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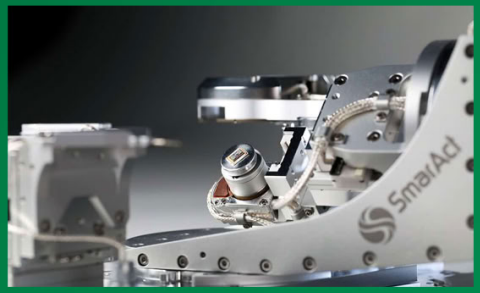
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Edaphic and microclimatic controls over permafrost response to fire in interior Alaska

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Abstract
Discontinuous permafrost in the North American boreal forest is strongly influenced by the effects of ecological succession on the accumulation of surface organic matter, making permafrost vulnerable to degradation resulting from fire disturbance. To assess factors affecting permafrost degradation after wildfire, we compared vegetation composition and soil properties between recently burned and unburned sites across three soil landscapes (rocky uplands, silty uplands, and sandy lowlands) situated within the Yukon Flats and Yukon-Tanana Uplands in interior Alaska. Mean annual air temperatures at our study sites from 2011 to 2012 were relatively cold (−5.5 °C) and favorable to permafrost formation. Burning of mature evergreen forests with thick moss covers caused replacement by colonizing species in severely burned areas and recovery of pre-fire understory vegetation in moderately burned areas. Surface organic layer thickness strongly affected thermal regimes and thaw depths. On average, fire caused a five-fold decrease in mean surface organic layer thickness, a doubling of water storage in the active layer, a doubling of thaw depth, an increase in soil temperature at the surface (−0.6 to +2.1 °C) and at 1 m depth (−1.7 to +0.4 °C), and a two-fold increase in net soil heat input. Degradation of the upper permafrost occurred at all burned sites, but differences in soil texture and moisture among soil landscapes allowed permafrost to persist beneath the active layer in the silty uplands, whereas a talik of unknown depth developed in the rocky uplands and a thin talik developed in the sandy lowlands. A changing climate and fire regime would undoubtedly influence permafrost in the boreal forest, but the patterns of degradation or stabilization would vary considerably across the discontinuous permafrost zone due to differences in microclimate, successional patterns, and soil characteristics.

Keywords: permafrost, fire, boreal forest

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1. Introduction

North American boreal forests are largely underlain by discontinuous permafrost. Because permafrost temperature in

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this zone is typically within a few degrees of thawing, it is potentially vulnerable to degradation due to changes in climate or surface disturbance (Osterkamp and Romanovsky 1999, Grosse *et al* 2011). Ecological succession is a strong negative feedback to permafrost degradation (Shur and Jorgenson 2007, Jorgenson *et al* 2010). With the development of evergreen stands with moss understories, surface organic material accumulates and soil moisture increases, creating cold subsurface conditions which support permafrost despite relatively warm air temperatures (Van Cleve and Viereck 1981, Osterkamp and Romanovsky 1999, Johnstone *et al* 2010a). Fire influences the surface energy balance primarily through the combustion of the insulating organic layer, so the response of permafrost to fire is mediated by fire severity (Yoshikawa *et al* 2003). High-severity fires which combust much of the insulating organic layer can increase soil heat flux and cause rapid permafrost degradation (Mackay 1995, Burn 1998, Yoshikawa *et al* 2003, Viereck *et al* 2008, Jiang *et al* 2012). If permafrost thaws beyond the depth of seasonal freezing, a perennially unfrozen layer, or talik, forms above the permafrost table. This talik decouples permafrost from the atmosphere and could continue to develop vertically and laterally over the long term (Osterkamp and Burn 2003, Yoshikawa *et al* 2003). However, degradation could be halted through the recovery of vegetation and the surface organic layer (Mackay 1995, Viereck *et al* 2008, Yi *et al* 2010). Fire severity also mediates the patterns of plant succession, and therefore, the recovery of the surface organic layer and the stabilization of permafrost (Shur and Jorgenson 2007, Viereck *et al* 2008, Johnstone *et al* 2010b, Shenoy *et al* 2011).

