

Soil carbon stabilization along climate and stand productivity gradients in black spruce forests of interior Alaska¹

E.S. Kane, D.W. Valentine, E.A.G. Schuur, and K. Dutta

Abstract: The amount of soil organic carbon (SOC) in stable, slow-turnover pools is likely to change in response to climate warming because processes mediating soil C balance (net primary production and decomposition) vary with environmental conditions. This is important to consider in boreal forests, which constitute one of the world's largest stocks of SOC. We investigated changes in soil C stabilization along four replicate gradients of black spruce productivity and soil temperature in interior Alaska to develop empirical relationships between SOC and stand and physiographic features. Total SOC harbored in mineral soil horizons decreased by 4.4 g C·m⁻² for every degree-day increase in heat sum within the organic soil across all sites. Furthermore, the proportion of relatively labile light-fraction (density <1.6 g·cm⁻³) soil organic matter decreased significantly with increased stand productivity and soil temperature. Mean residence times of SOC (as determined by $\Delta^{14}\text{C}$) in dense-fraction (>1.6 g·cm⁻³) mineral soil ranged from 282 to 672 years. The oldest SOC occurred in the coolest sites, which also harbored the most C and had the lowest rates of stand production. These results suggest that temperature sensitivities of organic matter within discrete soil pools, and not just total soil C stocks, need to be examined to project the effects of changing climate and primary production on soil C balance.

Résumé : La quantité de carbone organique du sol dans des réservoirs stables à renouvellement lent est susceptible de changer à la suite d'un réchauffement climatique parce que les processus qui influencent l'équilibre en C du sol (production primaire nette et décomposition) varient en fonction des conditions environnementales. Il est important de tenir compte de ce phénomène en forêt boréale où le sol constitue un des plus importants sites d'entreposage de carbone organique au monde. Nous avons étudié les changements de la stabilisation du carbone dans le sol le long de quatre gradients de productivité de l'épinette noire et de température du sol dans le but de mettre au point des relations empiriques entre le carbone organique du sol, les caractéristiques des peuplements et la physiographie du centre de l'Alaska. Le carbone organique total du sol dans les horizons minéraux a diminué de 4,4 g C·m⁻² pour chaque augmentation d'un degré-jour du sol organique observée dans l'ensemble des stations. De plus, la proportion de la partie relativement labile et légère (densité <1,6 g·cm⁻³) de la matière organique du sol a diminué significativement lorsque la productivité du peuplement et la température du sol augmentaient. La période moyenne de séjour du carbone organique du sol (déterminée à l'aide du ΔC^{14}) dans la partie dense (> 1,6 g·cm⁻³) du sol minéral a varié de 282 à 672 ans. Le plus vieil échantillon de carbone organique du sol a été observé dans les stations les plus froides qui renaient aussi les plus grandes quantités de C et où le taux de productivité des peuplements était le plus faible. Ces résultats indiquent qu'il est nécessaire d'étudier la sensibilité de la matière organique à la température pour des réservoirs du sol distincts, et non seulement pour les stocks totaux de C du sol, de façon à prédire les effets des changements climatiques et de la production primaire sur l'équilibre en C du sol.

[Traduit par la Rédaction]

Introduction

It is widely accepted that positive feedbacks exist between the increasing atmospheric concentration of CO₂ and global warming (e.g., Keeling et al. 1996; Chapin et al. 2000), and

therefore the ability of soil to accumulate and preserve mineralizable organic matter has received growing interest. The likely direction of change in soil organic carbon (SOC) in the boreal forest biome, which harbors the world's second largest SOC stock, is of marked concern because climate

Received 30 November 2004. Accepted 25 April 2005. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 14 October 2005.

E.S. Kane² and D.W. Valentine. Department of Forest Sciences, University of Alaska, Fairbanks, 303 O'Neill Building, Fairbanks, AK 99775, USA.

E.A.G. Schuur and K. Dutta. Department of Botany, University of Florida, Gainesville, 220 Bartram Hall, Gainesville, FL 32611, USA.

¹This article is one of a selection of papers published in the Special Issue on Climate–Disturbance Interactions in Boreal Forest Ecosystems.

²Corresponding author (e-mail: ftesk@uaf.edu).

warming is projected to be greatest in high latitudes (McGuire et al. 2000), and temperature is the cardinal determinant of soil C mineralization.

Black spruce (*Picea mariana* (Mill.) BSP) forests are a major component of the boreal system (Gower et al. 2001) and are the dominant cover type of Alaska, where they cover 26×10^6 ha (Heath et al. 2003) and harbor ~ 250 Mg C·ha⁻¹ (Johnson and Kern 2003). Our understanding of the soil C storage potential of black spruce forests is unclear because soil C balance in these forests, as in most forests, is determined by the balance between inputs from net primary productivity and outputs from decomposition, both of which are likely to change under a warmer climate.

Productivity in black spruce forests is largely limited by the rate of nutrient release from decomposing organic matter (Van Cleve et al. 1981), which often increases with higher soil temperatures (Van Cleve et al. 1990) and varies with landscape position (Van Cleve and Yarie 1986; Van Cleve et al. 1991). Landscape position, in turn, directly influences soil temperature and insolation on a seasonal basis. Dramatic temperature inversions are common in the winter and cause cold air to settle in valley bottoms. On the other hand, uplands are often cooler in the summer months in interior Alaska (Slaughter and Viereck 1986). Soils on northern aspects receive less insolation than do those on southerly slopes and therefore are cooler (e.g., Slaughter and Long 1975) and more likely to contain permafrost (Rieger 1983). The interaction between reduced nutrient release from arrested decomposition and decreased stand production on cold, north-facing aspects provides a niche for moss expansion (Oechel and Van Cleve 1986). Moss development and organic matter accumulation, in turn, increase the thermal buffering capacity of the soil (Bonan 1991), which significantly reduces the soil heat sum (Van Cleve and Viereck 1981). In addition to affecting local soil temperatures, relatively small-scale changes in topography can impact the lateral and vertical movements of water, which affect soil nutrient transformations and uptake in black spruce forests (Yarie and Van Cleve 1983; Grant 2004). For example, forests near summits are more prone to nutrient loss, whereas toe-slope forests are in regions of nutrient accumulation (Ping et al. 2005). Therefore, differences in physiographic features can create natural gradients in temperature and nutrient mineralization, which, in turn, impact stand production and the soil decomposition environment (Viereck et al. 1983). However, it is not yet clear how variations across the landscape in the relative rates of productivity and decomposition impact soil C accumulation and its resistance to decay in black spruce forests.

There have been few investigations of how SOC changes along landscape-induced thermal gradients in black spruce forests of interior Alaska. Dyrness and Grigal (1979) investigated vegetation–soil relationships along a 3-km elevational–slope gradient. Although the authors did not quantify SOC, they determined that the thickness, mass, and N concentration of the organic soil horizons all generally increased down-slope. However, relating soil properties to production and climate in this study was hampered by the low number of black spruce stands ($n = 6$), the narrow range in stand productivities investigated, and the lack of temperature data. Two later investigations have shown a decrease in mineral soil C and an increase in nutrient mineralization in organic

horizons with increasing soil temperature. However, these studies did not control for stand type (Viereck and Van Cleve 1984) or drainage class (Van Cleve et al. 1981), both of which affect SOC storage in boreal forests (Rapalee et al. 1998). Furthermore, the low number of black spruce stands compared in these two studies ($n = 5$ and 2 , respectively) precluded isolation of any pattern between SOC and stand productivity and temperature in interior Alaska.

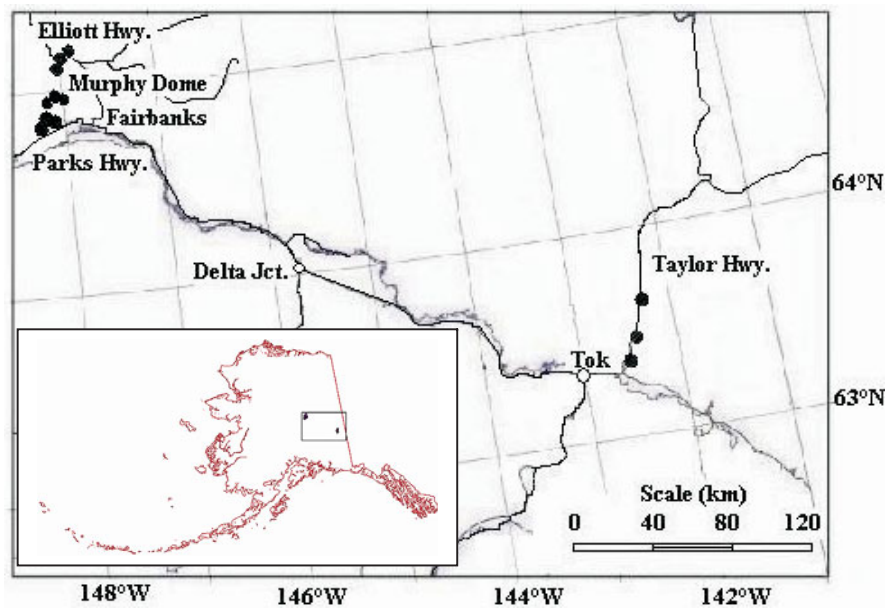
The bioavailability of surface organics decreases during humification, resulting in compounds that decay by orders of magnitude more slowly than fresh litter (Aber et al. 1990; Berg and Meentemeyer 2002). Soil organic C content and lability often decrease along a continuum with depth (Melillo et al. 1989; Winkler et al. 1996); however, the amount of relatively labile organic matter associated with mineral soil varies depending on the degree of organic matter illuviation (Kaiser et al. 2002), the sorptive capacity of the mineral soil (Kaiser and Guggenberger 2003; Moore 2003), and the decomposition environment within the mineral soil (Rodionov et al. 2000; Elberling and Brandt 2003). Since organic matter in the mineral soil increases in density as it decomposes (Baisden et al. 2002a), fractionating mineral soils into different density separates can shed light on the degree of organic matter decomposition (Schulten and Leinweber 1999) and lability (McLauchlan and Hobbie 2004) in a soil horizon. Therefore, quantifying the relative amounts of light and dense mineral associated organic matter along gradients in stand production (and hence, nutrient mineralization) might show how soil C stabilization is affected by the cycling of surface organic matter, but this has received little study.

