

Patterns of Total Ecosystem Carbon Storage with Changes in Soil Temperature in Boreal Black Spruce Forests

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ABSTRACT

To understand how carbon (C) pools in boreal ecosystems may change with warming, we measured above- and belowground C pools and C increment along a soil temperature gradient across 16 mature upland black spruce (*Picea mariana* Mill. [B.S.P]) forests in interior Alaska. Total spruce C stocks (stand and root C) increased from 1.3 to 8.5 kg C m⁻² with increasing soil summed degree-days (SDD > 0°C at 10 cm) across sites, whereas soil C stocks decreased from 11.9 to 6.3 kg C m⁻² with increasing SDD. Spruce C and organic soil C, which combined represent maximum C accrual since the last fire, increased with soil heat sums until 600 SDD, and then plateaued with increasing SDD across sites ($R^2 = 0.61$, $P = 0.002$; second-order polynomial regression). The sum of soil and total spruce C (total ecosystem C, TEC) reached its maximum in the middle-range of soil temperatures

measured (approximately 600 SDD), and was lower in the coolest (139 SDD) and the warmest (914 SDD) forests. The opposing trends between above- and belowground pools resulted in C shifting from the soil to spruce biomass with warmer soil temperatures. A shift in C distribution from below- to aboveground pools, as temperature increases, has implications for the vulnerability of C lost in boreal forest wildfires. The strongly negative relationship between surface mineral soil C stocks and increasing temperatures warrants further research into the potential loss of deep mineral soil C stocks with continued warming, especially in forests presently underlain with permafrost.

Key words: organic soil; carbon storage; biomass; climate change; fire; productivity; decomposition; permafrost; black spruce.

INTRODUCTION

Over the past four decades, arctic and boreal regions of the Northern Hemisphere have undergone greater climate warming than any other region on

earth (Serreze and others 2000), and continued warming is likely to affect ecosystem carbon cycling. Owing to the large amount of carbon harbored in boreal and arctic soils (> 400 Pg C), even small changes in how carbon is cycled in these systems has implications for global carbon (C) dynamics (Davidson and Janssens 2006). With a warming climate, increased decomposition rates of soil organic carbon could cause an increase in atmospheric CO₂ (for example, McGuire and others

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2006), thereby adding to the climate warming that is already occurring in the boreal forest (IPCC 2007). Alternatively, increased soil organic matter decomposition in a warmer climate could release nutrients that are used by plants to increase growth, and an increase in vegetation biomass may offset a portion of organic C release due to stimulated decomposition.

Soil temperature directly controls microbial activity (Ratkowsky and others 1982; Dioumaeva and others 2003), which in turn affects the pool size of plant-available nutrients (Van Cleve and others 1983 a,b). Cold soil temperatures also affect growing season length by suppressing early season root growth (Tryon and Chapin 1983; Alvarez-Uria and Korner 2007), and by limiting plant hydraulic conductivity and stomatal conductance (Jarvis and others 1997). Plant growth in boreal conifer ecosystems generally increases with experimental soil warming (Van Cleve and others 1990; Stromgren and Linder 2002), but the in situ response of microbial activity to warming has been difficult to disentangle from changes in spruce C allocation to roots (Stromgren 2001; Bronson and others 2008). Gradient studies that have related ecosystem C pools to soil temperature have found decreases in ecosystem C storage with warmer soil temperatures across mature forests in a successional sequence (for example, Van Cleve and others 1983 a,b; Yarie and Van Cleve 1986). Although these studies suggest that warming may stimulate microbial decomposition to a greater degree than plant primary production, the lack of control for changes in vegetation type precludes determining whether warmer temperatures lead to less C accumulation. In contrast, when species composition has been controlled for in boreal gradient studies, the accumulation of organic matter in vegetation and surface organic soil pools has been reported as insensitive to soil temperature (Vogel and others 2008 and air temperature (Reed and Nagel 2003). However, for these gradient studies precipitation co-varied with changes in regional temperature. Thus, uncertainty still exists as to how plant production and microbial decomposition of organic matter will respond to boreal climate warming.

Soil temperature is an interactive control on ecosystem function (Van Cleve and others 1991), meaning that it "both affects and responds to ecosystem processes" (Chapin and others 2006). In particular, soil temperature can decrease as organic matter accumulates at the soil surface, and the strength of this interaction varies based on topography (Viereck and Van Cleve 1984; Yarie and Van Cleve 1986), which directly affects soil heat balance

through changes in slope, aspect, and elevation (see Bonan 1982). We used this topographic variation in soil temperature to examine changes in net primary productivity and ecosystem C pools in upland black spruce (*Picea mariana* Mill. B.S.P.) forests of interior Alaska. The region studied had similar precipitation and soil parent material throughout (Kane and others 2006). Black spruce forests are a major component of the boreal system (Gower and others 2001), and are the dominant cover type of Alaska, where they cover 26×10^6 ha (Birdsey and Lewis 2003) and currently harbor approximately 250 Mg C ha^{-1} in soils (Johnson and Kern 2003). Because mineralization of soil organic carbon pools generally increases with temperature, and forest productivity increases with nutrient release from decomposing organic matter in warmer boreal forests, we hypothesized that aboveground forest C pools would increase, whereas soil C pools would decrease with increasing temperatures (when other factors are controlled for). Because soil C pools in boreal black spruce forests are generally much larger than stand biomass C pools (Gower and others 2001), we hypothesized that total ecosystem C would decline as temperatures increased across sites.

METHODS

STUDY SITES

The study area ranged from 63° to 65° N latitude (~ 365 km) and 142° – 148° W longitude (~ 550 km), in interior Alaska. We sampled 16 moderately well-drained (mesic) upland sites in this study, which were named for the roads used to access them and their mean soil temperature. The sites were established (from west to east) off of the Parks Highway (P), Cache Creek (C), Nenana Ridge (N), Murphy Dome (M), University of Alaska (U), and the Taylor Highway (T) (Table 1). Site soil temperature descriptors are the summed degree-days ($\text{SDD} > 0^\circ\text{C}$) measured at a depth of 10 cm into the organic soil (Table 1).