Changes in the fire regime, particularly coupled with a warming climate, can impact the distribution of permafrost by controlling the characteristics of the surface organic layer, both directly through combustion and indirectly through plant succession. There is evidence of climatically induced intensification of the fire regime in the North American boreal forest, with increased extent, frequency, and severity of fires, changes which would be expected to be unfavorable to permafrost stability in the marginal climates of the discontinuous permafrost zone (Gillett *et al* 2004, Kasischke and Turetsky 2006, Kasischke *et al* 2010, Johnstone *et al* 2010a, Barrett *et al* 2011). Permafrost degradation impacts hydrology, vegetation, and ecosystem processes which could feedback to influence climate through changes in carbon cycling; therefore, the response of permafrost to fire disturbance could have local, regional, and global-scale implications (Jorgenson *et al* 2010, Grosse *et al* 2011, O'Donnell *et al* 2011, Yuan *et al* 2012). The patterns of resilience or vulnerability of permafrost to the widespread disturbance of fire, though, are likely to differ across the discontinuous permafrost zone depending on numerous site factors that influence soil heat flux.

Variations in microclimate, soils, and vegetation create a wide range of thermal conditions that may modify the permafrost response to fire across the discontinuous permafrost zone. Air temperature and snowfall are important climatic controls on permafrost which vary regionally and topographically (Osterkamp and Romanovsky 1999, Jorgenson *et al* 2010). Soil texture and topography influence soil moisture and ice content, factors which strongly control heat flow through the ground (Shur and Jorgenson 2007). Soil moisture is of particular importance to soil thermal regimes in cold climates largely because the thermal conductivity of ice is four-fold greater than the conductivity of liquid water. Thus, the seasonal variation in the thermal conductivity of moist soils reduces heat conduction into the ground in summer, but enhances heat loss in winter, thereby typically creating colder soil conditions in fine-textured soils with high water-holding capacities (Williams and Smith 1991). The impermeability of the permafrost surface also contributes to high soil moisture in areas with a thin active layer (Woo *et al* 2008). The effects of permafrost thaw on soil moisture are likely dependent on the underlying soil texture (Jorgenson and Osterkamp 2005). For example, on slopes less susceptible to water impoundment with surface subsidence, the deepening of the active layer into coarse-textured soils would be expected to improve drainage, whereas drainage in fine-textured soils may be less affected by the change in thaw depth. By mediating the soil moisture regime after post-fire permafrost thaw, surficial geology may control the long-term stability of permafrost. Furthermore, the rate of thaw and resilience of permafrost is influenced by ice content (Jorgenson *et al* 2010). Permafrost with low ice content would be expected to thaw more rapidly after fire than permafrost with high ice content, due to differences in latent heat required for thawing. The focus of this research was to test how these edaphic factors influence the vulnerability of permafrost to degradation as a result of fire disturbance.

We examined the patterns of post-fire permafrost degradation in the discontinuous permafrost zone of the interior Alaskan boreal forest, a region with a continental climate and widespread fire disturbance. We compared recently burned and unburned evergreen stands across three soil landscapes (rocky uplands, silty uplands, and sandy lowlands). We examined how the permafrost response to fire, in terms of soil thermal regimes, moisture, and thaw depths, was mediated by vegetation, soil characteristics, and climate. The specific objectives of this study were to: (1) characterize the variation in vegetation composition and surface organic layer thickness in relation to soil properties, succession, and fire; (2) compare soil thermal regimes, moisture regimes, and thaw depths of burned and unburned stands across soil landscapes; and (3) monitor changes in active-layer depth and thaw settlement in ice-rich silty uplands under different disturbance regimes.

2. Methods

2.1. Study area and sampling design

The study area is within the interior Alaskan boreal forest, a region which is bounded by the Brooks Range to the north and the Alaska Range to the south (figure 1). The region is underlain by discontinuous permafrost and is characterized by a continental climate, with low precipitation and wide variation in air temperatures (figure 1, table 1). In interior Alaska, from 1971 to 2000, mean annual air temperature was

