

Wetland succession in a permafrost collapse: interactions between fire and thermokarst

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Abstract. To determine the influence of fire and thermokarst in a boreal landscape, we investigated peat cores within and adjacent to a permafrost collapse feature on the Tanana River Floodplain of Interior Alaska. Radioisotope dating, diatom assemblages, plant macrofossils, charcoal fragments, and carbon and nitrogen content of the peat profile indicate ~600 years of vegetation succession with a transition from a terrestrial forest to a sedge-dominated wetland over 100 years ago, and to a *Sphagnum*-dominated peatland in approximately 1970. The shift from sedge to *Sphagnum*, and a decrease in the detrended tree-ring width index of black spruce trees adjacent to the collapse coincided with an increase in the growing season temperature record from Fairbanks. This concurrent wetland succession and reduced growth of black spruce trees indicates a step-wise ecosystem-level response to a change in regional climate. In 2001, fire was observed coincident with permafrost collapse and resulted in lateral expansion of the peatland. These observations and the peat profile suggest that future warming and/or increased fire disturbance could promote permafrost degradation, peatland expansion, and increase carbon storage across this landscape; however, the development of drought conditions could reduce the success of both black spruce and *Sphagnum*, and potentially decrease the long-term ecosystem carbon storage.

1 Introduction

The spatial patterns of vegetation in the low lying flood plains of Interior Alaska are controlled by disturbances such as fire, permafrost degradation, flooding, and drainage. In particular, permafrost degradation is altering ecosystem structure and therefore, the capacity of northern wetlands to store carbon (Camill et al., 2001; Turetsky et al., 2002a). Because approximately one-quarter of the world's soil carbon is currently sequestered in boreal peatlands (Gorham, 1991; Apps et al., 1993; Turunen et al., 2002), degradation of permafrost could result in significant carbon emissions. Both carbon accumulation and methane emissions have been shown to increase in peatlands underlain by degrading permafrost as water tables increase and nutrients are released by the thawing soils (Robinson and Moore, 2000; Turetsky et al., 2000; Vitt et al., 2000; Camill et al., 2001; Turetsky et al., 2007). Permafrost thaw can also result in water body drainage (Yoshikawa et al., 2003; Jorgenson and Osterkamp, 2005; Riordan et al., 2006) potentially exposing wetlands to aerobic decomposition and carbon release. Different peatland communities store varying amounts of nutrients and maintain different soil environments (Camill and Clark, 1998). For these reasons, future carbon accumulation in permafrost peatlands will depend not only on plant and microbial responses to a warming climate, but on vegetation succession driven by fire and permafrost thaw.

Permafrost degradation observed over the last half century has altered ecosystem structure in boreal peatlands (Vitt et al., 2000; Camill et al., 2001; Jorgenson et al., 2001; Turetsky et al., 2002b; Christensen et al., 2004). In upland ecosystems permafrost thaw has resulted in patterned ground and



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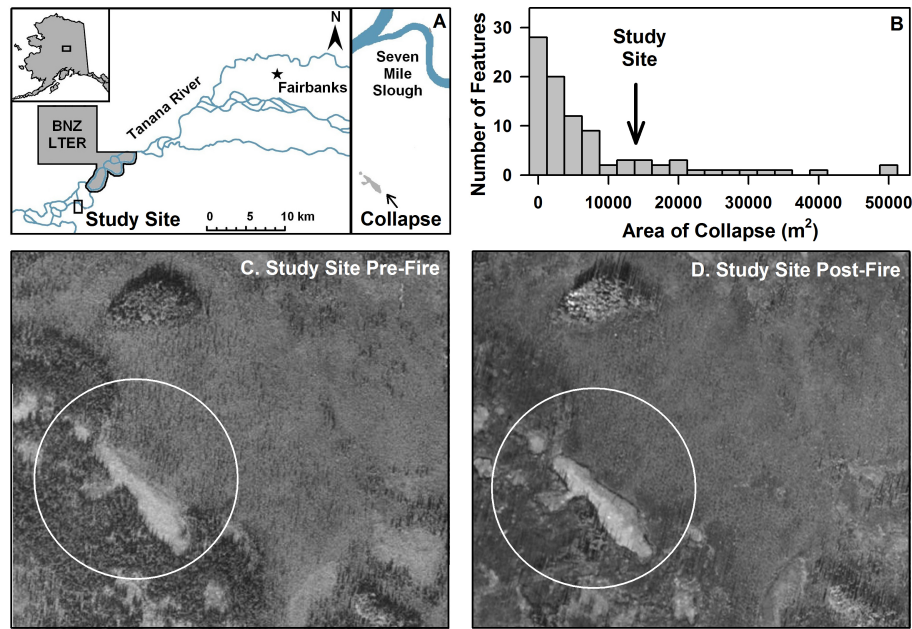


Fig. 1. Location of the study site, a permafrost collapse scar southwest of the Bonanza Creek experimental forest on the Tanana River floodplain in Interior Alaska (64° N $38.448'$, 148° W $20.009'$, 132 m elevation), (A). The distribution of discrete peat features that appear to be hydrologically isolated from the river, drainage channels or extensive fens in the 16 km² area around the study site estimated using digitized aerial photos (Photoshop 7.0, Adobe, San Jose, CA, USA, $n=91$), (B). Images show the collapse scar prior to (C) and after (D) the Survey-line Fire burned through the study site in late June 2001.

thermokarst pits (Osterkamp et al., 2000). In lowland ecosystems the loss of ice-rich permafrost has caused the conversion of forests to wetlands (Osterkamp et al., 2000; Jorgenson et al., 2001; Jorgenson and Osterkamp, 2005). Though air temperature influences the soil thermal regime, other factors such as ground ice content, soil texture, topography, slope, aspect, hydrology, winter snow fall and fire interact to determine rates of permafrost degradation (Osterkamp and Romanovsky, 1999; Jorgenson and Osterkamp, 2005). Discontinuous permafrost in Alaska is particularly sensitive to climate warming (Swanson, 1996) and warming of ground-ice has been observed at sites across the Interior (Osterkamp and Romanovsky, 1999). Since 1949, permafrost collapse has increased by 21% on the Tanana Floodplain of Interior Alaska (Jorgenson et al., 2001). By the end of the next century, permafrost could be eliminated from this landscape (Jorgenson et al., 2001).

Climate models project that the western boreal forest will experience significant warming over the next century (Stocks et al., 1998). Historical data indicate that between 1950 and 2000 annual surface temperatures in Interior Alaska have warmed by approximately 2°C (Keyser et al., 2000); however, during this period no clear trend in growing season precipitation has occurred (Keyser et al., 2000; Serreze et al., 2000). Warmer temperatures will increase evaporation and evapotranspiration; and therefore, peatlands are projected to

experience drier conditions in the future (Wrona et al., 2004). Warmer and drier summers could result in an increase in the frequency and severity of stand-replacing fires (Harden et al., 2000), and therefore, the extent of permafrost degradation (Jorgenson et al., 2001; Camill, 2005). These changes in the disturbance regime could have an even larger effect on the release of greenhouse gas emissions than direct physiological responses of plants and microbes to a warming climate (Chapin et al., 2000).

To understand the interactions between fire and thermokarst on wetland succession, we examined a *Sphagnum*-dominated permafrost collapse in a fire-scarred *Picea mariana* (black spruce) forest. We hypothesize that fire initiated collapse expansion at this site. The loss of transpiration, decrease in summer albedo, and decrease in organic matter thickness after fire can trigger permafrost degradation (Jorgenson et al., 2001; Yoshikawa et al., 2003). Though, fire has been linked with permafrost degradation in the peatlands of Western Canada, most studies identify climate warming as the dominant trigger of collapse in the boreal zone (Thie, 1974; Zoltai, 1993; Kuhry, 1994; Camill and Clark, 2000; Jorgenson et al., 2001). Furthermore, the connections between climate, fire, and fire induced thaw have been little studied because we are still developing the best techniques to address these complex ecological interactions.

