CARBON EXCHANGE AND PERMAFROST COLLAPSE:

IMPLICATIONS FOR A CHANGING CLIMATE

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

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Fairbanks, Alaska

May 2005

Abstract

With a warmer climate, the wetlands of Interior Alaska may experience more frequent or extensive stand-replacing fires and permafrost degradation. This, in turn may change the primary factors controlling carbon emissions. I measured carbon exchange along a moisture transect from the center of a *Sphagnum*-dominated bog into a burned forest (2001 Survey Line Fire) on the Tanana River Floodplain. Both the bog and the surrounding burn were sinks for CO_2, and the bog was a CH_4 source in the abnormally dry summer of 2004. Thermokarst and subsiding soils were observed on the margin of the bog in the three years since the fire, increasing the anaerobic portion of the soil landscape. I observed the greatest variation in carbon fluxes in this portion of the transect. I conclude that permafrost collapse is altering the pattern of emissions from this landscape. I tracked historical changes in vegetation, hydrology and fire at this site through macrofossil, charcoal and diatom analysis of peat cores. The paleoecological record suggests that fire mediates permafrost collapse in this system. This study indicates that future changes in temperature and precipitation will alter carbon cycling and vegetation patterns across this boreal landscape.

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PREFACE

This thesis is presented as two chapters in manuscript format. Chapter 1, "Carbon exchange in a recently burned permafrost wetland: the impact of growing season moisture", examines the controls on carbon exchange in a permafrost collapse bog and the impact of changes in precipitation scenarios on estimates of carbon dioxide, water and methane fluxes from this system. Chapter 2, "Interactions between fire and climate: wetland succession in a permafrost collapse", explores the mechanism of collapse, the controls of fire and hydrology on vegetation succession and carbon accumulation, and potential future scenarios for this ecosystem with climate change. Both chapters were written as manuscripts to be submitted for publication in peer-reviewed journals. Chapter 1 was co-authored with A. D. McGuire, J. W. Harden and F. S. Chapin III. Chapter 2 was co-authored with J. W. Harden, M. Wilmking, A. D. McGuire and F. S. Chapin III. The co-authors provided field and laboratory support and comments on the text; however, the execution of the majority of the research and the drafting of the manuscript was conducted independently.

I would like to thank my committee members Dave McGuire, Jennifer Harden, and Terry Chapin for their enthusiastic support of this research and valuable comments on the manuscripts. Thank you to Jill Bubier, Patrick Crill, Kathleen Rühland, and John Barron for assistance with the development of research hypotheses and methodology. Thank you also to Jamie Hollingsworth, Kaarle Strailey, Emily Sampson, Dan Ulliasi, and Merritt Turetsky for help with fieldwork, labwork and logistics. Thanks to Jay Jones for use of his laboratory. Thanks to my fellow graduate students Evan Kane, Jon O'Donnell, and Nick Lizusso for reading the manuscripts and providing advice and encouragement. Thanks to my officemates Teresa Hollingsworth, Nan Werdin, and Donie Bret-Harte and fellow students Morgan Peterson, Emma Betts, and Hannah Clilverd for their support. And lastly I want to thank my parents Judy Myers and Jamie Smith for providing endless advice and encouragement both scientific and otherwise.

This research was funded by the USGS Earth Surface Dynamics Program and the Bonanza Creek LTER (Long-Term Ecological Research) program (funded jointly by

NSF grant DEB-0423442 and USDA Forest Service, Pacific Northwest Research Station grant PNW01-JV11261952-231).

CHAPTER 1.

GENERAL INTRODUCTION

Approximately one-third of the world's soil carbon is sequestered in boreal peatlands (Gorham, 1991). This peat is protected from decomposition by cold temperatures and saturated soils (Bubier *et al.* 1998). Changes in drainage and increasing temperature could release these carbon stores to the atmosphere as CO_2 and CH_4 (Harden *et al.*, 2000). Enhanced carbon emissions from warmer and drier wetlands could feedback positively to accelerate global climate change (Chapin *et al.*, 2000).

Climate Projections

Climate models project that the North American boreal forest will experience more warming than any other terrestrial forest biome (Gower *et al.* 2001). Annual surface temperatures in Interior Alaska have increased by about 2°C in the last half century, and growing season length has increased by 2.6 days per decade; however, there has been no clear change in precipitation (Keyser *et al.*, 2000; Serreze *et al.*, 2000). Most peatlands will likely experience warmer, drier conditions; however, at the margins of continents, peatlands may become warmer and wetter (Öquist and Svensson, 1996). Model projections of precipitation for wetlands of Interior Alaska are subject to greater uncertainty due in part to the interaction of coastal and arctic air masses. Global climate model runs predict temperature increases of 2.5 to 6°C and precipitation changes ranging from -10% to 30% for the Fairbanks region by 2050 (Canadian Centre for Climate Modelling and Analysis, 2003). Precipitation and permafrost integrity are the primary controls of wetland water level. Therefore, the future precipitation regime will greatly influence the response of wetlands to climate change (Waddington *et al.*, 1998).

Disturbance

Climate warming will affect carbon cycling in northern peatlands by indirect mechanisms rather than through direct ecosystem responses to warmer temperatures (Gorham, 1991). Fire (Harden *et al.*, 2001) and thermokarst (Osterkamp *et al.*, 2000) are major disturbances in the low-lying forests and wetlands of Interior Alaska. On the ice-rich lowlands of the Tanana River floodplain, these disturbances are altering ecosystem structure and function (Jorgenson *et al.*, 2001). Areas of discontinuous permafrost are particularly susceptible to increases in methane emissions (Turetsky *et al.*, 2000). Future change to the disturbance regime may have the greatest impact on the emissions of greenhouse gases in this landscape (Chapin *et al.*, 2000).

Carbon Exchange

The net ecosystem exchange (NEE) of carbon is the sum of heterotrophic and root respiration minus plant uptake. NEE is an indication of whether the system is a net sink or source for CO_2. Root respiration and decomposition are the primary mechanisms accounting for CO_2 emissions from peat (Moore and Knowles, 1987). This ecosystem respiration depends primarily upon soil temperature, water level, and plant activity (Moore *et al.*, 1998). Uptake of CO_2 by plants depends principally on photosynthetically active radiation (PAR), air temperature, and plant community structure and composition (Moore *et al.*, 1998).

Methane is another important contributor to the total greenhouse gas budget. Since over a 100-year time span, a sustained emission of CH_4 has approximately 25 times the CO_2 global temperature change potential (Shine *et al.*, 2005), small emissions can contribute significantly to the total budget of radiatively active gases (Whalen, 2005). Although both CO_2 and CH_4 fluxes are mediated by temperature and moisture, CH_4 is produced in the absence of O_2. The primary controls of CH_4 emissions are water level, soil temperature and substrate quality (Moore and Knowles, 1989; Moore *et al.*, 1998; Bellisario, 1999). Fluxes of CO_2 and CH_4 can be used to calculate the net carbon emissions to the ecosystem over the growing season.

Wetland Succession

The succession of peatland vegetation has been described for permafrost collapse bogs in western Canada (Vitt *et al.*, 1994, Robinson and Moore, 2000) and Alaska

(Luken and Billings, 1983). These studies noted high rates of bryophyte production and carbon accumulation after permafrost collapse. *Sphagnum* species such as *S. riparium* thrive in the moist conditions that result from the raised water tables that accompany soil subsidence. High *Sphagnum* growth rates and low aerobic decomposition results in high rates of carbon accumulation.

Carbon Accumulation

The historic rate of carbon accumulation, through peatland succession, can be estimated by measuring carbon content of the soil profile and dating preserved macrofossils (Clymo *et al.*, 1998). The current carbon exchange, and historical rates of accumulation can be used to estimate the response of wetland systems to future climate (Gorham *et al.*, 1991).

This study

In this study I investigated spatial controls over carbon exchange and the impact of disturbance on the development of a permafrost collapse feature on the Tanana Floodplain. The aims of this study were to determine the influence of fire and thermokarst on carbon exchange and peatland succession. Understanding the response of this ecosystem to variations in climate and disturbance regime will improve estimates of future carbon emissions from this landscape.

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CHAPTER 2.

CARBON EXCHANGE IN A RECENTLY BURNED PERMAFROST WETLAND: THE IMPACT OF GROWING SEASON MOISTURE[1]

ABSTRACT

The Alaskan interior contains large pools of carbon stored in poorly drained ecosystems. With coupled warming and drying, this region of the boreal forest may experience more frequent or extensive stand-replacing fires and permafrost degradation. This may change the primary factors controlling carbon emissions. In a low-lying area of the Tanana River Floodplain, I established a 30-m transect from the center of a *Sphagnum*-dominated permafrost collapse bog, through a transitional aquatic moat, into a burned forest (2001 Survey Line Fire). I measured carbon exchange along the transect during the abnormally dry growing season of 2004. The relative importance of temperature and moisture in controlling carbon fluxes varied significantly along the transect. Both the bog and the surrounding burn were sinks for CO_2, with a mean daytime NEE of -1.4 μmol CO_2 m^{-2} s^{-1}. The moat was a CH_4 source with a mean growing season flux of 18 mg CH_4 m^{-2} d^{-1}. I observed permafrost degradation and subsided soils at the interface of the moat and forest in the second and third summer after the fire. The recently collapsed portion of the transect showed the greatest variation in carbon fluxes, indicating the importance of disturbance in altering the pattern of carbon emissions from this landscape. Regression model estimates suggest that, in a dry year (2004) CO_2 and CH_4 emissions are reduced, leading to greater net carbon uptake.

INTRODUCTION

Approximately one-third of the world's soil carbon is sequestered in boreal peatlands (Gorham, 1991). In boreal Alaska, 40 - 60% of the landscape is poorly drained, with underlying permafrost and a shallow water table (Harden *et al.*, 2003). In these low-lying

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[1] Myers-Smith, I. H., A. D. McGuire, J. W. Harden, and F. S. Chapin III. Carbon exchange in a recently burned permafrost wetland: The impact of growing season moisture. To be submitted to *Ecosystems*.

areas, *Sphagnum* peat contains 2-5 times the amount of carbon stored in upland black spruce stands (Goulden *et al.* 1998). Cold, water-logged soils prevent decomposition (Bubier *et al.* 1998); therefore, increasing drainage and temperature could release these stores of carbon to the atmosphere (Harden *et al.*, 2000).

Estimates of net emissions of greenhouse gases from northern systems vary greatly (Chapin *et al.*, 2000). Historically northern wetlands have functioned as carbon sinks (Gorham, 1991); however, under climate change these systems may shift to net sources. The response of wetlands to climate change involves both the direct control of peatland processes such as primary production, decomposition, and storage of organic matter and indirect landscape-level controls such as altered hydrology, thermokarst formation and fire (Gorham, 1991 and Hobbie *et al.*, 2000). In the low-lying forests and wetlands of Interior Alaska, both fire (Harden *et al.*, 2001) and thermokarst (Jorgenson *et al.*, 2001) are major landscape disturbances. Alteration of the disturbance regime and the direct ecosystem response to climate will influence future carbon emissions.

The controls on CO_2 and CH_4 fluxes can vary temporally throughout the growing season and spatially with changes in vegetation and micro-topography (Waddington and Roulet, 1996). It is the timing and magnitude of shifts in temperature and precipitation that determine the seasonal carbon balance in northern wetlands (Waddington and Roulet, 2000). This intra-annual variation may serve as a proxy for assessing carbon exchange under future climate scenarios.

In this study I investigate the spatial and temporal variation in controls on carbon exchange in a permafrost collapse peatland feature. The relative importance of process-level controls (temperature, moisture and substrate) and landscape-level controls (fire, thermokarst and drainage) were examined along the transition from a fire-scarred *Picea mariana* forest to *Sphagnum*-dominated bog. Empirical relationships between measured fluxes and meteorological variables were used to estimate carbon exchange for a wet and dry growing season.

The aims of this study were to 1) address the relative importance of moisture versus temperature as a control of spatial and temporal variation in CO_2 and CH_4 fluxes, 2) determine how landscape-level disturbances interact with process-level controls of carbon exchange, and 3) estimate the response of CO_2 and CH_4 emissions to changes in growing season moisture.

METHODS

Study Site

The study site (64^o N. 38.448', 148^o W. 20.009', 132 m elevation) was located southwest of the Bonanza Creek Experimental Forest on the Tanana River floodplain in Interior Alaska (Fig. 1). Water level 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 isolation from the Tanana River flow path. Paleo-records suggest that this area has not been part of the active floodplain for at least 600 years (Chapter 2). A transect from the center of a permafrost collapse peatland feature into the surrounding burn was established a month after the Survey Line fire (June-July 2001). In 2003, a boardwalk was built and sample sites were established every 6 m.

In 2004, there were three vegetation assemblages along the transect: the bog, moat and burn. These zones were characterized by distinct hydrologic conditions, vegetation type and disturbance legacy (Fig. 1). The maximum thaw depth in both the bog and moat was greater than 2 m (maximum sample depth), while the maximum thaw in the burn was approximately 80 cm. The bog was lower in elevation with a high relative water table and a 0.5 m-thick peat deposit above the mineral soil. In this portion of the transect, the dominant vegetation types 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 moat portion of the transect was the area of recent soil subsidence. It was dominated by *Eriophorum vaginatum* tussocks, *Carex* spp., and *Eriophorum angustifolium*. There was standing water present in the moat throughout the growing season, leading to a small biomass of aquatic vegetation. The burn was formerly a low-lying open-canopy black spruce forest with an understory of tussock vegetation. Most of the dead trees were still standing in the summer of 2004. Variable burn severity, the spacing of trees, and hummocks and hollows in the soil surface led to heterogeneous organic matter depths. By 2003, the dominant understory vegetation types were *Eriophorum vaginatum* tussocks, *Calamagrostis* spp., *Betula* spp., *Salix* spp., *Potentilla palustris*, *Ledum groenlandicum*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea* and *Chamaedaphne calyculata*. The vegetation recovered quickly after the burn. By the end of the 2003 growing season, the understory canopy reached over a meter in height. Vegetation patterns were similar in the third year, 2004, with continued growth of woody shrubs and tussocks. There were regenerating black spruce seedlings in the burn.

Climate

The study site has a climate typical of Interior Alaska. The winters are cold with mean temperatures below 0°C from October to April. The growing season is temperate but short, from early May to mid September, with three distinct stages: a cool dry period early in May after snowmelt (mean air temperature of 9°C with 15 mm of rain), a warm and dry mid summer in June (mean temperature of 15-16°C with rainfall of 35-45 mm per month), and a cool wet end of season in August and September (mean August temperature of 13°C and more than 50 mm of rain per month) (Viereck *et al.*, 1993). The summer of 2003 was wet with a significant rain event in late July. The summer of 2004 was warm and dry and precipitation was well below normal. At times during the growing season, smoke from wildfires reduced photosynthetically active radiation (PAR) (Myers-Smith, *unpublished data*).