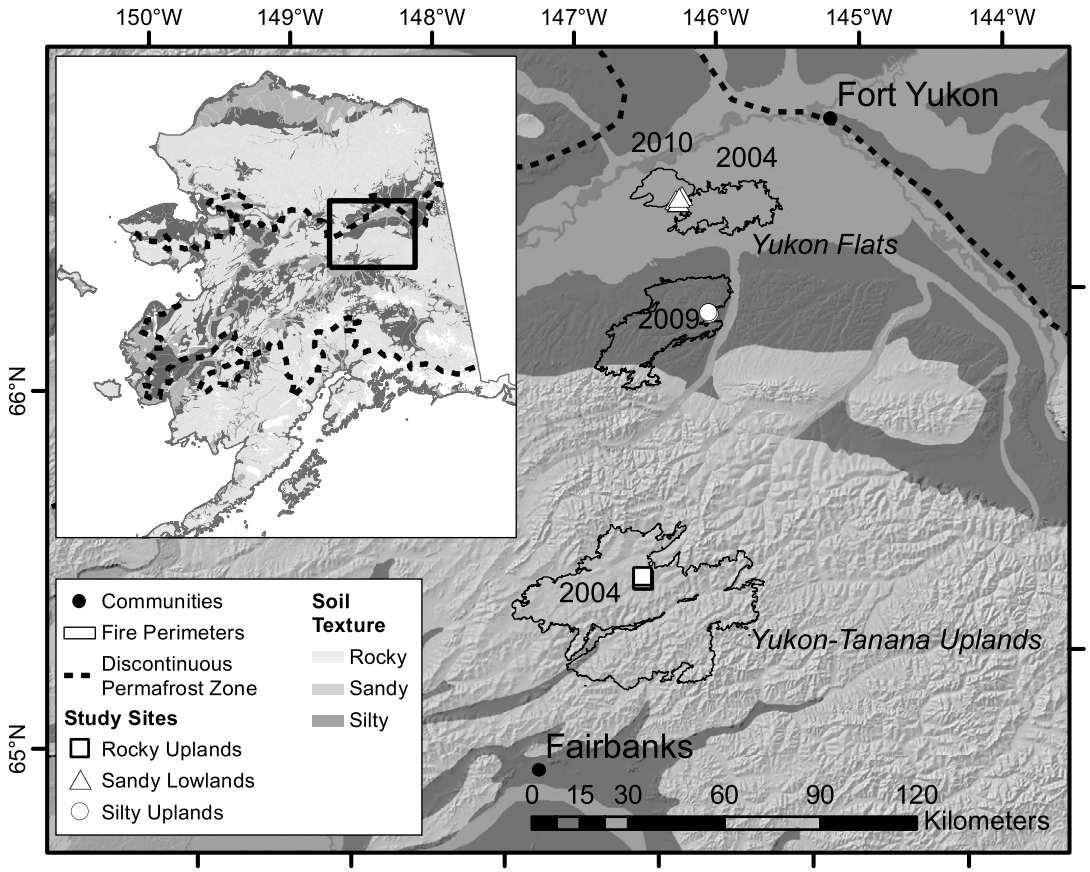


Figure 1. Topographic map of study area in interior Alaska. Dominant mineral soil textures are mapped with gray-scale symbology based on Karlstrom (1964) and Jorgenson *et al* (2008). The northern and southern boundaries of the discontinuous permafrost zone, from Jorgenson *et al* (2008), are represented with dashed lines. Study sites ($n = 18$) are indicated by open squares (rocky uplands), triangles (sandy lowlands), and circles (silty uplands). Fire perimeters and year of burn are shown for the recent fires studied.

Table 1. Characteristics of each landscape type, including region, mean elevation, mean annual air temperature (MAAT), air freezing degree days (FDD), air thawing degree days (TDD), and freezing *n*-factor (ratio of soil surface FDD to air FDD). The *n*-factor values are the least square means ±SE from a Tukey HSD post hoc test conducted after a significant effect of landscape type was found with a two-way ANOVA ($p = 0.01$); significant differences between means are denoted by different letters.

Landscape type	Region	Elevation (m)	MAAT (°C)	Air FDD	Air TDD	*n*-factor
Rocky uplands	Yukon-Tanana Uplands	604	−5.3	3437	1518	0.1 ± 0.0 *A*
Silty uplands	Yukon Flats	249	−6.1	4018	1780	0.3 ± 0.0 *B*
Sandy lowlands	Yukon Flats	123	−5.2	3904	1997	0.3 ± 0.0 *B*

−3.7 °C and mean annual precipitation was 323 mm (Alaska Climate Research Center 2013).

Our study focused on three soil landscapes: rocky uplands, silty uplands, and sandy lowlands, which respectively comprise approximately 30%, 5%, and 5% of the boreal region of Alaska (Karlstrom 1964, Jorgenson *et al* 2008) (figure 1, table 1). Within each landscape, we established three 'unburned' sites in mature evergreen forests (*Picea mariana* or *Picea glauca*), and three recently burned sites. Sites were selected using targeted sampling to establish plots in large homogeneous patches. Accessibility by floatplane or road was also considered in site selection. The range of variation in vegetation, fire severity, and soil characteristics that we captured was limited by the small sample size.

