typical vegetation such as *Sphagnum* (L.) mosses, black spruce (*Picea mariana* (Mill.) Britton, Sterns & Pogggenb.), tamarack (*Larix laricina* (Du Roi) K. Koch), sedges (*Carex* spp. L.), Labrador tea (*Rhododendron groenlandicum* (Oeder) Kron & Judd), bog rosemary (*Andromeda polifolia* L.) and leatherleaf (*Chamaedaphne calyculata* L.) (Kost and others 2007). The forested rich fens that we sampled were dominated by northern white cedar (*Thuja occidentalis* L.) with the presence of balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), hemlock (*Tsuga canadensis* L.) and a sparse understory due to heavy shading and deer herbivory (Kost and others 2007). Both the forested poor and forested rich fens featured more exposed muck due to shading from the forest canopy limiting moss cover. All soils sampled were Histosols ranging from terric to typic.

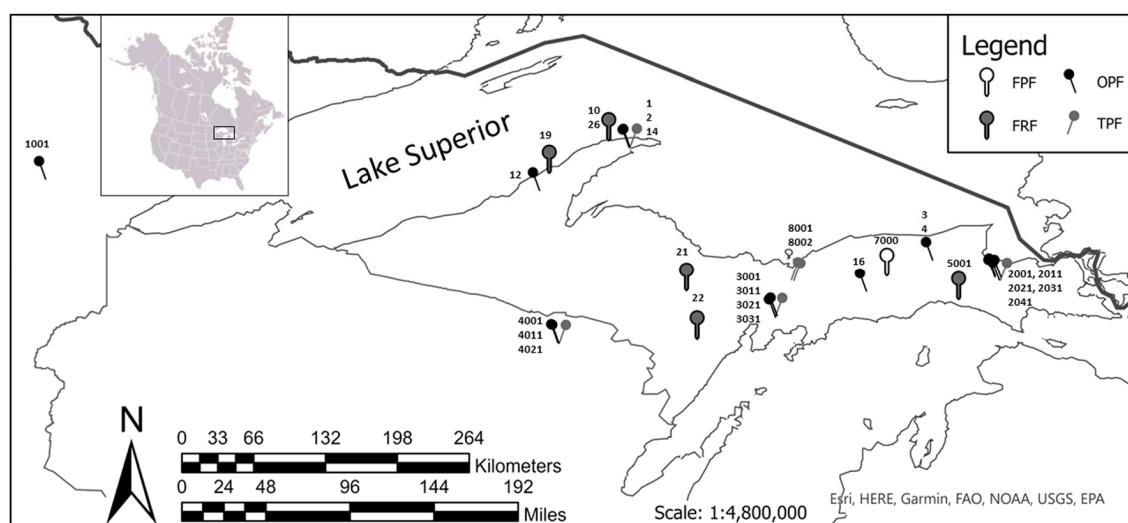


Figure 1. This map indicates the locations and ecotypes of all sampling locations used in this study. FPF = forested poor fen, OPF = open poor fens, FRF = forested rich fens, TPF = treed poor fens. Inset depicts study area in North America.

Sampling

We avoided coring in lags or ecotones which have variable hydrology. At each site we collected one peat profile by the following method. If a moss layer was present, we inserted a 15.2 cm diameter PVC tubes into the peat to a depth of 50 cm to collect the low bulk density surficial moss and peat. The surficial sample was carefully removed and cut into 10 cm depth increments. We then used a Russian peat corer to sample the peat profile down to the mineral soil. We immediately froze all samples upon return to the lab. We logged location data on a per site basis, using a Garmin eTrex 20. We classified our sample sites by peatland ecotype following the method used in the Hiawatha National Forest where many of our core samples were taken (Kudray 2019). This resulted in 4 classes: open poor fens (< 10% tree cover, acidic) ($n = 16$), treed poor fens (> 10% tree cover with mean height < 10 m, acidic) ($n = 6$), forested poor fens (> 10% tree cover with mean height > 10 m, acidic) ($n = 1$), and forested rich fens (> 10% tree cover, circumneutral) ($n = 6$).

Sample Processing

In the lab, for each peat profile, we cut the still-frozen peat 2 cm continuous increments before drying at 60 °C to constant mass, and then weighed the samples to determine bulk density. We ground and homogenized the samples using a Wiley mill equipped with a 40-mesh screen. This resulted in a powdered sample with a maximum particle size of 425 microns. We combusted one subsample of each peat sample at 500 °C for 12 h to establish the fraction organic matter (OM) by mass. We applied a conversion factor of 0.53 to estimate C mass from bulk density and %OM, chosen as a midpoint along the range of published values (Bhatti and Bauer 2002; Watmough and others 2022). We calculated the LARCA for each core by dividing the total C stock by the basal age (Clymo and others 1998). For open poor fens and treed poor fens, we eliminated the top 50 cm from the C stock to avoid bias from to more rapid and variable accumulation of undecomposed C in surficial moss (Clymo and others 1998; Young and others 2021).