Meteorological Measurements

In the beginning of the 2003 growing season, I installed meteorological instruments. I measured temperatures using copper-constantan theromocouples (Omega Engineering Inc., Stamford, CT, USA) at 5, 10, 20, and 50 cm depth on the east and west side of the boardwalk at 0, 10 (west side only), 20, and 30 m distance along the transect. I measured air temperature using PVC radiation shields at 30, 60, 120, and 240 cm height above the ground surface. I measured soil moisture using EC-20 ECH$_2$O dielectric aquameter probes (Decagon Devices Inc., Pullman, WA, USA) at 16 points along the transect at 30, 28, 26, 24, 18, 16, 14, and 12 m on the east and west side of the boardwalk. To measure rain, I installed a TE 525MM tipping bucket rain gauge (Texas Electronics Inc., Dallas, TX, USA) at 2 m on the tower. To measure water level, I installed a Druck[21] PDCR 1830-8388 submersible pressure transducer (5 psi range, Druck Inc., New Fairfield, CT, USA) inserted 60 cm down an 11 cm interior diameter PVC well. I measured photosynthetically active radiation with Apogee quantum sensors (Apogee Instruments Inc., Logan, UT, USA) at 30, 60, 120, and 240 cm above the soil surface. To monitor changes in thaw depth, I probed the soil at each visit to the site every three meters along both the east and west sides of the transect.

Fluxes

I measured CO_2, H_2O and CH_4 fluxes every one to two weeks throughout the growing season of 2004, using a Li-840 infrared gas analyzer (Licor Inc., Lincoln, NB, USA). The IRGA was calibrated before each trip in the field. For the flux measurements, I built plexiglass chambers with pipe insulation bases with dimensions of 61 × 61 × 30.5 cm, 61 × 61 × 61 cm, or 61 × 61 × 122 cm. Shorter chambers were used in the bog portion of the transect. Chambers included fans for air circulation, inlet and outlet ports for CO_2 measurements, or just outlet ports for CH_4 measurements (Carroll and Crill, 1997). I placed chambers directly on the soil surface and used pipe insulation and plastic sheeting used to make a solid seal during the measurement. To determine the volume for each chamber measurement, I measured the distance to the soil surface from a 6 cm grid suspended 30 cm above each plot. I then used the surface area to calculate the volume for chamber measurements at each plot.

To estimate net ecosystem exchange (NEE), I conducted chamber measurements of plant and soil respiration and plant uptake. Dark measurements were used to determine CO_2 derived from soil and root respiration (ecosystem respiration) using a two-layer cloth shroud with a reflective surface to exclude solar radiation. I measured gas exchange every 6 m from the center of the bog to the surrounding lowland burn. I logged data every 0.5 seconds for 2 min. To account for measurement variability, I conducted two measurements in succession at each location, after flushing the chamber for accumulated CO_2 and H_2O. I conducted CH_4 measurements for 40 minutes, with syringe samples taken after deploying the chamber and at 8 min intervals, totaling 6 gas samples. I analyzed gas samples using a Varian CP-3800 gas chromatograph with a flame ionization detector (Varian Inc., Palo Alto, CA, USA).

I calculated flux rates using linear regressions of gas concentrations over time ($r^2 > 0.9$). When calculating fluxes, I excluded all concentration data sets that did not exhibit linear change overtime.

Biomass

I established another 30-m transect from the bog into the surrounding lowland burn 30 m to the east of the intensively monitored transect. I established plots from the center of the bog into the surrounding burn at 0, 6, 12, 18, 24, and 30 m on the east and west side of the new transect. At each plot, I harvested a 61 × 61 cm area for above-ground biomass at the end of the growing season (DOY 231) in 2004. I sorted harvested above-ground biomass into plant type (*Sphagnum* spp., other moss, *Marchantia* spp., *Eriophorum vaginatum*, *Carex* spp., Grasses, *Betula* spp., *Salix* spp., *Potentilla palustris*, *Ledum groenlandicum*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea*, *Chamaedaphne calyculata*, other vascular, dead moss, dead *Carex* spp., dead Graminoid, dead *Potentilla palustris*, dead *Salix* spp., and other litter), then sorted into green-leaf and non-leaf aboveground biomass. I dried the samples at 60°C to determine the dry mass.

I calculated percent cover for the biomass and flux transects from digital photographs. Photographs were rectified to 10,000 x 10,000 pixels. A 20 x 20 grid was applied to the photograph and the percent of each plant type was estimated in each grid cell. The percent cover was regressed against the dry biomass measured for the biomass transect to project biomass for the intensively measured transect from percent cover. I did not project dead or moss biomass for the flux plots. Instead, I assumed moss biomass to be the same for the flux transect as in the biomass transect.

I projected change in biomass over the season from the change in greenness determined from digital photographs taken over the growing season. I chose five dates throughout the growing season with pictures of equal color quality, focus and of a similar aspect and estimated the percent of green-leaf biomass by selecting areas of green on the photograph and calculating the percent that these areas made up of the total pixels. I estimated curves for the change in % green vegetation over the growing season for 0 m, 6 m and a mean of the remaining distances along the transect (12, 18, 24, and 30 m), as these regions of the transect exhibited different patterns of % greenness across the growing season of 2004. To create a data set of green-leaf biomass over the growing season, I corrected the biomass estimates to account for the change in green vegetation.

Soils

I collected soil cores along the transect in March of 2003. I drilled cores using a gasoline-powered permafrost corer while soils were frozen. Two to four cores were drilled every 3 m along the transect, a total of 35 cores. I stored cores frozen and sampled in sections using a radial saw. Three well-preserved cores from the center of the bog, the moat and the burn were sampled every two cm for chemistry. Twenty three cores were sampled at the interface between different soil layers. Nine cores were sampled only to the mineral boundary. I measured bulk density for all soil samples.

Carbon and Nitrogen

I oven-dried at 50 - 65°C and ground all samples before analysis. I analyzed samples 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 error was ± 0.0093% for nitrogen, ± 0.45% for carbon. I analyzed biomass samples harvested from the biomass transect for %C and

%N when the samples were more than 10% of the plot biomass allowing for representative sampling of carbon and nitrogen from the dominant plant types.

Statistical Analysis

I performed all statistical analyses in SPSS 10.0 (SPSS Inc., Chicago, IL, USA). To identify the major controls of fluxes in this system, I used multiple linear regression to relate fluxes to six explanatory variables: soil temperature, thaw depth, PAR, green biomass, soil moisture, and water table depth. These variables are known to influence carbon exchange in wetlands (Gorham, 1991). Before analysis, I exponentially transformed the soil temperature data to meet assumptions of normality and equal variance. I assumed that multi-collinearity was minimal in these data because tolerance (1 - R^2 of each variable regressed upon the others) exceeded 0.5 for all explanatory variables. I developed separate empirical models for the bog and burn portions of the landscape. I interpolated CO_2, H_2O and CH_4 fluxes across the growing season (from day 149 to 261 of the year) of 2004 and extrapolated fluxes for the growing season of 2003. An exploratory analysis using stepwise multiple linear regression failed to reasonably estimate fluxes because biologically significant variables were eliminated. I, therefore, employed multiple linear regression without model selection or elimination of explanatory variables to improve predictive power. The ratio of dependent data points to independent variables ranged from 42:6 to 51:6 across the models that I developed.

RESULTS

Carbon Pools

The carbon stored in live aboveground vegetation was highest in the center of bog and lowest at positions 24 and 30 m in the burned portion of the transect (Table 1). The organic horizon was thicker (Fig. 2) and carbon storage was greater (Table 1) in the bog.

Growing Season Weather

I observed similar air temperature and thaw depth trends across the growing seasons of 2003 and 2004 (Fig. 3, A and B); however, precipitation differed significantly. May - September precipitation in 2003 was in the 90^{th} percentile and in 2004 was in the 20^{th} percentile for the frequency distribution of precipitation since 1909 (Alaska Climate Research Center). Precipitation data from 2003 indicated a significant rain event on days 207 and 208, when 80 mm of rain fell (Fig. 3, C), nearly one third of the mean annual precipitation. This triggered a rise in water levels and soil moisture that persisted through the rest of the growing season (Fig. 3, D and E). In the summer of 2004, there were no significant rain events (Fig. 3, C). The water level remained low throughout the growing season, and soil moisture never reached the levels observed in 2003 (Fig. 3, D).

Mean Fluxes Across the Transect

For all sites along the transect, the mean measured ecosystem respiration was 3.2 ± 0.30 μmol CO_2 m^{-2} s^{-1} (n = 6, ± SE); daytime NEE was -1.4 ± 0.38 μmol CO_2 m^{-2} s^{-1} (n = 6, ± SE), and water vapor flux was 1.7 ± 0.29 mmol m^{-2} s^{-1} (n = 6, ± SE) in the growing season of 2004 (Fig. 4). Methane fluxes in the burn were below measurement detection (3 mg CH_4 m^{-2} d^{-1}); however, the mean growing season CH_4 flux observed in the bog was 18 ± 3 mg CH_4 m^{-2} d^{-1} (n = 6, ± SE). I observed the highest variation in fluxes across the growing season in the moat portion of the transect (coefficient of variation, CO_2 respiration = -0.79, NEE = 0.49, H_20 = 0.78, CH_4 = 1.68).

CO_2, water vapor, and CH_4 fluxes differed from one another in their pattern of variation along the transect (Fig. 4). Ecosystem respiration was lowest in the bog and highest in the moat and burn portions of the transect. NEE in contrast was lowest in the moat, indicating higher rates of carbon uptake than at other points along the transect. The modest rates of NEE in the burn and bog portions of the transect reflected high rates of respiration balanced by high rates of photosynthesis. Water vapor flux declined with increasing distance from the bog, in association with decreasing soil moisture and biomass. Methane efflux was undetectable in the burned forest portion of the transect and highest in the moat and bog center, where soil moisture was highest.

Spatial and Temporal Variation

I developed empirical models (Table 2) from fluxes measured across the growing season for the burn (burned forest) and the collapse (moat and bog). These models showed variation in flux controls based on landscape unit (Fig. 5). Soil temperature was the dominant control on ecosystem respiration in the collapse; however, moisture was an important control in the burn. Net ecosystem exchange was primarily controlled by soil temperature, although these models explain less than 25% of the variation in observed fluxes in the collapse. In the collapse water vapor flux was controlled by temperature and soil moisture. In the burn, moisture was the dominant control; however, less than 30% of the variation was explained by the measured variables. Methane fluxes in the collapse were primarily controlled by soil moisture.

Estimated Growing Season Fluxes

Empirical models (from 2004 data) of ecosystem respiration, NEE, water vapor and CH_4 fluxes for both the collapse and burn (Table 2) were used to estimate fluxes under wet (2003) and dry (2004) growing seasons (Fig. 6). The estimated fluxes suggest that ecosystem respiration was reduced in the dry season relative to the wet season. The decreased ecosystem respiration would equal a cumulative decrease of 28 g C m^{-2} emitted to the atmosphere from the collapse and 67 g C m^{-2} from the burn. The empirical model of NEE in the bog explained less than 30% of the total variation (Table 2). Estimates of NEE indicate greater carbon uptake in the drier growing season, with 32 g C m^{-2} in the collapse and 20 g C m^{-2} in the burn. Water vapor fluxes were estimated to be higher in the drier growing season with an additional 110 g m^{-2} H_2O lost to the atmosphere in the collapse and 54 g m^{-2} H_2O in the burn. Methane fluxes were estimated to be three times lower in the dry growing season, with a cumulative emission of 1 g m^{-2} of carbon over the growing season.

DISCUSSION

Landscape-level Controls

The high observed spatial and temporal variability of fluxes observed along this moisture transect is typical of fluxes in other wetland systems (Bubier *et al.*, 1998). Fluxes were most variable in the moat, where water levels differed greatly during the 2004 growing season. In this region of the transect, active thermokarst and deep thaw promoted both aerobic and anaerobic decomposition, which released sufficient nutrients to support a high biomass of *Eriophorum vaginatum*. The net effect was a high rate of ecosystem respiration that was more than offset by high carbon uptake (and therefore a high NEE) in addition to high rates of evapotranspiration and methane release. Previous studies have documented high methane emissions at the margins of peat features (Bubier *et al.*, 2005). This study demonstrates that landscape-level disturbance, such as fire-initiated permafrost collapse, can alter carbon exchange by changing the relative water table level, soil thermal profile, and vegetation composition.

Process-level Controls

Temperature has often been shown to be the major controller of carbon fluxes in boreal systems (Moore *et al.*, 1998). However, in poorly drained ecosystems, water level controls oxygen diffusion, and hence the proportion of the soil profile undergoing aerobic versus anaerobic decomposition (Gorham *et al.*, 1991). Although low lying wetland ecosystems seem unlikely candidates to experience significant plant drought stress, the combination of root systems limited by a shallow active layer and rapid fluctuations in the water table led to periods of reduced water availability in the growing season of 2004. In the burn, the variable organic layer thickness produced to patches of dry soils across the landscape even when the water table was less than half a meter below the surface. In particular, the hummocks formed by the root matrices of the still standing dead trees dried out significantly over the summer. The drought limited ecosystem respiration and plant activity in the warmer parts of the growing season. Enhanced ecosystem respiration was not observed in the driest period of the 2004 growing season. The low mid-season ecosystem respiration can be attributed to moisture-limitation of soil microbial activity and plant metabolism.

Since soil moisture interacts with temperature to control carbon exchange, empirical models of NEE in wetlands differ from those for non-permafrost upland systems (Frolking *et al.*, 1998). In this study, models of NEE and water vapor flux explained less than half the variation across the growing season. The lack of variance explained is attributed to the interactive nature of plant responses to changes in temperature, thaw depth, soil moisture and PAR, especially when experiencing drought stress. Further investigations of ecosystem carbon exchange across the different vegetation communities in this system will improve our ability to effectively model carbon exchange in response to variations in climate.

Observed methane fluxes in the growing season of 2004 were low relative to other northern peatlands (Gorham, 1991; Bubier *et al.*, 1998; Moore *et al.*, 1998; Bellisario *et al.*, 1999) due to warm temperatures and low water levels. Soil moisture was the major controller of CH_4 emissions in the bog portion of the transect. The dry mid season led to redox conditions that were not conducive for methanogenesis. Estimates of fluxes for a wet growing season scenario suggest that CH_4 release may have been three times higher under precipitation levels experienced in 2003, equaling 76 g m^{-2} of CO_2 equivalent carbon (sustained global temperature change potential; Shine *et al.*, 2005) emitted to the atmosphere. Methane flux is particularly sensitive to precipitation in this hydrologically-isolated permafrost collapse. Our findings corroborate previous studies in that the response of methane fluxes to varying water level that will likely be the primary determinant of net greenhouse gas exchange in northern wetlands (Moore *et al.*, 1998).

Linking Landscape- and Process-level Controls

In this study the interactions between landscape-level disturbance and the primary controls on carbon exchange were assessed. The three zones across the transect, burned forest, moat and bog, interact with the primary landscape-level controls of fire, thermokarst and drainage (Fig. 7). Fire causes a loss of organic matter, a shift in summer albedo and a change in vegetation, which interact with the process-level controls of soil temperature, thaw depth, soil moisture, PAR, and biomass. Changes in soil temperature and soil moisture leading to increased thaw depth triggered thermokarst in the moat portion of the transect. The resulting soil subsidence caused aerobic soils to become saturated, changing the ratio of oxic- to anoxic-decomposition. Over time the bog vegetation will expand into the moat, increasing carbon accumulation in the landscape (Zoltai, 1993). These interactions between the landscape- and process-controls result in alterations to carbon exchange that emerge on different timescales: the impact of the 2001 fire on the burn portion of the transect will persist until the return of a mature black spruce forest. However, the impact of the thermokarst and resulting bog expansion will persist and be augmented by subsequent fire cycles in this landscape. Overall, the aerial cover of the forest will give way to collapse unless a cooling of climate reduces the sensitivity of permafrost to melting.