The rocky upland sites were located in the White Mountains National Recreation Area in the Yukon-Tanana Uplands ecoregion (∼600 m elevation). The colluvial substrate was dominated by channery rocks with fine-textured silt loams. The unburned rocky upland landscape had an ice-rich intermediate layer of permafrost just below the active layer ranging from 0.2 to 1.5 m thick, and was underlain by ice-poor permafrost. The burned rocky upland sites were affected by the 2004 Boundary Fire. The silty upland and sandy lowland study sites were located in the Yukon Flats National Wildlife Refuge, in a region with particularly strong variation in seasonal temperatures and low annual precipitation (∼170 mm) (Gallant *et al* 1995). The burned silty upland sites were affected by the 2009 Big Creek Fire. The silty upland sites (∼250 m elevation) were situated on hilly loess deposits. Yedoma deposits such as these were formed by ice-rich syngenetically frozen silt with massive ice wedges in areas that were unglaciated during

the late Pleistocene. In interior Alaska, large areas underlain by yedoma have been affected by thermokarst and thermal erosion during the Holocene, which resulted in formation of an ice-poor layer of thawed and refrozen soils up to 4 m thick on top of yedoma sections (Péwé 1975, Kanevskiy *et al* 2012). Our unburned silty upland sites had an ice-rich intermediate layer of permafrost approximately 0.6 m thick, underlain by a 2–3 m ice-poor layer, which was just above the extremely ice-rich yedoma. The sandy lowlands sites (∼100 m elevation) had a thin eolian loess cap (0.5–2.5 m) over an eolian sand sheet underlain by fluvial gravel and were ice-poor. The fire-affected sites burned in the 2004 Lower Mouth Fire and the 2010 Canvasback Lake Fire.

2.2. Data collection and analysis

Field sampling was conducted from 2009 to 2012. Air temperatures were recorded at one site within each landscape type. Two-channel dataloggers (HoboProV2, Onset Corp.) were installed at each study site to measure soil temperatures at the ground surface (5 cm) and at depth (100 cm). Temperatures were recorded at two-hour intervals and mean monthly air temperatures, mean annual air temperatures (MAAT), mean annual surface temperatures (MAST), and mean annual deep temperatures (MADT) were calculated. Thawing degree days (TDD) and freezing degree days (FDD) were the absolute value of the sum of the daily temperatures above and below 0 °C, respectively, for a one-year period. Freezing *n*-factors, i.e., the ratio of ground surface FDD to air FDD, were used to assess winter soil surface temperatures relative to local air temperatures to infer surface boundary effects and snow depth (Lunardini 1978). The temperature measurements reported were from the period 1 September 2011 to 31 August 2012. Note that surface temperature data were missing from two sites (in unburned silty uplands and unburned sandy lowlands) due to sensor failure and frost heave.

Soils were sampled near each soil temperature datalogger. Thaw depths were measured with a metal probe in late-August to mid-September. Minimum thaw depths were used for two of the burned sites due to the difficulty of accurately probing the rocky soils. Soil stratigraphy was described according to the methods of the Natural Resources Conservation Service. Soil pH and electrical conductivity were measured with hand-held meters in the field (PCTestr 35, Oakton) and values at 10 cm depth were used for site values. Soil samples were taken for bulk density and volumetric soil moisture, based on wet and oven-dried (60 °C) weights. Water storage (equivalent depth) was calculated as the total water content in the active layer or seasonally frozen layer. The net heat input into the active layer during the thaw season was estimated as the sum of latent and sensible heat in mid-August, based on moisture contents, mineral and organic soil fractions, and temperature gradients of the active layer (Jorgenson 1986). Landscape-level means and results of statistical tests that are reported for the above variables were from the 2012 field data.

Per cent cover of each plant species was estimated through point-sampling a 100-point grid within a 5 m × 10 m plot at each site. Species that were present but not captured by the point-sampling were recorded as having trace (0.1%) cover. Vegetation analysis was conducted with a multivariate ordination technique, nonmetric multidimensional scaling (NMDS), using PC-ORD 6.0 (McCune and Grace 2002, McCune and Mefford 2011). Ordination is used as a method of data reduction in which the dominant patterns of the variation in species composition are extracted into few continuous synthetic variables, the ordination axes. After the ordination of plant community data, correlation analyses of the axis scores with species and environmental data were conducted and presented as biplots, in which vectors represent the strength and direction of the correlations. NMDS is an iterative process that finds a low-dimensional representation of the dissimilarity matrix of sample units (sites) while preserving the ranking of distances. Distances between points in the ordination diagram approximate the dissimilarity of vegetation between sites. Species and environmental data were assessed for normality and were transformed as needed prior to ordination analysis.