Spectrometry

We followed the methodology outlined in Uhelski and others (2022a) to prepare our peat samples for Fourier-transform infrared (FTIR) spectrometry. In brief, we diluted one subsample of each dried and ground peat sample with KBr to 10% peat by mass.

We then collected the FTIR spectra of the samples using a Thermo Scientific Nicolet iS5 spectrometer, equipped with a standard fast recovery deuterated triglycine sulfate (DTGS) detector, and an iD Foundation—Diffuse accessory (Thermo Fisher Scientific, Ann Arbor, MI). Following the methodology of Uhelski and others (2022b), we baseline corrected and standardized each spectrum before using the peak fitting function in Origin (Origin 2019b 64-bit, OriginLab Corporation, Northhampton, MA) to condense the volume of data per sample by fitting 15 Gaussian peaks to the spectral features.

We used the peak areas fitted using this method as inputs to a char prediction model built using the methodology outlined in Uhelski and others (2022b). This model was optimally suited for the samples in this study because we developed them in parallel using peat samples and chars originating from the same region and even some of the same cores. In brief, we isolated 3 different chars indigenous to 3 separate North American boreal and hemi-boreal peatlands, produced admixtures of these chars and indigenous *Sphagnum* peat, and validated the char contents of these admixtures and several additional natural peat samples using Nuclear Magnetic Resonance (NMR) spectroscopy. Using this char content data and FTIR spectra of each sample, we built a model that predicts the mass fraction of char in each sample from the peak areas identified from its unique FTIR spectrum (Uhelski and others 2022b). The char concentration was validated by direct polarization NMR using the molecular mixing model (Baldock and others 2004). Using this model, we can make good estimates of char concentration throughout the peat column and use those estimates to detect fire events. While the model was fit to *Sphagnum* peat, we compared the spectra of *Sphagnum* and cedar peats using Mahalanobis distances (De Maesschalck and others 2000; Chapman and others 2001; Dudek and others 2021) and found that variance between peat types was less than variance within peat types. Therefore, we are confident our ability to accurately detect char concentration in all peat types sampled.

Fire Counting

For each core, individual fire events were inferred from char concentrations determined by FTIR spectrometry (Uhelski and others 2022b). When char content exceeded 11.37% we concluded that this likely reflected a fire event. We chose this threshold because it was the average char content

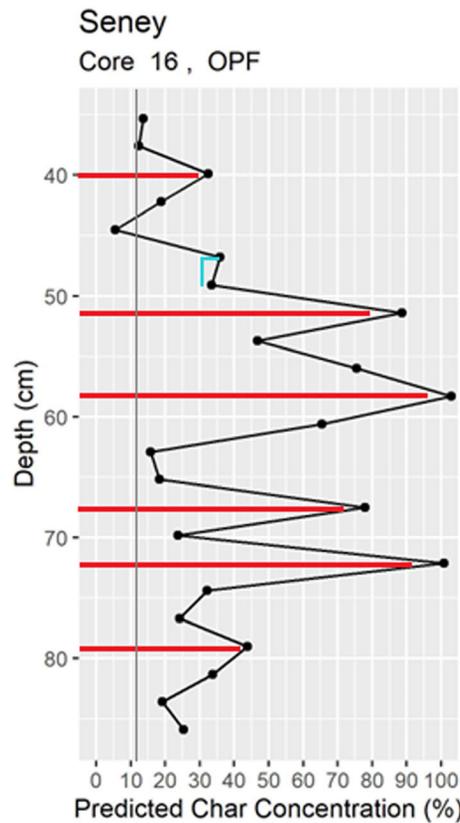


Figure 2. An example of the detection of past wildfires. The thin gray line indicates the minimum threshold (11.37%) for peaks to be considered. The red lines indicate counted fire events. The shoulder between 45 and 50 cm depth may have been a fire but was not counted because it was not sufficiently tall ($> 5\%$) compared to its lower neighbor, as indicated by the cyan line.

of the 3 endmembers used to build the model (Uhelski and others 2022b). In addition, we only indicated the presence of fire on the local maximum, so each spike was only counted once, even when it spanned multiple samples (Figure 2). Furthermore, we decided that each spike in char concentration had to be 5% higher than the local minima both above and below it to avoid minor fluctuations being considered separate events. The only exceptions to these rules were in cases where there were no samples either above or below the sample in question due to coinciding with the top or bottom of a core. Adhering to these rules ensured that our estimates were conservative, uniform, and repeatable.

We know that fire evidence can be erased by subsequent fires burning antecedent char layers, and low-severity fires may only burn vegetation without leaving detectable traces (Miyanishi 2001).

Furthermore, smoldering peat fires may consume much of the char produced, and peatland fires are known to be spatially heterogeneous on a micro-topographic scale (Benscoter and Vitt 2008; Benscoter and others 2015). As a result, our estimates of fire frequency (FF) are minima and likely represent the more impactful fires which yielded significant concentrations of residual char.