To determine how the complex interplay among stand production, nutrient mineralization, and soil temperature affects soil C stabilization, we investigated total SOC along four replicate gradients in black spruce productivity and climate in interior Alaska. Because turnover of soil pools is faster in warmer, more productive sites, we hypothesized (1) total SOC decreases as stand productivity and soil temperature increase because productivity depends on the amount of nutrients released with soil organic matter turnover, which also increases with temperature, the net result of which being that (2) SOC content in more stable soil pools is proportional to the amount of actively cycling SOC in surface soil pools.

Study sites

Four replicate gradients in black spruce productivity and soil temperature were established across interior Alaska, ranging in latitude from 63° to 65°N (~ 365 km) and in longitude from 142° to 148°W (~ 550 km). Study areas were named for the roads used to access them and were established (from west to east) off of the Parks Highway (P), Murphy Dome (M), the Elliott Highway (E), and the Taylor Highway (T) (Fig. 1). Each study area consisted of three sites, which were differentiated by their relative level of stand production, or site index. Site index (SI) is defined as the height of stand dominants attained after 50 years, and sites with low (L, 2.5–4.6 m), medium (M, 4.6–7.5 m), or high (H, 8.1–12.5 m) SI values occur within each study area. Site hierarchy, stand properties, and landscape characteristics are outlined in Table 1.

Fig. 1. Distribution of the 12 study sites (solid circles) in the Tanana Valley uplands of interior Alaska. Inset figure shows the relative position of the study region in the state of Alaska, USA. Low (L; site index (SI) = 2.5–4.6 m), medium (M; SI = 4.6–7.5 m), and high (H; SI = 8.1–12.5 m) productivity black spruce stands occur in the four study areas located off the Parks Highway (P), the Elliott Highway (E), Murphy Dome (M), and the Taylor Highway (T).



Vegetation at the low-productivity stands was dominated by *Ledum groenlandicum* and *Vaccinium* spp. (*V. vitis-idaea* and *V. uliginosum*) shrubs. *Betula nana* was also common at the TL site. *Vaccinium* spp. were common in the forb layers at the medium- and high-productivity stands, with *Equisetum sylvaticum* also being common at the high-productivity stands. Moss species were determined by harvesting all living moss in three 0.2-m² plots at each site. Dominant moss genera at all sites included *Hylocomium* and *Pleurozium*, as most sites were moderately to well drained. *Sphagnum* was also common at the PL site, however, as permafrost impeded drainage despite its relatively high slope and elevation.

Soils in interior Alaska, and in the Yukon–Tanana uplands in particular, are dominated by a mantle of mica-rich loess that continues to blow in from the outwash plain of the Tanana Valley (Pewe and Reger 1983; White et al. 2002). Although a thorough soil survey has not been conducted across much of interior Alaska, incipient loess parent material was dominant at all sites. Intermittent permafrost denotes a Gelisol, and the PL and EM soils were keyed as Typic Historthels, and the EL and TL soils were Aquic Haplorthels. Inceptisols occurred at all of the other sites. The ML and EH sites were keyed into the Cryaquept great group because the matrix showed redoximorphic features. The relatively low SOM content and a lack of long periods of inundation placed soils from the other sites into the Cryochrept great group. The Histic subgroup applied to the ML, PM, and EH sites. Inceptisols were within the Cryic temperature regime.

Methods

Methods of site establishment generally followed the protocols of the Growth and Yield Program at the University of Alaska, Fairbanks (E.C. Packee), and this study incorporated four sites from that study. Briefly, each site consisted of

three 20-m² plots, which were spaced 20 m apart (either in a triangle formation or perpendicular to slope). We sought backslopes to control for drainage, nutrient accumulation, and nutrient mobility across sites (Table 1). The primary landscape attributes selected were aspect and local relief because they determine insolation, which, in turn, drives changes in soil temperature and stand productivity. The colder, low-productivity stands occurred on north-facing slopes and typically received less insolation annually. Control over temperature and production at the T sites also included adiabatic cooling, which was driven mainly by elevation. Furthermore, only mature stands were selected. Chen et al. (2002) have shown that black spruce stand production dominated total aboveground productivity after approximately 30 years in Canadian uplands. Overstory production within a SI class declined gradually in later stages of stand development. Therefore, we avoided young (<60 years) and old (>150 years) stands so as to not confound changes in stand ontogeny with site and climatic limitations to stand production.

Stand density was determined by tallying every tree (>1.27 cm diameter) in each plot (0.04 ha) at each site. The height and diameter at breast height (1.37 m) of every tree in ten 0.001-ha randomly distributed plots at each site were measured. Age of dominant trees (at breast height) in each stand was determined by felling or coring four to six dominant trees at each site. The heights attained by dominant trees at 50 years of age (SI, metres) from each stand in this study were reconstructed through use of the height–age relationship developed by Rosner (2004). Actual ages of dominant trees (age at soil surface) in each SI class were derived from ages at breast height using growth–age relationships from cross-sections obtained at 1.2-m intervals along each tree harvested (following Carmean 1972). SI equations were developed from 292 trees harvested from 33 sites across interior Alaska (Rosner 2004), of which four sites have been

Table 1. Biophysical properties of the 12 black spruce sites in this study.

	Study sites*											
	PL	EL	TL	ML	EM	PM	TM	MM	PH	MH	EH	TH
Stand characteristics												
Site index (m) [†]	2.49	4.32	4.53	4.61	4.62	4.77	7.4	7.54	8.12	8.78	11.64	12.47
Dominant age	150	130	60	60	140	120	60	60	120	120	120	80
Dominant height (m)	5.41	8.66	5.18	5.28	9.62	8.95	8.38	8.53	13.34	14.02	16.61	15.32
Trees-ha ⁻¹	3085	4800	1111	1700	2525	6975	2667	6500	2475	6941	2683	3679
Basal area (m ² -ha ⁻¹)	4.6	15.06	1.84	3.54	17.48	21.22	13.51	22.72	21.32	26.8	21.47	31.38
Landscape properties												
Elevation (m)	427	335	993	549	366	470	877	549	455	412	427	730
Aspect (°)	360	330	283	330	330	315	328	180	165	190	360	147
Slope (%)	30	5	13	8	13	15	3	8	8	5	13	16
Hillslope position [‡]	BS	FS	H BS	H BS	BS	H BS	RI	BS	BS	BS	H BS	BS
Insolation (W·h·m ⁻² ·year ⁻¹ ; ×10 ⁵)	6.4	8.3	10.3	8.8	7.5	8.7	10.8	10	9.6	9.7	8.1	10.3
Latitude (°N)	64.77	65.108	63.66	64.958	65.106	64.767	63.46	64.955	64.765	64.977	65.102	63.397
Longitude (°W)	148.28	147.882	142.29	148.241	147.882	148.298	142.468	148.241	148.3	148.014	147.882	142.489

*Study site codes are denoted by their location near the Parks Highway (P), Elliott Highway (E), Taylor Highway (T), and Murphy Dome (M). Stands are ranked by productivity, with low (L), medium (M), or high (H) site index values occurring within each study area. Previous research incorporating or proximate to a given site includes: Barney et al. (1978) (PM), Rosner (2004) (TL, TM, TH, EH), Van Cleve et al. (1981) (PM), Viercek et al. (1983) (PL, PM), Vogel et al. (2005) (PM), and the Growth and Yield Program, University of Alaska, Fairbanks: E.C. Packee (TL, TM, TH, EH).

[†]Site index is the height (metres) obtained by dominant trees in the stand after 50 years.

[‡]Geomorphic descriptions as described by the USDA NRCS (Schoenberger et al. 2002) are as follows: BS, backslope; RI, rise in locally flat area; H (high) and L (low) describe microrelief.

incorporated in this study (Table 1). The utility of SI as a measure of site productivity is generally limited to mature, even-aged, undisturbed, monospecific stands (Carmean and Lenthall 1989), and these criteria were found at all of the sites in this study.

Soil temperatures from within the middle of the fibric and hemic soil horizons and from a depth of 5 cm into the mineral soil and air temperatures at 100 cm were monitored continuously from June 2003 to June 2004 at each site. Soil temperatures were monitored by genetic horizon because temperatures obtained from a fixed depth could lead to comparisons of pedogenically dissimilar horizons (such as organic versus mineral soils) across sites. Readings were recorded hourly using HOBO H8 data recorders (Onset Computer Corporation, Bourne, Massachusetts). Radiation shields were used to protect air temperature thermistors from direct solar radiation. Solar insolation (W·h·m⁻²·year⁻¹) was calculated for each site using Solar Analyst 1.0 (2000) software (Helios Environmental Modeling Institute, Lawrence, Kansas). This software uses digital elevation model input in reconstructing the angular distribution of sky visibility versus obstruction (from horizon angle) in conjunction with a raster representation of the apparent position of the sun as it varies through time.