Two 100–200 m transects were established in the silty uplands area with different fire disturbance histories to monitor annual changes in the permafrost table and thaw settlement through differential leveling and thaw probing (Viereck *et al* 2008, Osterkamp *et al* 2009). The intensive soil and vegetation monitoring sites for the silty uplands described above were located along these transects. Relative elevations were determined using differential leveling at 1 m intervals, and were tied to GPS-derived benchmark elevations to calculate absolute elevations of the ground surface. Thaw depths were measured at the same points and were subtracted from the surface elevations to determine the elevations of the permafrost table. Sampling dates were: 1–2 September 2009; 3–4 September 2010; 17–18 September 2011; and 7–8 September 2012. Note that initial sampling at the 2009 fire occurred the year following the fire. Changes were analyzed only from 2010 to 2012, the years with complete datasets across both transects.

Two-factor ANOVAs (JMP 10.0.0, SAS 2012) were conducted to determine the effects of landscape type, fire disturbance, and interactive effects on surface organic layer thickness, soil moisture, active-layer water storage, thaw depth, and net heat input. Diagnostic plots of residuals were used to assess normality and homoscedasticity. One outlier, a burned site in the rocky uplands with anomalously low fire severity, was removed from ANOVA analyses and the reported landscape-level means. Least square means differences were calculated using post hoc tests; Tukey HSD for multiple comparisons, and student's *t*-tests for pairs. Linear regression was used to examine relationships between surface organic thickness, thaw depth, and soil moisture. Shapiro–Wilk tests confirmed normal sampling distributions for these variables. Statistical significance was considered with $p < 0.05$. We used only the 2012 data for these analyses, which had a complete set of data across all sites. All datasets associated with this study are archived under the dataset title prefix 'Yukon River Basin Fire and Permafrost' at www.lter.uaf.edu/data_b.cfm.

3. Results and discussion

To evaluate factors controlling permafrost degradation after fire in the discontinuous permafrost zone, we compared ecological and thermal characteristics in burned and unburned forest stands among three soil landscapes in interior Alaska. Rocky upland, silty upland, and sandy lowland landscapes differed in terms of substrate and fire history (timing and severity), factors which influenced vegetation composition and its co-varying soil characteristics, such as surface organic layer thickness, thaw depth, and soil moisture. Fire, vegetation, soil, and topography interacted with climate to create varied soil moisture and thermal regimes and thaw depths that affect the stability of permafrost. Below we describe in detail the ecological, thermal, and physical patterns we observed and discuss the factors influencing permafrost.

3.1. Ecological patterns

The ordination shows the variation in plant community composition along gradients associated with edaphic characteristics and fire disturbance (figure 2). The points depicted in the ordination represent the community structure at each site, and the direction and length of the vectors indicate the direction and strength of the correlations of community composition with species cover (figure 2(a)) and environmental characteristics (figure 2(b)). The distance between points signifies the degree of dissimilarity in community composition among sites. The ordination axes were rotated by the treatment variable (fire) to differentiate the effects of fire on species composition from other sources of variation. Therefore, the effects of fire on vegetation were most pronounced along Axis 1, which accounts for most of the variation in community composition (54%). The unburned and burned sites of each soil landscape were clearly separated along this gradient, and the gradient was correlated with fire-related changes, such as decreased vegetation cover, increased cover of bare mineral soil, decreased surface organic layer thickness, increased thaw depth, and deep soil temperature (figures 2(a) and (b)). The increase of bare ground along Axis 1 was accompanied by increased cover of colonizing species that thrive on exposed mineral soils after fire (*Marchantia polymorpha, Ceratodon purpureus, Epilobium angustifolium, Populus tremuloides*) (figure 2(a)). Given the relationship between Axis 1 and fire, the distance between the unburned and burned sites along Axis 1 suggests the magnitude of change in community composition after fire. Axis 2 represents 39% of the variation in plant community structure. The clustering of the unburned sites by landscape type along this axis and the strong correlations between this axis and plant species found primarily in the unburned stands suggest that the variation along Axis 2 mainly reflects the differences in long-term successional patterns of the mature stands between landscape types (figure 2(a)). Additionally, Axis 2 was correlated with a number of soil characteristics (organic layer thickness, moisture, pH, electrical conductivity, thaw depth) (figure 2(b)), which reflect a combination of the underlying environmental characteristics and the influence of vegetation on soils.

