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Sphagnum mosses limit total carbon consumption during fire in Alaskan black spruce forests

Gordon Shetler, Merritt R. Turetsky, Evan Kane, and Eric Kasischke

Abstract: The high water retention of hummock-forming *Sphagnum* species minimizes soil moisture fluctuations and might protect forest floor organic matter from burning during wildfire. We hypothesized that *Sphagnum* cover reduces overall forest floor organic matter consumption during wildfire compared with other ground-layer vegetation. We characterized variability in soil organic layer depth and organic matter stocks in two pairs of burned and unburned black spruce (*Picea mariana* (Mill.) BSP) stands in interior Alaska. In the unburned stands, microsites dominated by *Sphagnum* had more than twice as much soil organic matter·m^{-2} as microsites dominated by feather moss and (or) lichens. Whereas 20% of soil organic matter was consumed during fire in microsites dominated by *Sphagnum*, 45% was consumed in microsites dominated by the feather moss and (or) lichens. Across 79 recently burned black spruce stands, unburned moss abundance (primarily remnant *Sphagnum* hummocks), landscape position (backslope, flat upland, flat lowland classes), and the interaction among these variables explained 60% of postfire organic soil depths. We suggest that "*Sphagnum* sheep" could serve as a useful visual indicator of variability in postfire soil carbon stocks in boreal black spruce forests. *Sphagnum* mosses are important ecosystem engineers not only for their influence on decomposition rates, but also for their effect on fuel consumption and fire patterning.

Résumé : La forte rétention d'eau par les espèces du genre *Sphagnum* qui forment des buttes minimise les fluctuations de la teneur en eau du sol et pourrait empêcher la matière organique du sol forestier de brûler pendant un feu de forêt. Nous posons l'hypothèse que le couvert de *Sphagnum* diminue globalement la consommation de matière organique au sol pendant un feu comparativement à d'autres types de végétation au sol. Nous avons caractérisé la variabilité de l'épaisseur et des stocks de matière organique dans deux paires de stations d'épinette noire (*Picea mariana* (Mill.) BSP) brûlées et non brûlées du centre de l'Alaska, aux États-Unis. Dans les stations non brûlées, les microsites dominés par *Sphagnum* avaient plus de deux fois plus de matière organique au sol·m^{-2} que les microsites dominés par les mousses hypnacées et les lichens. Alors que 20 % de la matière organique au sol était consumé pendant un feu dans les microsites dominés par *Sphagnum*, ce taux s'élevait à 45 % dans les microsites dominés par les mousses hypnacées et les lichens. Parmi 79 stations d'épinette noire récemment brûlées, l'abondance de mousses non brûlées (principalement des buttes rémanentes de *Sphagnum*), la position topographique (classes de revers, de sommet plat et de basse terre plate) et l'interaction entre ces variables expliquaient 60 % de l'épaisseur de la matière organique au sol à la suite d'un feu. Nous croyons que les monticules de *Sphagnum* pourraient être utiles comme indicateurs visuels pour établir la variabilité des stocks de carbone dans le sol à la suite du passage d'un feu dans les forêts boréales d'épinette noire. Les sphaignes sont des composantes importantes de l'écosystème non seulement à cause de leur influence sur le taux de décomposition, mais aussi à cause de leur effet sur la consommation des combustibles et le modelage du feu.

[Traduit par la Rédaction]

Introduction

Over the past 40 years, climate warming in the high latitude regions of North America has been dramatic (Chapin et al. 2005), and this warming trend is expected to continue over the next century (Hassol 2005). Several studies have documented increasing fire activity in the North American boreal region in recent decades, which is likely driven by climate change (Flannigan and Wotton 2001; Gillett et al. 2004; Kasischke and Turetsky 2006). In Canada over the last two decades, fires have burned an average of 2.8 million ha·year^{-1}, although more than 7 million ha can burn during extreme fire years. In 2004 and 2005, more than 4 million ha burned in interior Alaska (~ 10% of the land surface of this region). Along with the increase in burned area, there has been a shift in the seasonality of burning,

Received 7 January 2008. Accepted 28 March 2008. Published on the NRC Research Press Web site at cjfr.nrc.ca on 26 July 2008.

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 doi:10.1139/X08-057

with an increased number of fires occurring late in the growing season (Kasischke and Turetsky 2006).