Soil analyses

Soil descriptions were obtained from four randomly distributed pits dug at each plot, for a total of 12 pits at each site. Soil pits were approximately 60 cm², and dug into 5 cm of B1 horizon. Horizons were delineated based on the USDA Natural Resources Conservation Service classification scheme (Schoenberger et al. 2002). Organic soils were differentiated in the field by the degree of humification into fibric (Oi), hemic (Oe), and sapric (Oa, which rarely occurred) soil horizons. All living, green moss was discarded. Slightly or intermediately decomposed brown moss was designated as part of the Oi or Oe horizon, respectively. Mineral soils were separated into A and B1 (5 cm) horizons. Three cores (5.08 cm diameter) were obtained from the “best face” of each descriptive pit. Parsed soil cores were bulked by Oi, Oe and Oa, A, and B1 (depth of 5 cm) horizons at each descriptive pit.

Subsamples of homogenized organic soils were deprived of >2-mm roots and soil wood. Mineral soils were passed through a 2-mm sieve. All soils were dried at 105 °C. Organic soils were ground in a ball mill, but grinding of the fine-textured loess mineral soil was not required. Initial tests revealed that the carbonate content of mineral soil was negligible, and therefore soils did not undergo an acid treatment. Carbon content was determined through combustion in a LECO 2000 CNS analyzer (LECO Corporation, St Joseph, Michigan). Samples were run at least in duplicate, and the difference between replicates was <5% of the value.

The A horizons were homogenized, and 1.8 g was subsampled from six pits at each site, chosen at random, to be separated by density into fractions <1.6 g·cm⁻³ (light) and >1.6 g·cm⁻³ (dense) using sodium polytungstate solution (Sometu Co., Sherman Oaks, California). The choice of density was based on earlier studies in which fresh plant materials were separated from mineral-associated organic matter (Golchin et al. 1994). Although these are somewhat opera-

tional definitions, the light fraction is composed mainly of relatively undecomposed vegetation, whereas the dense fraction represents a mixture of more refractory material associated with the mineral soil (Schulthen and Leinweber 1999; Baisden et al. 2002a; McLauchlan and Hobbie 2004). We followed the density fractionation procedure described in detail by Baisden et al. (2002a); following Golchin et al. (1994). Generally, 1.8 g of A horizon soil was weighed into 50-mL centrifuge tubes filled with 35 mL of sodium polytungstate solution (SPT). The tubes were gently shaken, allowed to sit for >1 h, washed with an additional ~5 mL of SPT from a wash bottle, and centrifuged to aid in separation of particles <1.6 g·cm⁻³. The floating <1.6 g·cm⁻³ fraction was aspirated onto a prebaked quartz fiber filter (Tissuquartz, Pall Corporation, New York), rinsed with deionized water, dried, and weighed. Residual soil was resuspended in 35 mL of SPT and then was subjected to 6 min of ultrasonic disruption using a Biosonik probe style sonifier (Bronwill Scientific, Rochester, New York) with an energy output of approximately 40 J·mL⁻¹ (following North 1976). This liberated a negligible amount of soil organic matter (SOM) across all sites (<0.03 g·(g initial mass)⁻¹), showing that there was little occluded organic matter because of the low clay content and weak structure of the loess soils. This small mineral associated (<1.6 g·cm⁻³) fraction was aspirated onto a quartz filter as before, but no further analysis was conducted on this fraction. The dense (>1.6 g·cm⁻³) fraction was then rinsed with deionized water and collected as before. Recovery of fractionated soil across all samples deviated by 0.03 g·(g initial dry mass)⁻¹. The small amount of dissolved organic matter lost with the SPT was not recovered and could not be accurately calculated.

Stable isotope measurements were performed with a GEO 20–20 dual-inlet isotope ratio mass spectrometer coupled with a PDZ Europa solid preparation module (Sercon Co., Crewe, Cheshire, UK). Results are expressed in standard $\delta^{13}\text{C}$ notation, as the deviation (‰) relative to the isotopic ratio of Pee Dee belemnite standard. The samples used for $\delta^{13}\text{C}$ analysis were the same as those used for total C analysis and in the density fractionations. Samples were analyzed at least in duplicate, and the deviance was <0.2‰. For radiocarbon analysis, dense-fraction (>1.6 g·cm⁻³) soils were converted to CO₂ by combustion at 900 °C for 2 h in quartz glass tubes. Sample gas was purged of all non-CO₂ gasses by condensing in liquid nitrogen at -70 °C. Purified CO₂ was then graphitized with an iron powder catalyst (99.99%) in a method modified from Vogel et al. (1984). Graphite was sent to the Keck Carbon Cycle – Accelerator Mass Spectrometry facility at the University of California, Irvine, for radiocarbon analysis. Isotopic values for ¹⁴C are reported as the deviation (‰) from the ¹⁴C/¹²C ratio of oxalic acid, and the analytical precision was 3.8‰. The ¹⁴C values were also corrected for mass-dependent fractionation through use of the $\delta^{13}\text{C}$ value (Stuiver and Polach 1977). We used the ¹⁴C values to estimate the average age of SOM in dense-fraction mineral soil from the A horizon following methods described in detail by Trumbore (2000).

Data analyses

Site means in soil properties were composed of plot-level means ($n = 3$). Two soil samples were chosen at random

from each plot for $\delta^{13}\text{C}$ isotope analyses ($n = 6$). Density fractionations were bulked at the plot level, and one of the bulked dense fractions from each site was randomly chosen for radiocarbon analysis. However, graphite quality from the iron catalyzed reduction of CO₂ was unsuitable for radiocarbon analysis at four sites and therefore $n = 8$. All cross-site comparisons involving soil temperature have an $n = 10$ because the TH and TM sites were consumed in forest fires in the spring of 2004.

Differences among sites in mean annual temperature and soil profile depths were tested with one-way analysis of variance pairwise contrasts at $\alpha = 0.05$ (Scheffe error protection). Pearson's correlation coefficients demonstrated relationships between variables ($\alpha = 0.05$). Multiple regression analysis (forward selection procedure) developed empirical relationships between SOC and stand and physiographic properties ($n = 12$). Predictor variables were accepted at $\alpha = 0.05$ and if more than 5% of the variance could be explained. All descriptive statistics were performed with Analyze-it statistical module (Analyze-it Software, Ltd. Leeds, UK).

Results

Stand productivity and soil temperature

Mean stand basal area and diameter were highly correlated with SI ($r = 0.76$ and 0.83 , respectively; $p < 0.004$). SI, basal area, and stand diameter all increased with mean annual temperature ($r = 0.70, 0.55, 0.73$, respectively) and mean growing degree-days (GDD) >0 °C ($r = 0.69, 0.89, 0.83$, respectively; $p < 0.05$) of the organic soil horizons (see Table 2). Temperature measurements taken in the mineral soil (5 cm) did not significantly explain any of the variance in SI ($p = 0.14$), probably because the rooting depth of black spruce is largely limited to the organic horizons (e.g., Viereck and Johnston 1990).

Soil temperatures by genetic horizon varied among sites ($p < 0.001$). Mean annual temperatures (MAT) changed by ~2.5 °C in the organic horizons and by ~2.3 °C at a depth of 5 cm in the mineral soil across all sites (Table 2). Total organic matter depths varied significantly among study sites (Table 2). Soil heat sums decreased significantly with organic matter depth across all sites, with low-productivity sites exhibiting deeper organic soil horizons (Fig. 2). Mineral soil temperatures decreased marginally on sites with deeper total organic matter accumulation ($r = -0.59$ for both summed GDD and MAT at a depth of 5 cm into the mineral soil; $p = 0.07$). Mean annual soil temperatures obtained at a fixed depth (5 cm into the mineral soil) correlated well with MAT in the Oe horizon across sites ($r = 0.88, p < 0.001$).

SOC, productivity, and climate

The SOC content of different genetic horizons on an area basis (kg C·m⁻²) varied substantially along the four black spruce productivity gradients (Fig. 3). The proportion of total SOC in surface mineral soil horizons (A and 5 cm of B1) shifted from 52% ($\pm 3.3\%$) in low productivity stands to 41% ($\pm 1.1\%$) in stands exhibiting higher growth rates (Fig. 3). Low-productivity black spruce stands harbored significantly more C in the mineral soil horizons than did sites with higher stand productivity (Fig. 4). Carbon stocks in the combined organic horizons varied significantly among sites, and

Table 2. Mean soil profile depths (by genetic horizon) and temperature data for each horizon across the four black spruce gradients in productivity and temperature.

