

Rapid deglacial and early Holocene expansion of peatlands in Alaska

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Northern peatlands represent one of the largest biospheric carbon (C) reservoirs; however, the role of peatlands in the global carbon cycle remains intensely debated, owing in part to the paucity of detailed regional datasets and the complexity of the role of climate, ecosystem processes, and environmental factors in controlling peatland C dynamics. Here we used detailed C accumulation data from four peatlands and a compilation of peatland initiation ages across Alaska to examine Holocene peatland dynamics and climate sensitivity. We find that 75% of dated peatlands in Alaska initiated before 8,600 years ago and that early Holocene C accumulation rates were four times higher than the rest of the Holocene. Similar rapid peatland expansion occurred in West Siberia during the Holocene thermal maximum (HTM). Our results suggest that high summer temperature and strong seasonality during the HTM in Alaska might have played a major role in causing the highest rates of C accumulation and peatland expansion. The rapid peatland expansion and C accumulation in these vast regions contributed significantly to the peak of atmospheric methane concentrations in the early Holocene. Furthermore, we find that Alaskan peatlands began expanding much earlier than peatlands in other regions, indicating an important contribution of these peatlands to the pre-Holocene increase in atmospheric methane concentrations.

climate seasonality | Holocene thermal maximum | peatland carbon | Alaska | Siberia

Ongoing and future warming at high latitudes has generated significant interest in terrestrial carbon-cycle feedbacks to climate change (1). Of particular concern and considerable debate is the long-term effect of climate warming on soil carbon (C) pools (2–5). Numerous studies have documented that warming negatively impacts soil C storage by increasing respiration and decomposition (2, 4, 6). However, long-term effects of warming on C storage remain controversial (2, 3), in part because these studies only cover relatively short time scales. Furthermore, most of these studies were performed in mineral soils, and few studies consider long-term climate sensitivity of C storage in organic-rich peat soils (5), which represent up to one-third of the global soil C pool (7). In peatlands, climate warming has the potential to increase net C accumulation by stimulating net primary productivity (NPP) but also decrease it through greater ecosystem respiration (including decomposition of old peat C) (8). Peatlands accumulate carbon where productivity is greater than the rate of decay, which occurs when the soil is waterlogged and water tables are relatively stable (8, 9). Saturated soils are necessary for the existence of peatlands, but the role of moisture in peatland C accumulation remains unclear. On relatively short time scales, water table depth manipulations have not produced consistent results (10, 11), and numerous studies have shown stronger responses of C dynamics to temperature than moisture changes (10–13).

Most modern peatlands formed during the Holocene and thus represent a significant terrestrial carbon sink over this period (14, 15), as well as a methane (CH₄) source (16, 17). It is well known that boreal peatlands developed rapidly during the early Holocene (16–18) and are thought to have contributed to the early Holocene

CH₄ increase (16, 17), but results from previous studies do not show an early deglacial peatland initiation (16, 17) and thus cannot explain the deglacial increase in atmospheric CH₄ concentrations. In addition, how rapid peat formation relates to climate is not well understood. Previous peatland data synthesis studies do not identify climatic mechanisms of peatland expansion, in part because of the broad geographic reach and variable regional climate histories of these studies (17, 18), hindering understanding of climatic controls on peatland C dynamics. Here we place late-glacial and Holocene peatland C dynamics in Alaska into the context of the regional climate history through detailed peat-core analysis, focusing on the early Holocene, a time when summer temperatures were higher than the 20th century average, winter temperatures were lower, and conditions were drier overall, as indicated by low lake levels (19). In addition, we will examine the connection between deglacial increases in atmospheric CH₄ and expansion of Alaskan peatlands.

The Holocene thermal maximum (HTM) is a widely recognized period of warm climate in the high latitudes (19), attributed to an orbitally induced increase in summer insolation and a decrease in winter insolation (20). However, the HTM exhibits a spatio-temporal asymmetry across the northern hemisphere, owing to effects of the remnant Laurentide ice sheet and the large thermal inertia of the ocean (19). Extensive peatlands exist in Alaska and parts of Siberia (16, 17), each covering almost the same areas of 596,000 km² (21) and 592,440 km² (22), respectively. These two important peatland regions are located where the HTM coincided with maximum seasonality in insolation and presumably temperature (19, 23, 24), making these ideal locations for studying the effects of climate seasonality and temperature on peatland C dynamics. We also examine temporal patterns of C accumulation from four peatlands on the Kenai Peninsula, Alaska, where the climate at the present is semicontinental due to the rain shadow effect from the Kenai Mountains, resulting in comparable summer precipitation to interior Alaska.