2 Methods

2.1 Study area

In June 2001 an extensive fire, known as the Survey-Line fire burned south-west of Fairbanks, Alaska. In July 2001, one month following the fire, we established a transect from the centre of a permafrost collapse scar (64° N 38.448', 148° W 20.009', 132 m elevation) into the surrounding burned black spruce forest (Fig. 2) to monitor the ecological effects of this fire on a wetland permafrost landscape. Between our initial site survey and the summer of 2002, the periphery of the collapse feature had undergone a 6 m lateral expansion.

The field site is located southwest of the Bonanza Creek experimental forest in Interior Alaska, approximately 1 km south of the Tanana River (Fig. 1). Variable vegetation, hydrology, and topography from legacies of flooding, fire and thermokarst have created a complex landscape mosaic (Jorgenson et al., 2001). Approximately 5% of the area between the active floodplain and the extensive fens to the south is collapse. In a 16 km² area around the study site we identified 91 similar collapse features from aerial photographs which varied in size from 700–111 400 m². We surveyed the site on 5 August 2004, using a Topcon GTS 220 Series All-Weather Total Station (Topcon America Corporation, Paramus, NJ, USA), and found the area of the collapse to be 175 m long by 75 m wide or approximately 15 000 m² with a surface depression of up to 0.5 m (Fig. 2), slightly larger than the mean collapse size in the study region.

The study site is underlain by ice rich permafrost alluvial deposits of the Tanana River, and is located in an area of the floodplain that is not subject to groundwater upwelling (Jorgenson et al., 2001). Water level in wells (2 m screen depth) did not correlate significantly with river stage (National Water Information System, USGS) in the two years of this study (linear regression, inverse transformation, p-value=0.540), suggesting that this site is isolated from the active floodplain of the Tanana River (Myers-Smith, 2005). The peatland is best characterized as a poor fen, receiving the majority of its water and nutrients from atmospheric sources (*personal communication* Jill Bubier, August 2001, Mount Holyoke University and Merritt Turetsky, Michigan State University).

In 2004, three ecological zones with distinct vegetation assemblages were observed along the transect, and were characterized as the peatland, moat and burn. The peatland was considered to be the *Sphagnum* mat, the moat, the area of recent soil subsidence, and the burn, the adjacent burned forest. The dominant vegetation types in the peatland were *Sphagnum* spp. (primarily *S. riparium* with increased *S. squarrosum* towards the margins of the collapse), *Carex* spp. (primarily *C. canescens*, *C. aquatilis*, and *C. rostrata*) and *Eriophorum angustifolium*. The vertical mean growth of the *Sphagnum* mat was 2.5±1.2 cm per year (±SE, n=19, measured every 0.5 m along two transects from the edge to the centre of the permafrost collapse). The moat was dominated by *Erio-*

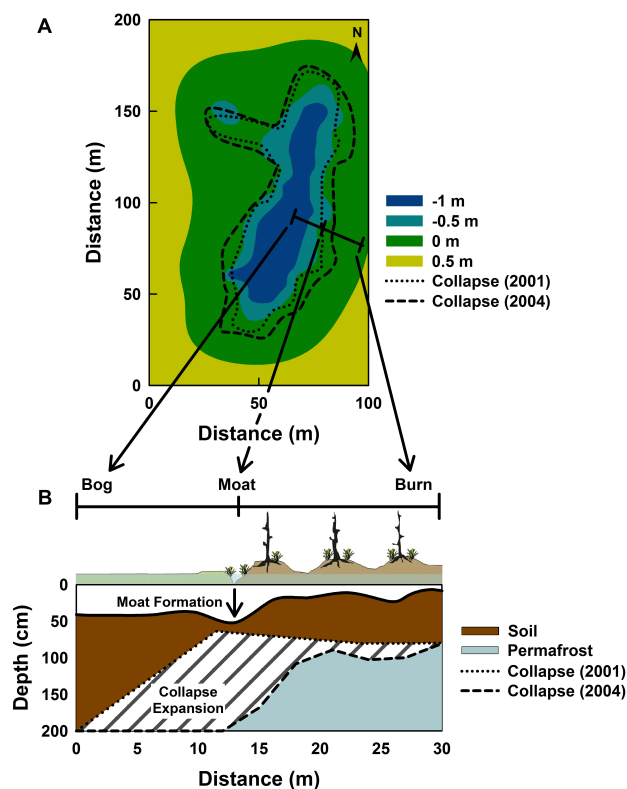


Fig. 2. Collapse expansion since the 2001 fire, illustrating the spatial extent of the collapse (A). The extent of the collapse in 2001 is indicated by the dotted line and in 2004 is indicated by the dashed line. Cross section of transect from centre of peatland to burn zone illustrating lateral subsidence and moat formation (B). The soil surface topography is indicated by the shades of colour in plot A and by the bold solid line in plot B. Frozen ground is represented by the blue polygon and the ground that has thawed since the fire is indicated by the hatched polygon. Cores were sampled along the transect at 0 m in the centre of the peatland, 12 m in the moat, and 27 m in the burned forest.

phorum vaginatum tussocks and *Carex* spp. Standing water was present in the moat throughout both the growing seasons of 2003 and 2004, allowing for the growth of aquatic vegetation. Prior to the Survey-Line Fire, the burn was a low-lying open-canopy *Picea mariana* forest with an understory of tussock vegetation. After the 2001 fire, the dominant vegetation types were *Eriophorum vaginatum* tussocks, Grasses, *Betula* spp., *Salix* spp., *Potentilla palustris*, *Rhododendron groenlandicum*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea* and *Chamaedaphne calyculata*.

The peatland, moat and burn zones had unique soil profiles (Figs. 2b, 3 and 4). The peatland organic layer was >0.5 m thick and the active layer was >2 m. The moat was the lowest portion of the transect, with an above surface water table for much of the growing season. The organic matter thickness was highly variable (2–40 cm) in the burn because of

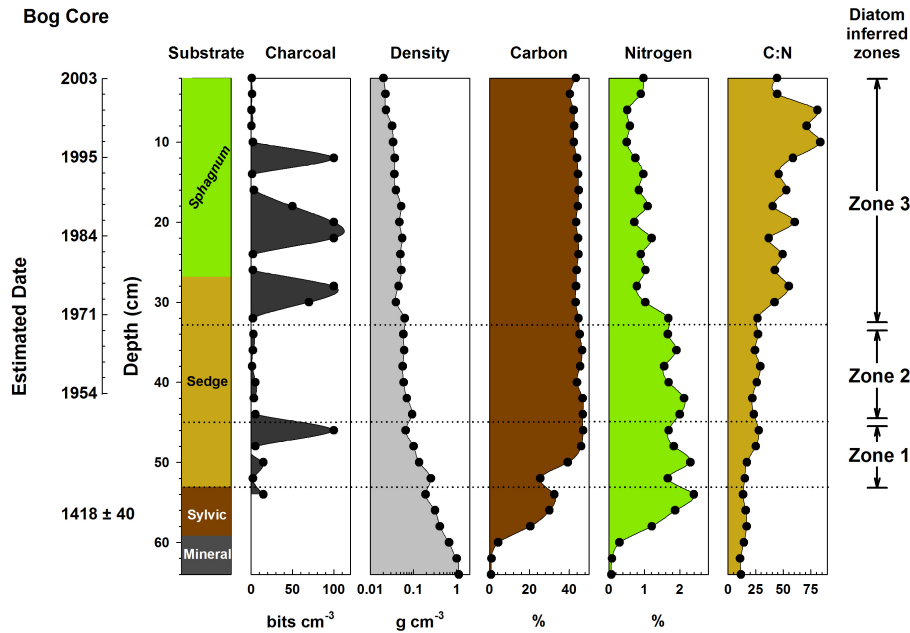


Fig. 3. Stratigraphy of a core from the centre of the peatland indicating charcoal remains, soil bulk density, %C, %N, and C:N. Dotted lines correspond to the diatom zones (Fig. 5). Estimated dates include the ^{137}Cs and ^{210}Pb derived age model (Table 2) and the ^{14}C date for a piece of charcoal in the sylvic peat (Table 1).

tussock-hollow microtopography, patchy fuel consumption, and variable soil subsidence patterns. The maximum thaw depth in the burn was ~ 80 cm.