The geospatial location of each plot at a site was recorded with a Trimble GeoExplorer III global positioning system (GPS; Trimble, Sunnyvale, CA). To within 95% confidence, spatial accuracy was estimated to be within 5 m of the true site center. The GPS position and a United States Geological Survey digital elevation model (1:63,630) were combined in the program ArcGIS 8.3 (ESRI, Redlands, CA), and annual potential insolation was estimated using the subroutine developed by Kumar (1997) (Table 1),

Table 1. General Biophysical Properties of the Interior Alaskan Black Spruce Ecosystems

Site ¹	Soil moisture ² (g g ⁻¹)	Latitude (°N)	Longitude (°W)	Elevation (m)	Slope (%)	Apect (°)	Mean DBH ³ (cm)	Basal age (years)	Density (trees ha ⁻¹)
C663	0.62 ± 0.21	64.890	148.271	184	6	180	6.2 ± 0.4	75	8,000
E338	1.59 ± 0.11	65.108	147.882	335	5	330	5.6 ± 0.5	144	4,800
E676	1.52 ± 0.11	65.106	147.882	366	13	330	8.7 ± 0.6	173	2,525
E771	1.27 ± 0.12	65.102	147.882	427	13	360	8.5 ± 0.6	120	2,683
M365	0.77 ± 0.10	64.958	148.241	549	8	330	4.6 ± 0.4	75	1,700
M605	0.95 ± 0.32	64.964	147.974	280	13	170	8.4 ± 1.3	86	5,173
M792	0.75 ± 0.07	64.976	148.012	476	11	180	7.0 ± 1.6	76	6,222
M854	0.66 ± 0.11	64.955	148.241	549	8	180	5.8 ± 0.5	74	6,500
M914	0.68 ± 0.15	64.954	147.992	227	10	200	5.7 ± 1.8	72	8,764
N598	0.74 ± 0.19	64.798	148.185	480	17	58	6.5 ± 1.7	91	6,902
N742	0.90 ± 0.12	64.816	148.107	270	12	130	5.7 ± 1.4	78	6,498
P423	1.82 ± 0.11	64.770	148.280	427	30	360	3.9 ± 0.3	153	3,085
P619	0.78 ± 0.16	64.766	148.295	520	12	340	7.4 ± 0.3	110	6,588
P889	0.55 ± 0.11	64.765	148.300	455	8	165	9.4 ± 0.7	160	2,475
T139	1.07 ± 0.11	63.660	142.290	993	13	283	4.1 ± 0.3	81	1,111
U684	0.85 ± 0.19	64.872	147.854	124	3	195	7.6 ± 0.4	120	6,941

¹First letter denotes the study area, with sites located off of the Parks Highway (P), the Elliott Highway (E), the Taylor Highway (T), and near Murphy Dome (M), the University of Alaska (U), Cache Creek (C), and Nenana Ridge (N). Letter is followed by summed degree-days (> 0°C) of organic soil measured at each site.

²Gravimetric mineral soil moisture (10 cm depth) at the end of the growing season.

³Diameter at breast height (1.4 m).

Sites with similar parent material were selected in this study; all sites were underlain with a mantle of mica-rich silt loam soil deposited since the end of the Pleistocene. This eolian loess continues to be carried in from glaciated regions of the Alaskan mountain range and from across the outwash plain or the Tanana Valley (Pewe and Reger 1983; White and others 2002), and has undergone relatively little weathering (Allan 1996; Ping and others 2006). Permafrost within 100 cm of the soil surface denotes a Gelisol (see Soil Survey Staff 2006), and soils at the cooler sites were keyed as Typic Historthels and Aquic Haplorthels (SDD 139-598, and SDD 676). Inceptisols occurring at the other sites were within the cryic temperature regime.

Stand Characteristics

Understory vegetation at the coldest sites (SDD 119-598) was dominated by *Ledum groenlandicum* and *vaccinium* spp. (*vitis-idaea* and *uliginosums* shrubs). *Vaccinium* spp. and *Equisetum sylvaticum* were common in the forb layers of warmer forests (SDD 605-925). Understory vegetation biomass harvests (all forbs, grasses, and shrubs above the living moss layer) on three 1 m² plots at 10 sites were conducted in the peak growing season prior to senescence. Vegetation biomass was dried to constant weight at 65°C in the laboratory. Living moss biomass was determined by harvesting all living

(green) moss in three 0.2 m² plots within the dominant moss patches at 10 sites. Dominant moss genera at all sites included *Hylocomium splendens* and *Pleurozium schreberii*, which are typical of moderately drained black spruce forests. *Sphagnum* spp. was also common at three cold sites (M365, P423, and E676), likely because permafrost impeded drainage. Standing water rarely occurred in these forests because of the sloped topography (Table 1).

The overstory at all sites consisted only of mature black spruce (stand age > 70 years, Viereck and Johnston 1990; Table 1), and stand age ranged from 72 to 173 years. Ideally, all forests would have been the same age because it is well established that mineral soil temperatures decrease as organic layers accumulate at the soil surface (Viereck 1970; Van Cleve and Viereck 1981; Simard and others 2007). To minimize the potential effect of the interaction between stand age and soil temperature, we selected mature but different aged forests in topographic positions that were expected to be either cool or warm (north and south facing toposequences, respectively). Thus, the age distribution of south-facing forests (72-160) was similar to that of north-facing forests (75-173). Moreover, the greatest periods of soil temperature cooling with stand development occur with rapid leaf area expansion in the early stages after fire (< 50 years; Bond-Lamberty and others 2005), and again later

in stand development when *Sphagnum* mosses may become more prevalent (> 300 years; Simard and others 2007). We selected forests within an age cohort that were unlikely to be affected by the interaction between stand succession and soil temperature.

Stand density and basal area were estimated with either variable radius or fixed area plots that were established within a 20 x 20 m area, as previously described (Kane and others 2005; Vogel and others

2005). Variable radius plots, or prism sweeps, were used for warmer stands where the average tree diameter was in excess of 4 cm (Gower and others 1997). A 10 basal area factor prism was used to select trees and the diameter of each tree was then measured at breast height (DBH at 1.4 m). Three plots were established at each site: a central one and two more that were randomly selected from one of the four cardinal directions and 20 m from the central plot. Spruce total aboveground and foliage biomass were estimated using interior Alaskan allometric equations (Yarie and others 2007) and measurements of mean DBH and stand density. Total aboveground biomass allometry was developed from 78 trees, 20 of which were harvested from two sites in this study (Yarie and others 2007). Foliage biomass was determined from a subset of 56 trees. These allometric equations were shown to be quite robust, and were not different from site-specific equations generated from other mesic black spruce forests of various ages (Mack and others 2008). Wood and foliage were assumed to be 48 and 46% C, respectively (Gower and others 1997), which agrees with previous analysis of over 600 spruce foliage and litter samples obtained in interior Alaska (John Yarie unpublished data; $47 \pm 0.1\%$ C).