Results

Our analysis of peat basal dates shows a steady increase in the number of newly formed peatlands across Alaska (Fig. 1) beginning at ~18 ka (1 ka = 1,000 cal yr BP; Fig. 2C). The highest rate of peatland formation occurred from 12 to 8.6 ka, with a peak initiation at 10.5 ka, concomitant with the highest insolation seasonality (Fig. 2A). By 8.6 ka, 75% of modern Alaskan peatland area (63% of total basal dates) formed (Fig. 2C), followed by a 6-fold decrease in the rate of new peatland formation.

To examine temporal variation of peatland C accumulation over the Holocene, we calculated C accumulation rates based on peat-core data from four peatlands in south-central Alaska (Fig. 2B).

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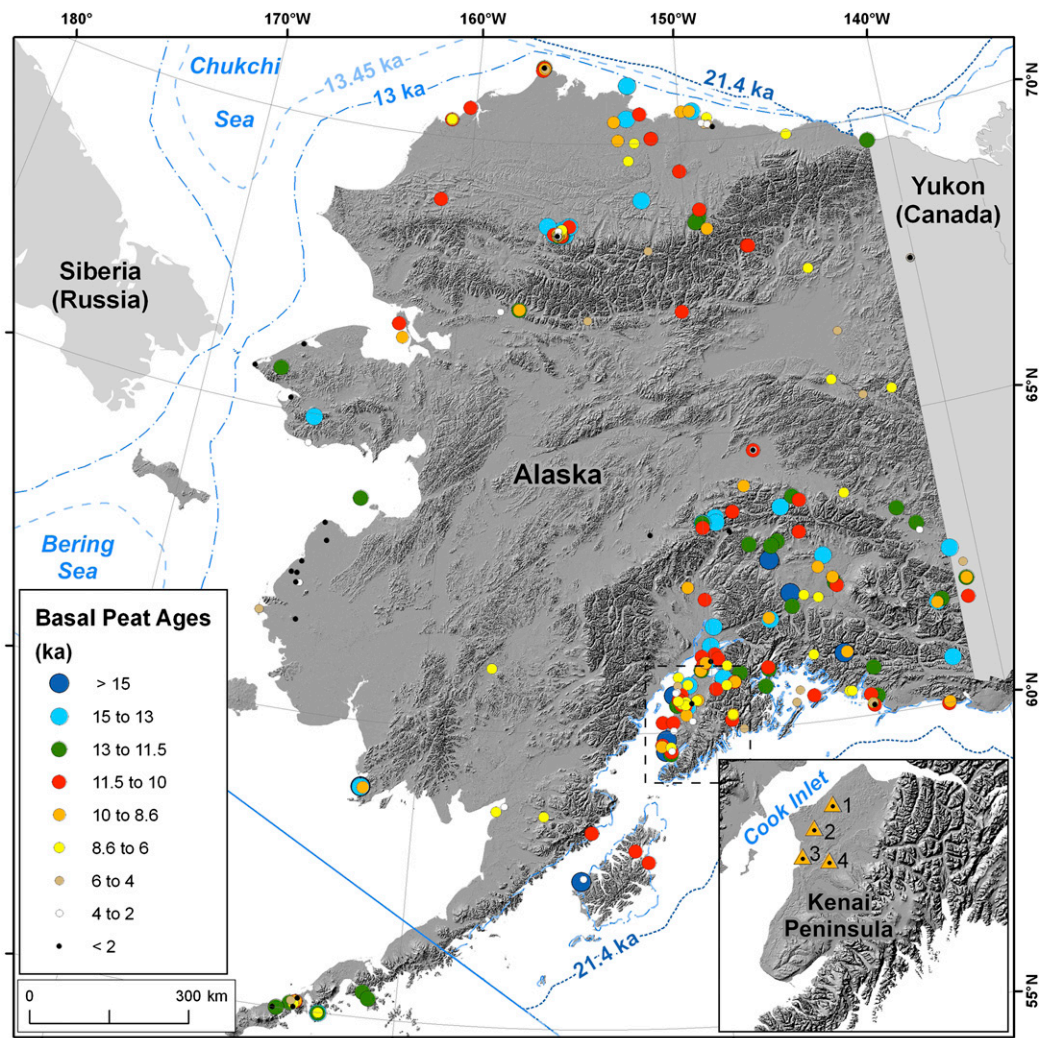