Depth (cm) (SE) [†]	Study sites [*]												
	PL	EL	TL	ML	EM	PM	TM	MM	PH	MH	EH	TH	
Oi	16.17b (1.48)	11.42ab (1.45)	11.83ab (1.9)	6.25a (0.69)	10.00ab (1.09)	5.58a (0.31)	4.92a (0.5)	4.25a (0.3)	5.08a (0.47)	4.00a (0.3)	5.83a (0.41)	5.08a (0.48)	
Oe, Oa	25.58b (1.03)	18.67ab (1.72)	19.17ab (1.64)	15.33ab (1.31)	24.42ab (1.11)	16.75ab (0.9)	12.67a (1.37)	12.58a (0.95)	14.67ab (0.99)	12.75a (0.84)	21.08ab (1.22)	13.33ab (0.96)	
A	27.91b (0.99)	19.91ab (1.77)	21.83ab (1.85)	17.67ab (1.41)	25.75ab (1.05)	18.75ab (0.97)	16.33ab (1.42)	14.25a (0.99)	17.00ab (0.93)	15.50ab (0.82)	22.42ab (1.28)	16.42ab (0.92)	
MAT (°C) (SE)[‡]													
Air (1 m)	-0.69a (0.77)	-1.81a (0.7)	-2.32a (0.74)	-1.86a (0.74)	0.30a (0.63)	-1.68a (0.74)	-1.95a (0.72)	-1.84a (0.74)	-1.40a (0.73)	-1.84a (0.74)	-0.26a (0.64)		
Oi	-0.06abc (0.33)	-0.06abc (0.33)	-0.72ab (0.25)	0.60bc (0.29)	1.53c (0.35)	-1.93a (0.45)	1.66c (0.31)	1.00bc (0.4)	1.28bc (0.32)	1.00bc (0.4)	1.64c (0.37)		
Oe, Oa	-0.09abc (0.2)	-0.87ab (0.19)	-1.14a (0.12)	0.53cd (0.11)	0.63cd (0.23)	0.30bcd (0.26)	1.35d (0.21)	1.30d (0.21)	1.30d (0.24)	1.02cd (0.2)	1.28d (0.21)		
Mineral soil (5 cm)	-0.36bc (0.15)	-1.38a (0.14)	-1.37a (0.08)	0.26de (0.06)	-0.61b (0.07)	0.49ef (0.1)	0.89f (0.11)	0.48def (0.06)	0.68ef (0.10)	0.48def (0.06)	0.10cd (0.05)		

Note: Values followed by different letters are significantly different (one-way analysis of variance pairwise comparisons; $\alpha = 0.05$).

^{*}See Table 1 for description of study site code.

[†]SE, standard error of the measurement.

[‡]MAT is the mean annual temperature (°C) from June 2003 – June 2004. Forest fires in 2004 prevented the collection of complete data sets at the TM and TH sites.

Fig. 2. Growing degree-day heat sums (daily summation of degrees above 0 °C) by genetic horizon decrease with cumulative depth of organic matter across the four black spruce productivity and climate gradients. Open symbols represent Oi horizons, shaded symbols represent Oe and Oa horizons, and solid symbols represent A horizons. Sites are ranked by productivity (site index (SI): stand height (metres) attained at 50 years).

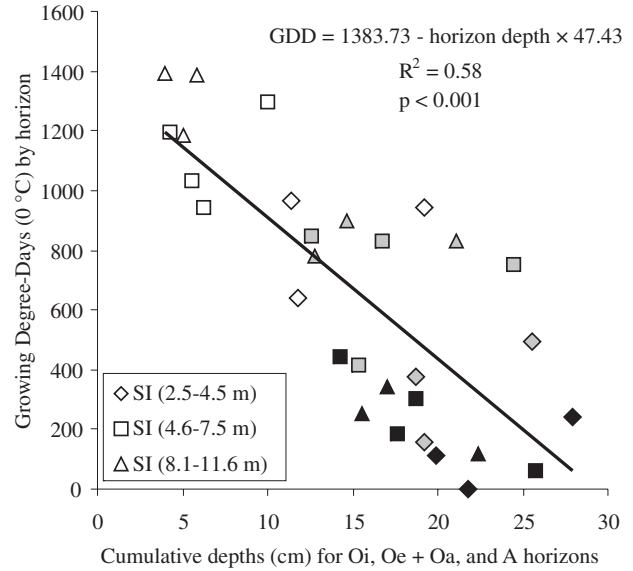
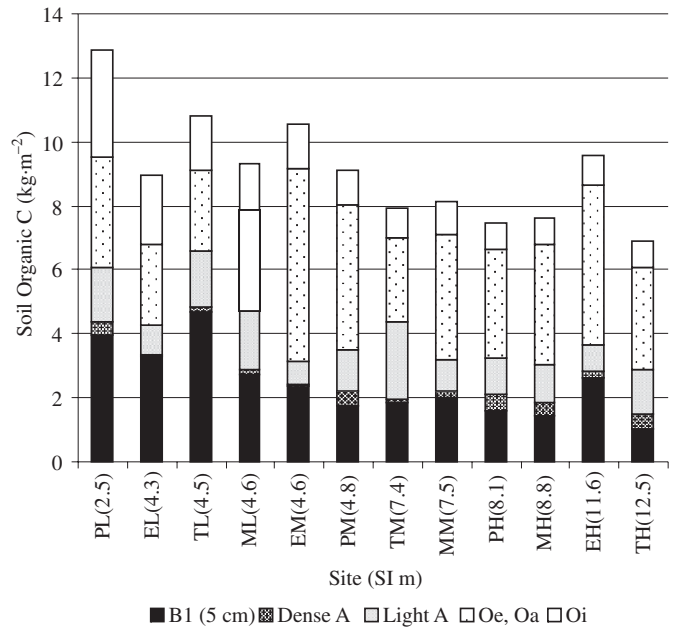
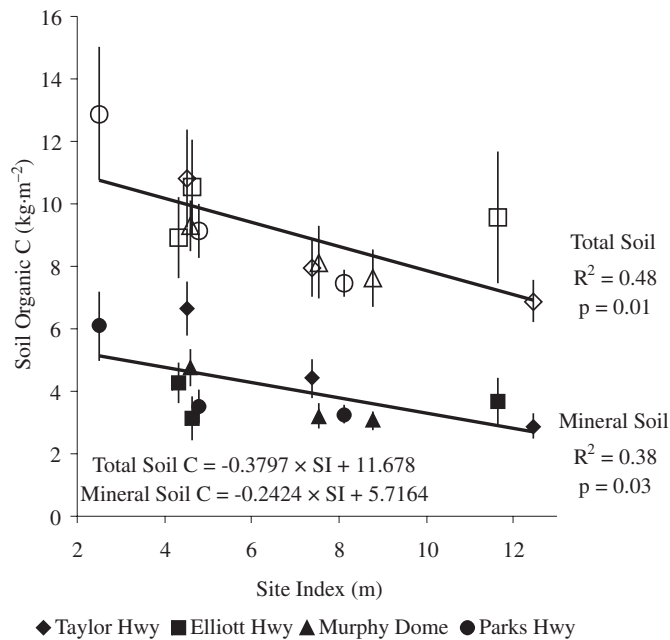


Fig. 3. Soil organic carbon content (kg C·m⁻²) for mineral (A and 5 cm B1) and organic (Oi, Oe, Oa) soil horizons across four black spruce productivity and temperature gradients. Mineral soil was fractionated into dense (>1.6 g·cm⁻³) and light (<1.6 g·cm⁻³) soil organic matter. Sites are ranked by productivity (site index (SI): stand height (metres) attained at 50 years).



SOC in the Oi horizons decreased with increasing SI across all sites ($r = -0.72$, $p = 0.01$). Moreover, total SOC (mineral and organic horizons) was inversely related to SI ($r = -0.69$, $p = 0.01$; Fig. 2) and stand basal area ($r = -0.72$, $p < 0.01$) across all sites. The observed decrease in total SOC with

Fig. 4. Total soil organic carbon content in all horizons (open symbols) and in the mineral soil horizons (solid symbols) decreases with stand productivity (site index (SI); stand height (metres) attained at 50 years) across four study areas in interior Alaska. Error bars represent standard errors of the mean.



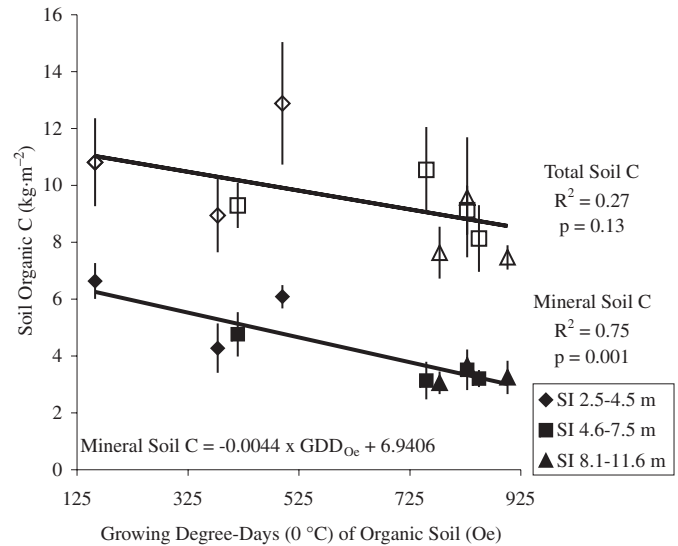
increased SI (Fig. 2) was significant even when the PL site (SI = 2.49 m) was removed from the analysis ($R^2 = 0.37$, $p < 0.05$).

Organic C harbored in mineral soil horizons decreased significantly with an increase in summed GDD within Oe soil horizons at a rate of $4.4 \text{ g C}\cdot\text{m}^{-2}$ for every GDD increase in heat sum (Fig. 5). This observed relationship between mineral SOC and summed GDD (Oe) across all sites (Fig. 5) was robust and significant even when the TL site (158 GDD) was removed from the analysis ($R^2 = 0.57$, $p = 0.02$). Furthermore, the most productive sites (SI = 8.5–12.0 m) also exhibited the warmest soil temperatures and had the lowest mineral soil C content (Fig. 5). Soil organic C in the mineral soil horizons decreased with increased summed GDD within Oi horizons ($r = -0.84$, $p < 0.01$) and also with increased MAT in the Oe horizons ($r = -0.74$, $p = 0.02$).

Depth and SOC content of Oi horizons decreased with an increase in the heat sum of the Oe horizons across all sites ($r = -0.67$ and -0.60 , $p = 0.03$ and 0.07 , respectively). However, the SOC content of the Oe and Oa horizons increased with heat sum ($r = 0.67$, $p = 0.03$) across all sites. As a result of this opposing trend, summed SOC in all genetic horizons did not vary with temperature ($p = 0.13$), despite a marked decrease in mineral soil C with an increase in soil temperature and stand productivity (Fig. 5).