Fires in boreal regions of North America and western Europe tend to be intense crown fires (Stocks and Kaufman 1997) that burn large areas and consume a significant component of forest floor organic matter (Stocks 1991; Kasischke et al. 1995). Fuel loading and continuity are important controls of the total area of burning and the ignition of surface organic matter. For example, black spruce (*Picea mariana* (Mill.) BSP) is the dominant forest cover type in interior Alaska and generally has a higher probability of burning than hardwood species, owing to greater flammability and a ladder fuel structure that leads to torching (Hely et al. 2000). Rupp et al. (2002) used a spatially explicit vegetation model to investigate the role of black spruce in fire regimes in Alaska's boreal forest and concluded that landscapes dominated by black spruce were likely to have more fires and greater burn area than landscapes dominated by white spruce (*Picea glauca* (Moench) Voss) or deciduous species. Following fire, forest stands are generally less susceptible to burning, owing to deciduous revegetation that can occur prior to conifer recolonization (Viereck 1973).

Several factors control the depth of burning of forest floor organic matter, but the primary controls are organic layer moisture and bulk density of the organic material exposed to combustion (Miyanishi and Johnson 2002). However, when surface organic layers become sufficiently dry, they can experience combustion all the way to mineral soil (Kasischke and Johnstone 2005). Burning of forest floor organic matter in black spruce forests is complex because of site-specific variations in the hydrologic status and composition of ground-layer fuels, ranging from drier stands with ground-layer vegetation dominated by feather mosses and lichens to more mesic ecosystems dominated by *Sphagnum* species (Hollingsworth et al. 2006). While ground-layer vegetation in mesic forests and wetlands frequently may experience low to moderate forest floor organic matter combustion, owing to its ability to harbor considerable moisture (e.g., >80% water by volume; Boelter and Verry 1977), surface vegetation typically has a very low bulk density and therefore can be prone to drying during periods of drought, thereby increasing fuel consumption rates (Van Wagner 1987).

In general, black spruce forests exhibit several traits that make wildfire nearly inevitable in this forest type regardless of landscape position (Dyrness et al. 1986; Harden et al. 2003). However, physiography at the local scale integrates soil temperature and moisture effects on forest structure and organic layer depth (e.g., Van Cleve and Yarie 1986), which largely determine the fuel types available for combustion (Ryan 2002; Kane et al. 2007). North-facing and toe-slope forests receive less insolation than forests on southerly slopes and therefore are cooler, wetter, have deeper organic layers, and are more likely to contain permafrost (Rieger 1983; Hinzman et al. 2006). Downhill movement of cold air during winter also contributes to colder microclimates in toe and foot slopes and constrained stream valleys. These factors provide a niche for the proliferation of bryophytes, including *Sphagnum* (e.g., Oechel and Van Cleve 1986).

Sphagnum mosses (the peat mosses) are widespread in boreal landscapes (Gajewski et al. 2001; Vitt et al. 2001), particularly in peatlands and forests underlain by surface permafrost. *Sphagnum* species wick water upwards through external capillary action and thus are able to store large volumes of water in dead hyaline cell structures. By increasing soil moisture, lowering soil temperatures, and producing recalcitrant litter that decomposes slowly, *Sphagnum* mosses inhibit decomposition and promote the accumulation of thick organic soil layers in boreal regions (cf. Yu et al. 2002). Owing to these controls on soil climate and ecosystem processes, *Sphagnum* mosses often are acknowledged as ecosystem engineers (cf. Van Breemen 1995). Because some *Sphagnum* species, particularly hummock-dwelling species, tend to have high water retention (Hayward and Clymo 1982), they can generally stay moist during periods of drought and low water table position (Kellner and Halldin 2002) and may also help protect the ecosystem from severe burning. For example, *Sphagnum* species that thrive in hummocks (cf. *Sphagnum fuscum*, *Sphagnum rubellum* and (or) *capillifolium*) are known as drought avoiders, as they maintain a high water retention capacity through structural and morphologic features such as dense capitula, spreading and hanging branches, and hyaline cells that store water (Rydin and McDonald 1985; Titus and Wagner 1984). Benscoter and Wieder (2003) found that spatial variability in organic matter consumption rates was correlated with microtopography and *Sphagnum* species. Even though hummock microtopographic positions were located farther from the regional water table than hollows, the hummocks dominated by *S. fuscum* burned less severely than vegetation in the hollows (likely *Sphagnum angustifolium* and (or) lichens) during a peatland fire.