We measured total biomass increment by collecting tree cores at 1.4 m from the ground, and then measuring the 5-year tree-ring increment using a digital micrometer. Power analysis indicated that as few as five trees could be cored to accurately estimate within 5% of the mean 5-year biomass increment ($n = 32-45$; Vogel and others 2005). Total biomass was estimated for the year of collection, and also for the tree diameter 5 years prior to tree core collection to determine biomass increment. Litterfall was collected in 0.5 m² traps (elevated above the moss layer) randomly distributed at 12 sites (six per site). Litterfall was collected annually throughout the growing season and estimates are the average of 2 years. Although inter-annual variability in black spruce litterfall can be high (for example, coefficient of variation in annual litterfall was 47% across a 30-year record in

upland black spruce forest at the Bonanza Creek Long-Term Ecological Research (LTER) site in interior Alaska), recent research has revealed that the majority of inter-annual variability in spruce litterfall measured across sites can be explained by site-and stand-specific factors (Saarsalmi and others 2007). Therefore, we use annual litterfall as an integrator of site and stand characteristics in making comparisons of production across sites.

Root biomass was estimated for two size fractions: larger than 5 mm and 2-5 mm. The larger size fractions were estimated using black spruce allometric equations and forest stocking information (Bond-Lamberty and others 2002), and the smaller size fraction was estimated by hand sorting and picking in 10-12 soil cores randomly collected from each site (7.5 cm diameter, cored to mineral soil surface). We used two techniques because large diameter roots, or roots near the root collar, are generally difficult to sample with soil coring equipment, but these roots are reasonably characterized with allometric equations (Santanlonio and others 1997). All data are available in an appendix:

www.lter.uaf.edu/pubs/research_vignettes.cfm.

Because forest biomass and soil organic layers follow fairly well-defined patterns with time since fire in boreal forests, stand age has to be accounted for to more directly examine how changes in climate affect carbon accrual. Forest biomass increases quickly with age until about 60 years, where it then plateaus and declines slowly with time (Yarie and Billings 2002; Chen and others 2002). Soil organic layers also accumulate carbon with stand age (Lecomte and others 2006). To account for these age effects, we normalized forest biomass and organic soil pools to the estimated Lire return interval [or interior Alaska (100 years; Yarie 1981). To do this, we first estimated total stand biomass for our sites using a generalized biomass versus age equation for interior Alaska (Yarie and Billings 2002; $R^2 = 0.86$, $P < 0.001$). The deviation of measured values from these estimates was assumed to be the result of soil temperature effects on biomass accrual, as the residual error was strongly correlated with SDD across sites ($R^2 = 0.48$, $P = 0.003$, logarithmic transformation), and was not related to stand age ($F = 0.71$, $P = 0.41$). Therefore, this equation was used to project site biomass to 100 years plus or minus the deviation of each site's measured biomass from the predicted values (Figure 1A). In effect, utilizing this residual error analysis removed any trend in biomass accrual as a function of age. We included root biomass C in the Yarie and Billings (2002) equation using an empirical relationship between root C and

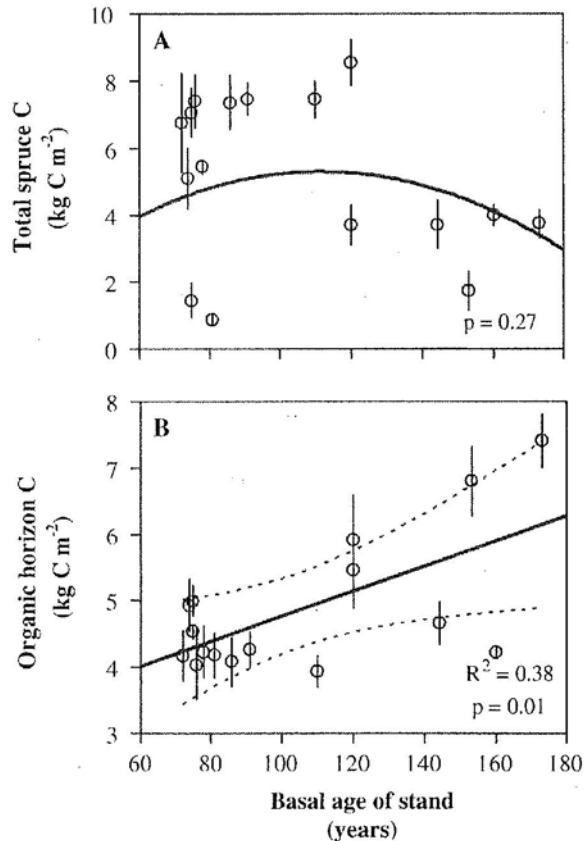


Figure 1. Total spruce C (stem, foliage, roots) did not change with age from 72 to 173 years across the sites in this study (A), but total organic horizon C accrual increased with stand age (B). The trend line in (A) was derived from a standard biomass versus stand age trend determined from USFS Inventory Analysis Unit data (means by 10 years age class; Yarie and Billings 2002) combined with root C changes with stand allometry determined in this study. The trend in (A) is described by the coefficients: $\beta_0 = -0.92 \pm 0.58$, $\beta_1 = 0.11 \pm 0.01$, $\beta_1^2 = -4.7 \times 10^{-4} \pm 7.3 \times 10^{-5}$; $R^2 = 0.86$, $P < 0.001$, $n = 15$. Data in (B) fit the line $\beta_0 = 2.86 \pm 0.67$, $\beta_1 = 0.019 \pm 0.006$. Error bars are standard errors of the mean values and dotted lines represent a 95% confidence interval about the regression line.

aboveground spruce C (kg C m^{-2}) from our data ($R^2 = 0.90$, $P < 0.001$, $n = 16$; $\beta_0 = 0.38 \pm 0.24$, $\beta_1 = 1.08 \pm 0.10$) to determine changes in total spruce C accrual with time. For surface organic layers, we used the equation generated within this dataset (Figure 1B), and normalized the data to 100 years using the same method as used for biomass. All spruce and organic soil C values reported herein were normalized to 100 years, and in all figures, trends in actual values (dashed trend lines) are presented alongside normalized values (solid trend lines). Trends for data normalized to

100 years and trends through non-normalized data were not different as total spruce carbon accrual did not change with stand age in the mature forests across the relatively narrow range of ages investigated in this study (72–173 years, Figure 1; see also Chen and others 2002). Mineral soil C was not normalized to 100 years because radiocarbon ages of this soil layer suggest it is generally 3–7 times older than the lire return interval (Kane and others 2005).