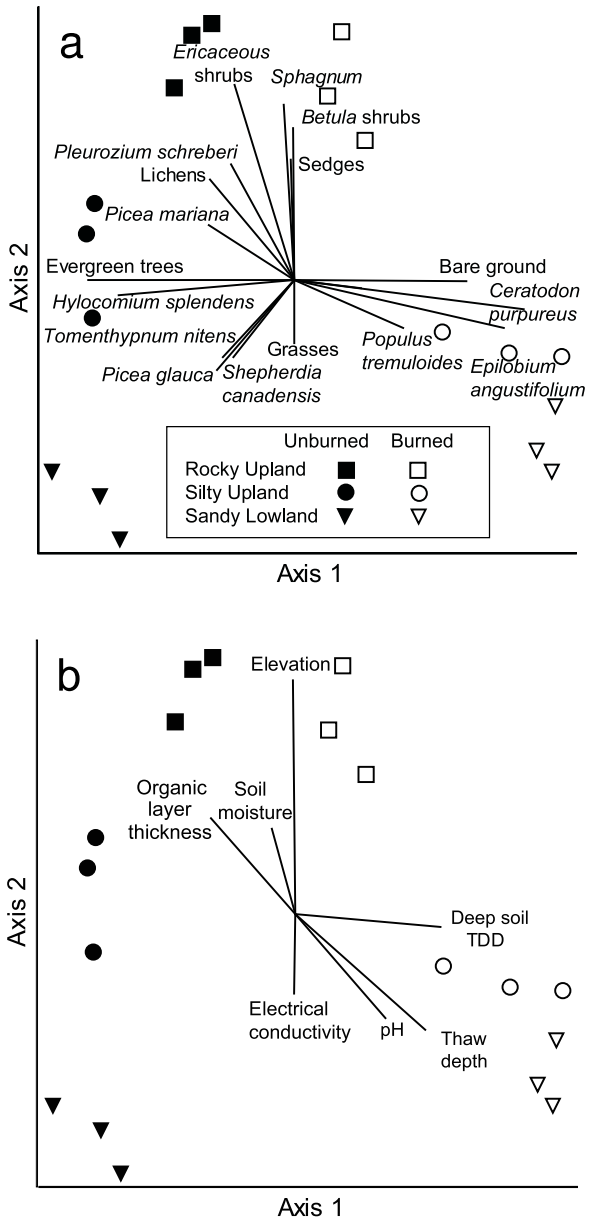


Figure 2. Nonmetric multidimensional scaling (NMDS) ordination of plant community structure and correlations with selected vegetation characteristics (a) and environmental characteristics (b). Points represent community structure at each site, and symbols differentiate between landscape types and treatment. Vectors show the direction and strength of the correlations. The ordination axes were rotated by the treatment variable (fire). The ordination axes represented 93% of the total variance in community structure, with 54% accounted for by Axis 1 and 39% by Axis 2.

The burned and unburned sites of the rocky landscape were clustered along Axis 1, revealing relatively similar community composition before and after the 2004 fire, and suggesting greater survival of pre-fire vegetation and/or greater post-fire recovery. The evergreen canopy (*Picea mariana*) was destroyed and colonizers had invaded, but overall the understory vegetation appeared to be recovering

towards pre-fire conditions, increasing the likelihood of permafrost recovery (Viereck *et al* 2008). At two of the burned sites, residual surface organic layer thicknesses were reduced to 4–9 cm. At one tussock-dominated site, fire severity was low, leaving 35 cm of organic material. The unburned sites in the rocky uplands were differentiated from others by the abundance of acidifying *Sphagnum* mosses (mainly *S. fuscum*), acidophilic dwarf birch and ericaceous shrubs, and were associated with strongly acidic soils, thick organic layers, high soil moisture, and shallow active layers (figures 2(a) and (b)).