Response to Precipitation

Alteration of the precipitation regime can change peatland systems from net sinks to sources of carbon (Bubier *et al.*, 1998, Schreader *et al.*, 1998). The net carbon budget for this ecosystem cannot be definitively determined from the flux measurements and modeling exercises conducted in this study. However, this study illustrates that changes in water regime have a significant impact on the relative contributions of different fluxes to the net carbon budget in this system. Projections of fluxes in this system under a dry growing season scenario suggest that decreased precipitation would reduce ecosystem respiration and CH_4 emissions. Understanding both the process-level controls and the impacts of landscape disturbance on carbon exchange in wetland systems will be crucial to our ability to project ecosystem feedbacks to climate change.

CONCLUSIONS

Heterogeneity caused by landscape disturbances such as fire and permafrost degradation and variation in soil drainage and vegetation has led to variable carbon exchange in this ecosystem. Both temperature and moisture interact to control the variation of fluxes across the landscape and throughout the growing season. In the dry growing season of 2004, both ecosystem respiration and CH_4 emissions were suppressed, and increased carbon uptake was observed. There is great uncertainty about the future precipitation regime in Interior Alaska. Change in water availability, rather than temperature, may be the most important determinant of the magnitude of feedbacks to climate change in these northern wetlands.

ACKNOWLEDGEMENTS

I thank Patrick Crill for training in field techniques, Jill Bubier for field reconnaissance and vegetation descriptions, Jeremy Jones for use of his laboratory, Jamie Hollingsworth, Kaarle Strailey, Emily Sampson, and Dan Ulliassi for field and laboratory assistance, and Evan Kane, Jon O'Donnell, and Nick Lizusso for reviewing the manuscript. This research was funded by the USGS Earth Surface Dynamics Program and the Bonanza Creek LTER (Long-Term Ecological Research) program (funded jointly by NSF grant DEB-0423442 and USDA Forest Service, Pacific Northwest Research Station grant PNW01-JV11261952-231).

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Table 1. Above- and below-ground carbon pools. Mean above-ground carbon pools for vegetation types across the transect (g m^{-2}, n = 2) and mean below-ground carbon pools for soil horizons (kg m^{-2}, n = 3) described using the Canadian Soil Classification system (Soil Classification Working Group, 1998).

		Distance (m)					
		Bog		Moat	Burn		
	Vegetation Type	0 m	6 m	12 m	18 m	24 m	30 m
Above Ground Carbon (g m^{-2})	*Carex* spp.	67.7 ± 23.1	39.2 ± 7.0	28.2 ± 28.2	-	-	-
	Eriophorum vaginatum	-	-	54.3 ± 54.3	43.8 ± 11.8	59.7 ± 8.3	31.2 ± 31.2
	Sphagnum spp.	157.5	143.5 ± 1.3	-	-	-	-
	Other Moss	-	-	16.7	49.5	15.3	15.6 ± 0.8
	Graminoid spp.	-	-	-	88.1 ± 89.2	1.3 ± 0.5	11.6 ± 9.7
	Betula spp.	-	-	-	1.1 ± 1.1	5.4 ± 3.5	3.0 ± 1.3
	Salix spp.	-	-	-	-	14.0 ± 14.0	-
	Other Vascular	-	1.1 ± 0.5	-	1.9 ± 0.3	0.5 ± 0.5	4.8 ± 3.2
	Total	**198.0**	**158.1**	**83.7**	**90.5**	**81.8**	**61.5**
	Soil Field Horizon Code						
Below Ground Carbon (kg m^{-2})	Live Moss	0.32 ± 0.07	0.11 ± 0.01	0.18 ± 0.06	0.35 ± 0.03	0.28 ± 0.00	0.40 ± 0.11
	Litter	2.23 ± 0.33	0.59 ± 0.06	0.78 ± 0.21	-	-	-
	Fibric	5.22 ± 0.40	6.40 ± 3.29	2.14 ± 0.29	-	-	-
	Mesic	14.17 ± 1.17	18.54 ± 3.67	9.04 ± 1.54	2.29 ± 0.60	3.93 ± 0.90	7.67 ± 1.11
	Humic	42.22 ± 3.98	-	16.38 ± 1.56	5.19 ± 0.00	-	-
	A Horizon	6.70 ± 1.38	-	6.39 ± 1.75	1.48 ± 0.40	1.98 ± 0.00	6.00 ± 0.82
	C Horizon	9.01 ± 1.34	8.00 ± 1.34	7.93 ± 0.58	8.00 ± 1.34	8.00 ± 1.34	13.61 ± 1.63
	Organic Soil Total	**11.41**	**6.73**	**6.12**	**3.46**	**3.55**	**5.54**

Table 2. Multiple linear regression model parameters. Model R^2, significance and unstandardized b-coefficients for multiple linear regression models of ecosystem fluxes for the collapse (0 - 12 m) and burn (18 - 30 m) portions of the transect. I used the b-coefficients to interpolate CO_2, H_2O and CH_4 fluxes across the growing season (from day 149 to 261 of the year) of 2004 and to extrapolate fluxes for the growing season of 2003.

	Ecosystem Respiration		Net Ecosystem Exchange		H_2O Flux		CH_4 Flux
	Collapse	Burn	Collapse	Burn	Collapse	Burn	Collapse
R^2	0.498	0.597	0.244	0.364	0.451	0.246	0.402
Significance	0.000	0.000	0.046	0.003	0.000	0.08	0.005
Constant	2.779	0.0116	-2.568	-4.620	5.990	5.800	-190.262
Soil Temperature	$3.36e^{-6}$	$2.27e^{-6}$	$3.11e^{-14}$	$3.47e^{-6}$	$1.07e^{-6}$	$-3.40e^{-8}$	$3.45e^{-5}$
Soil Moisture	-4.038	12.114	4.473	6.244	-19.227	-16.609	712.535
Water Level	1.096	1.027	0.592	0.108	-0.667	0.210	18.215
Thaw Depth	$-6.35e^{-3}$	$-2.46e^{-2}$	$1.83e^{-3}$	$2.51e^{-3}$	$1.28e^{-3}$	$2.26e^{-3}$	$-9.58e^{-2}$
PAR	$1.05e^{-3}$	$6.97e^{-3}$	$-1.48e^{-3}$	$1.01e^{-4}$	$1.52e^{-3}$	$-3.76e^{-4}$	$-4.61e^{-3}$
Biomass	$4.45e^{-3}$	$8.64e^{-3}$	$-6.33e^{-3}$	$-7.74e^{-3}$	$1.65e^{-3}$	$5.65e^{-3}$	0.101

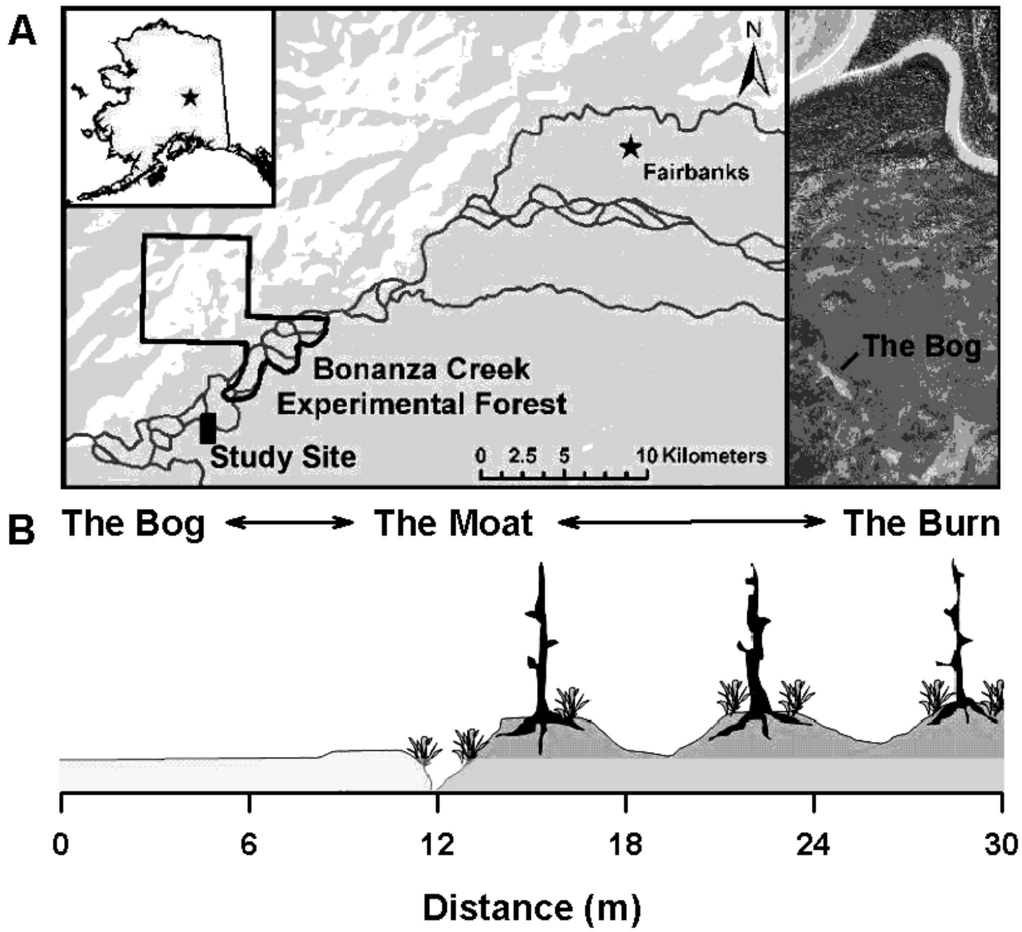

Figure 1. Site location and transect structure. (A) Map of the location of the study site in Interior Alaska. (B) Diagram illustrating bog, moat and burn portions along the transect.

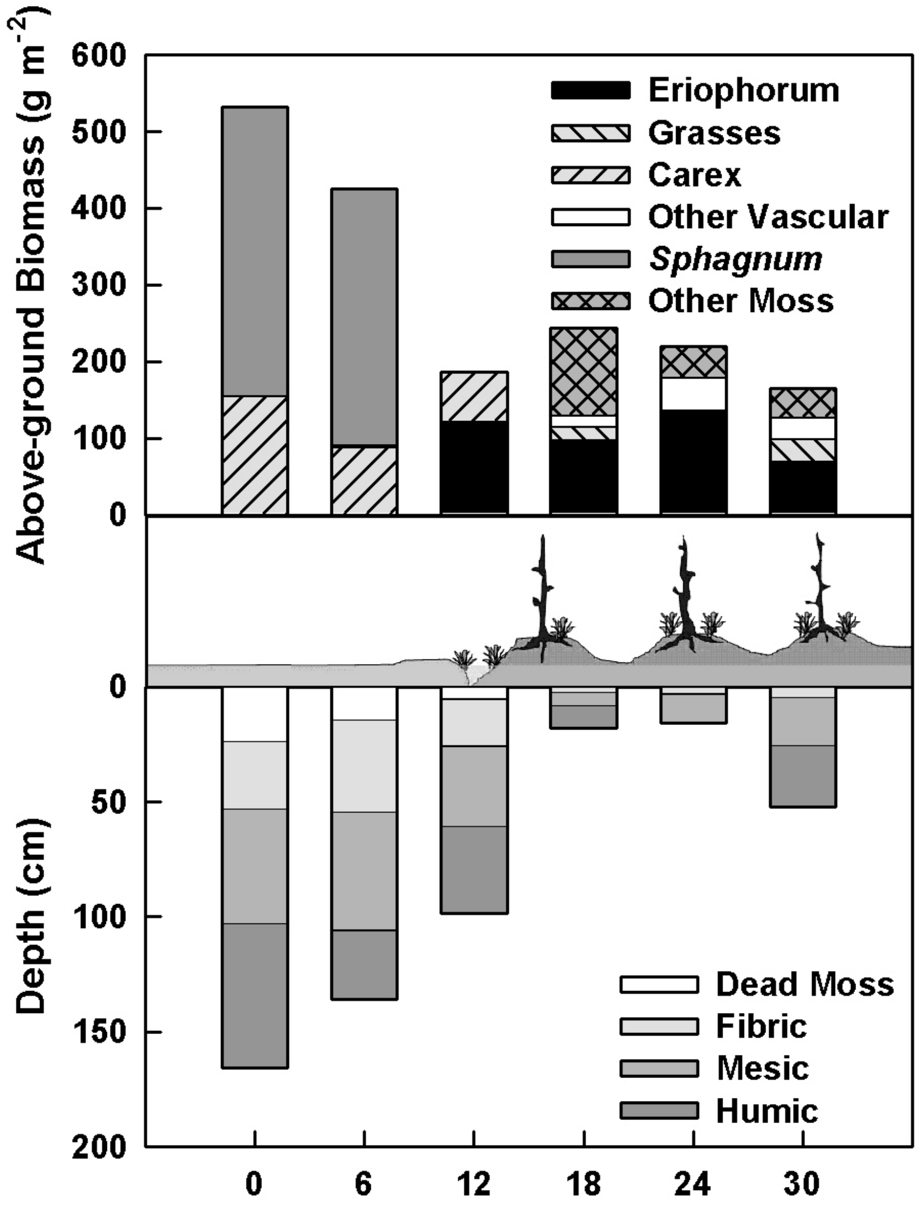

Figure 2. Biomass and soils across the transect. Mean above-ground biomass (g m^{-2}, n = 2) and mean measured soil horizon depths cm (n = 2) described using the Canadian Soil Classification system (Soil Classification Working Group, 1998).