Sphagnum mosses in boreal forests often do not burn, even when other ground-layer fuels are completely consumed. Hereinafter, we refer to *Sphagnum* that survive fire as "*Sphagnum* sheep" (Fig. 1). In our sites, *Sphagnum* sheep typically were associated with hummocks. We investigated the relationships between *Sphagnum* cover, organic soil depths and soil organic matter stocks, and fuel consumption rates in an intensive study of two pairs of burned and (or) unburned north-facing Alaskan black spruce forests. We also conducted an extensive study using a larger data set to explore the effects of remnant unburned moss, which was dominated by *Sphagnum* in most sites, on organic soil depth across 79 burned black spruce stands in interior Alaska. We hypothesized that the large soil organic matter stocks typical of boreal black spruce forests are caused at least in part by lower fuel consumption rates in areas dominated by *Sphagnum* compared with other dominant ground-layer fuel types (feather mosses and (or) lichen).

Methods

Intensive north-facing black spruce sites

Within the 217 000 ha Boundary fire that burned from mid-June through to late August 2004 in interior Alaska, we selected a burned north-facing site that was in close proximity to a natural fire break, allowing us to establish a pair of burned and unburned (representing mature, "prefire" conditions) stands. This pair of stands was located in the Nome Creek region (hereinafter referred to as NC; 65°20′N, 146°40.9′W) within the Boundary fire scar. The burned and

Fig. 1. Image of "*Sphagnum* sheep," which represent moss-dominated hummocks that did not burn. Image taken following the Ericson Creek fire that occurred in interior Alaska in summer 2003.

unburned stands were separated by a patch of deciduous vegetation and boulders and by Nome Creek.

Similarly, within the 12 600 ha Tors fire that burned from mid-July through to mid-September 2004, we chose a second pair of burned and unburned north-facing stands in the Granite Tors region (hereinafter referred to as GT; 64°53′N, 146°18.5′W). Burning in this area was extremely patchy, allowing us to identify a burned and an unburned stand adjacent to one another in similar vegetation types and on similar slopes. The NC and GT sites selected for this study were located approximately 55 km apart. Both pairs of sites were characterized by similar vegetation communities, with *S. fuscum* dominating hummocks and feather mosses (primarily *Pleurozium schreberi*) and lichen species in hollows and lawns.

Analysis of satellite hotspot signatures from the MODIS satellite showed that the NC stand burned on 29 June, whereas the GT stand burned on 11 August. Fuel moisture indices based on the weather station data were calculated by the Alaska Fire Service using the Canadian Fire Weather Index (FWI) system (Van Wagner 1987). Three indices were used to assess fuel moisture at the time of the burning of the stands. Two indices are indicative of moisture of the upper fuel layers (e.g., the mosses and upper duff) — the fine fuel moisture code (FFMC) and the duff moisture code (DMC). The drought code (DC) is indicative of moisture in the lower duff. For all these codes, higher values of the index indicate less fuel moisture. Average indices that included the two days before and after the observed burning date were calculated (Table 1).

At both the burned and unburned stands in each of the two study sites, we located a 40 m baseline transect in a homogeneous patch of forest. The baseline was oriented in a random direction and bisected three 30 m transects, one located at the center and two located at random distances in each direction from the center. Sample points were located every 5 m along each 30 m transect (7 sample points per transect) and an additional 4 sample points were located along the baseline (at 5, 15, 25, and 35 m), for a total of 25 sample points per site. The size of the plot was based on comparisons that were made with satellite data (Landsat TM/ETM+ imagery with a 30 m × 30 m pixel size), and the number of organic layer depth samples was based on the need to collect a sufficient number of samples to capture the variability in depth that occurs in these forest types (Kasischke et al. 2008). We sampled each black spruce tree ±1 m of each sample transect and measured its basal diameter. This tally of trees across the three 30 m transects (180 m^2) was used to calculate stand density and mean basal diameter at each site.

At each sample point, we identified ground-layer moss composition, which typically was dominated by *Sphagnum*

Table 1. Summary of stand characteristics and fire weather indices (FWIs) for the Nome Creek (NC) and Granite Tors (GT) intensive study sites.

	Stand characteristics								FWIs		
	Slope (°)		Elevation (m a.s.l.)		Stand density (trees·ha^{-1})		Mean basal diameter (m)				
Site	Unburned	Burned	Unburned	Burned	Unburned	Burned	Unburned	Burned	FFMC	DMC	DC
NC	11	11	705	705	2944	2111	4.0±0.4	8.1±0.8	94 (92)	116 (100)	296 (285)
GT	19	19	420	420	2444	5500	5.3±0.5	5.3±0.4	89 (91)	49 (44.7)	415 (401)