Total SOC accumulation was inversely related to insolation ($r = -0.73$, $p = 0.01$; Table 1). Mean annual air temperatures (1 m) increased with higher insolation ($r = 0.77$, $p < 0.001$), and organic soil horizon depths decreased with increasing insolation across all sites ($r = -0.85$, $p < 0.001$). However, the negative relationship between insolation and total SOC accumulation was confounded somewhat by the occurrence of cooler, low-productivity sites at relatively higher

Fig. 5. Soil organic carbon content in the mineral soil (solid symbols) decreases with increasing heat sum (growing degree-days (GDD) $>0 \text{ }^\circ\text{C}$) in the Oe horizon across four black spruce productivity gradients. Total soil organic carbon content (open symbols) showed no significant change with heat sum ($\alpha = 0.05$). Stand productivity was grouped into three site index (SI, metres) classes. Error bars represent standard errors of the mean.



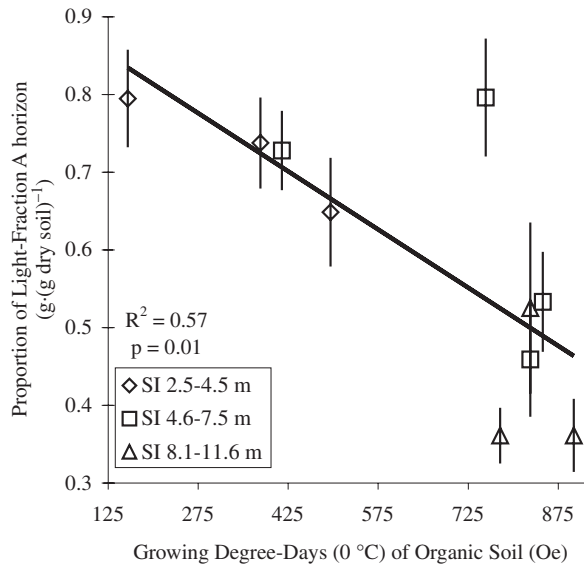
elevations where there was little obstruction of sunlight (i.e., the TL and ML sites). Elevation accounted for part of this variability and explained an additional 35% of the variance in total SOC accumulation when combined with insolation ($R^2 = 0.88$, $p < 0.001$).

Across all sites, the light-fraction ($<1.6 \text{ g}\cdot\text{cm}^{-3}$) SOM in the A horizon ($\text{g}\cdot(\text{g dry soil})^{-1}$) decreased with increasing soil MAT ($r = -0.67$ and -0.71 for Oe and mineral soil horizons, respectively; $p < 0.05$) and increasing GDD ($r = -0.75$ and -0.72 for Oe and mineral soil horizons, respectively; $p < 0.05$). Furthermore, the most productive sites (SI = 8.5–12.0 m) also exhibited the warmest soil temperatures and had the lowest proportion of light-fraction SOM in the A horizon (Fig. 6). This observed relationship between the proportion of light-fraction mineral soil and summed GDD (Oe) across all sites (Fig. 6) was significant even when the TL site (158 GDD) was removed from the analysis ($R^2 = 0.49$, $p = 0.04$). Light-fraction SOC on an area basis ($\text{kg C}\cdot\text{m}^{-2}$) also decreased with an increase in summed GDD (Oe) across all sites ($r = -0.62$, $p = 0.06$). SI was unable to explain any additional variance in light-fraction C content ($\text{kg C}\cdot\text{m}^{-2}$, $p = 0.16$), but SI explained 35% of the variance in decreasing light-fraction A horizon mass ($\text{g}\cdot(\text{g dry soil})^{-1}$, $p = 0.04$).

Soil carbon cycling and turnover

The degree of $\delta^{13}\text{C}$ enrichment in dense-fraction A horizon mineral soil relative to organic horizons was negatively related to C storage in underlying B1 mineral soil horizons (Fig. 7A). Furthermore, as $\Delta^{14}\text{C}$ enrichment in dense-fraction A horizon mineral soil increased, C storage in the underlying B1 horizon decreased across all sites (Fig. 7B). Total C accumulation in the mineral soil horizons ($\text{kg C}\cdot\text{m}^{-2}$, A and B1) showed a marginal inverse relationship with $\Delta^{14}\text{C}$ enrichment ($r = -0.64$, $p = 0.09$). Mean residence times (MRT)

Fig. 6. The proportion of light-fraction A horizon ($<1.6 \text{ g}\cdot\text{cm}^{-3}$) decreases with heat sum (growing degree-days $>0 \text{ }^\circ\text{C}$) in the Oe soil horizon across four black spruce productivity gradients. Stand productivity was grouped into three site index (SI, metres) classes. Error bars represent standard errors of the mean.



of C in dense-fraction A horizon SOM ranged from 282 to 672 years (Fig. 7B). Soil C turnover rate (MRT^{-1}) and soil temperature were both negatively related to SOC storage in the mineral soil horizons (Figs. 7 and 5, respectively).

As an independent test of how a change in fractionation density might affect the pool isolated, the A horizon from an additional black spruce site near Delta Junction, Alaska, (King et al. 2002) was fractionated at $2.0 \text{ g}\cdot\text{cm}^{-3}$ and analyzed for total C and $\Delta^{14}\text{C}$ in a similar manner. The $\Delta^{14}\text{C}$ value of this fraction was -18.2% (MRT of 415 years), and the SOC content of the underlying B1 horizon was $2.00 \text{ kg C}\cdot\text{m}^{-2}$. These values fall within 95% confidence limits of the relationship between $\Delta^{14}\text{C}$ in the $>1.6 \text{ g}\cdot\text{cm}^{-3}$ fractions and B1 horizon SOC across eight sites in this study (Fig. 7B). This suggests that loess-based mineral soil fractions >1.6 and $>2.0 \text{ g}\cdot\text{cm}^{-3}$ are composed of pedogenically similar SOM.

Discussion

Soil carbon cycling and turnover

The proportional amount of labile SOM in the mineral soil decreased with increasing temperature and stand productivity (Fig. 6), but the extent of these changes in SOM lability and the implications for increased C mineralization in a warmer climate are uncertain. Carbon mineralization in mineral soils at the cooler sites, with a higher proportion of light-fraction SOM, could exhibit a higher sensitivity to soil warming (Raich and Schlesinger 1992; Kirschbaum 1995; Bekku et al. 2003). On the other hand, C mineralization from soils obtained from the warmer sites, with a lower proportion of light-fraction SOM, could be relatively insensitive to warming (Liski et al. 1999; Giardina and Ryan 2000; Dalias et al. 2001). Previous research suggests that SOM diminishes asymptotically at higher temperatures because there is likely a limit to the amount of decomposition that is sensitive to temperature (e.g., Melillo et al. 1989; Aber et al.

1990), but our empirical data show linear decreases in SOC and light-fraction SOM in the mineral soil with increasing heat sum. Feedbacks among temperature, SOM depth, and SOC turnover may explain part of the linear decrease in SOC observed at warmer temperatures.

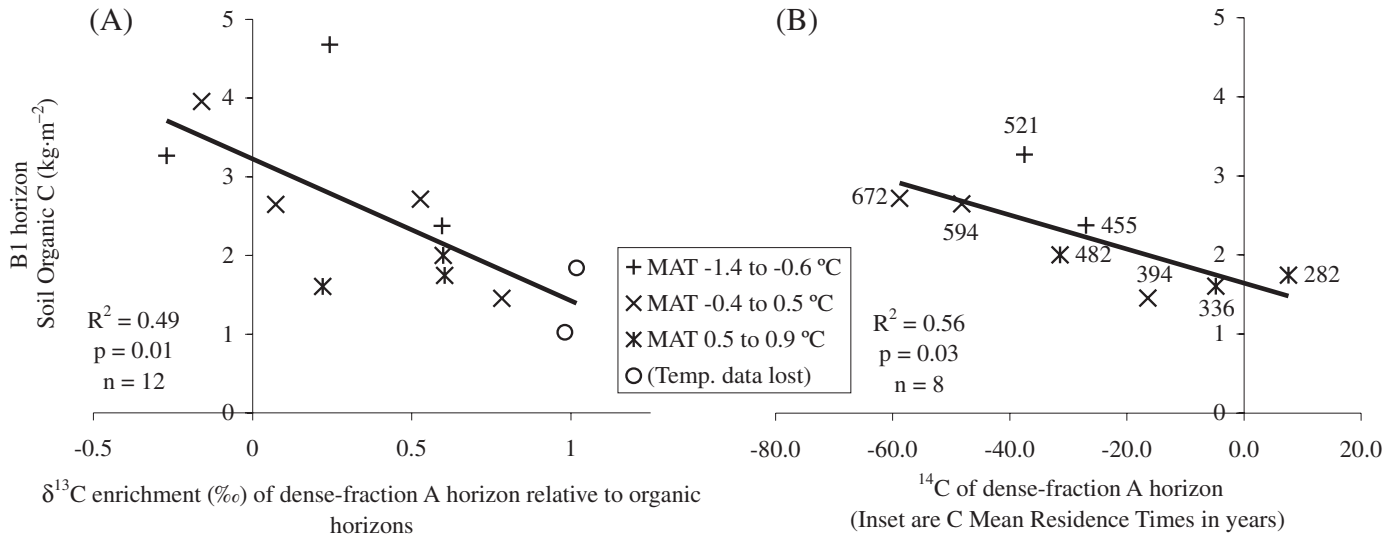
The stable isotopic composition ($\delta^{13}\text{C}$) of the light and dense soil fractions can be used to corroborate information gained from their relative quantities (Baisden et al. 2002b, 2002a). Although several factors can affect the fractionation of ^{13}C in soils (Ehleringer et al. 2000; Fernandez et al. 2003), SOM generally becomes more enriched in ^{13}C , as turnover processes preferentially mineralize ^{12}C (Nadelhoffer and Fry 1988; Boutton 1996). SOM density and $\delta^{13}\text{C}$ enrichment both increase with decomposition (Amundson and Baisden 2000; Baisden et al. 2002a) and follow a continuum from litter to mineral soil (Melillo et al. 1989; Balesdent et al. 1993; Ehleringer et al. 2000). Therefore, the greater degree of $\delta^{13}\text{C}$ enrichment in dense fractions relative to the lighter Oe horizons observed in the warmer, more productive stands (Fig. 7A) suggests C mineralization between the organic and mineral soil horizons increased with temperature and production.