Radiocarbon Dating

One subsample was taken from each selected ground peat sample for radiocarbon dating. Samples were graphitized in preparation for ^{14}C abundance measurement at the Carbon, Water & Soils Research Lab in Houghton, Michigan. Peat samples were dried, weighed into quartz tubes, and sealed under vacuum. Samples were combusted at 900 °C for 6 h with cupric oxide (CuO) and silver (Ag) in sealed quartz test tubes to form CO_2 gas. The CO_2 was then reduced to graphite through heating at 570 °C in the presence of hydrogen (H_2) gas and an iron (Fe) catalyst (Vogel and others 1987). Graphite targets were then analyzed for radiocarbon abundance by Accelerator Mass Spectrometry at either the Keck Carbon Cycle AMS Facility, Earth System Science Dept., University of California Irvine, or at the DirectAMS facility in Bothell, WA (Zoppi and others 2007) (Supplementary Table 1). Radiocarbon measurements were corrected for mass-dependent fractionation using AMS inline measurements of $\delta^{13}\text{C}$ following Stuiver and Polach (1977). Sample preparation backgrounds were subtracted, based on measurements of ^{14}C -free wood. Calibrated ages were calculated with OxCal v.4.4 (Bronk Ramsey 2009a, b) using the IntCal20 calibration curve. Calibrated median ages were used to determine peat initiation date (Figure 3) and calculate LARCA and fire frequency (Table 1). Basal peat was differentiated from mineral substrate by sample by its organic matter percentage. In some cases, the peat–mineral boundary was not

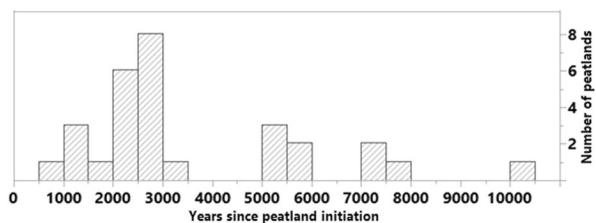


Figure 3. Frequency distribution of peatlands with different initiation ages, as determined by basal peat radiocarbon dating.

Table 1. Summary Table of Fire Frequency (FF, Fires per Thousand Years) and LARCA

	OVERALL (N = 29)		Open Poor Fen (N = 16)		Forested Rich Fen (N = 6)		Treed Poor Fen (N = 6)		Forested Poor Fen (N = 1)	
	FF (Fires ka ⁻¹)	LARCA (g m ⁻² y ⁻¹)	FF (Fires ka ⁻¹)	LARCA (g m ⁻² y ⁻¹)	FF (Fires ka ⁻¹)	LARCA (g m ⁻² y ⁻¹)	FF (Fires ka ⁻¹)	LARCA (g m ⁻² y ⁻¹)	FF (Fires ka ⁻¹)	LARCA (g m ⁻² y ⁻¹)
Maximum	5.9	43.0	4.6	43.0	5.9	35.4	1.9	9.0	0.7	37.1
3rd Quartile	2.4	29.5	3.1	24.0	4.0	32.2	1.9	9.0	0.3	32.6
Mean	1.7	20.1	2.0	17.6	2.6	26.0	1.9	9.0	0.2	22.7
Median	1.2	19.5	1.9	16.2	2.2	24.8	1.9	9.0	0.0	21.0
1st Quartile	0.4	10.8	1.0	8.8	1.1	20.0	1.9	9.0	0.0	13.9
Minimum	0.0	0.8	0.0	0.8	0.0	18.2	1.9	9.0	0.0	9.1

captured so initiation dates may be more recent than reality.

Age-depth models were constructed using the P_sequence function in OxCal v. 4.4 with atmospheric calibration curves IntCal20 and Bomb21NH1 (Bronk Ramsey 2008, 2009a; Reimer and others 2020). The presence of outliers was assessed using the TSsimple outlier test (Bronk Ramsey 2009b). Only one radiocarbon value was rejected based on the outlier test statistic (Core 12, sample 185).

Statistics

For dating of fire events, we used linear interpolation between two or more depth strata of known age. Each core was dated at the base using radiocarbon dating (open triangles on Figure 4) and the surface was assigned an age of 0 (open circles on Figure 4). For certain cores, we dated additional intermediate layers (triangles on Figure 4) and interpolated between them (Figure 4).

We used mean separation on fire frequency and LARCA to test our hypotheses about variance across peatland ecotypes, and linear regression to test our last hypothesis about the relationship between LARCA and FF. For any statistical analysis relating to ecotype comparison, the forested poor fen site was excluded due to insufficient sample size. For any analysis relating to LARCA, two samples from the Sleeper Lake location (Table 2) were excluded due to insufficient depth. For data analysis we used JMP Pro 14.0.0 (SAS Institute Inc.). We used non-parametric tests because of data heteroscedasticity. We began by running Levine's unequal variance test to determine whether to use Wilcoxon or Welch's test for significance testing. If

significant, we proceeded to use Steel-Dwass for mean separation (Fujiwara and others 2014). Before modeling the relationship between fire and LARCA, we limited our cores to those younger than 4000 years (see Figure 3) to avoid the known issues related to peatland age affecting LARCA results (Clymo and others 1998; Yu 2012; Young and others 2021). Normality was confirmed before modeling with linear regression.