Note: Analysis of MODIS hotspot data showed that the NC stands burned on 24–25 June 2004 and the GT stands burned on 11 August 2004. Fuel moisture indices were calculated for those days using data from the closest remote access weather station to either site (Angel Creek, see fire.ak.blm.gov/predsvcs/fuelfire.php), which was located 17 km from the GT sites and 42 km from the NC sites. We also calculated FWIs for these sites by averaging data generated from the four closest weather stations (which were an average of 56 km from the GT sites and 67 km from the NC sites). Values in parentheses are the averaged indices, based on data from 2 days prior to and 2 days after the days on which the stands burned (27 June – July 1 for the NC site and 9–13 August for the GT site). FFMC, fine fuel moisture code; DMC, duff moisture code; DC, drought code (Van Wagner 1987).

in hummocks and feather moss and (or) lichen species in hollows. In burned stands, partially burned moss stems frequently were used to reconstruct prefire forest floor moss composition. At each sampling point, we also extracted a 20 cm × 20 cm core of all soil organic layers to the top of the mineral soil using a flat-bladed shovel. These cores were used to measure the depth of each organic layer (live and (or) dead moss, and fibric, mesic, and humic soil) following Harden et al. (2004). At each sampling point along two transects, we also extracted soil cores (approximately 20 cm × 20 cm) using a bread knife from the surface moss layer down to mineral soil (14 per plot). Each organic layer was sectioned and placed in Ziploc bags. Samples then were transported back to the laboratory where they were oven-dried at 60 °C to a constant mass for bulk density and homogenized. Organic matter concentrations were determined by mass loss upon ignition at 550 °C for 5 h.

We used analysis of variance models to analyze controls on organic soil depth (cm) and soil organic matter stocks (kg·m^{-2}) using site (NC, GT), burn status (burned, unburned stands), ground-layer fuel type (*Sphagnum* versus feather mosses and (or) lichens), and all interactions among these variables as fixed effects.

Extensive black spruce forest sites

As part of ongoing studies designed to examine landscape and fire weather controls on ground-layer fuel consumption in boreal forests (see, e.g., Kane et al. 2007), we measured residual soil organic layer depths and the percentage of moss cover remaining postfire in 79 black spruce stands that burned during summers 2004 and 2005. Each stand was classified according to primary landscape attributes, including aspect (north, east, west, and south-facing slopes) and landscape position (back slope, flat uplands, flat lowlands). Backslopes are defined as having >5% slope and are situated midway up a hill slope (>1/3 from the bottom and <1/3 from the crest; Schoeneberger et al. 2002). The sites include stands located within 11 separate fire events. These 2 fire years represent the highest and third highest burned areas recorded for Alaska since 1940, and burned 2.72 million ha and 1.76 million ha of land in interior Alaska in 2004 and 2005, respectively.

In each site, the depth of the organic soil layer was measured to the mineral soil along spatial transects as described above. Sampling methods are described in more detail in Kasischke et al. (2008). We also recorded a visual estimate of the moss cover at each site that escaped burning by estimating the percentage of unburned moss within the four 20 m × 20 m subplots located around the center of the 40 m baseline. Post-hoc examination of photographs collected at each site as part of the Composite Burn Index protocol (Key and Benson 2006) revealed that residual moss cover was dominated by *Sphagnum* at most sites. We used a general linear model to analyze landscape position (back slope, flat uplands, flat lowlands), unburned *Sphagnum* abundance, and the interaction between landscape position × unburned *Sphagnum* abundance as controls on residual soil organic layer depth postfire.