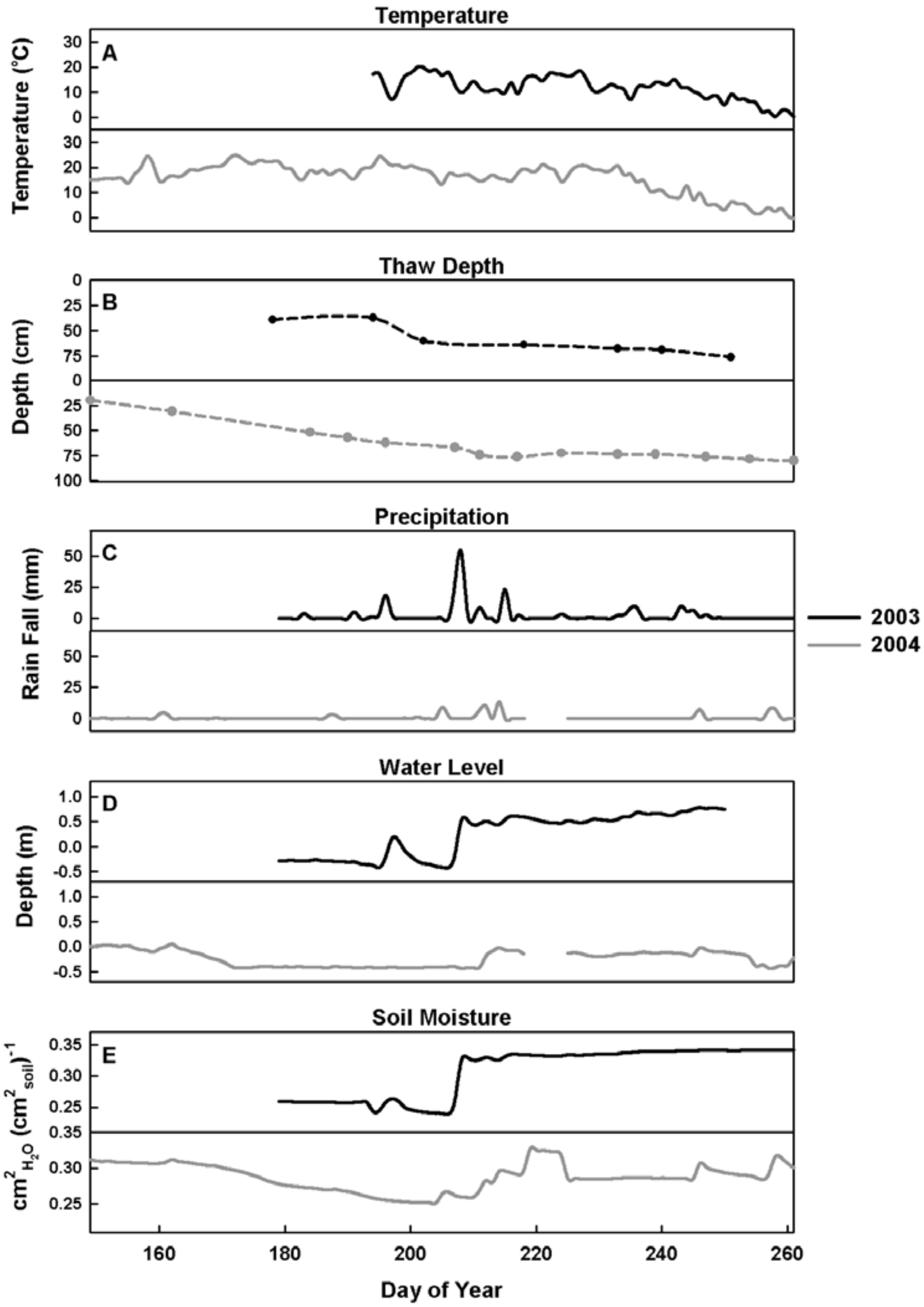

Figure 3. Meteorological variables for the growing season of 2003 and 2004. Air temperature (A), thaw depth (B), precipitation (C), soil moisture (D), and water level (E) for days 195 - 250 of 2003 and 2004. Thaw depth data are means for the forest portion of the transect.

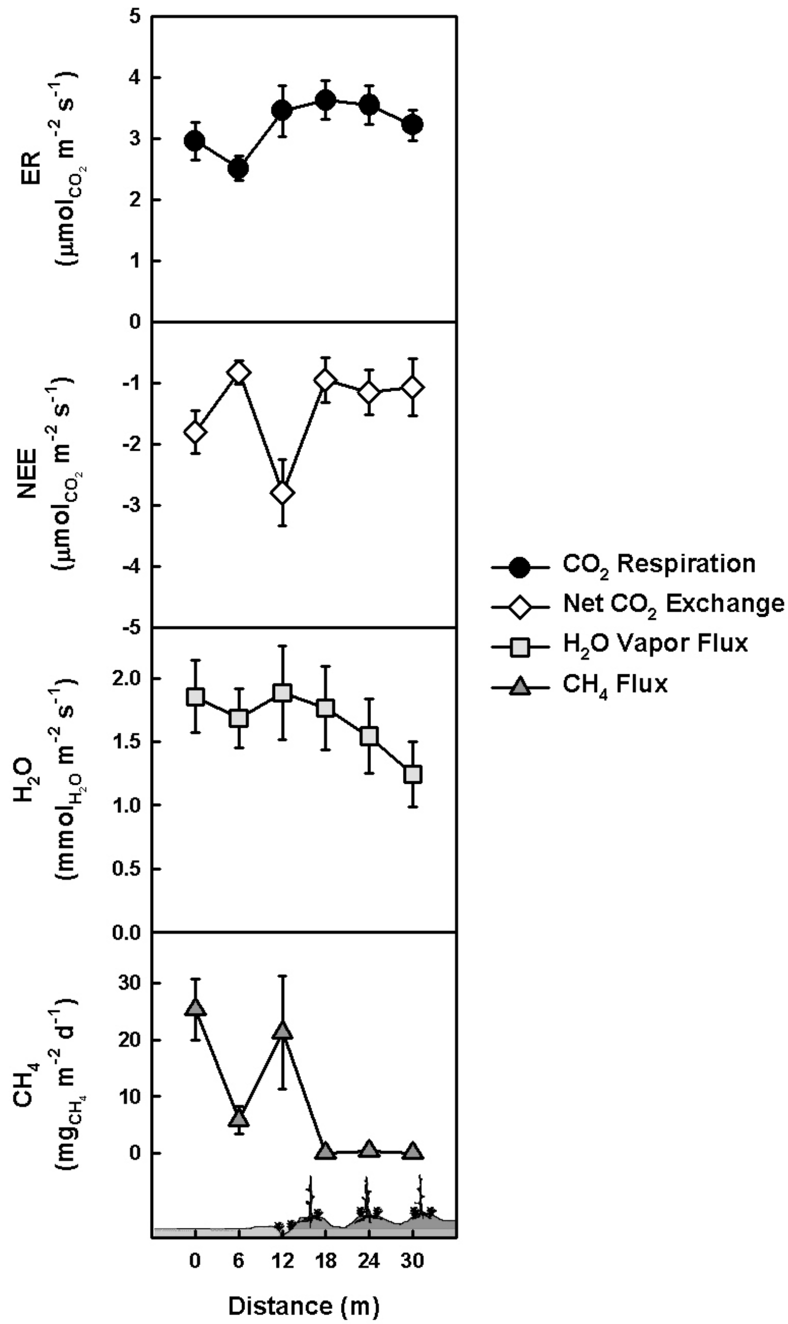

Figure 4. Mean fluxes across the transect. Mean ecosystem respiration (ER), NEE, water and CH_4 fluxes across the transect for the growing season of 2004 (error bars = ± SE, n = 16 for CO_2, NEE and H_2O and n = 13 for CH_4). Carbon uptake is denoted with negative numbers and carbon emissions with positive numbers.

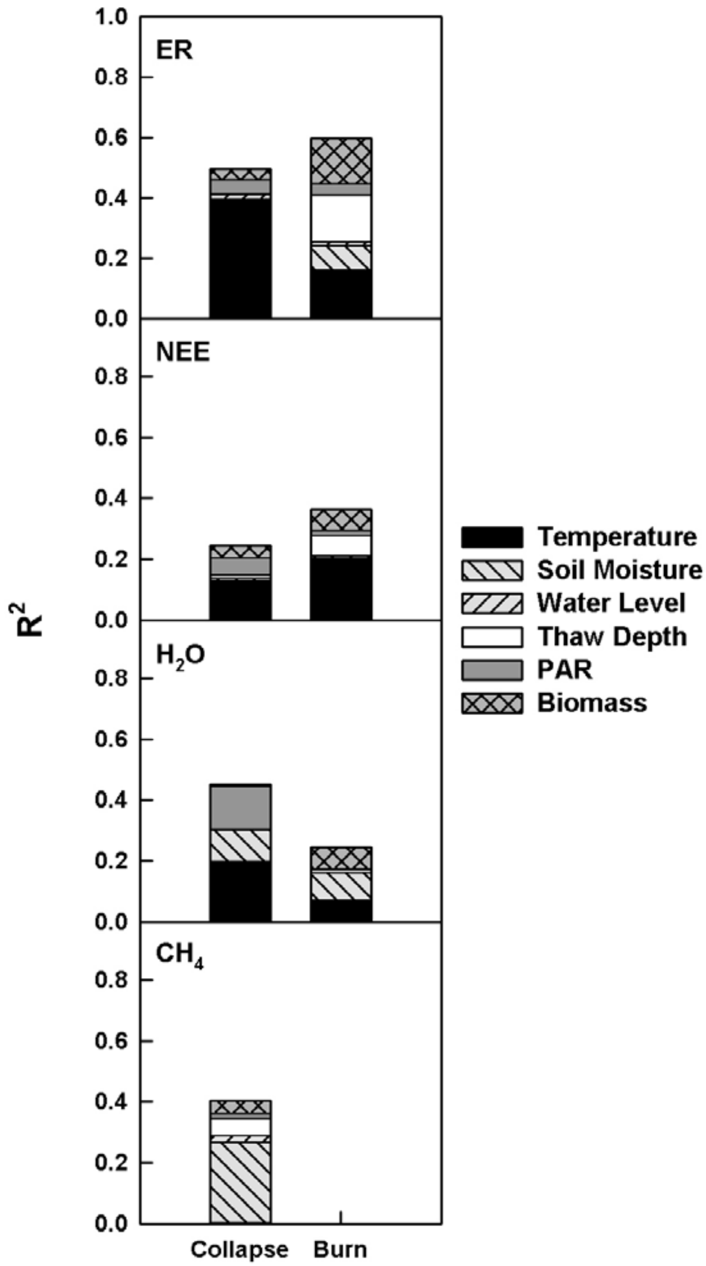

Figure 5. Multiple linear regression r^2 values for all significant parameters. The proportion of variation explained by each significant model parameter for multiple linear regression models of all fluxes for the collapse and burn portions of the landscape. All models are significant at $p < 0.05$ except for the H_2O burn model, which was marginally significant ($p = 0.08$).

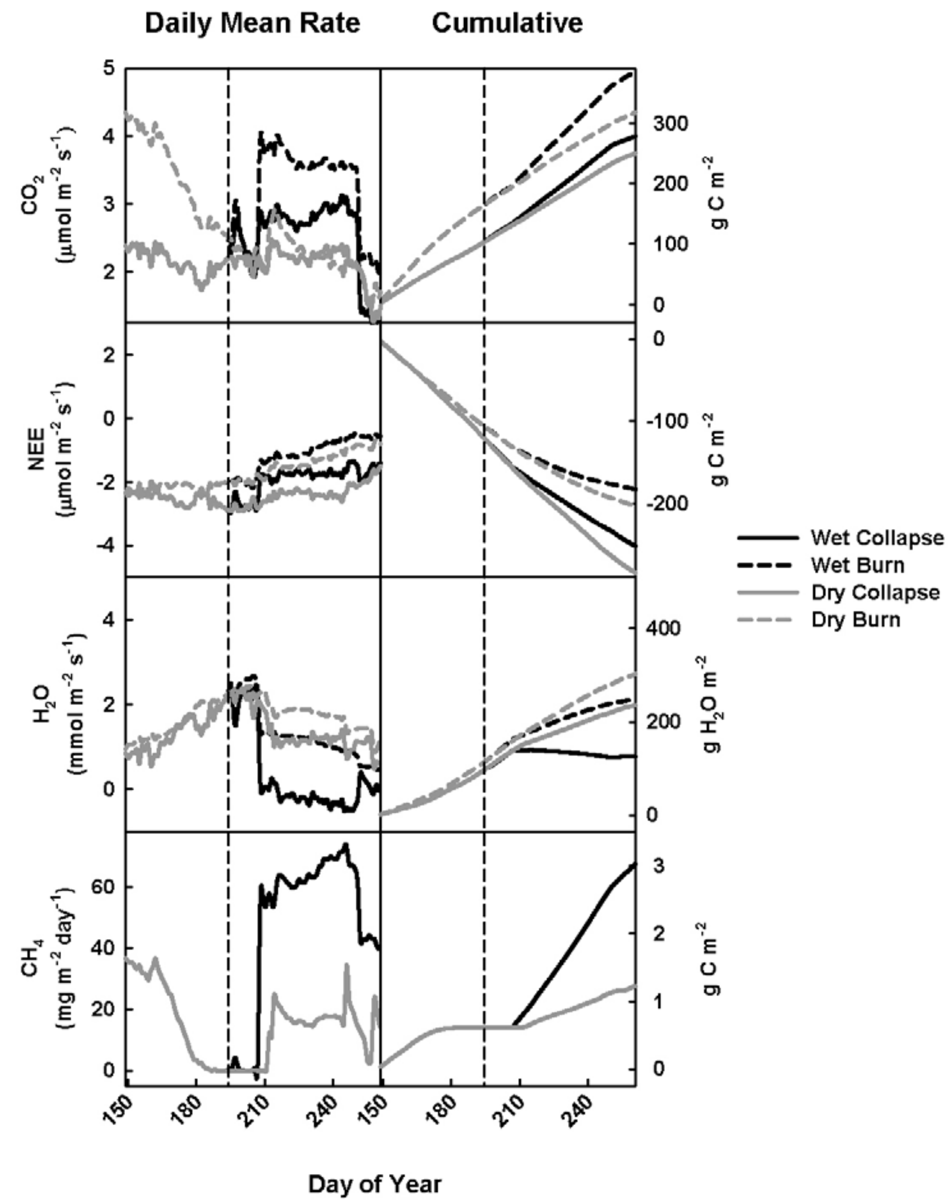

Figure 6. Predicted fluxes and carbon and water accumulation over the growing season for wet and dry scenarios. Predicted fluxes (left) and carbon accumulation (right) for wet (2003) and dry (2004) growing seasons for the collapse and burn portions of the transect. Wet and dry driving data were derived from hydrologic data from 2003 and 2004, respectively. All data were modeled in half hourly intervals and then averaged by day from day 149 to 261 of the growing season.