2.2 Active layer depth

To monitor changes in thaw depth, we pushed a 120 cm or 200 cm fiberglass frost probe into the soil until impenetrable ground was reached. The length of the probe inserted into the earth was considered to be the depth to frozen soil. We conducted three replicate measurements of the active layer every 3 m along both sides of the transect at each visit to the site (every one to two weeks throughout the growing season).

2.3 Soil coring

In March of 2003 we drilled 7.7 cm diameter-cores using a gasoline-powered permafrost corer from the centre of the peatland (peatland core, P26, 0 m along the transect, 64 cm long), the edge of the *Sphagnum* mat (moat core, M27, 12 m along the transect, 54 cm long) and within the burn (burn core, B22, 27 m along the transect, 45 cm long). We sampled three additional cores from the centre of the peatland (P1, P2, PS6, and PS5) for radio isotope dating (see Table 1 and Myers-Smith (2007) for further descriptions of cores at this site). Minimal rotation or deformation of soil layers and sediments occurred, because coring was conducted during winter when ambient temperatures were below freezing. Cores were stored frozen, until each were sectioned into 2 cm depth

increments using a radial saw. Samples were sub-divided: half of the sample was preserved frozen, one quarter was air dried, used to calculate bulk density and then prepared for diatom analysis, the final quarter was used for physical descriptions, plant macrofossil identification, dating, and chemical analysis. We oven-dried the chemical analysis soil samples at 50–65°C and ground them in a tumbling ball mill for 2–5 min, until a homogeneous powder was formed. These soil samples were analyzed for %C and %N using a Carlo Erba EA1108 CHNS analyzer (CE Instruments, Milan, Italy) and a COSTECH ECS 4010 CHNS-O analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA). Sample standard errors were $\pm 0.01\%$ for nitrogen, $\pm 0.45\%$ for carbon. We conducted gross-stratigraphic descriptions of plant microfossils and soils for each depth section of the three cores. We determined the dominant vegetation in the peat and moat core substrate, and sorted out peat fruiting bodies and leaves for isotopic analysis. We counted charcoal layers in the cores and estimated charcoal deposition by emptying dried samples of a known volume and depth (on mean 4.5 cm^{-3}) over a $10 \text{ cm} \times 10 \text{ cm}$ grid and counting macroscopic charcoal fragments (greater than 0.05 mm in diameter) in each cm grid cell. Due to the limited size of the sample, we did not measure total charcoal abundance in the core.

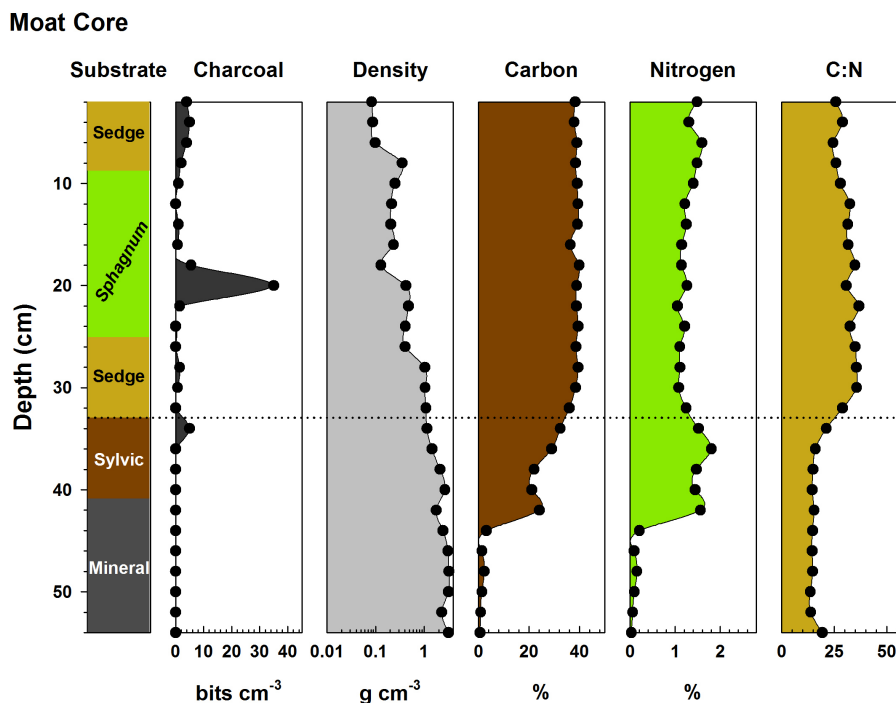


Fig. 4. Stratigraphy of a core from the moat portion of the transect indicating charcoal remains, soil density, %C, %N, and C:N. Dotted line corresponds to the transition from terrestrial organic matter to sedge-dominated peat.

Table 1. Radiocarbon results and the $\delta^{13}\text{C}$ values used to correct for isotopic fractionation (Stuiver and Poach, 1977). Samples from the transect on the north (P26, P2, P1) and south (PS6 and PS5) sides of the collapse. The sample material included *Sphagnum* fruiting bodies (fb), bulk peat (bp), and charcoal (c). Analyzes were conducted at the Lawrence Livermore National Laboratory Centre for AMS (LLNL) or the UC Irvine W. M. Keck Carbon Cycle AMS facility (KCC).

Transect Name	Smpl. ID	Anal. Loc.	Depth (cm)	Smpl. Mat.	$\delta^{13}\text{C}$ (‰)	$\delta^{14}\text{C}$ (‰)	^{14}C age (BP)
North	P26.20	LLNL	20	fb	-25	187.5±5.3	< modern
North	P26.34	LLNL	34	fb	-25	187.5±7.8	< modern
North	P26.40	LLNL	40	fb	-25	-18.0±4.4	145±40
North	P26.54	KCC	54	bp	-26.7±0.15	-36.3±1.8	245±20
North	P26.56	LLNL	56	bp	-25	-34.5±8.2	280±70
North	P26.56	KCC	56	bp	-26.6±0.15	-47.1±1.6	335±15
North	P26.56	LLNL	56	c	-25	-70.1±4.1	585±40
North	P26.58	KCC	58	bp	-27.2±0.15	-63.7±1.7	475±15
North	P2.60	KCC	60	bp	-27.2±0.15	-27.1±1.6	165±15
North	P1.65	KCC	65	bp	-27.2±0.15	-39.3±1.6	270±15
South	PS6.75	KCC	75	bp	-	-	505±40
South	PS5.77	KCC	77	bp	-	-	80±40

2.4 Diatoms

Diatoms have been shown to be a useful indicator of peatland succession, local hydrology, and fire disturbance (Kienel et al., 1999; Moser et al., 2000; Rühland et al., 2000) and can be more sensitive to changes in water chemistry than the com-

monly used peat indicators such as pollen and macrofossils (Rühland et al., 2000). In this study, we employed diatom analysis to indicate changes in pH and nutrients in the aquatic environment. To survey the diatom community, we processed the three cores from the peatland, moat and burn that were sampled every 2 cm by depth using methods described

by the Queen's University Paleocological Environmental Assessment and Research Laboratory (PEARL) and personal communications (K. Rühland, J. P. Smol, J. Barron, and M. Peterson). We digested the dried material, consisting of organic matter with varying amounts of sediment, in Kjeldahl digestion tubes in a heating block. We used 50:50 solution by molecular weight of concentrated H₂SO₄ and HNO₃ and digested for 3 days at 95°C or until the disappearance of all organic matter. We diluted the resulting solution with deionized water to a neutral pH. We mounted the samples using the Pleurax high refractive index mounting medium (prepared by W. Dailey, University of Pennsylvania). To determine the prevalence of the different diatoms, we counted 400 valves (or for one sparse sample, four slides) for each sample. Partial diatoms were only counted when more than half of the valve remained and the genus was clearly distinguishable. We identified samples according to Foged (1981), Krammer and Lange-Bertalot (1986–1991), and personal communications with K. Rühland and M. Peterson. All diatom valves were keyed out to genus, and when we were able we identified species, we refer to these taxa together (genus and species) as diatom categories (see Fig. 8).