The amount of ^{14}C incorporated into different density fractions is also capable of distinguishing turnover rates of SOM (Trumbore 2000; Baisden et al. 2002b, 2002a). The ^{14}C signature of SOM reflects that of the atmospheric CO_2 concentration at the time of fixation into the original plant material. The low $\Delta^{14}\text{C}$ values ($<0\%$) observed in dense-fraction soils from the cooler, low-productivity sites indicate that C exchange with modern (<40 years) atmospheric ^{14}C concentrations, which were enriched via thermonuclear weapons testing in the 1960s, is very slow (i.e., $\text{MRT} >300$ years). The higher $\Delta^{14}\text{C}$ values observed in the warmer, more productive sites reflect higher rates of exchange (i.e., higher C turnover) with the atmosphere (Fig. 7B).

Stand-soil interactions

The lower mineral soil C storage on more productive (Fig. 4), warmer (Figs. 5 and 6) sites with faster soil C turnover rates (Fig. 7) suggests that decomposition in the mineral soil may be more temperature sensitive than net primary productivity. However, total SOC in combined mineral and organic soil horizons did not significantly decrease with increased soil heat sum (Fig. 5), most likely because of increased C inputs to the soil in warmer, more productive forests. Mack et al. (2004) have similarly shown that while total SOC decreased with increased plant production (with nutrient availability increased via fertilization) in the Alaskan tundra, SOC in upper organic soil horizons ($>5 \text{ cm}$) increased with nutrient fertilization. Chen et al. (2002) demonstrated that although proportionally more of the total C fixed in low-productivity black spruce stands of Canada ($\text{SI} = 3$) was allocated below ground, total C inputs to the soil, above and below ground, were higher in more productive stands ($\text{SI} = 11$). Ruess et al. (2003) have similarly shown that belowground production increased in step with aboveground production in floodplain black spruce stands in interior Alaska. If these trends in stand production apply to this study, and one considers that SOC in organic soil horizons did not significantly change with productivity or climate, it follows that turnover of forest-derived C inputs to the organic soil must

Fig. 7. Carbon isotope enrichment in the dense-fraction A horizon mineral soil increases as the soil organic C content of the underlying B1 mineral soil horizon decreases. Sites are grouped by mean annual temperature (MAT) at a depth of 5 cm into the mineral soil (soil temperature data at two sites were lost because of forest fires; open symbols). (A) The $\delta^{13}\text{C}$ isotope enrichment in the dense-fraction A horizon mineral soil ($>1.6 \text{ g}\cdot\text{cm}^{-3}$) relative to organic soil horizons versus B1 horizon soil organic C. (B) The $\Delta^{14}\text{C}$ content of dense-fraction A horizon mineral soil versus B1 horizon soil organic C. Values next to symbols are mean residence times (years) of C in the dense fraction, as calculated from the degree of $\Delta^{14}\text{C}$ incorporation.



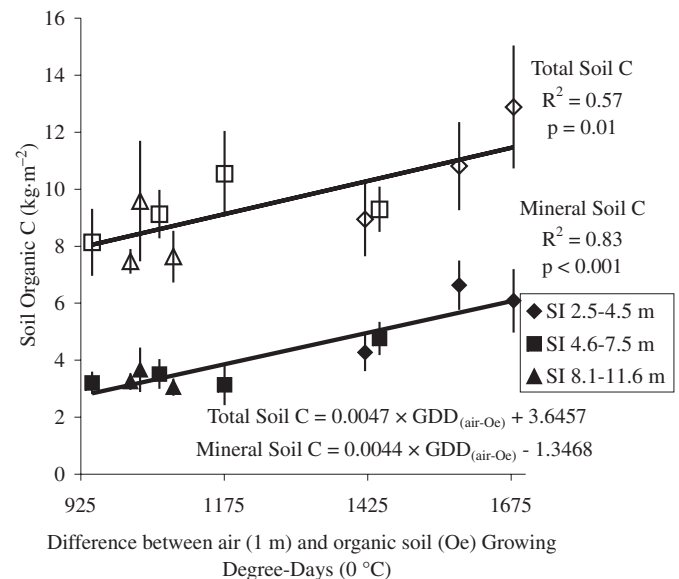
have increased with stand production and temperature. However, the products of SOM turnover did not accumulate in the mineral soil (Fig. 7), which could be due, in part, to the low sorptive capacity for the products of SOM turnover within incipient, loess-dominated mineral soil (Ugolini et al. 1987; Dahlgren and Marrett 1991; Moore 2003).

Biophysical controls over temperature and the “thermal advantage”

Moss significantly increases surface insulation and therefore exerts major control over soil temperatures (Rieger 1983; Bonan 1991; Beringer et al. 2001). It is no surprise, then, that soil temperatures in all horizons decreased with increasing organic matter thickness (particularly fibric material) across the productivity–temperature gradients in this study (Fig. 2). Air temperatures (1 m) did not significantly vary across all sites (Table 2), but soil temperatures in the lower-productivity sites (with deeper Oi) remained cooler and had a lower heat sum (Fig. 2). These data suggest that the moss layer increased the thermal inertia of soils relative to air temperature by insulating the soil.

Swanson et al. (2000) hypothesized that peat accumulation in cold climates increases with the divergence between warmer air temperatures and cooler soil temperatures, which gives a “thermal advantage” to biological processes occurring in the air (primary productivity) relative to biological processes occurring in the soil (microbial decomposition and mineralization). We tested this hypothesis across our four productivity–temperature gradients by subtracting the heat sum (GDD $>0 \text{ }^\circ\text{C}$) of the Oe soil horizon from the air (1 m) GDD. We found that the thermal environment of primary production relative to soil decomposition ($\text{GDD}_{(\text{air-Oe})}$) explained 57% of the variance in total SOC storage across all sites (Fig. 8). Furthermore, $\text{GDD}_{(\text{air-Oe})}$ explained 8% more of the variance in mineral soil C storage than did soil heat sum alone (Figs. 5 and 8).

Fig. 8. The difference between air (1 m) and soil (Oe horizon) heat sums (growing degree-days (GDD) $>0 \text{ }^\circ\text{C}$) compared with total (open symbols) and mineral (solid symbols) soil organic C storage. Stand productivity was grouped into three site index (SI, metres) classes. Error bars represent standard errors of the mean.



Another measure of the advantage of primary productivity over soil decomposition environment was the annual potential amount of incoming insolation at each site (Table 1). The thermal advantage of productivity relative to decomposition was lower on sites with greater amounts of insolation because organic matter depths, and hence soil insulating properties, decreased. This expectation was consistent with the decrease in total SOC harbored in all horizons with increasing insolation across all sites.

SOC in Alaska compared with other boreal forests

Upland spruce forests of interior Alaska harbor considerably more SOC than has been previously reported for other boreal forests. We sampled to 5 cm B horizon in this study, and Ping et al. (1997) identified an additional 5.9–7.6 kg C·m⁻² in underlying B and C horizons to 1 m depth in upland forests of interior Alaska that exhibited similar bulk densities and C concentrations to the sites in this study (total profile SOC ranging from 16.9 to 78.7 kg C·m⁻²). These SOC values for interior Alaska are 1 to 19 times greater than previously reported values for upland boreal forests spanning Sweden, Finland, Norway, and Denmark (Callesen et al. 2003). Moreover, the mean amount of SOC reported for organic horizons in these Fennoscandian forests was 29%–66% less than values observed in this study and was 38% and 64% less than organic horizon SOC reported for upland white spruce (*Picea glauca* (Moench) Voss) (Steltzer 2004) and upland black spruce (Ping et al. 1997) in northwest and interior Alaska, respectively.

The observed decline in mineral soil C with increasing heat sum and stand productivity in interior Alaska differs from previous reports along thermal – stand productivity gradients in Fennoscandian boreal forests (Liski and Westman 1995, 1997). Callesen et al. (2003) demonstrated that total SOC (across three texture classes to a depth of 1 m) in mixed boreal forests spanning four Nordic countries increased from 4.1 to 12.0 kg·m⁻² as mean annual temperature increased from 0 to 7.5 °C. Warmer temperatures and increased parent material development (Liski et al. 1998) across the Nordic study region are in sharp contrast with the cooler temperatures (Table 2; Ping et al. 1997) and incipient Gelisols and Inceptisols of interior Alaska (Allan 1969; Ping et al. 2005). These data suggest that SOC accumulation in upland boreal forests of interior Alaska is largely controlled by the degree to which decomposition is arrested at cooler temperatures, whereas soil textural properties exert more control over SOC in other boreal forests.