Decomposition Assays

Mass loss of spruce needle litter over one year (2003) was used as an assay of changes in surface soil decomposition with temperature across sites (10 sites; $n = 6$). Litterbags were made of 20 x 20 cm polypropylene fabric with 0.25 x 0.25 mm openings and were filled with 109 of air-dried black spruce needles obtained from a common pool that had been collected from elevated litter traps at the sites. All masses were related to oven-dry weights following Trofymow and others (2002). Litterbags were spread out flat within the surface litter (<1 cm depth).

Soil Sampling and Analysis

Soil C was estimated at each site by coring from the soil surface (beneath the living green moss layer) to 5 cm into the B mineral soil layer as previously described (Kane and others 2005; Vogel and others 2005). Twelve cores (7.5 cm diameter) were collected and divided into Oi and Oe (grouped as organic), and A and B to 5 cm (grouped as mineral) soil horizons. All samples were dried at 105°C, and mineral soils were sieved at 2 mm. A roller ball mill was used to grind the samples, which were then analyzed for C concentration on a LECO CNS-2000 analyzer (LECO Corp. St. Joseph, MI).

Soil temperature was measured at a minimum of two locations per site using Onset (Bourne, MA) 4-channel HOBO dataloggers. At all sites, probes were placed in the organic layer at 10 cm depth (Oe horizon), 5 cm into the mineral soil (10 sites only), and 1 m into the air (with a solar radiation shield), and were in place for 2–3 years at a given site. The mean daily temperature (hour timesteps) at 10 cm into the organic horizon was summed whenever it was above 0°C, over the course of a year, to develop the temperature index: soil summed degree-days (SDD). Some of the site temperatures were measured in different years (1999–2002 or 2003–2005). Because we chose to focus on spatial variation in soil temperature, rather than interannual temperature change, each

site's temperature was normalized to the mean annual SDD value (1999-2005) obtained from the Bonanza Creek LTER soil temperature record. Records for two black spruce forests (10 cm depth) within the same study area were used for the normalization. Mineral soil moisture was measured at each site at the end of the growing season (August-September) during the same years temperatures were measured. Soil cores (6.4 cm diameter) were harvested randomly within each site ($N = 6$) to a depth of 10 cm (incorporating both A and B horizons) and then were homogenized, subsampled, and dried at 105°C for gravimetric moisture determination.

Statistics and Analysis

Differences in carbon stocks between sites were tested using one-way analysis of variance (ANOVA) pairwise comparisons, LSD. All data were examined for normality and transformed if necessary. Pearson correlation coefficients demonstrated relationships between variables ($\alpha = 0.05$). Descriptive statistics were performed with Analyze-It statistical module (Leeds, UK) and regressions were developed (forward selection procedure) with PC SAS (version 9.1, SAS Institute, Cary, North Carolina).

RESULTS

Changes in Stand and Soil Characteristics with Soil Temperature and Moisture

Summed degree-days were negatively correlated with aspect (normalized to degrees from due south) and elevation, and together the two topographic variables were significant in a multiple regression analysis ($R^2 = 0.43$, $P = 0.03$). Adding slope, potential insolation, or soil moisture provided no additional explanatory power. Stand age was unrelated to SDD measured at 10 cm depth ($F = 0.03$, $P = 0.86$). Mineral soil moisture measured at the end of the growing season (Table 1) was positively related to aspect (normalized to degrees from due south; $R^2 = 0.47$, $P = 0.004$), but no further variance could be explained with the inclusion of elevation ($P = 0.35$). Mineral soil moisture was negatively correlated with SDD ($R^2 = 0.29$, $P = 0.03$) and positively correlated with stand age ($R^2 = 0.39$, $P = 0.01$) across sites.

Black spruce biomass C (roots, bole, and foliage) did not change with stand age across sites ranging from 72 to 173 years since establishment (Figure 1A), whereas organic horizon C accrual increased across sites over this 100-year interval

(Figure 1B). Spruce net primary production on an area basis ($\text{kg C m}^{-2}\text{y}^{-1}$) as well as per tree (kg C tree^{-1}), increased with increasing SDD across all sites (Figure 2). Stand density also increased with increasing soil heat sums across all sites ($R^2 = 0.27$, $P = 0.04$), with stands cooler than 600 SDD having (mean $\pm$ standard error) 2674 ± 821 trees ha^{-1} , and stands warmer than 600 SDD having 5773 ± 614 trees ha^{-1} . There were no changes in stand density with increasing soil temperatures across the warmer (>600 SDD) sites ($F_{1,11} = 0.04$, $P = 0.84$). Spruce needle inputs to the soil and needle decomposition rates at the soil surface both increased with SDD across sites (Figure 3), but there were no trends with mineral soil moisture ($F_{1,11} = 1.48$, $P = 0.25$ and $F_{1,9} = 2.16$, $P = 0.18$, respectively). However, organic soil C accumulation rare (horizon stock divided by mean age, as estimated by the age of the stand) did not change with increasing temperatures across all sites (Figure 3).

In all analyses relating soil temperature to C pools, trends for data normalized to 100 years and trends through non-normalized data were not significantly different from one another. Spruce C

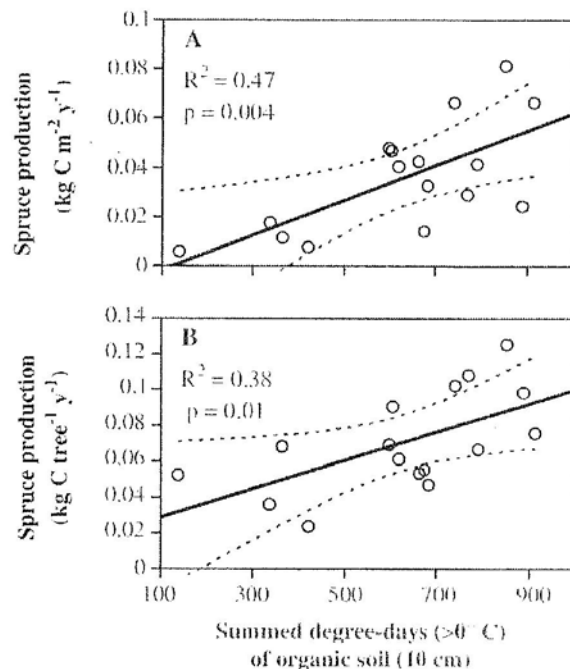


Figure 2. Spruce production on an area basis (A) and per tree (B) increases with increasing soil heat sums across sites. Dotted lines represent a 95% confidence interval about the regression lines. Spruce production in (A) fits the line $\beta_0 = -0.009 \pm 0.013$, $\beta_1 = 0.0001 \pm 0.00002$ and in (B) fits the line $\beta_0 = 1.40 \pm 1.44$, $\beta_1 = 0.007 \pm 0.002$.