RESULTS

Our basal dates indicate that many peatlands are relatively young and formed over past the 4000 years, but there are also older peatlands that originated between 5000–10,000 years ago (Figure 3). There is no discernable relationship between initiation date and ecotype. Carbon stocks ranged from 10.1 to 263.3 kg C m⁻² (Table 2) with a mean of 94.6 and median of 90.5 kg C m⁻². Much of the variance in this wide range is driven by peatland depth and age. Age-depth models also reflected a high degree of variance both within and across ecotypes (Supplemental Figure 1; Supplemental Table 1). Treed poor fens tended to have a much higher deposition rate than open poor fens ($p = 0.10$) and forested rich fens ($p = 0.19$), though statistical differences are not robust due to high variability within ecotype and the low number of replicates modeled.

There is considerable heterogeneity in fire occurrence within ecotypes, and even within cores. We observed distinctly fewer fires in forested rich fen peatlands compared to the poor fen peatlands (Figure 4). Poor fen sites do not have significantly different fire frequencies from one another. The mean fire frequency of forested rich fens is 0.18

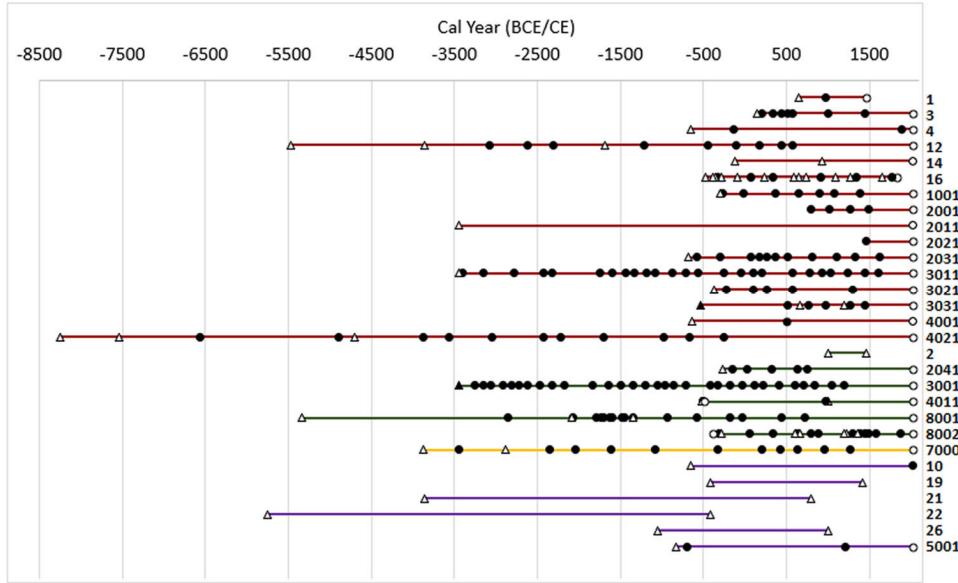


Figure 4. Calculated age of each identified fire by peat core. Peatland types are represented by colored lines: red, sites 1–4021 on the right-hand column, open poor fens, green, sites 2–8002, treed poor fens, yellow, site 7000, forested poor fen, purple, sites 10–5001, forested rich fens. Open circles represent tops of cores with modern material present, triangles represent radiocarbon dated samples between which dates are interpolated, filled symbols indicate fires.

fires ka^{-1} , with 4 out of 6 cores having no fire observations, and the most frequently burning core having 0.37 fires ka^{-1} (Table 1). This is significantly

lower than the mean of the open poor fens, which was 2.0 fires ka^{-1} (Table 1, Figure 5). Interestingly, the mean fire frequency of the open poor fens did not differ significantly from that of the treed poor fens (2.6 fires ka^{-1}) or the forested poor fen (1.9 fires ka^{-1}) (Table 1, Figure 5), and their medians and ranges were notably similar (Figure 5).

Despite the differences in fire frequency between the rich and poor fen ecotypes, we observed no significant LARCA differences between any of the four ecotypes (Figure 6). All peatland types with sufficient sample size (open poor fen, treed poor fens, and forested rich fens) had wide ranges in LARCA (~ 10 to $\sim 45 \text{ g m}^{-2} \text{ y}^{-1}$), with an overall average of $28 \text{ g m}^{-2} \text{ y}^{-1}$. We also found support for a negative relationship between fire frequency and C accumulation. Our model (based on a subsample of sites younger than 4000 years to avoid previously mentioned issues with LARCA, and excluding the largely non-burning forested rich fens) showed a significant ($p = 0.013$, $r^2 = 0.41$, $n = 14$) negative relationship between fire frequency and LARCA (Figure 7).