Conclusions

Near-surface SOC decreased with increased stand productivity (and hence, probable increases in nutrient availability) across four replicated gradients in black spruce stand production and climate in interior Alaska. In addition, the distributions of pools within the mineral soil (a decrease in total SOC and proportion of light-fraction SOM) and within the organic soil (a decrease in Oi horizon depth and SOC) were apparently driven by interactions between increased soil temperature and stand productivity across all sites. Variation in total SOC across all sites was best explained by the difference in aboveground and belowground heat sums, which we suggest is largely mediated by the insulative properties of surface organic horizons. The interactions among increased stand productivity, organic matter accumulation, and soil heat sum have altered the quality and quantity of different SOM pools through differences in decomposition environment and plant C inputs, even though total SOC appeared insensitive to temperature in some cases. These data suggest that temperature responsiveness of organic matter decomposition within discrete soil pools, and not just total soil C stocks,

needs to be examined to project the effects of changing climate and primary production on soil C balance.

Acknowledgments

We are indebted to Chien-Lu Ping and Edmond Packee for insight and advice in the early stages of this project. Wendy Loya and two anonymous reviewers significantly improved this manuscript with their suggestions, and Isla Myers-Smith and Jason Vogel furthered ideas through discussion. The Growth and Yield Program at the University of Alaska, Fairbanks (E.C. Packee) shared data incorporated in this study. Carolyn Rosner and Mike Hay helped greatly with site selection, GPS, and insolation calculations. We appreciate Lola Oliver and the University of California Irvine-Keck CC-AMS facility for help with isotope analyses. Two sites in this research are part of the Bonanza Creek Long Term Ecological Research program (funded jointly by National Science Foundation grant DEB-0423442 and USDA Forest Service, Pacific Northwest Research Station grant PNW01-JV11261952–231). Funding was received from the Center for Global Change and Arctic System Research (University of Alaska, Fairbanks) and the Inland Northwest Research Alliance (U.S. Department of Energy).

References

- Aber, J.D., Melillo, J.M., and McClaugherty, C.A. 1990. Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. *Can. J. Bot.* **68**: 2201–2208.
- Allan, R.J. 1969. Clay mineralogy and geochemistry of soils and sediments with permafrost in interior Alaska. Ph.D. dissertation, Dartmouth College, Hanover, N.H. pp. 5–20, 64–79.
- Amundson, R., and Baisden, W.T. 2000. Stable isotope tracers and mathematical models in soil organic matter studies. *In Methods in ecosystem science. Edited by O.F. Sala, R.B. Jackson, H.A. Mooney, and R.W. Howarth. Springer-Verlag, New York. pp. 117–134.*
- Baisden, W.T., Amundson, R., Cook, A.C., and Brenner, D.L. 2002a. Turnover and storage of C and N in five density fractions from California annual grassland surface soils. *Global Biogeochem. Cycles*, **16**: 1117–1132. doi:10.1029/2001GB001822.
- Baisden, W.T., Amundson, R.G., Brenner, D.L., Cook, A.C., Kendall, C., and Harden, J. 2002b. A multi-isotope C and N modeling analysis of soil organic matter turnover and transport as a function of soil depth in a California annual grassland soil chronosequence. *Global Biogeochem. Cycles*, **16**: 1135–1160. doi:10.1029/2001GB001823.
- Balesdent, J., Girardin, C., and Mariotti, A. 1993. Site-related δ¹³C of tree leaves and soil organic matter in a temperate forest. *Ecology*, **74**: 1713–1721.
- Barney, R.J., Van Cleve, K., and Schlentner, R. 1978. Biomass distribution and crown characteristics in two Alaskan *Picea mariana* ecosystems. *Can. J. For. Res.* **8**: 36–41.
- Bekku, Y.S., Nakatsubo, T., Kume, A., Adachi, M., and Koizumi, H. 2003. Effect of warming on the temperature dependence of soil respiration rate in arctic, temperate and tropical soils. *Appl. Soil Ecol.* **22**: 205–210.
- Berg, B., and Meentemeyer, V. 2002. Litter quality in a north European transect versus carbon storage potential. *Plant Soil*, **242**: 83–92.

- Beringer, J., Lynch, A.H., Chapin, F.S., III., Mack, M., and Bonan, G.B. 2001. The representation of Arctic soils in the land surface model: the importance of mosses. *J. Clim.* **14**: 3324–3335.
- Bonan, G.B. 1991. A biophysical surface energy budget analysis of soil temperature in the boreal forests of interior Alaska. *Water Resour. Res.* **27**: 767–781.
- Boutton, T.W. 1996. Stable carbon isotope ratios of soil organic matter and their use as indicators of vegetation and climate change. *In* Mass spectrometry of soils. *Edited by* T.W. Boutton and S. Yamasaki. Marcel Dekker, Inc., New York. pp. 47–82.
- Callesen, I., Liski, J., Raulund-Rasmussen, K., Olsson, M.T., Tau-Strand, L., Vesterdal, L., and Westman, C.J. 2003. Soil carbon stores in Nordic well-drained forest soils—relationships with climate and texture class. *Global Change Biol.* **9**: 358–370.
- Carmean, W.H. 1972. Site index curves for upland oaks in the central states. *For. Sci.* **18**: 109–120.
- Carmean, W.H., and Lenthall, D.J. 1989. Height-growth and site-index curves for jack pine in north central Ontario. *Can. J. For. Res.* **19**: 215–224.
- Chapin, F.S., III., McGuire, A.D., Randerson, J., Pielke, R., Sr., Baldocchi, D., Hobbie, S.E., Roulet, N., Eugster, W., Kasischke, E., and Rastetter, E.B. 2000. Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biol.* **6**(Suppl. 1): 211–223.
- Chen, W., Chen, J.M., Price, D.T., and Cihlar, J. 2002. Effects of stand age on net primary productivity of boreal black spruce forests in Ontario, Canada. *Can. J. For. Res.* **32**: 833–842.
- Dahlgren, R.A., and Marrett, D.J. 1991. Organic carbon sorption in arctic and subalpine Spodosol B horizons. *Soil Sci. Soc. Am. J.* **55**: 1382–1390.
- Dalias, P., Anderson, J.M., Bottner, P., and Couteaux, M.M. 2001. Temperature responses of carbon mineralization in conifer forest soils from different regional climates incubated under standard laboratory conditions. *Global Change Biol.* **7**: 181–192.
- Dyrness, C.T., and Grigal, D.F. 1979. Vegetation–soil relationships along a spruce forest transect in interior Alaska. *Can. J. Bot.* **57**: 2644–2656.
- Ehleringer, J.R., Buchmann, N., and Flanagan, L.B. 2000. Carbon isotope ratios in belowground carbon cycle processes. *Ecol. Appl.* **10**: 412–422.
- Elberling, B., and Brandt, K.K. 2003. Uncoupling of microbial CO₂ production and release in frozen soil and its implications for field studies of arctic C cycling. *Soil Biol. Biochem.* **35**: 263–272.
- Fernandez, I., Mahieu, N., and Cadisch, G. 2003. Carbon isotopic fractionation during decomposition of plant materials of different quality. *Global Biogeochem. Cycles*, **17**: 1075–1095. doi:10.1029/2001GB001834.
- Giardina, C.P., and Ryan, M.G. 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature (London)*, **40**: 858–861.
- Golchin, A., Oades, J.M., Skjemstad, J.O., and Clarke, P. 1994. Study of free and occluded particulate organic matter in soils by solid state ¹³C CP/MAS NMR spectroscopy and scanning electron microscopy. *Aust. J. Soil Res.* **32**: 285–309.
- Gower, S.T., Krankina, O., Olson, R.J., Apps, M., Linder, S., and Wang, C. 2001. Net primary production and carbon allocation patterns of boreal forest ecosystems. *Ecol. Appl.* **11**: 1395–1411.
- Grant, R.F. 2004. Modeling topographic effects on net ecosystem productivity of boreal black spruce forests. *Tree Physiol.* **24**: 1–18.
- Heath, L.S., Smith, J.E., and Birdsey, R.A. 2003. Carbon trends in U.S. forestlands: a context for the role of soils in forest carbon sequestration. *In* The potential of U.S. forest soils to sequester carbon and mitigate the greenhouse effect. *Edited by* J.M. Kimble, L.S. Heath, R.A. Birdsey, and R. Lal. CRC press, Boca Raton, Fla. pp. 35–46.
- Johnson, M.G., and Kern, J.S. 2003. Quantifying the organic carbon held in forested soils of the United States and Puerto Rico. *In* The potential of U.S. forest soils to sequester carbon and mitigate the greenhouse effect. *Edited by* J.M. Kimble, L.S. Heath, R.A. Birdsey, and R. Lal. CRC press, Boca Raton, Fla. pp. 47–72.
- Kaiser, K., and Guggenberger, G. 2003. Mineral surfaces and soil organic matter. *Eur. J. Soil Sci.* **54**: 219–236.
- Kaiser, K., Guggenberger, G., Haumaier, L., and Zech, W. 2002. The composition of dissolved organic matter in forest soil solutions: changes induced by seasons and passage through the mineral soil. *Org. Geochem.* **33**: 307–318.
- Keeling, C.D., Chin, J.F.S., and Whorf, T.P. 1996. Increased activity of northern vegetation inferred from atmospheric CO₂ measurements. *Nature (London)*, **382**: 146–149.
- King, S., Harden, J., Manies, K.L., Munster, J., and White, L.D. 2002. Fate of carbon in Alaskan landscapes project—Database for soils from eddy covariance tower sites, Delta Junction, AK. U.S. Geological Survey preliminary report. U.S. Geological Survey, Menlo Park, Calif.
- Kirschbaum, M.U.F. 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biol. Biochem.* **27**: 753–760.
- Liski, J., and Westman, C.J. 1995. Density of organic carbon in soil at coniferous forest sites in southern Finland. *Biogeochemistry*, **29**: 183–197.
- Liski, J., and Westman, C.J. 1997. Carbon storage in forest soil of Finland. 1. Effect of thermoclimate. *Biogeochemistry*, **36**: 239–260.
- Liski, J., Ilvesniemi, H., Makela, A., and Starr, M. 1998. Model analysis of the effects of soil age, fires and harvesting on the carbon storage of boreal forest soils. *Eur. J. Soil Sci.* **49**: 407–416.
- Liski, J., Ilvesniemi, H., Makela, A., and Westman, C.J. 1999. CO₂ emissions from soil in response to climatic warming are overestimated — the decomposition of old soil organic matter is tolerant of temperature. *Ambio*, **28**: 171–174.
- Mack, M.C., Schuur, E.A.G., Bret-Harte, M.S., Shaver, G.R., and Chapin, F.S., III. 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature (London)*, **431**: 440–443.
- McGuire, A.D., Clein, J., Melillo, J.M., Kicklighter, D.W., Meier, R.A., Vorosmarty, C.J., and Serreze, M.C. 2000. Modelling carbon responses of tundra ecosystems to historical and projected climate II. The sensitivity of pan-Arctic carbon storage to temporal and spatial variation and climate. *Global Change Biol.* **6**: 141–150.
- McLauchlan, K.K., and Hobbie, S.E. 2004. Comparison of labile soil organic matter fractionation techniques. *Soil Sci. Soc. Am. J.* **68**: 1616–1625.
- Melillo, J.M., Aber, J.D., Linkins, A.E., Ricca, A., Fry, B., and Nadelhoffer, K.J. 1989. Carbon and nitrogen dynamics along the decay continuum: Plant litter to soil organic matter. *Plant Soil*, **115**: 189–198.
- Moore, T.R. 2003. Dissolved organic carbon in a northern boreal landscape. *Global Biogeochem. Cycles*, **17**: 1109–1116. doi:10.1029/2003GB002050.
- North, P.F. 1976. Towards an absolute measurement of soil structural stability using ultrasound. *J. Soil Sci.* **27**: 451–459.
- Nadelhoffer, K.J., and Fry, B. 1988. Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. *Soil Sci. Soc. Am. J.* **52**: 1633–1640.