2.5 Treerings

We used dendrochronology to link the below ground data to above ground observations of the response of this system to collapse. Tree-ring analysis provides a record of the response of the black spruce trees to changing climate and ongoing thermokarst, allowing for speculation about the response of this landscape to future climate change. We harvested twenty-one fire-killed tree cross-sections from the margin of the collapse and in the surrounding burn in the growing season of 2004 (Wilmking and Myers-Smith, 2008). We measured ring width (sliding stage, Velmex Inc., Bloomfield, NY, USA, resolution: 0.001 mm) for two radial transects of the tree cross-sections, which showed the least amount of compression wood. To build site chronologies, we first cross-dated tree ring series with the program Cofecha (R. Holmes, Laboratory of Tree Ring Research, University of Arizona) and adjusted possible dating errors and then standardized ring-widths with the program ARSTAN using traditional negative exponential or straight line fits (R. Holmes, Laboratory of Tree Ring Research, University of Arizona) to remove the age-related variation in growth rate. These site chronologies were used for climate-growth correlations with temperature and precipitation data from a composite of climate data from the University Experiment Station (1906–1947) and Fairbanks International Airport (1948–2000; Wilmking et al., 2004). In addition, we recorded the presence and amount of compression-wood for each year in the disk, an indicator of leaning which is interpreted to be related to frost-heaving and permafrost collapse (Camill and Clark, 1998).

2.6 Core dating

To estimate the age of peat deposits we utilized AMS radiocarbon, ²¹⁰Pb and ¹³⁷Cs isotopic dating techniques (Oldfield et al., 1995; Turetsky et al., 2004, ; Table 1). We used the ²¹⁰Pb and ¹³⁷Cs data to develop three age estimate models. Two mass accumulation rates (MAR, g cm⁻² yr⁻¹) derived from unsupported ²¹⁰Pb are the constant flux-constant accumulation rate (CF-CS) and the constant rate of supply (CRS) methods (Appleby and Oldfield, 1992). The CF-CS MAR is derived from the slope of the ln (unsupported ²¹⁰Pb) versus cumulative dry mass. The CRS method (CRS) assumes a constant rate of supply of unsupported ²¹⁰Pb and calculates the MAR of each successive layer by creating a ratio of the unsupported ²¹⁰Pb activity (decays per minute (dpm) × cm⁻²) below the layer to the total integrated activity to derive the age of the layer. The ¹³⁷CS-MAR is derived by assigning dates of 1964 to the peak activity in ¹³⁷Cs (34 cm) and 1952 to the depth of first occurrence of measurable ¹³⁷Cs 1952 assuming a constant mass accumulation rate at this depth range (Fuller et al., 1999). In Table 2, we report the mean and range (minimum and maximum) of these three age models. The ¹³⁷Cs and ²¹⁰Pb ages agree to within 10 to 15 years, with the divergence likely due to differing mobility in the deposit.

Sphagnum fruiting bodies, charcoal and bulk peat samples from the core collected from centre of the peatland were analyzed for ¹⁴C using accelerator mass spectrometry (Table 1; AMS, 1.5 SDH.1 Pelletron Accelerator, National Electrostatics Corporation, Middleton, Wisconsin, USA) at the Lawrence Livermore National Laboratory Centre for AMS and the UC Irvine W. M. Keck Carbon Cycle AMS facility. Peat samples from 2, 8, 20, and 24–54 cm-depths were analyzed for ¹³⁷Cs, total ²¹⁰Pb and ²²⁶Ra activity by gamma spectrometry at the USGS Sediment Radioisotope Laboratory in Menlo Park (Fuller et al., 1999).

2.7 Statistical analysis and data reporting

We determined diatom-delineated zones using constrained cluster analysis by information content (CONIIC) by the program Psimpoll 3.01 (K. D. Bennett, Uppsala University). We performed regressions in JMP IN 5.1.2 (SAS Institute Inc., Cary, NC, USA). Field and analytical data are reported for all sites and samples at the Bonanza Creek LTER website <http://www.lter.uaf.edu> listed under the investigator Isla Myers-Smith. Archive samples are stored at US Geological Survey at Menlo Park.

3 Results

3.1 Age estimates

Ages as a function of depth were estimated for the top 54 cm of the peatland core from radioisotope profiles with

Table 2. Sample results for ^{137}Cs and ^{210}Pb (mean \pm SE), the isotope derived age model (mid point of the 3 age estimates \pm range), and estimated carbon accumulation for the peatland core. The supported ^{210}Pb activity, defined by the ^{226}Ra activity, was determined on each interval by subtracting the ^{226}Ra activity, defined as the average of the measured ^{214}Pb and ^{214}Bi from total ^{210}Pb . In many intervals no correction was made because the measured ^{226}Ra was less than the method detection limit of 0.3 dpm/g.

Depth (cm)	^{137}Cs (pCi/gm)	^{210}Pb Total	Sup. Act. ^{226}Ra	Unsup. ^{210}Pb	Age Model	C Acc. (kgC m $^{-2}$)
2	0.26 \pm 0.26	8.48 \pm 4.41	<0.3	8.48 \pm 4.41	2003 \pm 0	0.2
8	0.16 \pm 0.11	9.32 \pm 1.76	0.55 \pm 0.39	8.77 \pm 1.47	1999 \pm 2	0.8
10	0.15 \pm 0.13	5.61 \pm 2.20	<0.3	5.61 \pm 2.20	1998 \pm 3	1.1
12	0.24 \pm 0.13	4.68 \pm 2.20	0.41 \pm 0.47	4.27 \pm 1.64	1996 \pm 4	1.4
14	0.12 \pm 0.14	9.06 \pm 2.38	0.70 \pm 0.54	8.37 \pm 1.71	1994 \pm 5	1.7
16	<0.07	8.97 \pm 2.87	0.71 \pm 0.67	8.27 \pm 1.88	1992 \pm 6	2.0
20	0.40 \pm 0.13	8.20 \pm 2.11	0.41 \pm 0.47	7.79 \pm 2.16	1987 \pm 8	2.9
24	0.31 \pm 0.07	5.16 \pm 1.08	<0.3	5.16 \pm 1.08	1981 \pm 11	3.8
26	0.51 \pm 0.08	4.10 \pm 1.15	<0.3	4.10 \pm 1.15	1979 \pm 12	4.3
28	0.62 \pm 0.08	4.97 \pm 1.14	<0.3	4.97 \pm 1.14	1976 \pm 14	4.7
30	1.66 \pm 0.10	4.48 \pm 1.89	<0.3	4.48 \pm 1.89	1974 \pm 14	5.0
32	2.75 \pm 0.12	5.48 \pm 1.33	<0.3	5.48 \pm 1.33	1971 \pm 15	5.5
34	2.78 \pm 0.10	8.11 \pm 1.16	<0.3	8.11 \pm 1.16	1967 \pm 15	6.1
36	1.46 \pm 0.08	5.48 \pm 1.09	<0.3	5.48 \pm 1.09	1964 \pm 17	6.6
38	2.03 \pm 0.09	5.59 \pm 1.12	<0.3	5.59 \pm 1.12	1961 \pm 18	7.1
40	1.66 \pm 0.10	6.52 \pm 1.35	<0.3	6.52 \pm 1.35	1958 \pm 19	7.6
42	0.95 \pm 0.10	4.30 \pm 1.52	<0.3	4.30 \pm 1.52	1954 \pm 21	8.3
44	1.08 \pm 0.09	3.70 \pm 1.31	<0.3	3.70 \pm 1.31	1950 \pm 22	9.1
46	1.08 \pm 0.08	2.06 \pm 1.12	<0.3	2.06 \pm 1.12	1945 \pm 24	9.8
48	1.19 \pm 0.07	2.84 \pm 1.05	<0.3	2.84 \pm 1.05	1941 \pm 26	10.7
50	1.29 \pm 0.09	4.36 \pm 1.24	<0.3	4.36 \pm 1.24	1935 \pm 29	11.7
52	0.27 \pm 0.03	1.98 \pm 0.52	1.16 \pm 0.12	0.81 \pm 0.53	1915 \pm 52	13.0
54	<0.07	1.48 \pm 0.41	0.86 \pm 0.09	0.62 \pm 0.42	1889 \pm 85	14.2