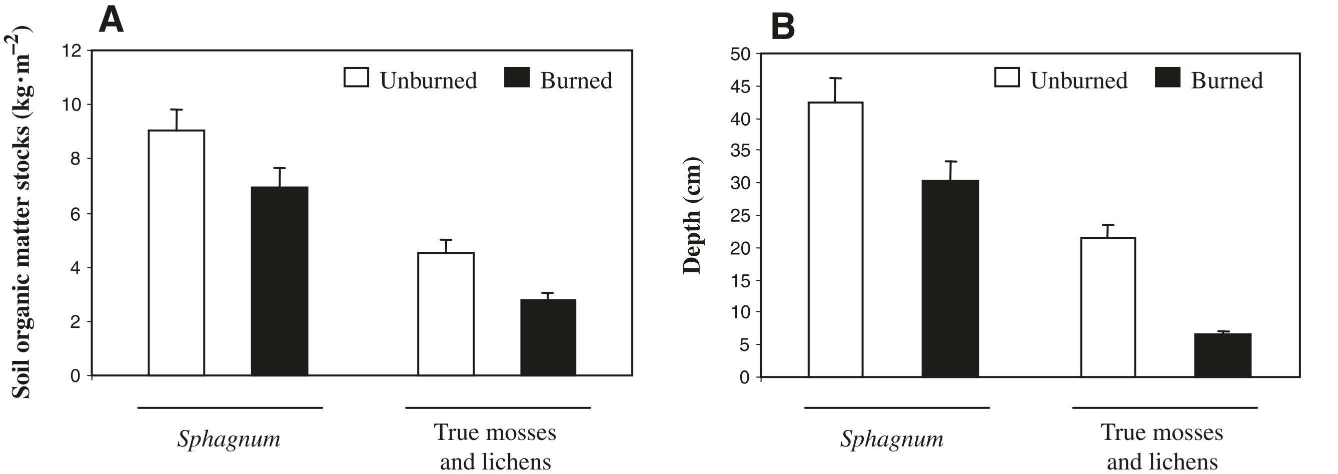
Results

Intensive north-facing black spruce sites

There was little difference in the fuel moistures of the mosses and upper duff layers at the times of the fires in the NC and GT sites, while the deep duffs were likely much drier at the GT site than the NC site, based on the DC (Table 1). Both pairs of stands were characterized by similar slopes and elevations (Table 1). The NC sites had lower stand densities but greater mean basal diameters than the GT sites (Table 1). At the NC sites, the stand density was similar between the burned and unburned stands, but the mean basal diameter was greater at the burned stand (Table 1). At the GT sites, mean basal diameter was similar between the burned and burned stands, while stand density was higher at the burned stand. In the NC burned stand, 100% of the canopy trees were left as standing snags, whereas 77% of the canopy trees were standing as snags at the burned GT stand 1 year postfire.

Organic soil depth varied with burn status (1 df, F = 27.09, p = 0.0001) and surface fuel type (1 df, F = 73.23, p = 0.0001), but did not vary between regions (GT site vs. NC site). Organic soil depth also showed no significant interactions between regions (GT site vs. NC site), burn status (burned vs. unburned stands), and (or) surface fuel type (*Sphagnum* vs. feather moss and (or) lichen). Soil organic matter stocks followed similar trends, with significant differences among burn statuses (1df, F = 12.13, p = 0.0012) and surface fuel type (1df, F = 60.30, p = 0.0001), but no study region effect or interactions among study regions, burn statuses, and (or) surface fuel types. Across

Fig. 2. Organic matter stocks (A) and organic burn depths (B) in burned and unburned north-facing black spruce stands as a function of ground-layer vegetation type, averaged across the Nome Creek and Granite Tors intensive study regions. Values are given as mean + 1 SE.



sites and surface fuel types, organic soil depth in the unburned stands averaged 31 ± 3 cm and contained 6.51 ± 0.61 kg ash-free dry mass organic matter·m^{-2}, whereas organic soil depth in the burned stands averaged 14 ± 3 cm and contained 4.14 ± 0.55 kg ash-free dry mass organic matter·m^{-2} (Fig. 2; all data are means ± 1 SE). Thus, on average, burning reduced organic soil depth by 55% and organic matter stocks by 36% in these stands.

Across study region and burn status, mean organic soil depths and organic matter stocks were 38 ± 3 cm and 8.30 ± 0.57 kg ash-free dry mass organic matter·m^{-2}, respectively, in microsites dominated by *Sphagnum*, whereas mean values for microsites dominated by feather mosses and lichens were 15 ± 2 cm and 3.70 ± 0.32 kg ash-free dry mass organic matter·m^{-2}, respectively (Fig. 2). Thus, microsites dominated by *Sphagnum* had more than twofold greater soil organic matter stocks than microsites dominated by other ground-layer vegetation.

Across sites, unburned microsites dominated by *Sphagnum* species were associated with 42.5 ± 3.6 cm mean organic soil depth and mean soil organic stocks of 9.06 ± 0.73 kg ash-free dry mass organic matter·m^{-2}, whereas burned microsites dominated by *Sphagnum* species were associated with 30.3 ± 3.1 cm mean organic soil depth and mean soil organic stocks of 6.92 ± 0.70 kg ash-free dry mass organic matter·m^{-2}. Unburned microsites dominated by feather mosses and (or) lichen species had mean organic soil depths and organic matter stocks of 21.5 ± 2.1 cm and 4.51 ± 0.46 kg ash-free dry mass organic matter·m^{-2}, respectively. Burned microsites dominated by feather mosses and (or) lichen species had mean organic soil depths and organic matter stocks of 6.5 ± 0.6 cm mean organic soil depth and mean soil organic stocks of 2.75 ± 0.26 kg ash-free dry mass organic matter·m^{-2}, respectively. Thus, using this paired site approach, burning in the *Sphagnum* microsites reduced organic soil depths and organic matter stocks by 23% and 22%, respectively (Fig. 3), whereas burning in microsites dominated by feather mosses and (or) lichen species reduced the depth of organic soil layers by 65% and total soil organic matter stocks by 44% (Fig. 3).