Fig. 1. Digital elevation model (DEM) of Alaska. Dots indicate peatland sites with basal dates. Colors and sizes indicate paleoclimatically significant age groupings, including the deglacial (>15 ka), the Bølling-Allerød (15–13 ka), the Younger Dryas (13–11.5 ka), the early Holocene (11.5–10 ka and 10–8.6 ka), the mid-Holocene (8–6 ka and 6–4 ka), and the late Holocene (4–2 ka and <2 ka). Paleo-shorelines are depicted with dotted blue lines (adapted from ref. 25). The location of the *Inset* is outlined by a dashed-line. (*Inset*) Four peatland sites on the Kenai Peninsula used for carbon accumulation rate curves (Fig. 2B). 1, Swanson; 2, No Name Creek; 3, Kenai Gasfield; 4, Horse Trail.

Our results show an average C accumulation rate of $\sim 20 \text{ g C m}^{-2} \text{ a}^{-1}$ (grams of carbon per square meter per year) from 11.5 to 8.6 ka, four times higher than the average rate of $\sim 5 \text{ g C m}^{-2} \text{ a}^{-1}$ over the rest of the Holocene. Visual examination of peat cores and macrofossil analysis of all four cores showed well preserved peat in the early Holocene compared with a much lower degree of preservation for mid- to late-Holocene peat (Fig. S1) (30).

Discussion

Rapid Peatland Expansion and Carbon Accumulation During the HTM.

Rapid peatland expansion from 12 to 8.6 ka with a peak at ~ 10.5 ka coincides almost exactly with maximum insolation seasonality and the HTM in Alaska (19) (Fig. 24). The subsequent decline in rates of peatland initiation occurs concomitantly with decreasing insolation and climate seasonality, suggesting that a strong link exists between temperature seasonality and peatland development. Comparable explosive peatland expansion in the early Holocene has been observed in Siberia (16), which experienced a similar early Holocene climate and seasonality as in Alaska, but with a slightly later peak in summer temperatures at ~ 9 ka (23, 24), roughly concurrent with the maximum peatland expansion there (Fig. 2C).

Our data show both the most rapid peatland expansion and C accumulation during the early Holocene, a period that was previously deemed unsuitable for peatland development in high northern latitudes (7, 31). In the four C accumulation records from the Kenai Peninsula (Fig. 2B), Holocene C accumulation rates show a remarkably similar pattern despite differences in vegetation composition (30) and timing of peatland initiation (Fig. S1). Peat accumulation rates are controlled by both autogenic and allogenic factors. Under a steady climate, the rate of peat accumulation is sometimes higher initially and slows down over time, especially in continental peatlands (32, 33), as the peat surface becomes isolated over time from the groundwater source (32), and also as continued decomposition of the deeper anoxic peat layers reduces hydraulic conductivity (33). However, our records show well preserved early Holocene peat, despite botanical differences and having $\sim 10,000$ years to decompose (Fig. S1). In addition, two of these records initiated during the late-glacial period (~ 14 ka) but did not begin significantly accumulating peat until the early Holocene, presumably when the climate was more favorable. These observations rule out autogenic peatland processes as the dominant factor in controlling C accumulation at these four sites.

cores. Particularly low accumulation rates beginning ~4 ka correspond with the onset of neoglaciation in Alaska (35), which has been shown to have decreased and even stopped peat accumulation processes in other boreal regions such as Siberia (37).