correction for compaction within the core (Table 2). The radiocarbon age estimates for the sylvic (tree derived) peat samples in the peatland core are 335 yr BP at 56 cm, 475 yr BP at 58 cm, and 585 yr BP for a piece of charcoal at 56 cm depth. The age estimate for a sedge peat sample from 54 cm in the peatland core is 245 years before present (yr BP).

3.2 Core stratigraphy

Stratigraphic analyses of the sediment cores from the centre of the peatland and moat, include records of carbon, nitrogen, charcoal, soil density, and vegetation assemblage (Figs. 3 and 4). Soil bulk density and the percent nitrogen were variable with depth through both cores; however, following peaks in charcoal deposits, greater bulk density corresponded with lower C:N.

We found three distinct organic matter substrates in the core from the centre of the peatland: sylvic peat from 53–59 cm, sedge-dominated peat from 27–53 cm, and *Sphagnum*-dominated peat from 0–27 cm (Fig. 3). We identified four organic matter substrates in the moat core: sylvic peat from 33–41 cm, sedge-dominated peat from 25–33 cm,

Sphagnum-dominated peat from 9–25 cm and a return to sedge-dominated peat from 0–8 cm (Fig. 4). Diatom assemblages were very well preserved in the peat sediments in the top 48 cm of the peatland core, and the top 44 cm of the moat core; however, at the base of both cores diatoms were sparse, many of the valves were broken and sediment obscured the slides. The diatom assemblages for the peatland core delineated with CONIIC into three zones that agreed loosely with the three substrates: sylvic, sedge-dominated, and *Sphagnum*-dominated peat (Fig. 5); however, in the moat core the patterns are less clear (Fig. 6).

3.3 Peatland core zone 1

Zone 1 (53–59 cm) consisted of charred sylvic peat and well decomposed sedges. Bulk density in this region of the core was high (0.1–1.1 g cm $^{-3}$) and C:N ratios were low (11–28). The diatom species *Pinnularia* spp., *Hantzschia amphioxys* var. *major*, *Eunotia praeurupta*, *Navicula amphibola*, *Stauroneis phoenicentreon* were present in low densities at the bottom of the sedge-dominated portion of the core. The diatom assemblages in zone 1 were similar to that at 4 cm depth in the terrestrial soil core from the adjacent burned

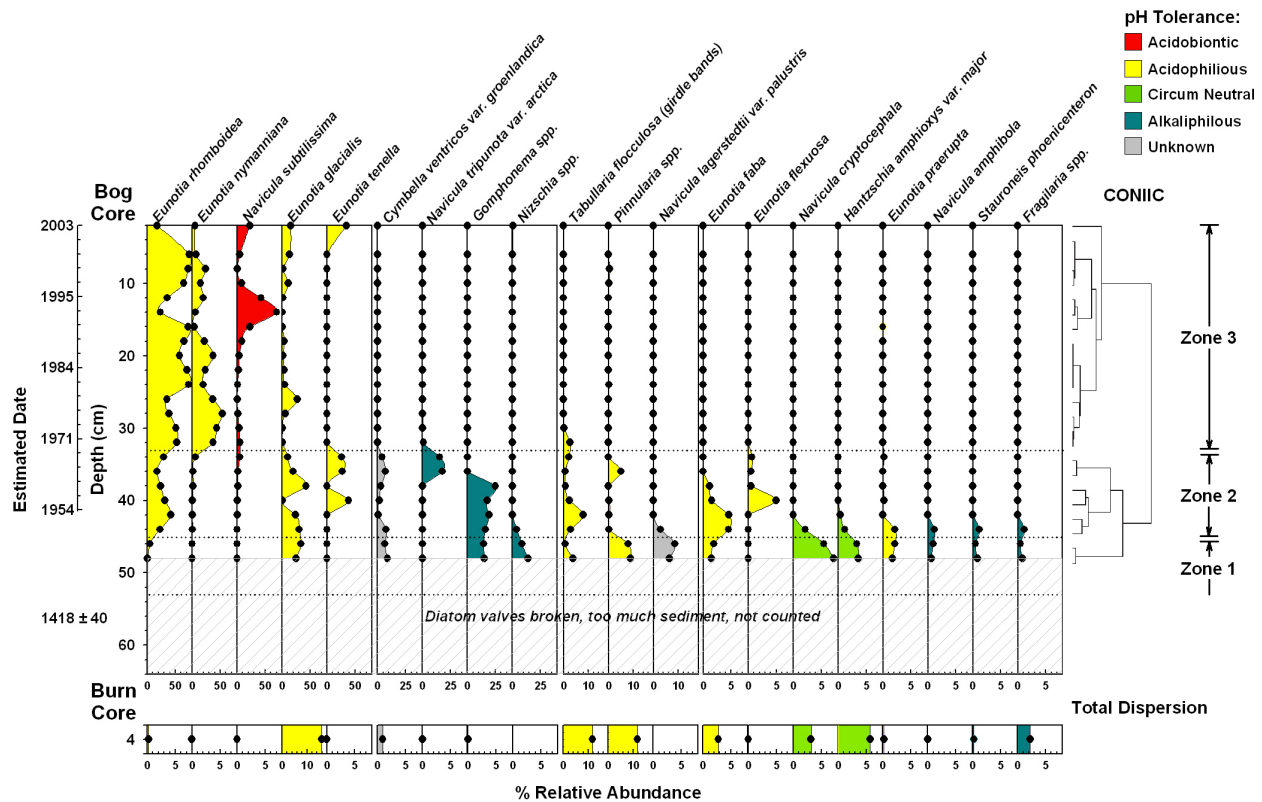


Fig. 5. The percent relative abundance of key diatom species/genera assemblages for the peatland core. Diatom-delineated zones were determined using constrained cluster analysis by information content (CONIIC). We consider the first diatom zone to begin at 53 cm where the sedge-dominated substrate begins; however, diatoms were not counted below 48 cm due to a high proportion of broken valves, residual organic matter and inorganic sediment on the slides. The diatom taxa are presented from most dominant to least dominant from left to right across the figure, the colour of the area under each curve corresponds to the pH tolerance of each diatom (see legend). The abundance of diatom species in the terrestrial soil core at 4 cm is included below the peatland core data. Estimated dates include the Cs and ^{210}Pb derived age model (Table 2) and the ^{14}C date for a piece of charcoal in the sylvic peat (Table 1).

forest (Fig. 7), with high densities of *Pinnularia* spp., *Eunotia Faba*, *Navicula cryptocephala*, *Fragilaria* spp., and the aerophilic species *Hantzschia amphioxys* var. *major*. Conspicuous (~ 0.5 mm in diameter) charcoal pieces were found in the sylvic peat deposits, and a peak of charcoal was found at 46 cm depth just prior to the transition to the second diatom zone.