The sandy lowland sites were affected by severe fires in both 2004 and 2010. Less than 2 cm of surface organic material remained after the first fire. The second fire combusted the remaining organic layer and exposed bare mineral soil over much of the spatial extent of the fire. The magnitude of the effects of the high-severity fire on vegetation in the lowlands was apparent in the wide separation between burned and unburned sites along Axis 1 (figure 2(a)). The above-ground portions of pre-existing vegetation were virtually all consumed, and cover of mineral soil colonizers increased. The high abundance of *Populus tremuloides* seedlings after fire in these sites suggests a shift to deciduous successional trajectory, which would be expected to postpone the development of a thick moss layer that facilitates permafrost recovery (Viereck *et al* 2008, Johnstone *et al* 2010a). The unburned sandy lowlands had distinct plant species assemblages, which were likely influenced by the alkaline soils and relatively low soil moisture (20 vol%), as suggested by the correlation of Axis 2 with these environmental variables (figure 2(b)) and with several indicator species described below (figure 2(a)). We attribute the low soil moisture to the arid climate and to the good drainage due to the deep active layer and underlying sandy soils. The active layer of these soils was thick even in the unburned sites (∼100 cm). In contrast to the other areas where late successional forests were dominated by *Picea mariana*, the unburned evergreen sites were dominated by *Picea glauca*, a species which tends to occupy well-drained soils. *Tomenthypnum nitens*, a common feathermoss indicative of calcareous soils, occurred exclusively in these sites. The calciphilic shrub *Shepherdia canadensis* was common, whereas *Sphagnum* and ericaceous shrubs were notably absent. The surface organic layer was about 15 cm thick and dominated by feathermosses.

In the silty uplands, the 2009 fire reduced surface organic layer thicknesses from 14 to 7 cm on average, and caused a large shift in vegetation, with colonizers establishing on mineral soils and the regrowth of willow species (figure 2(a)). The exposure of mineral soils and recruitment of deciduous seedlings (*Populus tremuloides*) suggest a shift towards a deciduous successional trajectory. The unburned vegetation was characterized by a high density of *Picea mariana* trees, abundant ericaceous shrubs, and a feathermoss-dominated moss layer. The silt loam soils were weakly acidic, had a moderately thick organic layer and a shallow active layer, and were saturated at depth.

Low-severity fires in which a thick surface organic layer remains typically result in the re-establishment of pre-existing vegetation (Johnstone *et al* 2010b). Many of the dominant species in boreal spruce forest understories are able to resprout after a low-severity fire, thereby speeding the recovery of the pre-fire vegetation (Johnstone *et al* 2010a, Bernhardt *et al* 2011, Hollingsworth *et al* 2013). Further, the low albedo and high porosity of the charred organic surface create dry conditions unfavorable for the establishment of small-seeded deciduous tree species, which typically have greater success on the moist seedbeds of mineral soils (Johnstone and Chapin 2006). The larger seeds of evergreen trees have greater carbohydrate reserves, which allow rapid root growth and thus a greater ability to access the scarce soil moisture in burned organic seedbeds (Greene and Johnson 1999). The variation in these plant traits helps explain why low-severity fires perpetuate self-replacement and high-severity fires are associated with a shift in the successional trajectory towards deciduous dominance. Deciduous stands are characterized by relatively high rates of evapotranspiration, high litterfall, rapid nutrient cycling, thin organic layers, and limited moss development, factors which contribute to high soil temperatures, low soil moisture, and the absence of, or greater depths to, permafrost (Van Cleve and Viereck 1981, Flanagan and Van Cleve 1983, Johnstone *et al* 2010a). By contrast, evergreen stands are associated with low litterfall, moss understories, slow rates of decomposition, and the subsequent accumulation of thick organic layers, which insulate soils and reduce heat input.

3.2. Moisture and thermal regimes

Fire disturbance and landscape type each had significant effects on a wide range of soil properties, and interactive effects on surface organic thickness, soil moisture, and water stocks were found (figures 3(a)–(e) and 4). Overall, there was a large decrease in surface organic layer thickness (from 21 to 4 cm) in burned sites across all soil landscapes. There was no significant change in mean volumetric moisture content overall, but there was a large increase in water storage above the permafrost (from 247 to 431 kg m^{-2}) due to increases in thaw depth after fire (from 72 to 152 cm). Fire caused an increase in MAST (from −0.6 to +2.1 °C), MADT (from −1.7 to +0.4 °C), and seasonal heat gain (from 86 to 183 MJ m^{-2}). We attribute the higher ground temperatures at the burned sites in winter to the increase in summer ground heat flux after the reduction of the surface organic layer thickness (figure 4). Winter cooling of the soils in the burned sites was likely slowed by the combined effect of snow and an increase of heat released from the deeper active layer. Similar seasonal ground thermal patterns after fire have been observed in other studies (Burn 1998, Yoshikawa *et al* 2003).