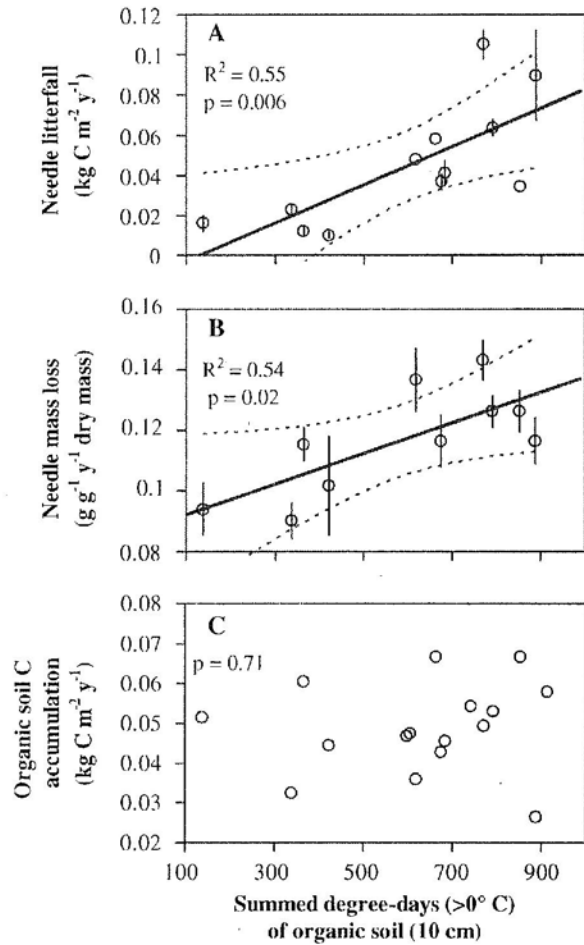


Figure 3. Spruce needle litterfall (A) and mass loss of spruce needles within the surface organic soil (<1 cm) over one year (B) both increased with increasing soil heat sums across sites, but organic soil C accumulation (stock divided by stand age) did not change with increasing temperature (C). Error bars are standard errors of the mean values and dotted lines represent a 95% confidence interval about the regression lines.

pools normalized to an age of 100 years increased markedly with increasing soil heat sums to 600 SDD (Figure 1A), but there was no increase with increasing soil heat sums in the relatively warmer stands with greater than 600 SDD ($F_{1,11} = 1.77$, $P = 0.21$). There was a negative relationship between mineral soil moisture and total spruce C accrual across sites ($R^2 = 0.26$, $P = 0.04$). Sites with greater than 600 SDD exhibited average spruce C pools (6.69 ± 0.42 kg C m⁻²) and mean rates of biomass increment (0.044 ± 0.006 kg C m⁻² y⁻¹) that were more than double those of cooler sites with less than 600 SDD (2.54 ± 0.61 kg C m⁻² and 0.011 ± 0.003 kg C m⁻² y⁻¹, respectively). In contrast, sites with greater than 600 SDD exhibited

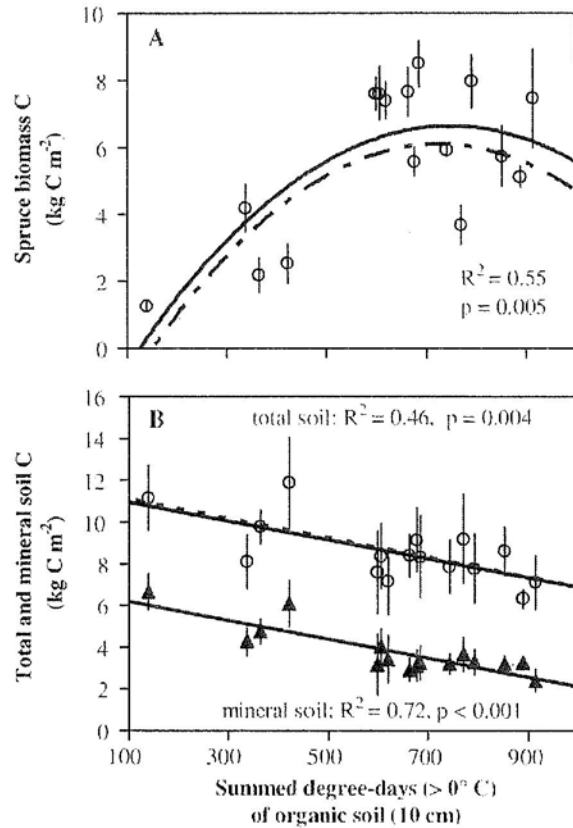


Figure 4. Spruce biomass C (stand, foliage, roots) increased with soil summed degree-days (SDD) to 600 SDD, and then did not change (A), whereas mineral soil (solid triangles) and total soil (open circles) organic carbon stocks declined with increasing SDD across all sites (B). Spruce biomass and organic soil C were normalized to 100 years, as in Figure 1. Solid lines are linear trends through data normalized to 100 years and dashed lines are trend fits for the non-normalized data (points not shown). Error bars are standard errors of the mean values. Spruce biomass C (A) fits the second order polynomial: $\beta_0 = -2.953 \pm 2.495$, $\beta_1 = 0.026 \pm 0.009$, $\beta_2 = -1.711 \times 10^{-5} \pm 8.375 \times 10^{-5}$ and total soil C stocks (B) fit the line $\beta_0 = 11.40 \pm 0.87$, $\beta_1 = -0.0045 \pm 0.0013$.

total soil C stocks (8.00 ± 0.25 kg C m⁻²) that were approximately 23% lower than cooler sites with less than 600 SDD (10.23 ± 0.83 kg C m⁻²) when normalized to 100 years since last disturbance. Total soil C pools declined with increasing soil SDD across all sites, owing to a substantial decline in mineral soil C (Figure 1B). Organic soil horizon C stocks did not change with increasing SDD ($P = 0.98$), or with changes in soil moisture ($F = 2.37$, $P = 0.15$). However, mineral soil SDD measurements (5 cm) decreased as organic layer depths increased ($R^2 = 0.53$, $P = 0.01$; exponentially transformed). In addition, mineral soil mois-

ture increased with increasing organic layer depths across sites ($R^2 = 0.78$, $P < 0.001$). Organic layer depths increased from 17 ± 1 cm on warmer (> 600 SDD) sites to 20 ± 2 cm on cooler (< 600 SDD) sites.