3.4 Peatland core zone 2

Zone 2 (27–53 cm) was composed of sedge-dominated peat. Bulk densities were less in this portion of the core (0.06 – 0.09 g cm $^{-3}$); however, C:N ratios remained low (22–29). The diatom species *Gomphonema* spp., *Cymbella ventricosa* var. *groenlandica*, *Navicula tripunctata* var. *arctica*, and *Nitzschia* spp. were common in this middle portion of the peatland core. A peak of *E. rhomboidea*, *Tabularia flocculosa* (girdle bands), and *E. faba* at 42 cm coincided with a peak in % nitrogen. A peak of *E. tenella*, *C. ventricosa*, *N.*

tripunctata, *Pinnularia* spp., and *E. flexuosa* at 36 cm corresponded to another peak in bulk density and % nitrogen. Estimated carbon accumulation averaged 171 ± 42 gC m $^{-2}$ y $^{-1}$ (or 6 ± 2 mm y $^{-1}$, \pm range) for this sedge-dominated zone.

3.5 Peatland core zone 3

Zone 3 (0–27 cm) was made up of primarily *Sphagnum*-dominated peat. In this portion of the transect bulk densities were lowest (0.02 – 0.06 g cm $^{-3}$) and C:N ratios were highest (27–84). Three peaks in charcoal abundance were found during this zone of the core (Fig. 3). A shift in the diatom assemblage was initiated 6 cm beneath the shift to *Sphagnum*-domination at 33 cm (Fig. 5) in the macrofossil record. In the uppermost *Sphagnum*-dominated portion of the core (zone 3), *Eunotia rhomboidea*, *E. nymanniana*, *E. glacialis*, and *Navicula subtilissima* were prevalent. Peaks in specific diatom abundance (Fig. 5) often correlated with specific physical and chemical characteristics of

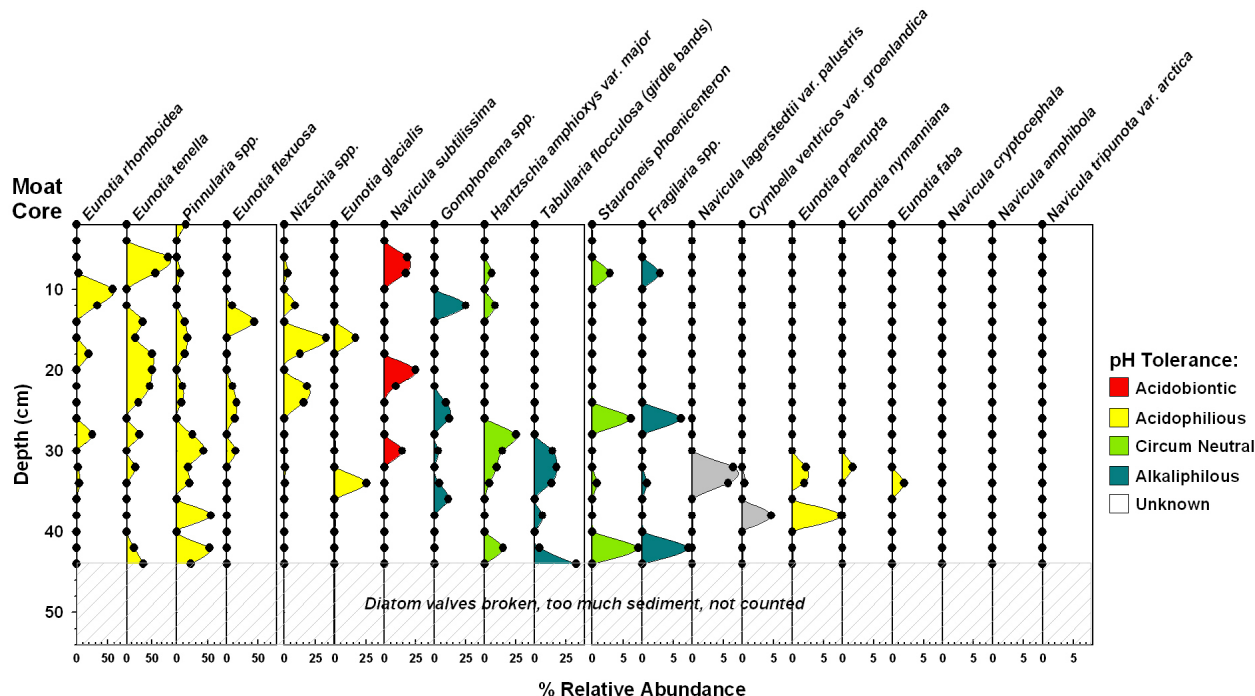


Fig. 6. The percent relative abundance of key diatom species/genera assemblages for the moat core. Diatoms were not counted below 44 cm due to sparse diatom densities, a high proportion of broken valves, residual organic matter and inorganic sediment on the slides. The diatom taxa are presented from most dominant to least dominant from left to right across the figure, the colour of the area under each curve corresponds to the pH tolerance of each diatom (see legend).

the core. For example, the abundance of *E. nymanniana* responded positively to charcoal deposits and tracked bulk density (cross correlation, $r=0.62$, $p\text{-value}<0.003$, $d=-1$; Figs. 3 and 5). Estimated carbon accumulation averaged $172\pm 154\text{ gC m}^{-2}\text{ y}^{-1}$ (or $11\pm 7\text{ mm y}^{-1}$, \pm range) for the *Sphagnum* dominated portion of the core.

3.6 Treerings

For the period from 1930 to 2000, we found a negative relationship between growing season air temperature and the detrended tree-ring width index for black spruce in the terrestrial portion of the landscape (Fig. 8; Wilmking and Myers-Smith, 2008). The tree ring width index for trees growing in the wetter environment at the margins of the collapse feature showed weaker relationship with temperature (linear regression, $R^2=0.04$, $P=0.11$). Compression-wood was observed in 14 of the 21 trees sampled.

4 Discussion and conclusions

Diatom assemblages, plant macrofossils and soil chemistry in the sylvic soil layers from both peatland and moat cores indicate that a terrestrial forest pre-dated the initiation of the collapse. The %C, %N, C:N, and density in the organic mat-

ter above the mineral horizon was similar in all of the cores from the transect, and woody peat and charcoal were found at the base of both the peatland and moat cores. The diatom assemblage above the sylvic peat layer in the peatland and moat cores were analogous to assemblages observed in modern soils from the terrestrial black spruce forest adjacent to the peatland. This assemblage of alkaliphilous to pH neutral, salt tolerant, and mesotraphentic to eutraphentic (tolerant of nutrient enrichment) taxa of diatoms (*Pinnularia* spp., *Navicula amphibola*, *Stauroneis phoenicenteron*) and the aerophilic diatom taxon *Hantzschia amphioxys* var. *major* indicate less acidic, nutrient rich soil (Van Dam et al., 1994).