Extensive black spruce forest sites

All of the extensive sites burned between mid-June and the end of August 2004, with the exception of three sites that burned in late June and early July 2005. Of the 79 stands included in our extensive site data set, 34 burned in June 2004, 20 burned in July 2004, and 22 burned in August 2004. Throughout the summer of 2004, precipitation levels were less than half the long-term average (50 year means) in interior Alaska, whereas during summer 2005 they were 2/3 of the long-term normal (climate records from www.wrcc.dri.edu/summary/climsmak.html). Based on data from six remote access weather stations (RAWS), the average FFMC remained relatively constant throughout the summer, except for a period during late July and early August when scattered showers occurred across the region (Fig. 4). The DMC rose in mid-June and early July and remained high (mean = 98) until the period of rain at the end of July. At the end of the rainy period, the DMC rose continuously throughout August (Fig. 4). Because it is based on cumulative data from the previous 52 days, DC experienced less day-to-day fluctuation than either the FFMC or the DMC and rose continuously throughout the study period (Fig. 4). Indices for the three stands that burned in the 2005 fires were based on data collected from the Hodzana RAWS. Between mid-June and early July, mean FFMC was 88, mean DMC was 84, and mean DC was 275, values which were similar to those observed in 2004 for the same time periods (Fig. 1).

Across all of the extensive burned black spruce forest stands, a model including (*i*) the abundance of unburned moss, which was dominated by *Sphagnum* in most stands; (*ii*) landscape position; and (*iii*) the interaction between unburned *Sphagnum* abundance and landscape position explained about 60% of site-averaged organic soil layer depth (Table 2). We used separate regression models for data within each landscape position to further explore the interaction between unburned *Sphagnum* abundance and landscape position. The abundance of unburned *Sphagnum* was a significant predictor of site-averaged organic soil depth in back slope and flat wetland sites, but had no relationship

Fig. 3. Percent reduction of organic soil depths (A) and soil organic matter stocks (B) during wildfire in microsites dominated by *Sphagnum* compared with microsites dominated by true moss and (or) lichens, averaged across the NC and GT intensive study sites (Table 1). Values are given as mean + 1 SE.

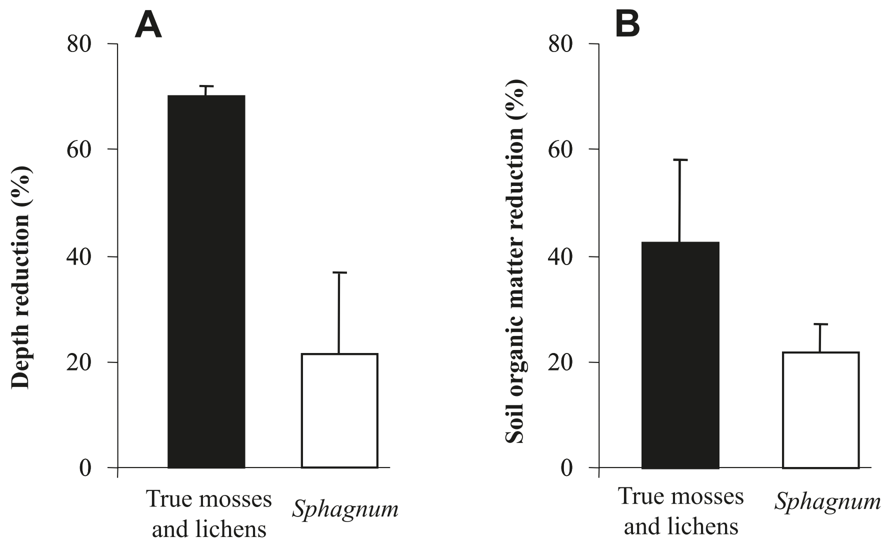
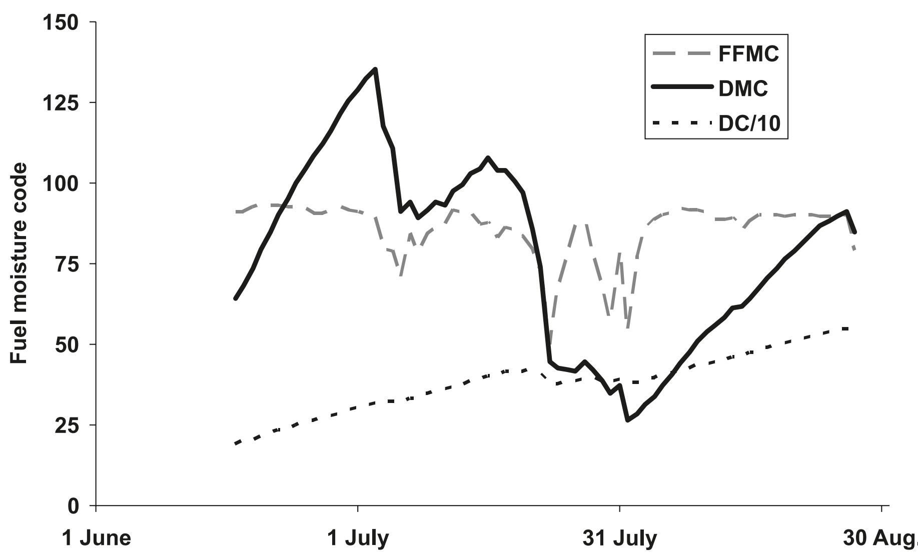