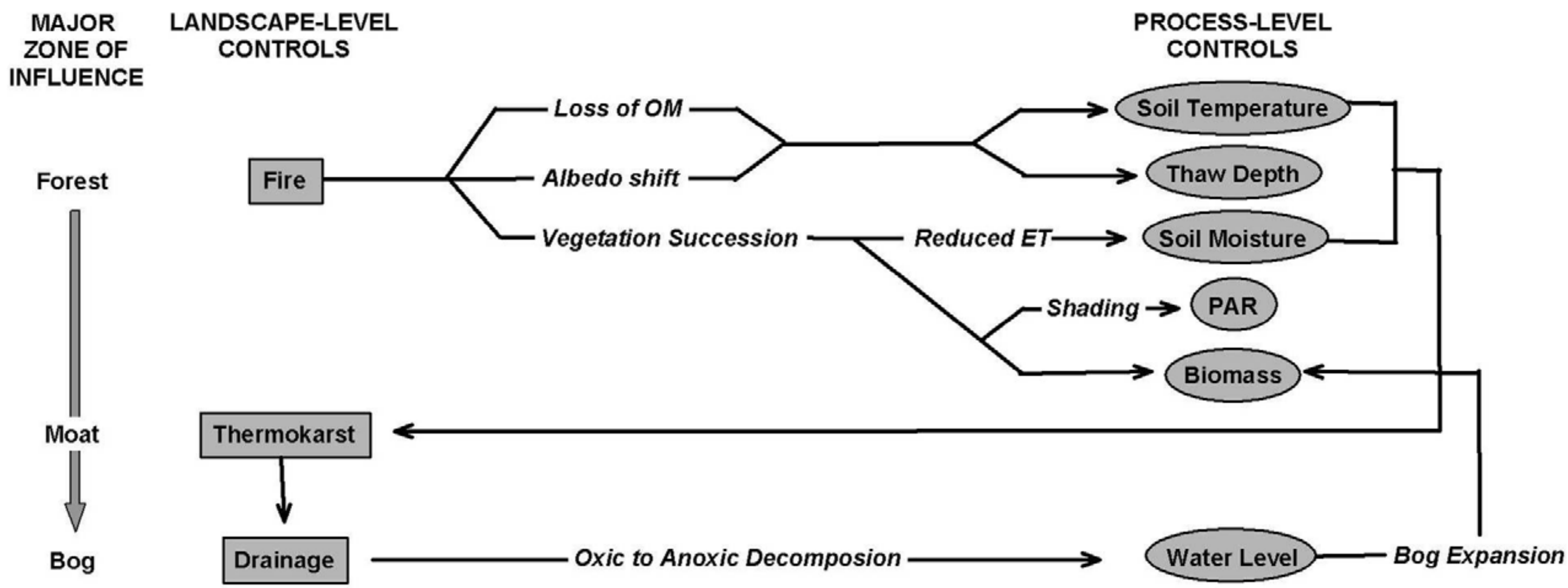

Figure 7. Conceptual model of interactions between controls of carbon exchange. Conceptual model of the interaction between landscape-level and process-level controls on carbon exchange in this ecosystem.

CHAPTER 3.

INTERACTIONS BETWEEN FIRE AND CLIMATE: WETLAND SUCCESSION IN A PERMAFROST COLLAPSE[1]

ABSTRACT

The spatial patterns in poorly drained ecosystems are controlled by vegetation succession and landscape-level disturbance. With warming and drying, wetland regions of the boreal forest may experience more frequent or extensive stand-replacing fires and permafrost degradation. This disturbance will alter the structure and function of this northern carbon sink. To determine the influence of fire and thermokarst on the development of this landscape, I investigated the succession of a *Sphagnum*-dominated permafrost collapse located on the Tanana River Floodplain. Fire in the adjacent forest initiated permafrost collapse approximately 600 years ago. Diatom data indicated a change in water chemistry preceded the shift from a sedge to *Sphagnum*-dominated ecosystem approximately 250 years ago. If precipitation patterns remain unchanged over the next few centuries, the trajectory of fire, collapse and bog expansion will continue. However, significant drying could initiate a return to terrestrial vegetation or reduce the success of black spruce in this landscape. The development of new ecosystem states could lead to reduced carbon storage and would be a positive feedback to climate warming.

INTRODUCTION

Boreal ecosystems are projected to be some of the most sensitive to future climate forcing. Projected changes in temperature and precipitation could alter disturbance regimes, potentially increasing the frequency of fire and thermokarst. Change in the disturbance regime may have a larger effect on the release of greenhouse gas emissions than direct physiological responses of plants and microbes to climate (Chapin *et al.*,

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[1] Myers-Smith, I. H., J. W. Harden, M. Wilmking, A. D. McGuire, and F. S. Chapin III. Interactions between fire and climate: Wetland succession in a permafrost collapse. To be submitted to *Journal of Geophysical Research-Biogeosciences.*

2000). Since disturbance is integral to vegetation succession, climate warming could trigger the development of new ecosystem states in the boreal region (Chapin *et al.*, 2004).

Climate models project that the boreal forest will experience significant warming over the next century (Gower *et al.*, 2001). Annual surface temperatures in Interior Alaska have increased by about 2°C in the last half century; however, there has been no clear trend in precipitation (Keyser *et al.*, 2000; Serreze *et al.*, 2000). Under climate change most peatlands will likely experience warmer, drier conditions; however, in areas like Interior Alaska, they may become warmer and wetter (Öquist and Svensson, 1996).

Localized processes such as aspect, shading, drainage, and insulation may exert more direct control over the stability of permafrost in peatlands than regional climate (Camill and Clark, 1998). Because permafrost degradation and vegetation succession are controlled by microclimate and hydrology, and localized variation in ecosystem response to climate change, vast areas of the boreal forest could respond faster, and along different trajectories than predicted by coarse-scale models (Camill and Clark, 1998).

Half of the boreal region in Alaska is underlain by soils that have developed under conditions of near-surface water tables, much of which is underlain by permafrost (Harden *et al.*, 2004). The thawing of ice-rich permafrost can lead to the transformation of terrestrial systems to wetlands through collapse (Osterkamp *et al.*, 2000, Jorgenson *et al.*, 2001). Collapse is a vertical subsidence and therefore, a lateral expansion of low-lying soils on the landscape. Permafrost temperatures in Interior Alaska have warmed 1.5 °C since the mid - 1980's (Osterkamp and Romanovsky, 1999) and permafrost collapse has increased by 21% on the Tanana Flats since 1949 (Jorgenson *et al.*, 2001). By the end of the next century, climate warming may eliminate permafrost in this landscape (Jorgenson *et al.*, 2001).

In this study I investigated the impacts of fire disturbance and thermokarst on wetland succession in a collapse feature. I examined the relative importance of fire and collapse expansion in the evolution of this landscape along the transition from a fire-scarred *Picea mariana* forest to a *Sphagnum*-dominated bog. I used paleoecological methods, namely diatom taxonomic shifts through a pedogenic sequence, to develop conceptual models of collapse development and their implication for future landscape patterns under scenarios of climate change.

The aims of this study were to 1) document succession in this collapse feature, 2) determine whether fire initiates collapse expansion, and 3) document changes in wetland moisture to understand how climate change may impact the structure and function of this ecosystem.

METHODS

Study Site

This study was conducted in a permafrost collapse (64^{o} N. 38.448', 148^{o} W. 20.009', 132 m elevation) southwest of the Bonanza Creek experimental forest on the Tanana River floodplain in Interior Alaska (Fig. 1). Variable vegetation, hydrology, and topography from legacies of flooding, fire and thermokarst have created a complex landscape mosaic in the Tanana Flats (Jorgenson *et al.*, 2001). Unlike much of this landscape, this region is not subject to upwelling of groundwater; therefore, these wetlands are best characterized as ombotrophic bogs, receiving the majority of their water from atmospheric sources. In this area, water level in wells 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.

In July 2001, within a month of the Survey-line fire, a transect was established from the center of a permafrost collapse peat land feature into the surrounding burn. By August 2002, the periphery of the collapse feature had undergone a 6 m lateral expansion, indicating inundation of the burn. On August 5th 2004, I surveyed the site using a Topcon GTS 220 Series All-Weather Total Station (Topcon America Corporation, Paramus, NJ, USA). The collapse is 175 by 75 m and the surface depression is 0.5 m (Fig. 2).

In 2004, there were three ecological zones along the transect: the bog, moat and burn. These three portions of the transect had distinct soil profiles (Fig. 2) with a maximum 0.5 m organic matter (OM) accumulation in the bog. Thaw depth was greater than 2 m below this portion of the transect. The moat, the transition between the bog and surrounding burned forest, was the area of recent soil subsidence. This was the lowest portion of the transect, with a high relative water table level. In the burn, the maximum thaw depth was approximately 80 cm. The organic matter thickness was highly variable because of tussock-hollow microtopography, variable fuel comsumption, and variable soil subsidence patterns.

The three ecological zones along the transect had distinct vegetation assemblages. In the bog portion of the transect, the dominant vegetation types 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 moat portion of the transect was the area of recent soil subsidence and was dominated by *Eriophorum vaginatum* tussocks and *Carex* spp. There was standing water present in the moat throughout both the growing seasons of 2003 and 2004, with a small biomass of aquatic vegetation. The burn was formerly a low-lying open-canopy *Picea mariana* forest with an understory of tussock vegetation. The dominant vegetation types after the fire were *Eriophorum vaginatum* tussocks, Grass spp., *Betula* spp., *Salix* spp., *Potentilla palustris*, *Ledum groenlandicum*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea* and *Chamaedaphne calyculata*.

Soil Temperature

In 2003, I installed meteorological instruments along the transect. I measured temperatures using copper-constantan theromocouples (Omega Engineering Inc., Stamford, CT, USA) at 5, 10, 20, and 50 cm depth on the east and west side of the boardwalk at 0, 10 (west side only), 20, and 30 m distance along the transect. To monitor changes in thaw depth, I probed the soil to a depth of 120 cm at each visit to the site every three meters along both the east and west sides of the transect.

Soil Sampling

Two to four replicate frozen soil cores, 35 cores total, were collected every 3 m along the transect in March 2003 with a gasoline-powered permafrost corer. Cores were stored frozen and sampled using a radial saw. Three well-preserved cores from the center of the bog, the moat and the burn were sampled every two cm for macrofossil, diatom analysis and chemistry. I calculated bulk density for all depths.

Carbon and Nitrogen

Core samples were analyzed for %C and %N to estimate rates of peat accumulation. I oven-dried at 50 - 65°C and ground all samples before analysis 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 error was ± 0.0093% for nitrogen, ± 0.45% for carbon.

Core Dating

A charcoal piece from 56 cm depth and *Sphagnum* head capsules from 40 cm depth in the core from the center of the bog were analyzed for ^{14}C was conducted at Lawrence Livermore National Laboratory, Center for Accelerator Mass Spectrometry. Dates were reported relative to the standard NIST Oxalic Acid I ($C_2H_2O_4$), with additional correction for fractionation, based on generalized ^{13}C.

Charcoal Estimates

To indicate fire events in the surrounding ecosystem, charcoal layers in the cores were quantified. I estimated charcoal by emptying dried samples of a known volume and depth (on mean 4.5 cm^3) over a 10 cm x 10 cm grid and counting macroscopic charcoal fragments (greater than 0.05 mm in diameter) in each cm grid cell.

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). Diatoms are more sensitive to changes in water levels than the commonly used peat indicators such as pollen and macrofossil analysis (Rühland *et al.*, 2000). In this study, I employed diatom analysis to indicate shifts in water chemistry and to ascertain the response of this ecosystem to disturbance.

To survey the diatom community, I processed three cores sampled every 2 cm by depth from the bog, moat and burn using methods described by the Paleoecological Environmental Assessment and Research Laboratory (PEARL) at Queen's University and personal communications (Kathleen Rühland and John P. Smol). I digested the dried material, consisting of organic matter with varying amounts of sediment, in Kjeldahl digestion tubes in a heating block. I used 50:50 solution by molecular weight of concentrated H_2SO_4 and HNO_3 and digested for 3 days at 95°C or until the disappearance of all organic matter. I diluted the resulting solution with deionized water to a neutral pH. I 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, I counted 400 valves (or for one sparse sample, four slides) for each sample. I identified samples according to Foged (1981), Krammer and Lange-Bertalot (1991) and personal communications with K. Rühland.

Dendrochronology

I used dendrochronology to link paleoecological data with modern observations of the response of this system to fire. 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. My collaborator, Martin Wilmking, and I 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. We measured ring width (sliding stage, Velmex Inc., Bloomfield, NY, USA, resolution: 0.001mm) for two radial transects of the tree cross-sections. To remove the age-related variation in growth rate, we crossdated trees with Cofecha and standardized ring-widths with the program ARSTAN (Richard Holmes, Laboratory of Tree Ring Research, University of Arizona). We recorded the presence of compression-wood for each tree ring, an indicator of leaning which is interpreted to be related to frost-heaving and permafrost collapse (Camill and Clark, 1998). We correlated tree ring widths 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).

Sphagnum Growth

I measured current rates of the growth of the *Sphagnum* mat relative to horizontal wires buried in peat over the two years of this study. At the end of the second growing season in 2004, I measured *Sphagnum* height above the wire every 50 cm along the 10 m wire path.

Statistical Analysis

I determined diatom-delineated zones using constrained cluster analysis by information content (CONIIC) by the program Psimpoll 3.01 (K.D. Bennett, Uppsala University). I performed regressions and ANOVAs in SPSS 10.0 (SPSS Inc., Chicago, IL, USA).

RESULTS

Core Stratigraphy

Soils from the center of the bog (Fig. 3) and moat (Fig. 4) provided records of both carbon accumulation and disturbance. I found three distinct organic matter substrates in the core from the center of the bog: sylvic OM from 53 - 59 cm, sedge-dominated peat from 27 - 53 cm, and *Sphagnum*-dominated peat from 0 - 27 cm (Fig. 3). I identified four organic matter substrates in the moat core: sylvic OM from 41 - 33 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. Charcoal residues in the bog core indicated four fire events at 12, 21, 28, 46 cm over the last 600 years. In the moat core, there was one strong fire signal at 20 cm and another smaller peak in charcoal at 34 cm. Soil bulk density and the percent nitrogen were variable with depth through both cores. There were peaks in bulk density after all fire events that corresponded with peaks in the C:N.

Diatoms

Diatom assemblages indicated three successional stages in the bog core (Fig. 5). These three zones delineated with CONIIC agreed loosely with the three substrates: sylvic OM, sedge-dominated, and *Sphagnum*-dominated peat. *Eunotia rhomboidea*, *E. nymanniana*, *E. glacialis*, and *Navicula subtilissima* (zone 3) were prevalent in the *Sphagnum*-dominated portion of the core. A shift in the diatom assemblage was initiated 6 cm beneath the shift to *Sphagnum*-domination in the macrofossil record. *Gomphonema* spp., *Cymbella ventricosa var. groenlandica*, *Navicula tripunctata var. arctica*, and *Nitzchia* spp. (zone 2) were common in this portion of the core. There were some conspicuous diatoms in low densities at the bottom of the sedge-dominated portion of the core (zone 1). These were *Pinnularia* spp., *Hantzschia amphioxys var. major*, *Eunotia praerupta*, *Navicula amphibola*, *Stauroneis phoenicenteron*. There was a similar diatom assemblage at 4 cm in the terrestrial soil core (Fig. 5).

Peaks in specific diatom abundance often correlated with specific physical and chemical characteristics of the soil core. The abundance of *E. nymanniana* responded positively to burn events and tracked bulk density (cross correlation, r = 0.62, *p-value* < 0.003, d = -1). *E. tenella*, *C. ventricosa*, *N. tripunctata*, *Pinnularia* spp., and *E. flexuosa* peak at 36 cm, which corresponded to a peak in density and % nitrogen. A peak of *E. rhomboidea*, *Tabellaria flocculosa* (girdle bands), and *E. faba* at 42 cm coincided with another peak in % nitrogen.

Dendrochronology

Trees in the forest responded negatively to summer temperatures (r^2 = 0.25, *p-value* < 0.001, n = 11), whereas trees growing in the collapse showed no relationship (*p-value* = 0.28, n = 10) to temperature. Compression-wood was observed in 14 of the 21 trees sampled.