Radio isotope dating of the transition from (burned) sylvic organic matter to sedge-dominated peat layers in the peatland and moat cores help to reveal the history of this permafrost collapse. Though uncertain, the radio isotope age estimates suggests that the collapse likely formed over 100 years ago (Figs. 3 and 5), from a landscape similar to the present-day black spruce forest. The charcoal date of 585yr BP in the sylvic peat may not represent the age at the time of the collapse, because this soil likely underwent cryoturbation, organic matter loss from fire, and mixing from root growth, combining older soil layers with younger. There are no dates for the older sedge dominated peat just above the sylvic peat;

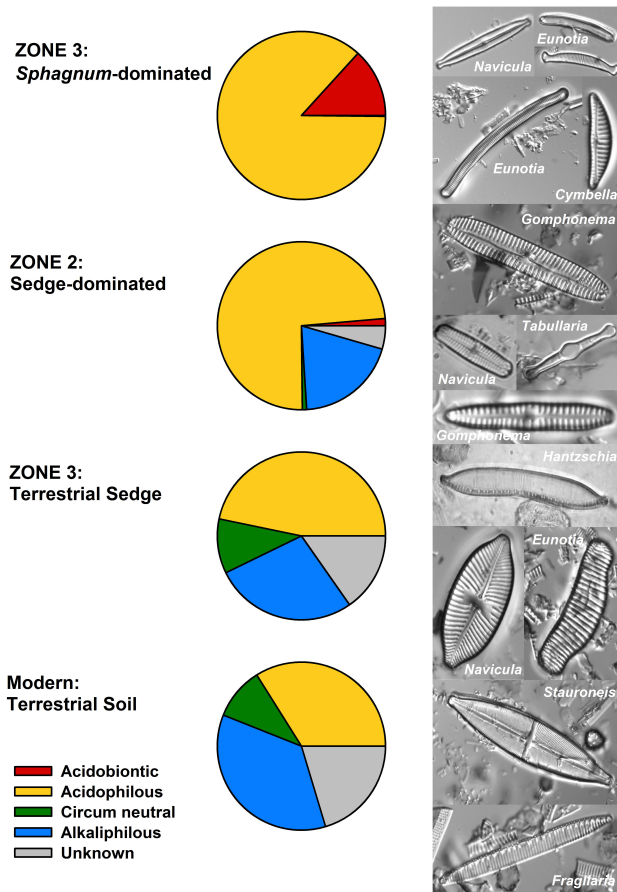


Fig. 7. Diatom species assemblages for the peatland, moat and terrestrial soil cores classified by pH tolerance. Photographs indicate the dominant diatom species found with depth in the core, with the diatoms found in the *Sphagnum*-dominated zone at the top, the sedge-dominated zone in the centre, and the sylvic zone at the base of the figure.

however, this portion of the peatland core has a lower C:N ratio and likely a much slower peat accumulation rate. The dating estimate for the youngest portion of the core is also imprecise because there is uncertainty and error associated with ^{210}Pb and ^{137}Cs dating technique.

During the initial collapse, the sedge-dominated zone (zone 2) was colonized by circum-neutral, mesotraphentic (indifferent to trophic conditions) and epiphytic (growing on plants, rather than planktonic) diatom species. This is consistent with a nutrient rich peatland environment found in sedge-dominated ecosystems today (Rühland et al., 2000). The dominant vegetation, diatom assemblage, and peat chemistry changed at the beginning of zone 3 (between 26 and 32 cm depth in the core). The shift in the diatom assemblage occurred around 1969 ± 15 yrs and predated the shift from sedge to *Sphagnum* peat and C:N ratio that occurred around 1978 ± 13 yrs. Diatoms in Siberia have previously

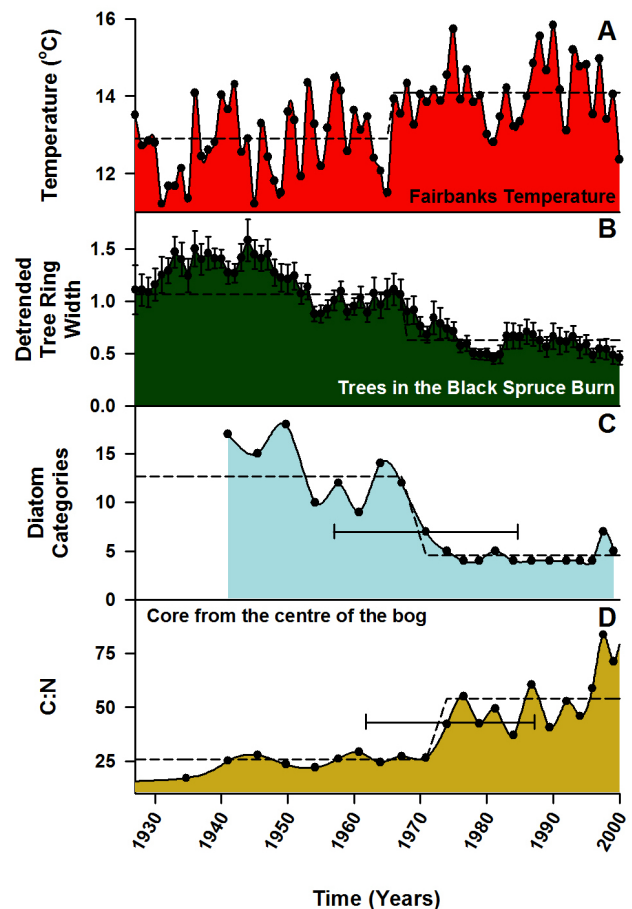


Fig. 8. Growing season temperature (May, June, July and August) from a composite of University Experiment Station (1906–1947) and Fairbanks International Airport (1948–2000, Wilmking and Myers-Smith, 2008), (A) detrended tree-ring width index for black spruce trees in the ecosystem surrounding the collapse (mean \pm SE, $n=11$, Wilmking and Myers-Smith, 2008), (B) number of diatom categories (diatom genus or species, error bar indicates the error in the age estimate at 1965), (C) and the ratio of carbon to nitrogen (error bar indicates the error in the age estimate at 1965), (D). Dashed lines indicate the shift in each of the data sets.

been shown to respond first to changes in peatland chemistry and then secondarily to changes in bryophytes (Rühland et al., 2000). In our study, the shift in diatom assemblage may be in response to the shift in temperature in the Fairbanks region (Fig. 8), which seemed to be part of a synoptic scale shift to warm and dry conditions since 1974 (Barber et al., 2004). Since a sedge-dominated wetland is consistent with wetter, more nutrient rich conditions (Zoltai, 1995), the change to *Sphagnum*-domination suggests that conditions became drier, more acidic and/or more nutrient poor in the collapse perhaps as a result of consecutive warm growing seasons in the late 1970s.

Diatom assemblages and plant macrofossils comprise the most recent zone of the peatland core (zone 3) and indicate that the peatland collapse has become an acidic poor fen within the past 3 decades (Fig. 6). This *Sphagnum*-dominated portion of the core contained predominantly acidophilous (mainly occurring below pH 7) *Eunotia* spp., and a peak in the acidobiontic (optimal occurrence at pH 5.5; Van Dam et al., 1994) species *Navicula subtilissima* at 14 cm, suggesting a period of low pH during the recent history of the peatland environment.

The shorter organic profile at the edge of the peat mat (Myers-Smith, 2007) and the single charcoal peak in the moat core may indicate that the sylvic organic matter in the moat core is younger than in the peatland core, suggesting a lateral, outward expansion of the permafrost collapse. The moat core also showed less clear changes in diatom assemblages with depth. Acidophilous diatoms were found throughout the core. The eutraphentic *Stauroneis phoenicenteron* and aerophilic *Hantzschia amphioxys* var. *major* were counted at 8 cm depth in the core, coincident with a return of sedge-dominated substrate in the moat core.