- Oechel, W.C., and Van Cleve, K. 1986. The role of bryophytes in nutrient cycling in the Taiga. *In* Forest ecosystems in the Alaskan taiga. *Edited by* K. Van Cleve, F.S. Chapin III, P.W. Flanagan, L.A. Viereck, and C.T. Dyrness. Springer-Verlag, New York. pp. 121–137.
- Pewe, T.L., and Reger, R.D. 1983. Guidebook to permafrost and quaternary geology along the Richardson and Glenn Highways between Fairbanks and Anchorage, Alaska. Division of Geological and Geophysical Surveys publication, Department of Natural Resources, State of Alaska, Fairbanks, Alaska.
- Ping, C.L., Michaelson, G.J., and Kimble, J.M. 1997. Carbon storage along a latitudinal transect in Alaska. *Nutr. Cycl. Agroecosyst.* **49**: 235–242.
- Ping, C.L., Michaelson, G.J., Packee, E.C., Stiles, C.A., Swanson, D.K., and Yoshikawa, K. 2005. Characterization and formation of soils in the Caribou–Poker Creek Research Watershed, Alaska. *Soil Sci. Soc. Am. J.* **69**: 1761–1772.
- Raich, J.W., and Schlesinger, W.H. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus Ser. B Chem. Phys. Meteorol.* **44**: 81–99.
- Rapalee, G., Trumbore, S.E., Davidson, E.A., Harden, J.W., and Veldhuis, H. 1998. Soil carbon stocks and their rates of accumulation and loss in a boreal forest landscape. *Global Biogeochem. Cycles*, **12**: 687–701.
- Rieger, S. 1983. The genesis and classification of cold soils. Academic Press, New York. pp. 1–47.
- Rodionov, A., Amelung, W., Urusevskaja, I., and Zech, W. 2000. Carbon and nitrogen in the enriched labile fraction along a climosequence of zonal steppe soils in Russia. *Soil Sci. Soc. Am. J.* **64**: 1467–1473.
- Rosner, C. 2004. Growth and yield of black spruce, *Picea mariana* (Mill.) B.S.P., in Alaska. M.Sc. thesis, University of Alaska, Fairbanks, Alaska.
- Ruess, R.W., Hendrick, R.L., Burton, A.J., Pregitzer, K.S., Sveinbjornsson, B., Allen, M.F., and Maurer, G.E. 2003. Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. *Ecol. Monogr.* **73**: 643–662.
- Schoenberger, P.J., Wysocki, D.A., Benham, E.C., and Broderson, W.D. 2002. Field book for describing and sampling soils. Version 2.0. Natural Resources Conservation Service, National Soil Survey Center, Lincoln, Nebr.
- Schulten, H.R., and Leinweber, P. 1999. Thermal stability and composition of mineral-bound organic matter in density fractions of soil. *Eur. J. Soil Sci.* **50**: 237–248.
- Slaughter, C.W., and Long, K.P. 1975. Upland climatic parameters on subarctic slopes, central Alaska. *In* Climate of the arctic. *Edited by* S.A. Bowling and G. Weller. Geophysical Institute of Alaska, Fairbanks, Alaska. pp. 276–280.
- Slaughter, C.W., and Viereck, L.A. 1986. Climate characteristics of the Taiga in interior Alaska. *In* Forest ecosystems in the Alaskan taiga. *Edited by* K. Van Cleve, F.S. Chapin III, P.W. Flanagan, L.A. Viereck, and C.T. Dyrness. Springer-Verlag, New York. pp. 9–21.
- Steltzer, H. 2004. Soil carbon sequestration with forest expansion in an arctic forest–tundra landscape. *Can. J. For. Res.* **34**: 1538–1542.
- Stuiver, M., and Polach, H. 1977. Reporting of ¹⁴C data. *Radiocarbon*, **19**: 355–363.
- Swanson, D.K., Lacelle, B., and Tarnocai, C. 2000. Temperature and the boreal–subarctic maximum in soil organic carbon. *Geogr. Phys. Quatern.* **54**: 157–167.
- Trumbore, S.E. 2000. Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecol. Appl.* **10**: 399–411.
- Ugolini, F.C., Stoner, M.G., and Marrett, D.J. 1987. Arctic pedogenesis: 1. Evidence for contemporary podzolization. *Soil Sci.* **144**: 90–100.
- Van Cleve, K., and Viereck, L.A. 1981. Forest succession in relation to nutrient cycling in boreal forest of Alaska. *In* Forest succession: concepts and application. *Edited by* D.C. West, H.H. Shugart, and D.B. Botkin. Springer-Verlag, New York. pp. 203–208.
- Van Cleve, K., and Yarie, J. 1986. Interaction of temperature, moisture, and soil chemistry in controlling nutrient cycling and ecosystem development in the taiga of Alaska. *In* Forest ecosystems in the Alaskan taiga. *Edited by* K. Van Cleve, F.S. Chapin III, P.W. Flanagan, L.A. Viereck, and C.T. Dyrness. Springer-Verlag, New York. pp. 160–189.
- Van Cleve, K., Barney, R., and Schlentner, R. 1981. Evidence of temperature control of production and nutrient cycling in two interior Alaska black spruce ecosystems. *Can. J. For. Res.* **11**: 258–273.
- Van Cleve, K., Oechel, W.C., and Hom, J.L. 1990. Response of black spruce (*Picea mariana*) ecosystems to soil temperature modification in interior Alaska. *Can. J. For. Res.* **20**: 1530–1535.
- Van Cleve, K., Chapin, F.S., III, Dyrness, C.T., and Viereck, L.A. 1991. Element cycling in taiga forests: state factor control. *Bio-science*, **41**: 78–87.
- Viereck, L.A., and Johnston, W.F. 1990. Black spruce. *In* Silvics of North America. Vol. 1. Conifers. *Edited by* R.M. Burns and B.H. Honkala. U.S. Dep. Agric. Agric. Handb. 654. pp. 227–237.
- Viereck, L.A., and Van Cleve, K. 1984. Some aspects of vegetation and temperature relationships in the Alaska taiga. *In* The potential effects of carbon dioxide-influenced climatic changes in Alaska. *Edited by* J.H. McBeath. School of Agriculture and Land Resources Management, University of Alaska, Fairbanks, Alaska. Misc. Publ. 83-1. pp. 129–142.
- Viereck, L.A., Dyrness, C.T., Van Cleve, K., and Foote, M.J. 1983. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. *Can. J. For. Res.* **13**: 703–720.
- Vogel, J.S., Southon, J.R., Nelson, D.E., and Brown, T.A. 1984. Performance of catalytically condensed carbon for use in accelerator mass spectrometry. *Nucl. Instrum. Methods Phys. Res.* **B5**: 289–293.
- Vogel, J.G., Valentine, D.W., and Ruess, R.W. 2005. Soil and root respiration in mature Alaskan black spruce forests that vary in soil organic matter decomposition rates. *Can. J. For. Res.* **35**: 161–174.
- White, J.D., Koepke, B.E., and Swanson, D.K. 2002. Soil survey of North Star area, Alaska. USDA Natural Resources Conservation Service, North Star Borough, Alaska.
- Winkler, J.P., Cherry, R.S., and Schlesinger, W.H. 1996. The Q₁₀ relationship of microbial respiration in a temperate forest soil. *Soil Biol. Biochem.* **28**: 1067–1072.
- Yarie, J., and Van Cleve, K. 1983. Factors which determine site productivity in interior Alaska taiga ecosystems. USDA For. Serv. Gen. Tech. Rep. PNW-163. pp. 94–100.