DISCUSSION

Mechanism of Collapse

Collapse has been attributed to fire in the peatlands of Western Canada; however, fire has not been identified as the dominant mechanism of collapse (Thie, 1974, Zoltai, 1993). In this study, the soil profiles across the transect included deep humified organic layers that contained charcoal and macrofossils indicative of cyclic disturbance and succession sequences. Charcoal residues in the bog indicate that four fires have occurred in the terrestrial forest adjacent to the bog in the past 600 years since the initiation of the collapse. This indicates a fire return interval of approximately 150 years. In the three growing seasons following the 2001 fire, my collaborators and I observed a 6 m lateral expansion of the collapse. 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). Therefore, I hypothesized that fire may be the primary cause of thermokarst in this ecosystem.

Macrofossils and soil chemistry indicated that a terrestrial forest pre-existed the collapse. There was a layer of well-decomposed organic matter above the mineral horizon that was similar in %C, %N, C:N, and density in all cores along the transect. Woody peat was found at the base of both the bog and moat cores. The diatom assemblage above this sylvic organic matter was very similar to the assemblage observed in soils from the terrestrial portion of the transect. Alkaliphilous to pH neutral, salt tolerant, and mesotraphentic to eutraphentic (tolerant of nutrient enrichment) taxa (*Pinnularia* spp., *Hantzschia amphioxys var. major*, *Navicula amphibola*, *Stauroneis phoenicenteron*) found at the base of the bog core indicate a less acidic, nutrient rich soil

(Van Dam *et al.*, 1994). The terrestrial layer in the bog and moat cores suggests that the collapse formed out of a landscape very similar to the present-day black spruce forest.

The varying depths of the organic signal along the transect may imply that this collapse has developed in punctuated stages of disturbance and succession. Sylvic peat occurred at 53 cm below the surface in the bog core; however, in the moat core it was found at only 33 cm. The varying depth to terrestrial OM may indicate a previous collapse preserved in the profile at approximately 7 m from the center of the bog.

These multiple lines of evidence suggest a conceptual model for collapse development over time at this site (Fig. 6). Given a black spruce forest with a thin active layer growing over ice-rich permafrost, I propose the following sequence. After burning of the forest, an initial collapse is formed. This is then colonized by wetland vegetation such as sedges and *Sphagnum*. Over successive fire sequences the collapse expands and the wetland vegetation colonizes the newly subsided margins.

However, fire is not the only trigger of collapse and wetland expansion. The presence of compression-wood in the growth rings of trees at the margin of the collapse feature indicate that subsidence has occurred since the last stand replacing fire. Evidence from this study supports the hypothesis that fire is the dominant driver of spatial patterning in this ecosystem after isolation from the active floodplain. However, permafrost degradation and wetland succession has proceeded in the recovery periods between fires.

Wetland Succession

Diatom assemblages indicate three successional stages in the bog core. The most recent zone, roughly coincident with the *Sphagnum*-dominated zone, was dominated by acidophilous (mainly occurring below pH 7) *Eunotia* spp. The diatom assemblage in the top 32 cm of the bog core is consistent with the modern state of the collapse as an acidic ombitrophic bog. There was a significant increase in the acidobiontic (optimal occurrence at pH 5.5) species *Navicula subtilissima* at 14 cm, suggesting a period of low pH during the recent history of the bog environment.

A shift in the diatom assemblage was initiated 6 cm beneath the shift to *Sphagnum*-domination in the macrofossil record. Diatoms in Siberia have been shown to respond first to changes in the chemical environment and then secondarily to vegetation changes (Rühland *et al.*, 2000). The shift in the diatom community observed in my study may indicate the initial environment perturbation that lead to vegetation succession in the collapse.

The diatom-inferred zone from 33 - 45 cm was dominated by circum-neutral, mesotraphentic (indifferent to trophic conditions) and epiphytic (growing on plants, rather than planktonic) species consistent with a more nutrient rich sedge-dominated ecosystem (Rühland *et al.*, 2000). At the base of the 33-45 cm sedge-dominated zone, acidophilous diatom species were less prevalent, suggesting a more nutrient rich and less acidic system in the past.

The fluctuations in diatom assemblage after charcoal peaks suggest that the algal community is sensitive to fire. The increase in *Eunotia nymanniana* post fire may indicate a response to increasing pH caused by the flush of nutrients from the adjacent burned forest. Ash remaining after the fire and leaching ammonia can increase the soil pH. This change to soil water chemistry can persist for multiple growing seasons after fire (Certini, 2005). Other studies also document diatom responses to fire and attribute the assemblage shifts to changes in pH (Rühland *et al.*, 2000). Decreases in bulk density and increases C:N in the bog, after fire in the surrounding forest, indicate a response of carbon accumulation to the fire-induced nutrient flux. In this study, the peat preserved a record of the response of this wetland ecosystem to fire events in the adjacent forest.

Fire preceded the shift away from pH neutral and mesotraphentic diatoms in the sedge-dominated zone of the bog core. However, there is no indication of fire before the shift to the acidophilous, oligotraphentic (mainly occurring in low nutrient conditions) community prior to the *Sphagnum*-dominated zone. A change in local hydrology or precipitation inputs may have instigated the second change in vegetation and diatom assemblage. Further investigation may isolate the cause of this autogenic succession.

Carbon Accumulation

Approximately one-third of the world's soil carbon is currently sequestered in boreal peatlands (Gorham, 1991). Since carbon accumulation is greater in permafrost collapse scars than in other peat features (Camill and Clark, 1998; Robinson and Moore, 2000), future climate shifts may lead to increased collapse and peat expansion, leading to greater carbon storage. However, if 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).

Vegetation succession inferred from macrofossil and diatom analysis, in addition to the significant shift in C:N at transition from sedge to *Sphagnum*-dominated peat, suggest a change in carbon accumulation in the core. Since there is only one reliable date (585 ± 50 years at 56 cm in the bog core), it is difficult to calculate carbon accumulation rates in the two differing successional stages of the bog. I used literature values for carbon accumulation of a *Sphagnum riparium* collapse (Robinson and Moore, 2000) and the age at depth to estimate historic carbon accumulation rates in this system (Table 1). Over the growing seasons of 2003 and 2004, the annual rate of *Sphagnum* growth in the collapse was 2.5 ± 1.5 cm (n = 19), a reported literature value for carbon accumulation in a similar collapse feature is 25.6 gC m^{-2} y^{-1} or 1.56 mm y^{-1} (Robinson and Moore, 2000). The estimated rate of carbon accumulation for the sedge-dominated zone is 10.0 - 11.7 gC m^{-2} y^{-1} or 0.53 - 0.63 mm y^{-1} (Table 1). This estimated carbon accumulation rate is lower than the estimated mean carbon accumulation for boreal peatlands of 21 gC m^{-2} y^{-1} (Clymo *et al.*, 1998). A shift away from a *Sphagnum*-dominated community to a sedge dominated wetland could lead to a decrease in carbon accumulation of approximately 15 gC m^{-2} y^{-1} in this ecosystem.

Future Trajectories

I found a negative relationship between growing season air temperature and tree growth in the terrestrial portion of the landscape, relative to trees growing in the wetter environment at the margins of the collapse feature. I attribute this relationship to drought-inhibited growth. Although low lying wetland ecosystems seem unlikely candidates 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 Leiffers, 1989). Annual growth in black spruce was negatively correlated with temperature and positively correlated with precipitation in other boreal forest stands (Dang and Lieffers, 1989; Brooks *et al.*, 1998). Using tree ring width as an indicator of tree growth response to temperature-induced drought stress (Barber *et al.*, 2000), warming may reduce the success of this forest type on the landscape.

If this region of Interior Alaska experiences warming and drying in the active layer of the soil profile, black spruce trees may exceed a drought-stress threshold. Climate change could lead to a decline in black spruce success across this landscape and a transition to more drought-tolerant species. Severe warming resulting in wetland drainage might initiate the development of a steppe-like community (Chapin *et al.*, 2004).

The bog portion of the transect has shown previous shifts from sedge to a *Sphagnum*-dominated plant community. Under warming and drying this ecosystem may return to a more terrestrial plant community. Both the potential future transition away from black spruce in the forest portion of the landscape and away from *Sphagnum* in the collapse could lead to decreased inputs from NPP relative to decomposition (Goulden *et al.* 1998). Since carbon accumulation is more strongly controlled by vegetation succession than a direct response to climate (Camill *et al.*, 2001), future vegetation succession away from *Sphagnum* could reduce carbon storage in this ecosystem (Fig. 7). If large climate shifts occur in Interior Alaska and lead to increased fire frequency and severity in addition to an increased rate of permafrost degradation, novel states could develop in this landscape.

CONCLUSIONS

The spatial mosaic of the Tanana Floodplain is formed by landscape-level disturbance. Fire leads to the development and expansion of permafrost collapse. Vegetation succession is driven by fire-induced collapse and has occurred independently of fire disturbance, perhaps initiated by a change in climate or local hydrology. If the precipitation regime in Interior Alaska remains unchanged, this system will likely continue on a trajectory of fire mediated collapse and bog expansion. An expansion of wetland will increase carbon storage and methane emissions in this landscape. However, if significant drying occurs this could trigger a return to terrestrial vegetation in the collapse and potentially prevent the regeneration of black spruce in the forest after fire. These novel states would likely decrease carbon storage and methane emissions in this system, creating a positive feedback to future climate change.

ACKNOWLEDGEMENTS

Jill Bubier was intimately involved in the reconnaissance and site selection when I formed the fire-based hypothesis for permafrost collapse and I thank her sincerely for her valuable insight. Kathleen Rühland provided valuable support with peat diatom preparation and identification. I thank John Barron, Elizabeth Fourtanier, and Morgan Peterson for assistance with diatom procedures, identification and literature. I thank Jamie Hollingsworth, Merritt Turetsky, Kaarle Strailey, and Dan Ulliassi for field and laboratory assistance. And I thank Evan Kane, Jon O'Donnell, and Nick Lizusso for reviewing the manuscript. This research was funded by the USGS Earth Surface Dynamics Program and the Bonanza Creek LTER (Long-Term Ecological Research) program (funded jointly by NSF grant DEB-0423442 and USDA Forest Service, Pacific Northwest Research Station grant PNW01-JV11261952-231).

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Table 1. Estimated carbon accumulation rates. Estimated accumulation rates for the sedge-dominated zone adjusted to the ^{14}C date for the bog core at 56 cm. To estimate carbon accumulation rates in this study, I used rates for a permafrost collapse reported in Robinson and Moore (2000) and the estimated age at depth for the *Sphagnum*-dominated zone of the bog core from this study.

Depth (cm)	Soil Carbon (gC m^{-2})	Age (years)	Accumulation Rate (gC m^{-2} y^{-1})	(mm y^{-1})
		Inferred age	*From Literature*	
2 - 28	2400	94 - 167	25.6	1.56
		^{14}C age	*Estimated*	
30 - 54	4894	585	10.0 - 11.7	0.53 - 0.63

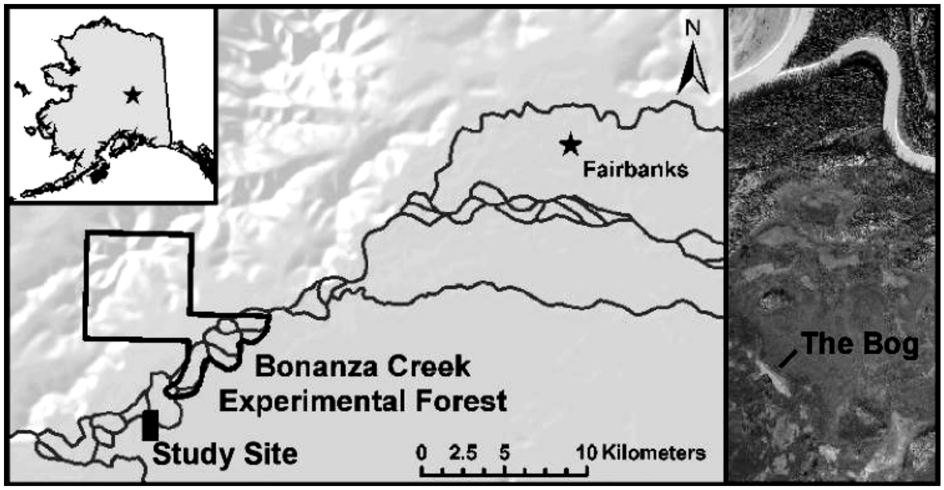

Figure 1. Site location. Map of the location of the study site in Interior Alaska.

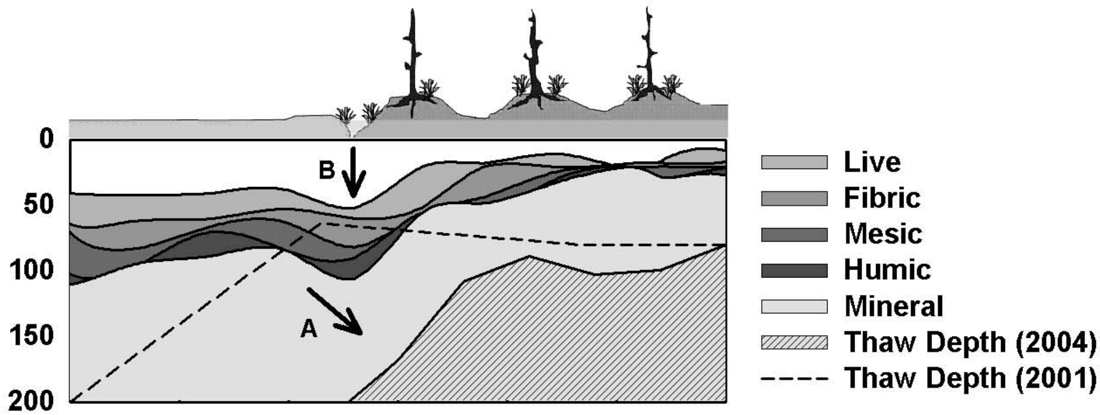

Figure 2. Soil profile, permafrost and soil subsidence across the transect. Soil profile across the transect. Maximum thaw depth in 2001 is indicated by the dashed line. Permafrost at the maximum thaw depth in 2004 is indicated by the second dashed line above the white polygon. Since the fire in 2001, permafrost thaw (A) has lead to soil subsidence (B) in the moat portion of the transect.