The charcoal peaks and remains observed in the peatland and moat cores indicate that fire is a frequent disturbance in this region. Though we have only measured the peaks in macroscopic charcoal deposition, we can use these visible charcoal remains to piece together the fire history of this region. Peat accumulation rates were variable across the peatland surface (range = 1–7 cm growth per year), we therefore attribute the most recent charcoal peaks in the peatland core (at 12 cm) and moat core (at 20 cm) to ash deposits from the Survey-line fire of 2001. The ages inferred from the radioisotope profiles indicate that the two charcoal peaks at 20–22 cm and 28–30 cm depth in the peatland core are likely fallout from historic regional fires that did not directly affect the forest stand adjacent to the permafrost collapse. The charcoal peak at 46 cm depth could indicate a localized fire; however, the dating is uncertain. The maximum ages of the trees (182, 172 and 169 years old) in the adjacent black spruce stand indicate that the last stand-replacing fire would have been prior to 1821.

Subtle changes in the diatom assemblages following charcoal peaks suggest that the algal community is sensitive to charcoal deposition and changes in pH. For example, when the change in diatom species abundance are plotted with charcoal with depth in the peatland core, the greatest shift in both charcoal and *E. nymanniana* are nearly coincident (data not shown). The increase in *Eunotia nymanniana* (optimal occurrence at pH of 6.1; Weckström et al., 1997) after charcoal peaks may indicate a response to increasing pH caused by the flush of nutrients from charcoal deposition. Ash remaining after the fire and leaching of ammonia can increase the soil pH (Smithwick et al., 2005). This change to soil solution chemistry can persist for multiple growing seasons after fire (Certini, 2005). Diatom responses to fire were documented in a core from Siberia in which Rühland et al. (2000)

attributed the assemblage shifts to changes in silt influx from the recently denuded catchment. In this study, decreases in bulk density and increases in C:N in the peatland core may also indicate a response of the wetland vegetation in addition to diatoms to nutrient flux from charcoal deposits (Figs. 3 and 4).

4.1 Triggers of collapse

At our study site in the three growing seasons following the 2001 fire, we observed a 6 m lateral expansion of the collapse. We also observed compression-wood in the growth rings of trees at the margin of the collapse feature, this suggests ground movement which could be evidence of subsidence since the last stand-replacing fire. We cannot gauge the rate of permafrost degradation that occurred prior to the 2001 fire; however, the extensive permafrost degradation post-fire indicates that fire is an important driver of ecological change in this ecosystem. Given a black spruce forest with a thin active layer growing over ice-rich permafrost, we hypothesize the following sequence for collapse development. After burning of the forest, permafrost thaw due to darker surface albedo, decreased evapotranspiration, and loss of insulating organic soils results in the formation of an initial collapse. The lowered landscape, now partially submerged in thaw water, is then colonized by wetland vegetation such as sedges and *Sphagnum*. Subsequent fire events in the adjacent forest lead to lateral expansion of the collapse. As the collapse expands, wetland vegetation colonizes the newly subsided margins.

While results from this study supports the hypothesis that fire is an important driver of collapse in this ecosystem after isolation from the active floodplain, permafrost degradation and wetland succession likely proceed in the recovery periods between fires. Approximately 5% of the area between the active floodplain and the extensive fens to the south is collapse, and 80% of these collapse features are smaller than the bog investigated in this study. If collapses exhibit radial growth in response to fire and climate disturbance, smaller features were likely initiated more recently. The high proportion of small collapse features in this landscape corroborate the findings of (Jorgenson et al., 2001), and suggest accelerated permafrost degradation on the Tanana Floodplain.

4.2 Future trajectories

Since carbon accumulation is greater in permafrost collapse scars than in other peat features, future climate warming could lead to increased collapse and peat expansion and greater carbon storage (Camill and Clark, 1998; Robinson and Moore, 2000). If, however, pervasive drying of wetlands occurs, increased storage may be offset by greater aerobic decomposition (Hilbert et al., 2000) or vegetation shifts (Payette and Delwaide, 2004). Carbon accumulation rates estimated in this study, $172 \pm 154 \text{ gC m}^{-2} \text{ y}^{-1}$

(or $11 \pm 7 \text{ mm y}^{-1}$, \pm range) for the *Sphagnum* dominated portion of the core, though based on uncertain age estimates, are significantly higher than that reported for a similar *Sphagnum riparium* collapse feature in Western Canada of $25.6 \text{ gC m}^{-2} \text{ y}^{-1}$ or 1.56 mm y^{-1} (Robinson and Moore, 2000), and for boreal peatlands in general of $21 \text{ gC m}^{-2} \text{ y}^{-1}$ (Clymo et al., 1998); however, they are similar to those reported for a permafrost inception in peatland in the European Russian Arctic of $181 \text{ gC m}^{-2} \text{ y}^{-1}$ (Oksanen et al., 2001). This young collapse should continue to accumulate carbon unless future warming or permafrost degradation results in drainage of the wetland.

We attribute the negative relationship between growing season air temperature and the detrended tree-ring width index for black spruce growing in the terrestrial portion of the study site (Fig. 8; Wilmking and Myers-Smith, 2008) to drought-inhibited growth. Although this poorly drained forest seems an unlikely candidate to experience significant plant drought stress, the combination of root systems limited by a shallow active layer and rapid fluctuations in the water table may lead to periods of reduced water availability (Dang and Lieffers, 1989). Annual growth in Western Canadian black spruce stands has previously been shown to be negatively correlated with temperature and positively correlated with precipitation (Dang and Lieffers, 1989; Brooks et al., 1998). In Interior Alaskan white spruce (*Picea glauca*) tree-ring width, ^{13}C and maximum latewood density was shown to be an indicator of tree growth response to temperature-induced drought stress (Barber et al., 2000). In our study, the observed decreased black spruce growth in warmer growing seasons may indicate reduced success of this forest type with climate warming.

The spatial mosaic of the Tanana Floodplain landscape is formed by fire, permafrost degradation and vegetation succession. If drought conditions do not increase in Interior Alaska, this system will likely continue on a trajectory of fire mediated collapse and peatland expansion. An expansion of wetland could increase carbon storage and methane emissions in this landscape (Turetsky et al., 2000; Vitt et al., 2000; Camill et al., 2001; Myers-Smith, 2005). Results from this study indicate that both the succession from a sedge- to a *Sphagnum*-dominated wetland and the decrease in the detrended tree-ring width index of black spruce trees surrounding the collapse were coincident with a non-linear climate shift (Fig. 8). This stepwise increase in summer temperature in Interior Alaska in the late 1970s has been attributed to a regime change in the Pacific Decadal Oscillation (?). A significantly drier future climate or the initiation of subsurface drainage could trigger a return to terrestrial vegetation in the collapse and potentially prevent the regeneration of black spruce in the forest after fire, resulting in the development of a novel ecological state such as a steppe-like community (Chapin et al., 2004). Since it is suspected that carbon accumulation is more strongly controlled by vegetation succession than responding directly to climate (Camill

et al., 2001), future vegetation succession away from *Sphagnum* and sedge species could lead to reduced carbon storage in this ecosystem, particularly if decomposition is not nitrogen limited (Mack et al., 2004).

In this study, we combine paleo-ecological tools including soil chemical analysis, diatom and plant macrofossil analysis, and tree ring data. By combining these different techniques we can begin to piece together the mechanisms driving succession and project future scenarios in this permafrost landscape. Paleo-ecological records are powerful techniques for inferring past climate (Blackford, 2000). With uncertain future climate scenarios, we must continue to expand paleo-ecological studies utilizing all tools available including diatoms, testate amoeba, plant macrofossils, stable and radio isotopes. By refining our understanding of the influence of the disturbance regime over succession and spatial patterning, we can continue to improve projections of ecological feedbacks to climate change in boreal wetlands.

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