Fig. 4. Fuel moisture codes (Van Wagner 1987) from the 2004 fire season calculated from six weather stations in interior Alaska situated in the vicinity of our extensive black spruce sites that burned in 2004. FFMC, fine fuel moisture code; DMC, duff moisture code; DC, drought code.



with average organic soil depth in flat upland stands (Fig. 5).

Discussion

Sphagnum is a dominant component of ground-layer vegetation in interior Alaskan peatlands and mesic black spruce forests, where some dominant *Sphagnum* species such as *S. fuscum* form hummocks or areas of elevated microtopography. Feather moss species and lichens often dominate lawn (flat areas) and (or) hollow microtopographic positions in these continental sites. Even though hummocks are elevated above other ground-layer fuel types and thus are farther from the water table, soil moisture can be much wetter in *Sphagnum*-dominated hummocks than in hollows, owing to the wicking abilities and water retention traits of the dominant hummock-forming species (Rydin and McDonald 1985).

In our unburned stands, areas dominated by *Sphagnum* had more than twice as much organic matter as did areas dominated by other ground-layer vegetation (Fig. 2). *Sphagnum* mosses typically are associated with slow decomposition rates, due to their formation of recalcitrant tissue that inhibits microbial activity (reviewed in Van Breemen 1995; Turetsky 2003). This biochemical control often is regarded as being critical to the accumulation of peat in many types of boreal peatlands. However, the strong water retention characteristics of some *Sphagnum* species that allow them to serve as drought avoiders and survive well above the water table (Rydin and McDonald 1985) also appear to protect *Sphagnum*-derived organic matter from consumption during wildfire (Benscoter and Wieder 2003). Our results

Table 2. Results of a general linear model predicting site-averaged organic soil layer depths in 80 burned black spruce stands across interior Alaska ($p < 0.0001$, $F = 17.59$; model df = 5; model SS 1761.7; $R^2 = 0.59$).

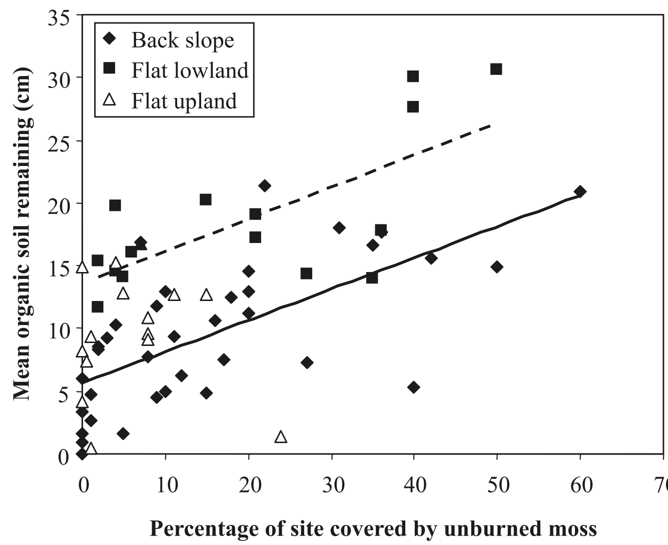
	df	SS	*F*	*p*
Unburned moss	1	328.73	16.41	0.0001
Landscape class	2	303.34	7.57	0.0012
Unburned moss × landscape class	2	124.20	3.10	0.0522
Model	5	1761.72	17.59	<0.0001
Error	61	1222.20	—	—

show that rates of forest floor organic matter consumption were considerably lower in microsites dominated by *Sphagnum,* which had 20% forest floor organic matter reduction on average, compared with microsites dominated by feather mosses and (or) lichens, which had 45% forest floor organic matter consumption during the same fire events (Fig. 3).