Net C accumulation is a function of, and long-term difference between, NPP and ecosystem respiration (including peat C decomposition). NPP is controlled primarily by summer temperature and growing season length, whereas respiration is controlled mostly by soil temperature and waterlogged conditions, with aerobic respiration occurring at a higher rate than anaerobic respiration (38). Although moisture is an important control on ecosystem respiration rates, recent studies have documented that temperature increases generate a stronger response in CH₄ and CO₂ fluxes than water-table changes in modern peatland manipulation studies (11, 12, 39, 40). Warmer temperatures have been shown to significantly increase NPP (41), suggesting that longer, warmer early Holocene summers would have resulted in enhanced productivity. During winter, a decrease in frost depth and moderate increases in snow depth (42, 43) can increase respiration rates enough to turn an ecosystem from a C sink to a source (43). A combination of diminished snowfall and lower winter temperatures during the early Holocene would have significantly reduced winter respiration rates, resulting in greater C sequestration, a climate pattern that can be explained by a weakening of the Aleutian Low in winter and a strengthening of the subtropical high in summer (44).

The high temperature seasonality during the early Holocene in Alaska was likely similar to the continental climate that characterizes several important modern peatland regions, including western Canada and the West Siberian lowlands. These two regions experience warm summers and cold winters and moderate rates of precipitation, and have the highest average rates of Holocene peat accumulation of all northern high latitude peatland regions (8). The difference in timing of the HTM across the northern boreal regions (19, 24) allows for further examination of the role of the HTM on peat C accumulation rates. The cooling effect of the Laurentide ice sheet in eastern Canada delayed the HTM until 5–3 ka, a time that corresponds with high C accumulation rates there (8). It should be noted that the timing of the HTM in eastern Canada is out of synch with maximum insolation seasonality, and true examination of the role of early Holocene seasonality must take this into account. This hypothesis can be tested in the southern hemisphere where the maximum insolation seasonality and HTM timing occur at 5–2 ka (20). Although data are sparse, one peatland record from Patagonia appears to show higher peat accumulation rates at this time compared with the rest of the Holocene (45).

Role of Northern Peatlands in Controlling Atmospheric Methane Concentrations. Although peatlands represent a significant C reservoir, they also are a source of CH₄ to the atmosphere (16, 17). Atmospheric CH₄ concentrations began increasing during the last deglaciation, with two large and abrupt increases, one at the start of the Bølling-Allerød (Termination 1A) and another at the beginning of the Holocene (Fig. 2E), but the cause of the increases remains the subject of much debate (28, 29, 31, 46–49). Several hypotheses have been proposed, the first of which suggests that releases from methane hydrates caused the atmospheric CH₄ increase (46). This hypothesis is considered by some to be increasingly unlikely (47, 48). A second hypothesis suggests that extensive wetland development caused the increase atmospheric CH₄, particularly the abrupt increase at the beginning of the Holocene (16, 17, 48). Finally, a recent study (28) proposes that thermokarst lake formation in Siberia, Alaska, and northwestern Canada during the early Holocene explains most of the atmospheric CH₄ increase and maintains that the northern peatland basal date synthesis curve (17) lacks the rapid early Holocene increase evident in thermokarst lake formation (Fig. 2D). The lag in peatland initiation dates may partially be explained by the large

number of sites located in Canada and Western Europe (17) where ice sheet dynamics and thermal inertia in the North Atlantic delayed the onset of Holocene warming (19).

Alaskan peatlands began gradually expanding ~18 ka, almost 5,000 years before Siberian peatlands (Fig. 2C) and >1,000 years earlier than was previously recorded for northern boreal peatlands (17). This early peatland expansion was largely possible because of a lack of an ice sheet over most of Alaska. The gradual increase in Alaskan peat basal dates corresponds with the beginning of the increase in atmospheric CH₄ concentrations, which suggests that these peatlands contributed to the initial deglacial increase in atmospheric CH₄ concentrations. The inter-polar gradient in CH₄ concentrations at this time implies that a northern wetland source must exist (49), but no sharp increase in peatland area in Alaska is observed at Termination 1A (~14.9 ka) to explain the sharp increase in atmospheric CH₄ concentrations, suggesting that other factors may have contributed to that observed sharp CH₄ rise. Because CH₄ production shows a strong temperature dependence (12, 39, 40), it is conceivable that the warm Bølling-Allerød temperatures could have increased CH₄ emissions in existing peatlands at that time, even with no additional new peatland formation. Furthermore, colder temperatures have been shown to decrease the residence time of CH₄ in the atmosphere (50). It is also likely that by that time, peatland expansion had begun to the south of the Laurentide ice sheet and Europe (17). In addition, it remains possible that the CH₄ increase at Termination 1A was caused by a northern hemisphere source of methane hydrates (46), although available isotopic data argue against this explanation (48, 50). It is also possible that thermokarst development increased as temperatures rose (28), or that subglacial methane was released from retreating ice sheets (51).