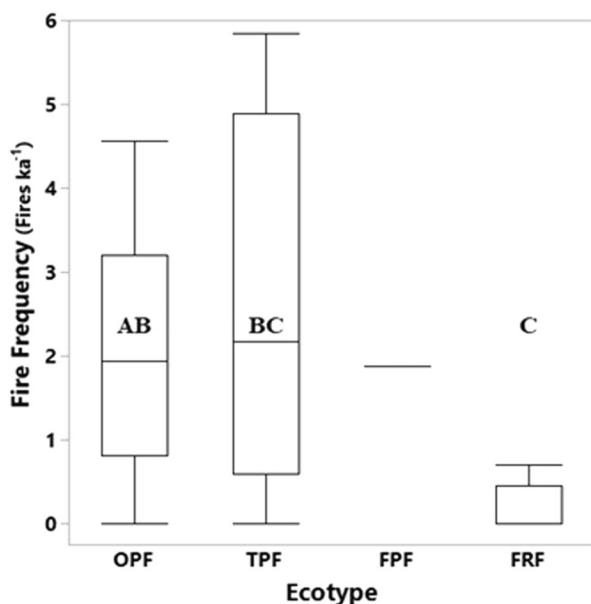


Figure 5. The quartiles of the mean fire frequency estimates for the 4 ecotype classes examined. Fire frequency is measured in fires per kiloannum (per thousand years). OPF = open poor fens, TPF = treed poor fens, FPF = forested poor fen, FRF = forested rich fens. Different letters indicate statistical differences (FPF not included in this analysis because $n = 1$).

DISCUSSION

We calculated fire histories for 29 peatlands in the hemi-boreal zone of North America. This represents the first comprehensive, direct long-term

Table 2. Summary Data for the 29 Peat Cores Evaluated in This Study

Ecotype	Name	Lat (dd) (WGS84)	Long (dd) (WGS84)	Depth (cm)	Calibrated Age (Cal Y BCE/CE)	Lower 95.7% CI (Cal Y BCE/CE)	Upper 95.7% CI (Cal Y BCE/CE)	# Fires ka ⁻¹	FF (Fires ka ⁻¹)	Mean Peat Acc. (g m ⁻² y ⁻¹)	LARCA (g m ⁻² y ⁻¹)	Carbon Stock (kg m ⁻²)
OPF	Betchler Lake.2001	46.302510	-84.910710	71	798	688	878	4	3.3	9.8	12.0	20.6
OPF	Betchler Lake.2011	46.314020	-84.955690	247	-3444	-3519	-3372	0	0.0	43.2	27.1	78.9
OPF	Betchler Lake.2021	46.303450	-84.960460	55	1462	1422	1621	1	1.8	3.6	14.5	10.1
OPF	Betchler Lake.2031	46.279850	-84.924260	149	-680	-789	-568	11	4.1	26.0	16.2	65.9
OPF	Bete Grise.1	47.381900	-87.973601	71	652	610	666	1	0.7	27.8	35.4	70.2
OPF	Bete Grise.14	47.376510	-87.979389	93	-122	-193	-50	0	0.0	37.4	42.6	90.5
OPF	Elmer, MN.1001	47.116033	-92.796300	147	-302	-354	-168	7	3.0	62.6	45.6	58.8
OPF	Hedmark Pines, WI.4001	45.761210	-88.560040	447	-637	-786	-541	1	0.4	81.1	44.8	129.2
OPF	Hedmark Pines, WI.4021	45.765060	-88.568460	223	-8254	-8284	-8225	11	1.1	18.9	12.2	129.3
OPF	Painesdale.12	47.022795	-88.719401	238	-5476	-5535	-5380	9	1.2	51.7	33.9	263.2
OPF	Ramsey Lake.3011	45.970990	-86.771700	247	-3454	-3516	-3365	25	4.6	71.2	40.8	130.1
OPF	Ramsey Lake.3021	45.983670	-86.759490	95	-380	-401	-232	5	2.1	33.2	12.0	46.3
OPF	Ramsey Lake.3031	45.984300	-86.758090	99	-539	-750	-412	6	2.3	20.3	12.5	54.5
OPF	Seney.16	46.186584	-86.020793	86	-483	-734	-403	6	2.4	36.8	25.7	120.5
OPF	Sleeper Lake.3	46.449698	-85.474701	53	152	81	210	7	3.7	-	-	58.3
OPF	Sleeper Lake.4	46.450797	-85.475000	51	-652	-753	-423	3	1.1	-	-	50.3
TPF	Alt Sph Lake.8001	46.275058	-86.627725	489	-5334	-5376	-5224	16	2.2	37.7	24.0	157.1
TPF	Betchler Lake.2041	46.2776960	-84.922150	91	-275	-388	-206	5	2.2	37.8	40.1	55.0
TPF	Bete Grise.2	47.383634	-87.977336	84	1007	977	1025	0	0.0	55.7	65.0	76.1
TPF	Hedmark Pines, WI.4011	45.759110	-88.563520	413	-485	-746	-397	2	0.8	66.8	39.1	121.0
TPF	Peck Lake.8002	46.281630	-86.647683	167	-387	-401	-235	11	4.6	34.4	20.3	101.8
TPF	Ramsey Lake.3001	45.982170	-86.777370	249	-3448	-3622	-3371	32	5.9	62.5	37.9	115.8
PPF	Seney Forested.7000	46.334880	-85.855840	184	-3869	-3951	-3797	11	1.9	17.1	12.2	73.5
FRF	Bob's Lake.21	46.210278	-87.509721	94	-3868	-3978	-3794	0	0.0	26.3	13.9	136.9
FRF	Eagle Harbor.10	47.452501	-88.151389	140	-652	-758	-416	1	0.4	52.8	43.6	113.1
FRF	Eagle Harbor.26	47.451385	-88.151669	144	-1059	-1197	-933	0	0.0	70.1	37.1	117.2
FRF	Marsin.19	47.183333	-88.642780	74	-413	-513	-396	0	0.0	64.5	34.2	111.3
FRF	Rexton.5001	46.137160	-85.263730	49	-831	-900	-807	2	0.7	17.2	9.1	31.9
FRF	Whitney.22	45.811943	-87.422222	99	-5756	-5829	-5721	0	0.0	26.4	14.0	155.5