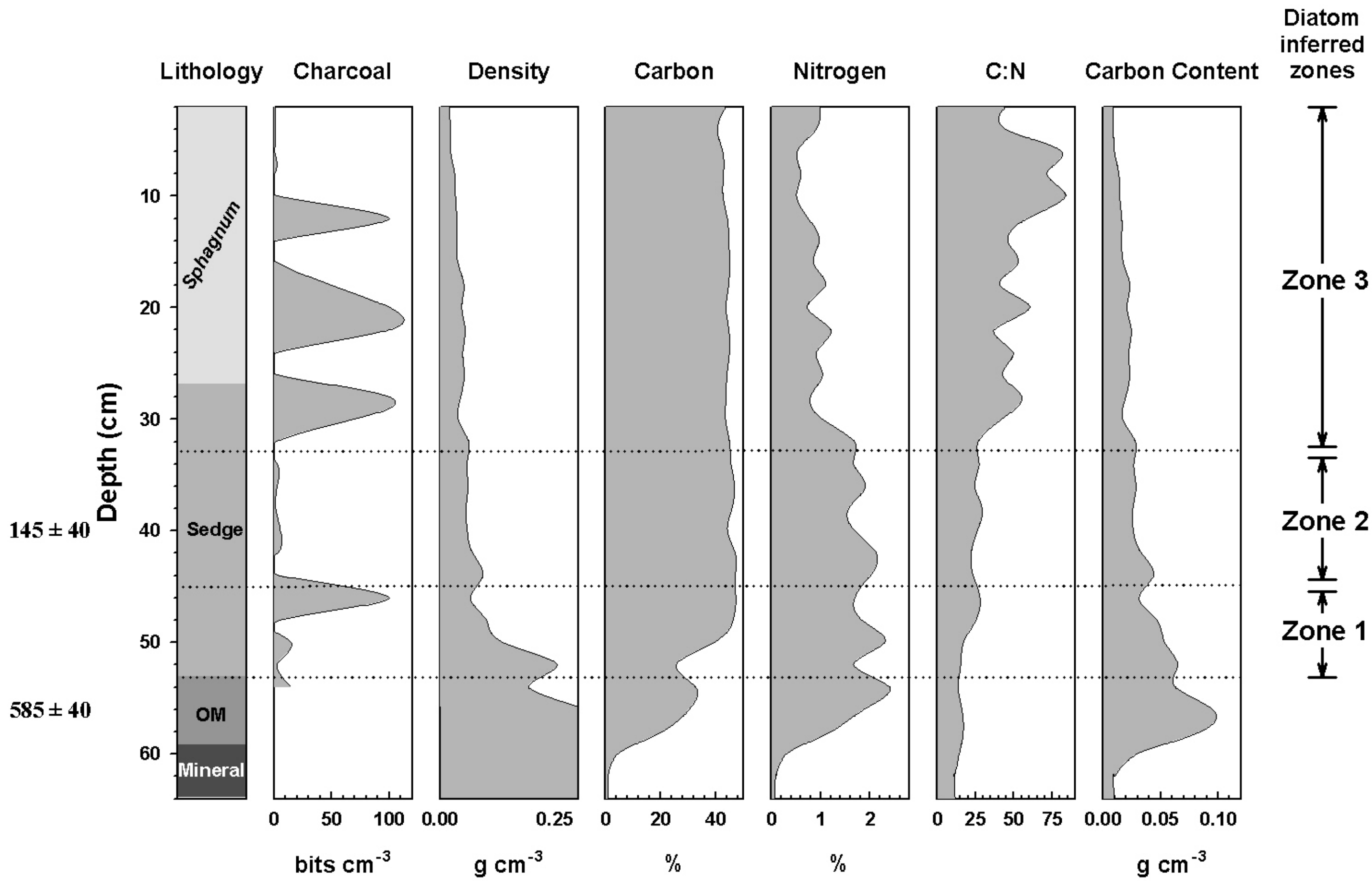

Figure 3. Bog core stratigraphy. Stratigraphy of a core from the center of the bog indicating charcoal remains, soil bulk density, %C, %N, C:N, and carbon content. Dotted lines correspond to the diatom inferred zones (Fig. 5). Dates indicate radio carbon ages for the core at depth (40 cm = 145 ± 40, $\delta^{14}C$ = -18.0 ± 4.4; 56 cm = 585 ± 40, $\delta^{14}C$ = -70.1 ± 4.1).

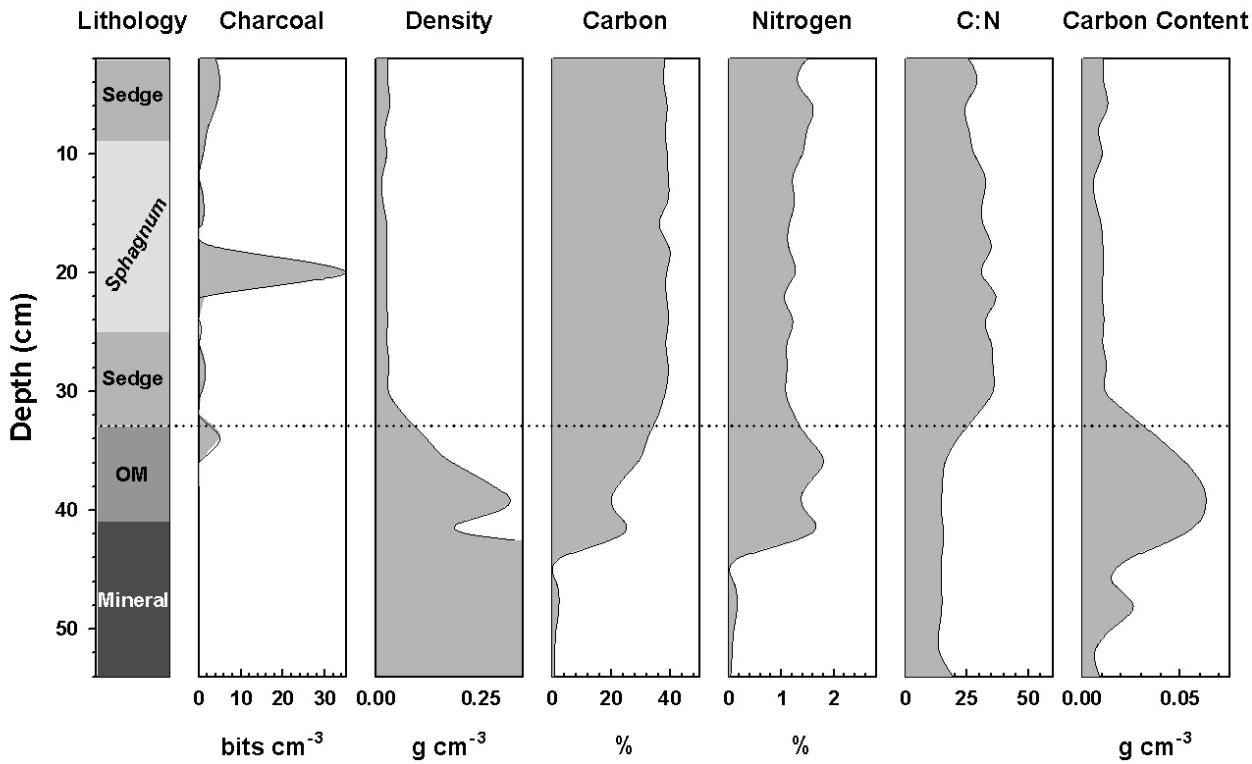

Figure 4. Moat core stratigraphy. Stratigraphy of a core from the moat portion of the transect indicating charcoal remains, soil density, %C, %N, C:N, and carbon content. Dotted line corresponds to the transition from terrestrial OM to sedge-dominated peat.

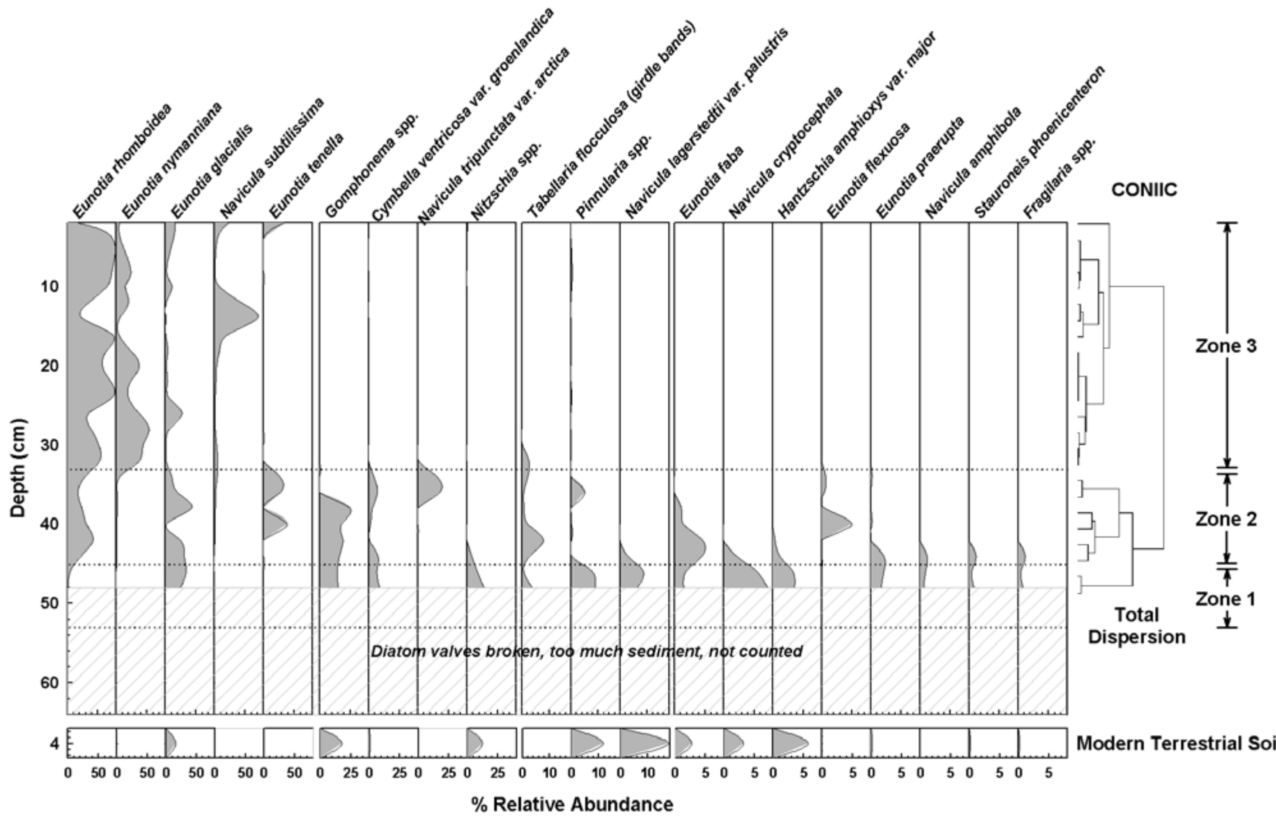

Figure 5. Diatom assemblages with depth in the bog core. The percent relative abundance of key diatom species/genera from the bog core. Diatom-delineated zones are determined using constrained cluster analysis by information content (CONIIC). Diatoms were not counted below 48 cm due to a high proportion of broken valves and residual organic matter and sediment at the bottom of the core. The abundance of diatom species in the terrestrial soil core at 4 cm is included below the bog core data. The diatom taxa are presented from most dominant to least dominant from left to right across the figure.

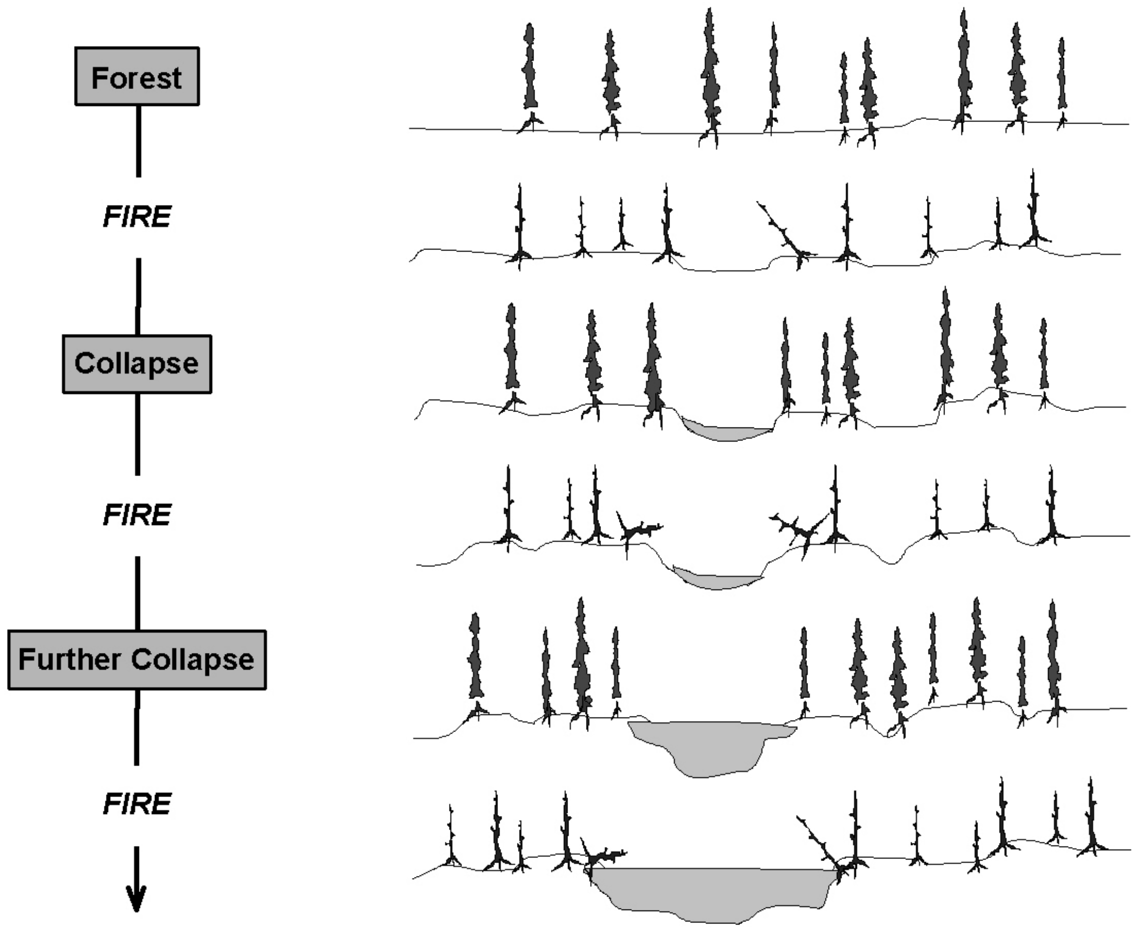

Figure 6. Conceptual model of the collapse development. Collapse expansion over successive fire cycles.

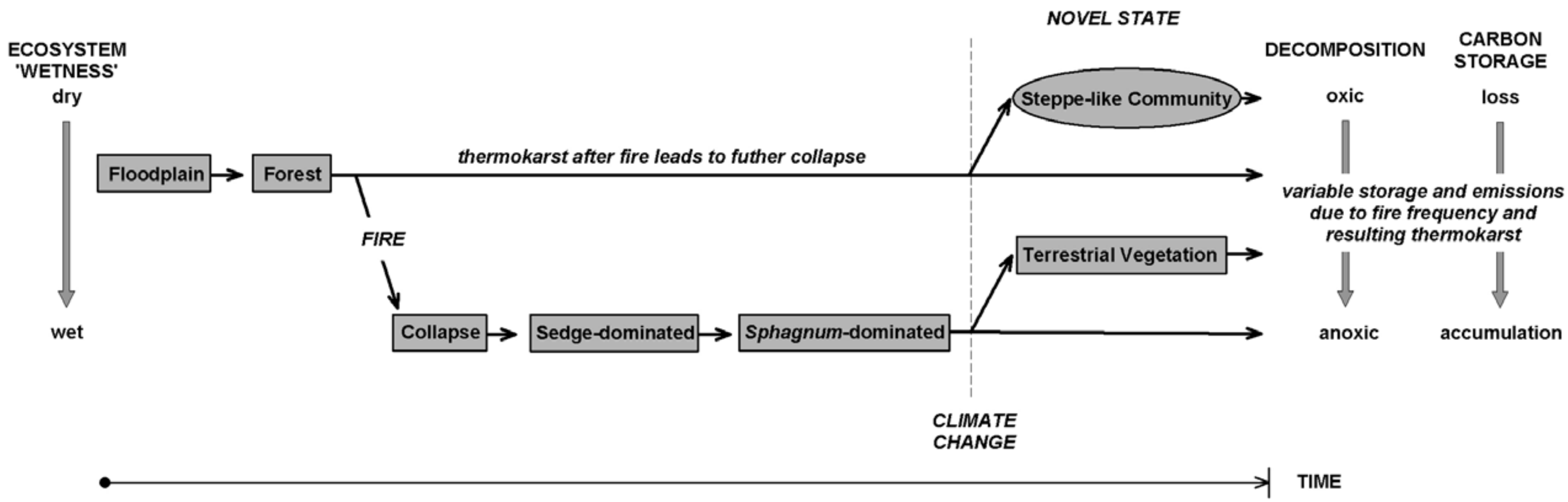

Figure 7. Conceptual model of ecosystem development over time. Ecosystem succession including the potential development of novel states under climate change and the impacts on carbon exchange.