Mean biomass C in the living moss layer (0.22 ± 0.02 kg C m⁻²) did not change with temperature ($F_{1,9} = 0.01$, $P = 0.91$) or stand age ($F_{1,9} = 0.57$, $P = 0.47$) across sites. Shrub and forb layer biomass C decreased with increasing temperatures across sites ($R^2 = 0.74$, $P < 0.001$), with 0.16 ± 0.05 kg C m⁻² being stored in forests with less than 600 SDD and 0.02 ± 0.004 kg C m⁻² being stored in forests with greater than 600 SDD. Both of these C pools were relatively insignificant in comparison to soil and black spruce C pools ($< 2\%$), and were not measured at all sites, and therefore were not included in the analysis of total ecosystem C (TEC).

Changes in Total Ecosystem C Pools with Soil Temperature

Total ecosystem C (total spruce and soil C pools) increased with SDD until approximately 600 SDD, and then declined at a rate of 7.4 ± 3.5 g C m⁻² for every degree-day increase in soil heat sums over 600 SDD ($R^2 = 0.31$, $P = 0.06$, $SE = 1.29$, $n = 12$; Figure 5A). Mineral soil moisture was not related to TEC accrual across sites ($F = 0.36$, $P = 0.56$). Spruce C and organic soil C, which combined represent maximum C accrual since the last fire, increased with soil heat sums until 600 SDD, and then did not significantly change with increasing SDD (Figure 5B; $R^2 = 0.61$, $P = 0.002$, $SE = 1.55$, $n = 16$; second-order polynomial regression). There was no trend between spruce C plus organic soil C and soil heat sums across the warmer sites (> 600 SDD; $F_{1,11} = 2.14$, $P = 0.17$). At sites with greater than 600 SDD, spruce biomass C pools comprised $45 \pm 2\%$ of TEC, whereas at cooler sites with less than 600 SDD, spruce biomass C comprised only $20 \pm 5\%$ of TEC. The distribution of C shifted from the mineral soil to spruce biomass with warmer temperatures across all sites (Figure 6). Any increases in total spruce biomass C across all sites occurred at an equal loss in total soil C (Figure 7).

DISCUSSION

Patterns of Total Ecosystem C Pools Along the Temperature Gradient

The balance between plant productivity and microbial decomposition determines the direction

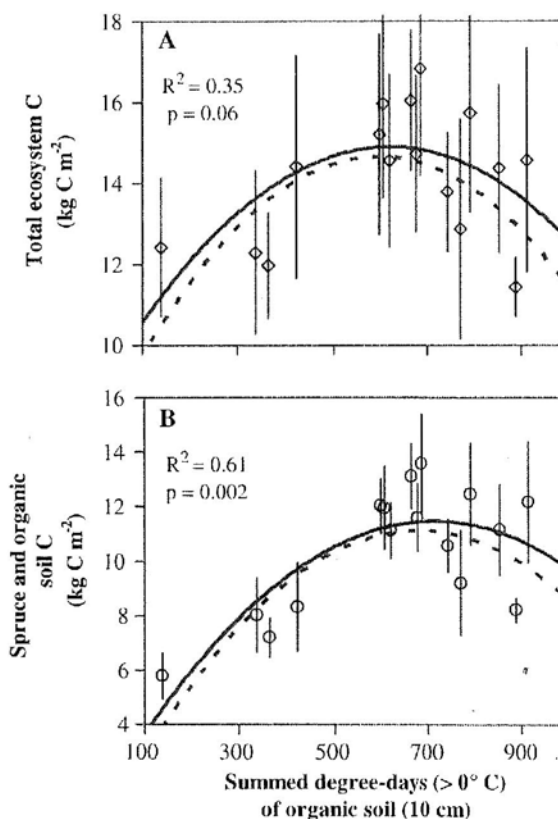


Figure 5. Total ecosystem carbon (spruce and soil C) varied curve-linearly with increasing soil heat sums (A). Spruce and organic soil C, which represent maximum C accrual since the last wildfire, also varied curve-linearly with increasing soil heat sums (B). Solid lines are polynomial trends through data normalized to 100 years and dashed lines are trend fits for the non-normalized data (points not shown). Error bars represent standard errors of the mean values, summed for all pools. Coefficients describing the polynomial trend in (A) are: $\beta_0 = 8.74 \pm 2.11$, $\beta_1 = 0.020 \pm 0.008$, $\beta_2^2 = -1.60 \times 10^{-5} \pm 7.10 \times 10^{-6}$. Coefficients describing the polynomial trend in (B) are: $\beta_0 = 0.859 \pm 2.35$, $\beta_1 = 0.030 \pm 0.009$, $\beta_2^2 = -2.09 \times 10^{-5} \pm 7.90 \times 10^{-6}$.

of change in TEC storage with warming, and our data suggest that TEC varies curve-linearly with increasing temperature in these black spruce ecosystems. TEC increased with soil heat sums until approximately 600 SDD, mostly due to relatively greater increases in spruce biomass than declines in soil C (Figures 2, 4). As temperatures increased above 600 SDD, however, TEC declined with increasing temperature, primarily because of decreasing mineral soil C. An increase in TEC with warmer temperature agrees with predictions for arctic regions where vegetation biomass is expected to increase (Shaver and others 1992); McKane and

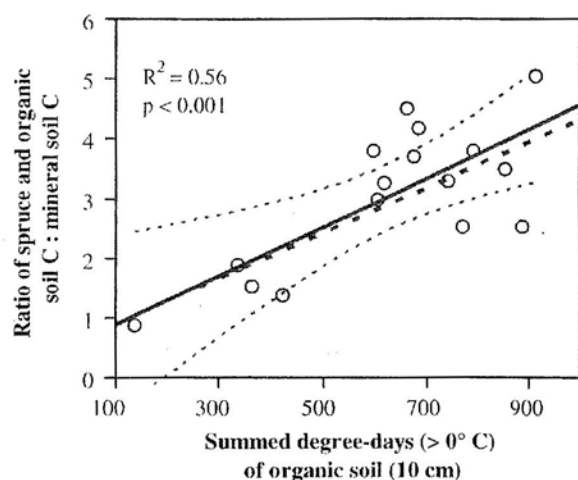


Figure 6. Carbon found in spruce and organic soil horizons increased relative to mineral soil C with increasing soil heat sums. *Solid line* is a linear trend through data normalized to 100 years and *dashed line* is a trend fit for the non-normalized data (points not shown). *Dotted lines* represent a 95% confidence interval about the regression line. Coefficients describing the line in arc: $\beta_0 = 0.47 \pm 0.64$, $\beta_1 = 0.0041 \pm 0.0010$.