OPF open poor fens, TPF treed poor fens, FRF forested rich fens. Names go by the convention Location. Core#. This is useful when cross-referencing with Appendix 2.

evaluation of hemi-boreal regional peatland fire frequency.

Fire Frequency of Hemi-boreal Peatlands

The range of our observations ($0\text{--}5.8$ fires ka^{-1}) fell nearly exactly into the range of observations published for similar peatlands in western Canada ($0\text{--}5.3$ fires ka^{-1}) (Kuhry 1994). Our fire frequency range and estimates fell within the wider ranges published for some Finnish peatlands (Pitkänen and others 1999, 2001), but below the range estimated for others (Tolonen 1985). Our estimates of fire frequency are notably far lower than those suggested for the same region by upland proxies, which range from $30.6\text{--}142.9$ fires ka^{-1} (Drobshev and others 2008; Sutheimer and others 2021). However, care must be taken in interpreting upland proxy data; these proxy estimates contain records of fires which burned either (1) through both upland and peatland and which were recorded in both, (2) through both upland and peatland and which were recorded only in upland proxies due to low severity, fire heterogeneity or other cause or, (3) which burned in uplands while skipping peatlands due to higher moisture content. Therefore, while upland proxies can be informative, potentially filling in the lower severity and more contemporary components of the fire regime, there remain barriers to direct comparison, even when

care is taken to sample in the same locations as was the case with Sutheimer and others (2021).

Our data suggest that rich forested fens dominated by northern white cedar experience very little fire, with only 3 total fires observed in over 18,000 collective recorded years. In comparison, the *Sphagnum* dominated poor fens show evidence of 2.1 fires ka^{-1} (mean fire return interval of 476 years). This supports our hypothesis that forested rich fens experience fire significantly less often than poor fens in the same region. This is supported by multiple studies which describe a negative association between northern white cedar and wildfire disturbance (Fenton and Bergeron 2008; Taylor and Chen 2011; Appelbaum and others 2017; Jules and others 2018; Rayfield and others 2021). Though we have not established the cause, we suspect this to be due to a combination of stable water tables and a closed canopy increasing humidity and reducing ground cover capable of carrying a fire.

The poor fens are represented in this study by three ecotypes: open poor fens, treed poor fens, and a forested poor fen. The open poor fens and treed poor fens do not differ significantly in fire frequency and the one forested poor fen site that we sampled appears to follow this same broad pattern of poor fen fire frequency. The implication of this finding is that poor fen ecotypes have comparable fire regimes regardless of present-day tree cover, which is the main differentiator between these 3 ecotypes. Our prior work has also found that peat quality was similar between these three poor fen ecotypes throughout the entire length of the peat cores (Uhelski and others 2022a). The main difference between the three poor fen types is the cover of trees, which can vary due to changes in hydrology or time since last major fire (Harris and others 1996; Rydin and Jeglum 2013). The time since last fire is greater in the treed poor fens (median = 1046 years since 2021) than in the open fens (median = 572 years since 2021), though this difference was not statistically significant due to high variance in time since fire. There are also a few open fens that have not had fires in several thousand years, which may indicate that these sites are too wet for both fire and forest development.