The rate of Alaskan peatland expansion does not decrease during the Younger Dryas (YD), and therefore it cannot explain the reduction in atmospheric CH₄ concentrations. Closer examination of the spatial expansion pattern (Fig. 1) shows a lower rate of expansion on the North Slope of Alaska but continued expansion in south-central and eastern Alaska during the YD, a pattern confirmed by a detailed peatland and paleoclimate analysis from the Arctic Foothills (52). The decrease in peat expansion on the North Slope is attributed to colder, drier conditions (52), whereas the continued expansion in south-central Alaska suggests a weaker YD cooling with greater southerly atmospheric flow, a pattern simulated by numerous climate models (53–55). The smooth increase may also be attributed to opening of the Bering Sea, which may have altered sea ice extent and atmospheric circulation patterns (Fig. 1) (55) to allow for continued peatland initiation. If cooling slowed peat formation and halted thermokarst development during the YD because of colder conditions across much of the ice-free boreal region, then these changes could explain the decline in atmospheric CH₄ concentrations. A recent isotopic analysis of methane from the Greenland GRIP ice core suggests that a reduction in boreal wetland emissions should have occurred as a result of a decrease in wetland area (50), but these changes may have largely occurred outside of Alaska. A portion of the methane change can also be explained by biomass burning, which was likely lower during the YD (50).

During the early Holocene, expansion of Alaska peatlands preceded the expansion of Siberian peatlands by almost 1,000 years and occurred during the period of low thermokarst lake formation at the beginning of the Holocene, suggesting that Alaskan peatlands may have contributed most to the initial early Holocene increase in atmospheric CH₄ concentrations at Termination 1B (11.6 ka). The delayed timing of peatland development in Siberia can be explained by dry conditions caused by the diversion or dismantling of westerly air masses by the Eurasian ice sheet (56) and may also explain the delayed onset of thermokarst lake formation, because the majority of sites are from Russia (28). The slight difference in timing of initiation

ages in these vast peatland areas, in addition to the increased rate of thermokarst lake formation (28), may help explain the broad early Holocene peak in atmospheric CH₄ concentrations.

By comparing peatlands and thermokarst lakes from the same region of Siberia and Alaska, where warmer-than-present summer temperatures (19) correspond to maximum insolation seasonality (Fig. 2A), we find that 70% of the combined Alaskan and West Siberian peatlands (Fig. 2C) developed by 8.6 ka, similar to thermokarst lake pattern (28) (Fig. 2D). We suggest that extremely rapid expansion of peatlands in Alaska and Siberia (16) during the early Holocene represents a significant contribution to the peak CH₄ concentrations in the early Holocene. If we conservatively assume that the average early Holocene rate of peat accumulation was 15 g C m⁻² a⁻¹ and that the rate of peatland area expansion corresponds with the frequency of basal dates as a percent of total peatland area (Fig. 2C), we find that Alaskan peatlands would have sequestered 14.8 Pg of C between 11.6 and 8.6 ka. This suggests that Alaskan peatlands contributed significantly to the global soil carbon stock and that the previous estimates of 29–58 Pg of C uptake from all northern boreal peatlands in the early Holocene (17) are likely highly conservative. Although CH₄ emissions from peatlands are highly variable, if we assume a conservative rate of 9 g CH₄ m⁻² a⁻¹ (11), we estimate that Alaskan peatlands emitted 3 Tg CH₄ a⁻¹ during the early Holocene. If we assume a percent total of basal dates by 8 ka represent the percent of peatland area present, then we estimate that Alaskan peatlands contributed between 3 and 5 Tg CH₄ per year, based on the estimate of 20–45 Tg CH₄ released every year by present boreal peatlands (57). Our estimate is conservative, because many of these peatlands likely began as minerotrophic fens, which emit more CH₄ than the oligotrophic peatlands found more often on the landscape today. In addition, the effect of warm early Holocene temperatures likely also contributed to greater CH₄ emission (11, 40). By combining the Siberia and Alaska peatland datasets (Fig. 2C), an abrupt decline in peatland expansion is observed at 8.6–8.2 ka, slightly earlier in Alaska than in Siberia, corresponding with a nearly 100-ppbv decrease in atmospheric CH₄ concentrations (Fig. 2E), which is attributed to the 8.2 ka cooling event (31). Although the established peatland area did not decrease, the cooler climate, combined with the drastic decrease in the rate of new peatland formation, may partially explain the decrease in CH₄ concentrations.