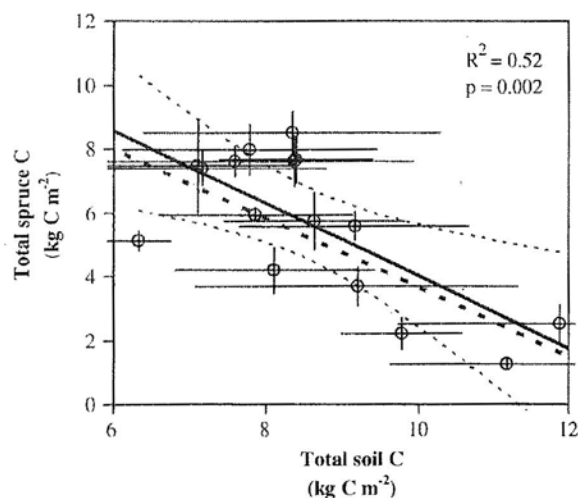


Figure 7. Spruce biomass C (stand, foliage, roots) decreased as total soil C in organic and mineral (5 cm) horizons increased, with a slope not different from 1 ($\beta_0 = 15.39 \pm 2.55$; $\beta_1 = -1.14 \pm 0.29$). Error bars represent standard errors of the mean; error terms for spruce biomass were derived from the standard errors of stand distributions and allometric equations. *Dashed regression line* is a trend fit for the non-normalized (to 100 years) total soil and total spruce C data (points not shown). *Dotted lines* represent a 95% confidence interval about the regression line.

others 1997), primarily because of an increase in nutrient mineralization (for example, Chapin and others 1995). In contrast, in a region of the boreal

forest warmer and wetter than where we studied, Goulden and others (1998) reported that warming caused a black spruce forest to lose C because of soil organic matter mineralization deep in the soil profile. At the cooler sites in this study (<600 SDD), shallow permafrost likely restricted soil organic matter decomposition even as soil heat sums increased from 139 to 423 SDD, resulting in no significant downward trend within this narrow temperature range (Figure 1B). At the warmer end of the gradient (>600 SDD), the thin organic layers were likely poor insulators of the mineral soil, allowing for deeper thaw and/or a longer duration of ice-free conditions with the progression of the growing season (for example, Dyrness 1982; Yoshikawa and others 2002; Harden and others 2006).

There was a strong negative relationship between soil temperature and soil C stocks across all sites (Figure 4B), and the curve-linear TEC relationship would likely be more evident had we measured soil C deeper in the profile. Although we sampled to 5 cm in the B horizon, Ping and others (1997) identified an additional 5.9–7.6 kg C m⁻² in 1 m deep soil profiles for upland forests of interior Alaska that had similar bulk densities and C concentrations to those in this study. Moreover, much more soil C has been reported for mineral soil profiles in permafrost-dominated sites in arctic Alaska (for example, 12–53 kg C m⁻²; Ping and others 1997; Bockheim and others 1999). If deeper soil C stocks follow the same trends as the surface mineral soil horizons observed in this study (Figure 4B; see Bockheim and Hinkel 2007), then these data suggest that soil organic matter decomposition would outstrip primary production with continued warming in the relatively warmer regions of Alaska.

Changes in Mineral Soil C with Increasing Temperatures

The observed decline in mineral soil C with increasing heat sums and stand productivity in interior Alaska differs from previous reports along thermal-stand productivity gradients in Fennoscandian boreal forests (Liski and Westman 1997). Callesen and others (2003) demonstrated that mineral soil organic C (across three texture classes) in mixed boreal forests spanning four Nordic countries increased as mean annual temperature increased from 0 to 7.5°C. Moreover, increases in nitrogen deposition co-occurred with increases in temperature across the Nordic study region, and nitrogen fertilization increased C inputs to the soil by increasing plant primary production (Hyvonen

and others 2007). Soil C inputs owing to nitrogen fertilization are thought to be stabilized in these podzolised soils (Kleja and others 2007). However, warmer temperatures and increased parent material development (podzolization) across the Nordic study region (Callesen and others 2003) are in sharp contrast with the cooler temperatures and incipient Gelisols and Inceptisols of interior Alaska (Ping and others 2006). These data suggest that mineral soil organic C accumulation in upland boreal forests of interior Alaska is largely controlled by the degree to which decomposition is arrested at cooler temperatures, whereas textural properties (soil development) may exert more control over mineral soil organic C in other boreal forests.

Changes in Spruce Biomass Pools with Soil Temperature and Moisture

The marked increase in spruce biomass C in warmer forests (> 600 SDD) compared with cooler forests (<600 SDD) was due to increased production per tree and increased stand density (for example, Figure 1). Previous studies have shown increased black spruce production with increased temperatures from cold, north-facing forests compared with warm, south-facing stands (Van Cleve and others 1981; Kane and others 1998), and also when cool black spruce forests have been experimentally heated (Horn 1964; Van Cleve and others 1981). Vogel and others (2008) reported an increase in black spruce production per tree across a continental gradient in soil temperature, but the study design included a co-varying precipitation gradient and relatively warmer (> 600 SDD; 10 cm) temperatures. In contrast, Pare and Van Cleve (1992) found that aboveground production in relatively warm white spruce forests was insensitive to temperature in interior Alaska, and tree-ring studies have shown reduced growth of Alaskan white spruce with increasing temperatures (Barber and others 2000; Wilmonk and others 2004). In our study, production in relatively warmer black spruce forests (> 600 SDD) was also insensitive to increasing soil heat sums, suggesting that warming only increases stand production to some upper limit (see Way and Sage 2008).