Like many other published works (Tolonen 1985; Pitkänen and others 1999, 2001; Sillasoo and others 2011), we found that there is considerable heterogeneity in the timing of fires within a given core (Figure 4). Some cores appear to have relatively uniform fire histories, while others have notable “boom and bust” periods. Some cores have long time spans post initiation without fire obser-

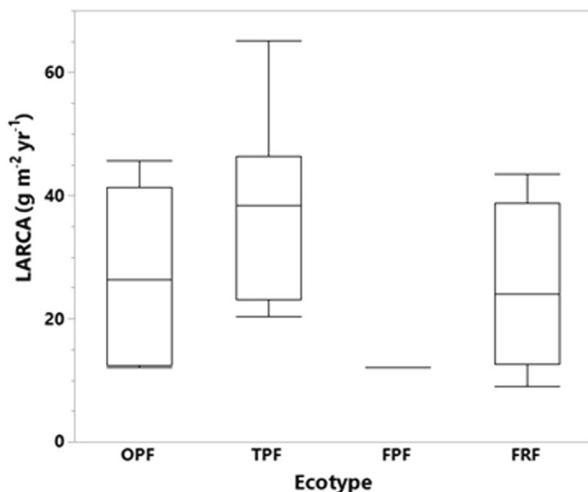


Figure 6. This box-and-whisker plot indicates the quartiles for the long-term apparent rate of carbon accumulation (LARCA) of the ecotypes. They vary widely within ecotypes, but we found no significant difference between classes ($p = 0.298$). OPF = open poor fens, TPF = treed poor fens, FPF = forested poor fen, FRF = forested rich fens.

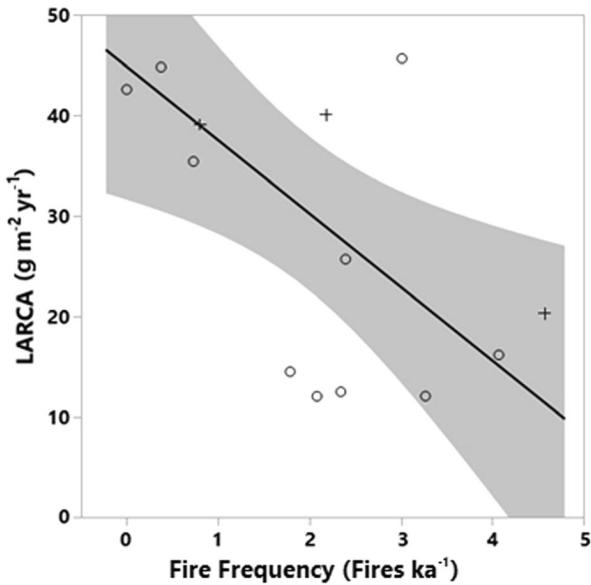


Figure 7. This plot shows the fitted relationship ($p = 0.013$, $r^2 = 0.41$, $n = 14$) between the long-term apparent rate of carbon accumulation (LARCA) and fire frequency for peatlands younger than 4000 years old. Fire frequency is measured in fires per kiloannum (per thousand years). O symbols are open poor fens and + symbols are forested poor fens. Forested rich fen sites are omitted due to lack of fire. The modeled relationship is $\text{LARCA}(\text{gm}^{-2}\text{y}^{-1}) = 44.84(\text{SE : } 6.08) - (7.31(\text{SE : } 2.51) \times \text{FF(fireska}^{-1}\text{)})$.

vations, while others burned frequently from the start. These patterns can be due to land management by indigenous communities, climate, and other natural causes. Large scale synchronization of fire events, presumably due to regional drought, appears to have occurred at least once, around 1500 years ago (Figure 4), but this has not been verified by radiocarbon dating of all relevant char layers. Due to our sampling design (using 10 cm increments for the top 50 cm of peat in open and treed poor fens) reducing the chance to detect char layers, we were unable to compare recent fire history to the fire history of the deep past. Due to this, and the heterogeneity in fire history, we are unable to discern any consistent pattern of fire through time.

Fire Frequency and Carbon Accumulation in Hemi-boreal Peatlands

We were able to support our hypothesis of a negative relationship between fire frequency and long-term C accumulation (Kuhry 1994; Robinson and Moore 2000), which suggests that increased fire occurrence can lower peatland C stocks over time.

The relationship of our model of fire frequency to LARCA is based on conservative estimates of fire frequency, so the true slope of the relationship may in fact be shallower than we observed here, which could explain why our model displays a steeper negative relationship than that of Kuhry's (Kuhry 1994). We stress that our method reflects the occurrences of char-producing wildfires, which likely exhibited smoldering combustion (Hungerford and others 1995; Miyanishi 2001). Our method does not likely capture fires with primarily flaming modes of combustion, such as occurs with surface fuels like sedges; these fires could be stand-replacing (Bourgeau-Chavez and others 2020) and yet would produce little char. With that in mind, based on our model, LARCA approaches 0 when fire frequency approaches 6.15 fires ka^{-1} (fire return interval of 162 years), implying more frequent severe fires would result in extirpation of the peatland. However, negative feedbacks to fire frequency and intensity such as increasing moisture and reduced fuel load likely serve as counteracting forces keeping peatlands stable outside of severe and/or persistent disturbances. For example, Indonesian peatlands were stable for millennia prior to the severe and persistent hydrological disturbance produced by ditching projects which precipitated massive changes to peatland fire regimes and consequent C losses (Sazawa and others 2018; Vetrata and Cochrane 2020).