CHAPTER 4.

GENERAL DISCUSSION AND CONCLUSION

Landscape-level disturbance interacts with climate to create the vegetation mosaic across the Tanana Floodplain. Both permafrost collapse and fire are likely to increase with climate warming (Jorgenson, 2001). This will change the primary controls on carbon exchange across this landscape.

Collapse in the Landscape

Unlike the peatlands of Western Canada (Zoltai, 1993), landscape development on the Tanana Floodplain is controlled by interactions between primary succession in the active floodplain and secondary succession instigated by fire and thermokarst (Jorgenson, 2001). The changing physical environment and the ecological response to disturbance have formed a complex landscape mosaic (Fig. 1). Permafrost collapse features dot the floodplain between the remnants of river channels. This study focused on carbon exchange and succession of one collapse bog; however, results can be scaled to account for landscape patterns and carbon exchange across this region. 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 (Fig. 2). 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 Jorgensen et al. (2001), and suggest accelerated permafrost degradation on the Tanana Floodplain.

Collapse Expansion

In this study, my collaborators and I observed a 6 m lateral expansion of soil subsidence after fire on the east side of the collapse (Fig. 3). A survey of the moat around the collapse indicates a 27% increase in collapse area. The charcoal record in the bog suggests that this collapse may have developed over 5 fire cycles. If the increase in collapse area is constant among all collapse features, the Survey-line fire led to a 1.4% increase in collapse area in this region of the Tanana Floodplain.

Collapse Margins

It is the margin of the collapse features that will vary most in response to climate. In the moat, active thermokarst, a high relative water table level, and flourishing tussock vegetation are leading to high net ecosystem exchange of CO_2 and high emissions of CH_4. The increase in collapse area after each successive fire leads to an increase in anoxic soils across the landscape. The bog and moat portions of the transect were the greatest sinks for carbon and sources of methane. If this ecosystem remains on a trajectory of fire-mediated collapse, carbon exchange will increase. However, this study indicates that magnitude of carbon storage will be determined primarily by the precipitation regime.

Climate Response

There has been no clear trend in precipitation over the last 50 years in Interior Alaska (Serreze *et al.*, 2000), and global climate models project both increases and decreases in precipitation regime for Interior Alaska over the next century (Canadian Centre for Climate Modelling, 2003). A shift in precipitation will change the fire regime, pattern of vegetation, and development of collapse. Changes to any of these ecosystem variables will have feedbacks to carbon exchange and climate. If Interior Alaska becomes wetter over time, wetland vegetation will continue to flourish and methane emissions will increase. However, if Interior Alaska experiences drier growing seasons in the future, black spruce success may be reduced in elevated portions of the landscape and *Sphagnum* growth may be suppressed in collapses. These vegetation shifts could lead to reduced below-ground carbon accumulation and methane emissions across the landscape.

Future Research

Future research in this system should focus on replicating approaches employed in this study to determine if fire-mediated collapse is ubiquitous across the landscape. Dating the initiation of collapse features in relation to collapse size will help determine the rate of permafrost degradation. The use of diatoms as indicators of historic hydrology and water chemistry is a rarely used but promising technique to monitor ecosystem change in peatlands. Better characterizations of diatom assemblages across the landscape and in relation to moisture, pH, and vegetation will assist the interpretation of these data. Continued monitoring of carbon exchange in this and other landscape features on the Tanana Floodplain, such as the sedge fens and mature black spruce and deciduous forest, will allow for estimates of carbon exchange across the ecosystem complex. Finally, better projections of the future precipitation regime will improve forecasts of future collapse, vegetation change, and carbon exchange in this system.

Conclusion

Temperature and moisture were important controls in the variation of carbon exchange across this landscape. In the dry growing season of 2004 ecosystem respiration and methane emissions were suppressed and the net carbon uptake increased. Estimates of fluxes during a wet growing season suggest that ecosystem respiration would increase and methane emissions would nearly triple. Wetter conditions, therefore, may result in enhanced emissions of carbon dioxide and methane.

Paleoecological records indicate that fire is the primary control over permafrost collapse in this system. However, permafrost degradation and vegetation change are occurring independent of fire disturbance during the collapse history. If climate in this region of the Tanana Floodplain remains unchanged, fire mediated collapse will increase on the landscape. Collapse expansion will increase emissions of methane while increasing carbon stores in peat systems. If, however, climate change results in drier growing seasons vegetation may shift away from *Sphagnum*-dominated ecosystems and black spruce forests to drought-tolerant communities. Any loss in carbon storage or increase in methane emissions, possible under both wet and dry future climate scenarios, could result in a positive feedback to climate change.

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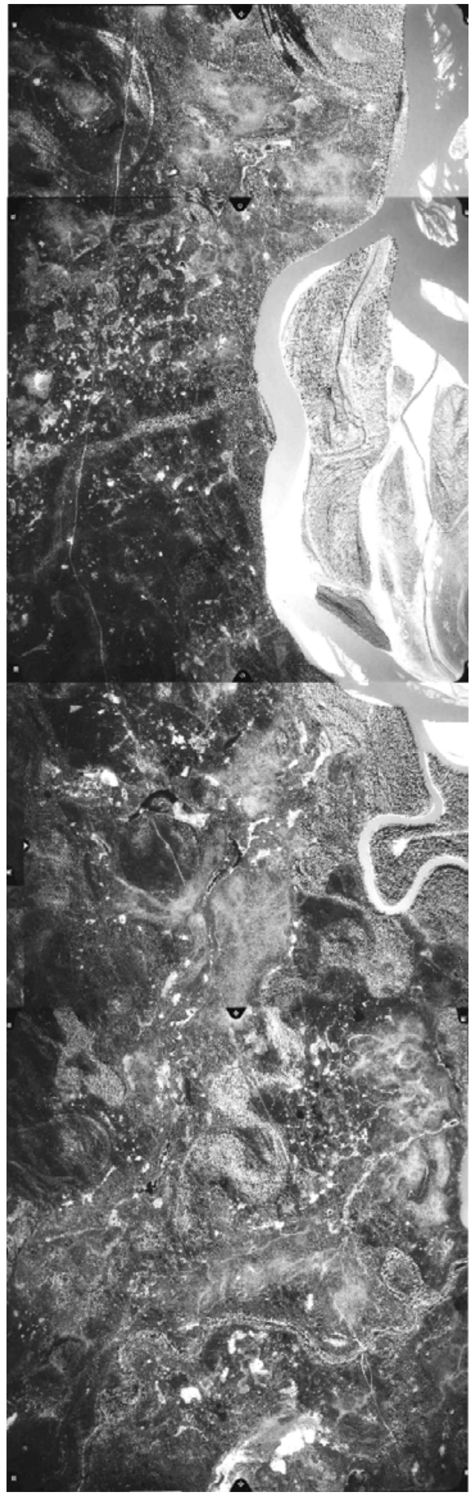

Figure 1. The study region. Aerial photograph of the 16 km^2 area around the study site.

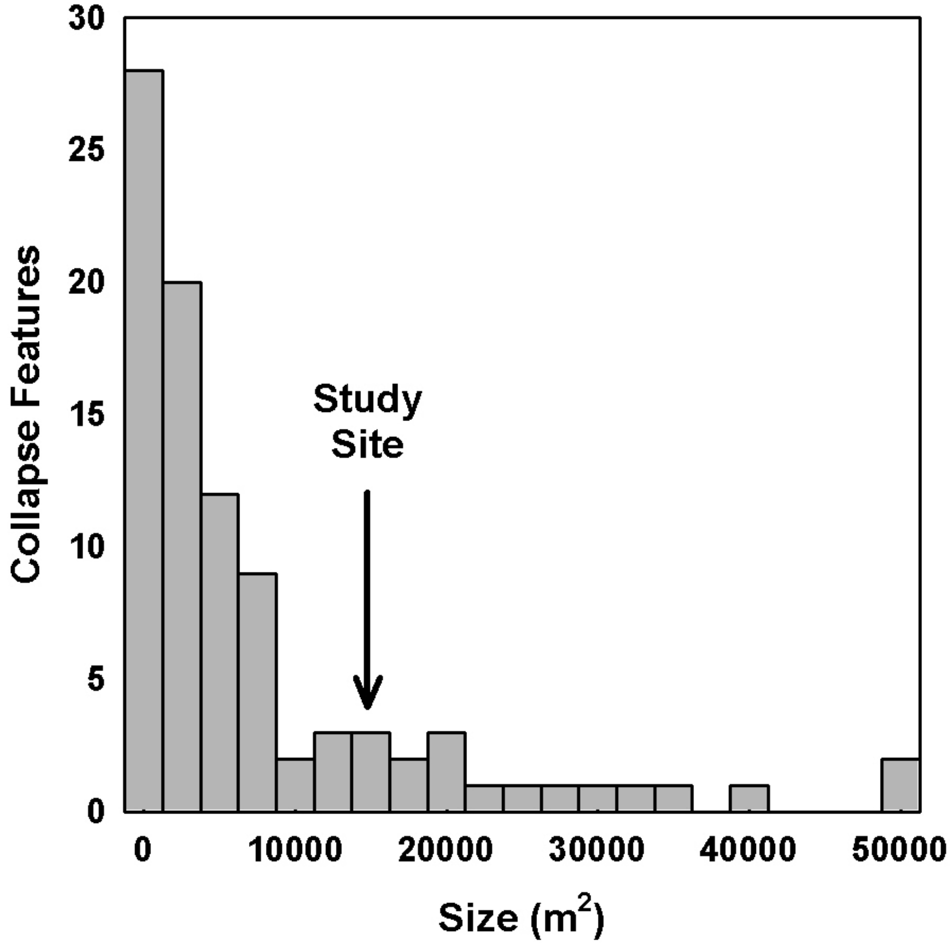

Figure 2. Collapse features across the landscape. The distribution of collapse features across the 16 km^2 area around the study site (n = 91). The number and area of discrete peat features that appeared hydrologically isolated from the river, drainage channels or extensive fens was estimated using digitized aerial photos (Photoshop 7.0, Adobe, San Jose, CA, USA).

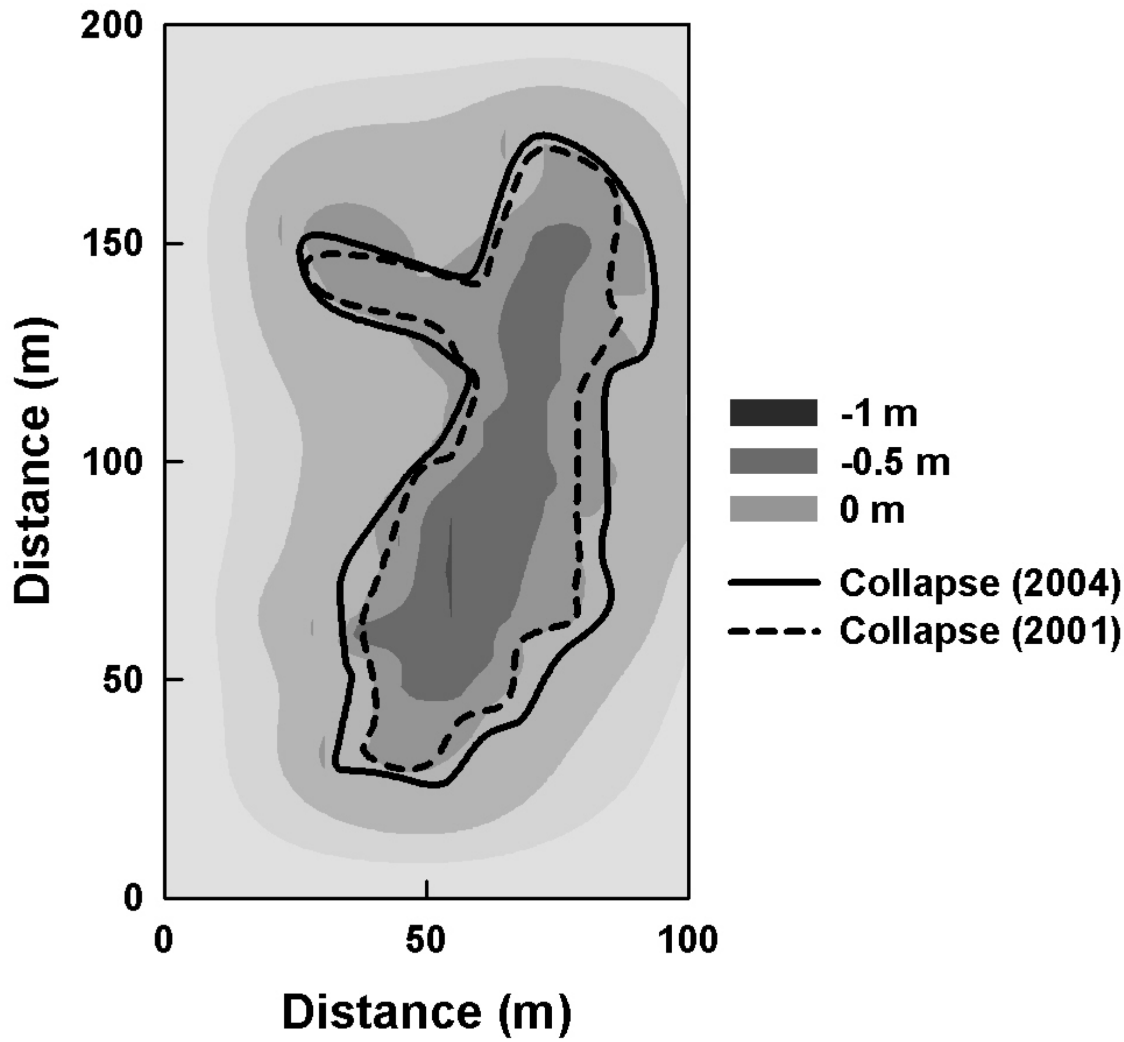

Figure 3. The expansion of the collapse bog. A survey of the extent and depth of the collapse. The dashed line is the margin of the collapse in 2001 and the solid line that in 2004. Gradients indicate collapse depth (m).