In our intensive paired burned and unburned data set, there was no significant interaction between fuel type and burn status, which suggests that high *Sphagnum* cover was associated with thicker organic soils that contained more organic matter than other ground-layer vegetation both before and after fire. Thus, it is possible that much of the within-site variability in soil carbon storage in these ecosystems can be explained by ground-layer distributions and fuel consumption patterns that likely persist over multiple fire cycles. Harden et al. (2006) also concluded that interactions between water retention (via vegetation or underlying mineral soil characteristics), soil climate, and consumption during fire likely perpetuate spatial variation in organic soil layers in boreal ecosystems through repeated fire cycles.

Following burn activity in mesic and more poorly drained black spruce stands, *Sphagnum* hummocks can be the dominant fuel type remaining on the landscape, forming *Sphagnum* sheep that can be easily detected even from a distance (Fig. 5). We quantified the abundance of unburned *Sphagnum* remaining after fire in 79 black spruce stands in Alaska to determine whether the abundance of unburned *Sphagnum* was a significant predictor of site-averaged postfire organic layer depths. *Sphagnum* abundance, landscape position class, and the interaction between these two variables cumulatively explained 60% of residual organic soil depth across these sites. We suggest that additional variation in organic soil depth could be explained with species-specific moss distribution data, though that was beyond the original intent of this study. To investigate the interaction between unburned *Sphagnum* and landscape position, we analyzed the relationship between unburned moss abundance and postfire organic soil depths separately for each landscape position class. There was no relationship between these variables in flat upland stands, which tended to have both low *Sphagnum* cover and postfire organic soil depths. Flat upland stands are drier than our other landscape classes, and thus tend not to accumulate thick duff and organic soils. However, the dry ground-layer fuels in these stands (in part due to low *Sphagnum* cover) can also burn completely, exposing mineral soil. In contrast, the abundance of *Sphagnum* sheep alone explained 30% and 50% of the variability in site-averaged organic soil depths in back slope and flat lowland stands, respectively. The flat lowland stands both had larger areas of postfire unburned *Sphagnum* and thicker organic soils remaining compared with back slope stands (Fig. 5). This is not surprising, given that these lowland stands not only tend to correspond to wetter soil environments that likely started with more *Sphagnum* cover, but also may have experienced less severe burning than the back slope stands (Kane et al. 2007). Given that that the abundance of unburned *Sphagnum* served as a significant predictor of organic soil depths postfire across the backslope and flat lowland stands, we suggest that *Sphagnum* sheep could serve as a useful visual indicator of variability in postfire organic matter stocks in black spruce ecosystems that contain thick forest floor organic layers (Fig. 5).

Fig. 5. Effect of unburned moss abundance on site-averaged organic soil layer depth across 80 burned black spruce stands in interior Alaska. Data are separated by three landscape position classes (back slope, flat lowland, flat upland) to investigate the interaction between moss abundance and landscape position (Table 2). No model result is given for flat uplands ($p > 0.05$, $n = 16$). The solid line depicts the relationship for back slope sites (slope = 0.20 ± 0.05, intercept = 7.76 ± 1.32, $R^2 = 0.35$, $p = 0.001$, $n = 47$). The broken line indicates the relationship for flat lowland sites (slope = 0.26 ± 0.07, intercept = 13.57 ± 1.85, $R^2 = 0.50$, $p = 0.003$, $n = 16$).



Sphagnum mosses are widely recognized as ecosystem engineers for their important controls on decomposition, cation exchange, and peat accumulation in boreal ecosystems. Here, however, we argue that these species also serve as important ecosystem engineers for their strong water retention traits that control patterns of fuel consumption, thereby influencing variability in soil organic matter stocks in boreal forests that likely persists over multiple fire rotations. The loss of key *Sphagnum* species, for example under future climate regimes that involve severe drought, may have large implications for fire behavior and organic matter stocks in boreal soils.

Acknowledgements

We thank Elizabeth Hoy, Evan Ellicott, Nancy French, Lucas Spaete, Sam Upton, and Claire Treat for assistance in the field. We also thank Dale Vitt for inventing the term *Sphagnum* sheep and Brian Benscoter, Dan Thompson, and Mike Waddington for insightful discussions on *Sphagnum* traits in relation to fire ecology. This research was supported by a NASA grant (NNG04GD25G) to E. Kasischke and M. Turetsky and the Bonanza Creek Long-Term Ecological Research Program, which is supported by the USDA Forest Service (PNW01-JV11261952–231) and the National Science Foundation (NSF; DEB-00 80609).

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