While we found a significant negative relationship between fire frequency and LARCA, we were not able to support our hypothesis that forested rich fens would have lower LARCA than other peatland ecotypes. We found no significant difference in LARCA between ecotypes (Figure 6), though we did note that the weak trend was for forested rich fens to have lower LARCA than the poor fens despite having much fewer fire observations. This agrees with Robinson and Moore's findings that along a gradient from ombrotrophic bog to poor fen to rich fen, recent rate of C accumulation trended downward (Robinson and Moore 1999). The large variability that we found in LARCA within ecotypes rather than across them leads us to conclude that LARCA values are unique to each specific peatland. Indeed, the range of LARCAAs we observed span the range of observations in the literature ($0\text{--}40 \text{ g m}^{-2} \text{ y}^{-1}$) (Kuhry 1994; Pitkänen and others 1999; Robinson and Moore 1999, 2000; Loisel and others 2014).

Given the observed negative relationship between fire frequency and LARCA, we can use a simplified mass-balance approach to assess the C balance associated with peatland fire. There is

concern that the incidence of fire in peatlands can release “irrecoverable carbon,” that is, C that could not be recaptured by the same area in time to limit the effects of anthropogenic climate change (Goldstein and others 2020; Harris and others 2021; Loisel and others 2021). For example, we observed widely variable LARCA values with an average of $28 \text{ g m}^{-2} \text{ y}^{-1}$ resulting in an average of 0.84 kg C m^{-2} sequestered in 30 years [the mid-century target (Goldstein and others 2020)]. If this is compared to the average $\sim 3 \text{ kg C m}^{-2}$ consumed in each fire (Turetsky and others 2011; Walker and others 2020a) this leaves a deficit of 2.16 kg C m^{-2} , which could be considered “irrecoverable”. In other words, the average peat fire will release more C than that same area burned can recapture in over 100 years, creating a local C deficit during humanity’s window of opportunity to act. This back-of-the-envelope calculation leaves out many nuances, but is supported by our observed decline in LARCA with increased fire frequency. We can thus expect that more frequent and more severe peatland wildfires will decrease the average C sink strength of dominant peatland types in the hemi-boreal region.

Syntheses of current trends in climate indicators for the Great Lakes region already report increased temperature, earlier thaws, and greater numbers of extreme heat and precipitation events (Hayhoe and others 2010). Meanwhile, the North American boreal region has exhibited increasing trends in fire occurrence and extent (Kasischke and Turetsky 2006). Regional predictions for future climate scenarios still have wide margins of certainty, but generally indicate decreasing snowfall and snowpack, increasing mean annual and seasonal temperatures and increasing interannual variability among all of these variables (Giorgi 2006; Hayhoe and others 2010; Šeparović and others 2013; Ashley and others 2020). While the Great Lakes provide some moderating influence on regional climate change, the area is not immune, and climate-driven changes to fire regime and species distribution in hemi-boreal wetlands should be expected. Notably, the three most common tree species present in peatlands of this biome, *Picea mariana*, *Larix laricina*, and *Thuja occidentalis* all exist at their southernmost native extent in this hemi-boreal zone (Burns and Honkala 1990). These wetland species could have their natural ranges exceeded by midcentury even under a lower emissions scenario (Hayhoe and others 2010), with unknown consequences for disturbance and ecosystem ecology within hemi-boreal peatlands.

CONCLUSION

We established conservative fire frequencies for peatlands in the hemi-boreal region of northern Michigan and Wisconsin (USA), with the median poor fen experiencing $2.1 \text{ fires ka}^{-1}$ (median fire return interval of 476 years) and the median rich fen experiencing no fire. We found a significant negative relationship between fire frequency and LARCA. Within our regional focus, we observed a wide range of LARCA. Despite the difference in vegetation and fire regimes between poor and rich fen classes, their LARCA did not differ significantly from one another. Our findings imply that fire is a natural part of poor fen peatlands in the hemi-boreal region. However, with greater occurrence of peat fires, these ecosystems overall will likely be weaker long-term sinks for atmospheric C, while individual burned peatlands act as short-term sources of atmospheric C.

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DATA AVAILABILITY

Additional data are available in Michigan Technological University’s Digital Commons, including location, depth, bulk density, organic matter, carbon, char content values and FTIR spectra for each sample within each core. Radiocarbon data are available. Also included are code and configuration files that are used following the methods of our previous publication (Uhelski and others 2022b) to produce our char content estimates. The dataset doi is: <http://doi.org/10.37099/mtu.dc.all-datasets/39>

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