The current distribution of peat basal dates is sparse over much of Siberia (8, 16) and much of the lowland area in Alaska (Fig. 1), suggesting that sampling of these vast areas may help us to better understand the impact these peatland regions had on increasing atmospheric CH₄ concentrations. Furthermore, information about whether peatlands formed by paludification (peatland initiated or expanded onto uplands) or by terrestrialization (lake-infilling process) will improve our understanding of climate controls—specifically, increases or decreases in precipitation—on peat formation processes (8).

Implications for Carbon-Cycle Feedback to Present Climate Change. Our data from Alaskan peatlands, along with Siberian peatland data (16), indicate that peatlands responded strongly to the heightened seasonality in the early Holocene by sequestering large amounts of C as well as emitting significant quantities of

CH₄. Early deglacial peatland development in Alaska may help explain the early increase in atmospheric CH₄ concentrations, but the gradual increase in peatland initiation cannot explain the sharp increases and decreases in atmospheric methane concentrations over the Bølling-Allerød and Younger Dryas periods, suggesting that an additional northern hemisphere wetland source outside of Alaska contributed to the marked CH₄ changes, or that changes in CH₄ production within existing peatland during these known climatic intervals contributed to the CH₄ concentration changes. Peatland expansion in Alaska is well timed with increasing insolation and temperature seasonality. Earlier studies pointed to the role of greater summer insolation and warm climate on early Holocene peatland expansion (16, 17), but our present study is, to our knowledge, the first to suggest that winter processes may also play an important role in carbon accumulation. Specifically, colder winters with low snowfall may have decreased peat temperatures to significantly reduce winter ecosystem respiration during the early Holocene. Our data suggest that high early Holocene temperature seasonality played a primary role in controlling the high rates of peatland C accumulation, and adequate moisture is necessary to maintain the presence and persistence of peatlands, but it does not determine the rate of C accumulation in these peatlands. Although we show that peatlands expanded and accumulated carbon under a climate warmer than today, we emphasize the importance of strong temperature seasonality in peat C accumulation at that time. As opposed to the early Holocene, recent and projected warming in high-latitude regions is most pronounced in winter and autumn seasons, owing to strong positive snow and ice feedbacks (1). Although our study implies that Alaskan peatlands responded favorably to a warmer climate, we caution that these results do not necessarily imply that peatlands will increase long-term C storage under current climate warming, particularly if warmer winters increase snow depths in these peatland regions (1), which would likely increase carbon loss from decomposition.

Methods

We compiled 284 basal peat ¹⁴C dates from both previously published sources and our own dating results (Table S1) across Alaska (Fig. 1) to assess the temporal pattern of peatland initiation and expansion in a region where the well established warm early Holocene climate (19) is concurrent with maximum seasonality (20). Basal peat ¹⁴C dates (Table S1) were calibrated to their 2σ age ranges using the program Calib 5.0 based on the INTCAL04 calibration dataset (58), and the calibrated 2-sigma age ranges were placed into 50-year bins. This was done to account for older bulk dates with larger calibrated age ranges and potentially imprecise mean ages. The number of sites in each bin was tallied to generate Fig. 2C. The percentage of peatland area was calculated based on cumulative numbers of these 50-year bins.

Carbon accumulation rates (Fig. 2B) are based on 1-cm measurements of C content and bulk density obtained through combustion (loss-on-ignition) and dated by 9–13 AMS ¹⁴C dates for each of the four cores (Table S2). The mean of the four sites was calculated for each 1,000-year bin using time-weighted averaged C accumulation rates for each core, and errors are standard errors of the mean.

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