The difference in biomass accumulation between cold and warm sites was also affected by site differences in stand density. At the cold sites, we suspect low tree densities and low biomass were due to poor seedling establishment rather than self-thinning with stand-age because self-thinning is generally followed by a commensurate increase in

biomass (Reineke 1933; Oliver and Larson 1996). Boreal black spruce forests are often under-recruited (see Johnstone and others 2004), with seedling mortality coinciding with thick organic matter layers that likely cause moisture stress (Black and Bliss 1980; Johnstone and Chapin 2006) because organic layers have low bulk densities and thus are prone to drying out on the surface during the summer (Van Wagner 1987). In addition, cooler forests with deeper organic soil depths generally have more organic soil remaining after a wildfire (Kasischke and Johnstone 2005; Kane and others 2007), which also provides a less-favorable soil seedbed for spruce regeneration (for example, Greene and others 2007). Not only does temperature affect the physical and moisture characteristics of surface organic layers, but temperature also directly affects seedling germination. Meunier and others (2007), used a climate gradient across Canada to confirm that black spruce seed germination requires a thermal sum threshold of approximately 800-940 SDD (5°C), with no increase in germination occurring with further warming. Variation in germination at temperatures above this heat sum was best explained by local site factors, including organic matter thickness. Therefore, low seedling establishment in relatively cold black spruce forests with deep organic layers offers a parsimonious explanation for the marked increase in spruce density from cooler forests (<600 SDD) to warmer forests (>600 SDD).

Although greater mineral soil moisture measured in cooler, north-facing forests in this study is perhaps not surprising because of increased organic layer depths (and thus, increased soil water storage deeper in the profile; Yarie and Van Cleve 1986; Sharratt 1997), it is also likely that the age-related increase in organic layer depths contributed to variation in soil moisture between sites (for example, Van Cleve and others 1983a). When an interactive control like soil moisture becomes affected by the variable of interest (for example, soil organic layer depth or temperature), then the cause-effect relationship among variables becomes impossible to disentangle (Van Cleve and others 1991). As a counterexample, SDD was measured at a fixed depth (10 cm) in the soil profile, which resulted in it being unrelated to organic matter accumulation with stand age and more directly affected by topography. Thus, we caution against interpreting the negative relationship between soil moisture and tree biomass as indicative of tree stress or nutrient limitation related to excess soil moisture. Rooting depths are largely confined to organic horizons in black spruce forests (Vioreck

and Johnston 1990; Vogel 2004), but seasonal changes in active layer depths are very different on different aspects, and therefore, there is likely a difference between mineral soil moisture and free water in the rooting zone. Indeed, individual tree growth, litterfall, and litter decomposition rates were all unrelated to mineral soil moisture, suggesting mineral soil moisture was more directly affected by organic matter accumulation rather than vice-versa. To understand the role of soil moisture in affecting TEC accumulation, soil water that is actually plant available (that is, free water in the rooting zone during peak growing season) will need to be measured as it changes with topography and soil temperature.

Changes in Total C Accrual in Between Fire Cycles

The sum of organic soil layer and spruce C stocks, which reflects an estimate of net ecosystem production since the last stand replacing fire (for example, O'Neill and others 2003; Bond-Lamberty and others 2004; Simard and others 2007), had an increasing trend with soil heat sums until 600 SDD, which then declined with increasing temperatures (Figure 5B). Understanding how this trend might affect C storage in Alaska would require some estimate of the spatial distribution of soil temperatures, which currently does not exist. However, these data suggest that there is an upper limit to total C accrual between fire cycles in response to increasing temperatures. Our estimates of stand biomass and organic layer C (mean of $11.2 \pm 0.6 \text{ kg C m}^{-2}$); normalized to 100 years,

are similar to those reported for warmer and wetter regions of the North American boreal forest, which range from 10.5 kg C m^{-2} in northern Manitoba ($n = 2$, Wang and others 2003) to 13.5 kg C m^{-2} in central Quebec ($n = 8$, estimated from Lecomte and others (2006); Simard and others (2007). Based on our study, a profound effect of soil temperature appears to be its influence on the relative rate of tree growth versus C accumulation in the soil (Figure 6). For upland forests of interior Alaska, previous studies have shown a negative trend between indexes of aboveground tree production and soil e stocks in black spruce forests (Kane and others 2008). Rollingsworth and others 2008. These studies and ours suggest that any increase in spruce biomass C accrual with warming in Alaska is unlikely to represent a substantial increase in net ecosystem production, especially considering co-occurring losses in soil C (Figure 7).

Consequences of Increased Aboveground C Allocation in a Warmer Climate

A redistribution of ecosystem C from belowground to aboveground pools with increasing temperature has important implications for the vulnerability and susceptibility of C loss at the landscape level, especially through disturbances such as wildfire (Bond-Lamberty and others 2007). This is important to consider, because the frequency of fire in the North American boreal forest region has more than doubled over the last four decades (Gillett and others 2004; Kasischke and Turetsky 2006), largely as a consequence of increased warming (Flannigan and others 2005). In this study, spruce C pools were larger in sites with warmer soil temperatures (Figures 2, 4), but gains in spruce C co-occurred with a loss in soil e across sites (Figure 7). Increases in black spruce standing biomass are also strongly correlated to the total amount of C lost during wildfires in interior Alaska ($R^2 = 0.80$, $P < 0.001$, $n = 12$; data from Kasischke and others 2000). Thus, not only are more productive black spruce forests likely to lose more C in a wildfire, but warmer forests with deeper depths to seasonal ice lose a greater proportion of their total soil C stocks in wildfire than do cooler forests (Harden and others 2000; Kane and others 2007. These data suggest that C stocks are likely to become more susceptible to combustion in wildfire as proportionally more ecosystem C is harbored in above ground biomass pools with increasing soil temperatures.

CONCLUSIONS

Our findings suggest that soil C pools are likely to decline with climatic warming in Alaskan black spruce ecosystems, whereas spruce C pools only increase to an upper limit. As a result of these two patterns, total ecosystem carbon storage may increase or decrease with warming, depending on the pre-existing temperature of an area. For cooler forests, the decline in soil organic C with increasing soil temperatures may not constitute a net loss of total ecosystem C due to co-occurring increases in aboveground production. In warmer forests, however, the rate of C accrual from increased forest growth will eventually decrease and be exceeded by declines in soil C as temperatures increase; this is especially evident if one considers the potential for C loss from deeper mineral soil pools. Moreover, the shift in C distribution from below- to aboveground pools as temperatures increase could have important implications for the vulnerability

and susceptibility of C loss in boreal forests, especially through disturbances such as wildfire.

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