The thickness of the surface organic layer was a strong predictor of thaw depth across all landscape types and treatments in our study (figure 5(a)), underscoring the importance of the interplay between ecological succession, in which organic material accumulates, and fire, which combusts the surface organic material, to the soil thermal regime and permafrost. Increased surface organic layer thickness was also associated with increased volumetric soil moisture content

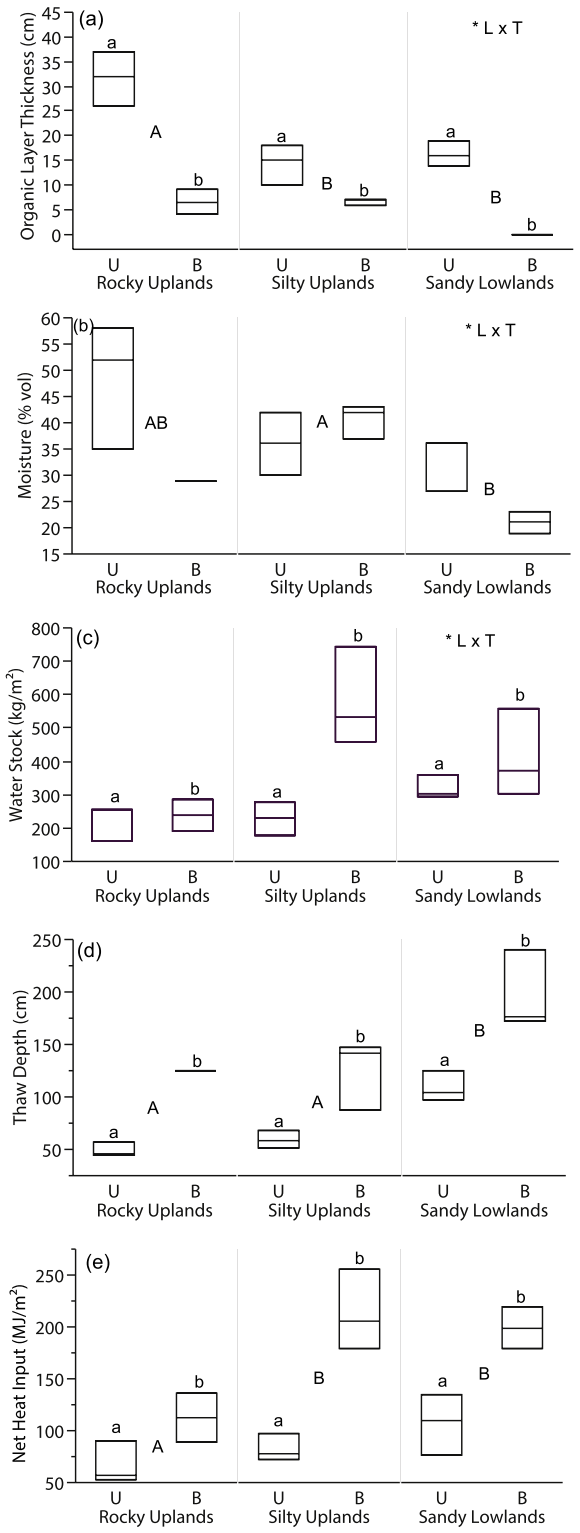


Figure 3. Box plots of surface organic layer thickness (a), volumetric soil moisture (b), water stock (c), thaw depth (d), and net seasonal heat input (e) across landscape types and treatments ($n = 17$). Note, one outlier from a low-severity burn in the rocky uplands was excluded. Two-way ANOVAs and post hoc tests (Tukey HSD and student's *t*-tests) were conducted. Significant differences ($p < 0.05$) between means are denoted by lowercase letters for treatment (unburned/burned) and uppercase letters for landscape type. Positioning of uppercase letters indicate the landscape-level means on the *y*-axes. Interactive effects of landscape and treatment ($^*L \times T$) are displayed when significant.

of the active layer/seasonally frozen layer (figure 5(b)). We attribute this relationship to the high water-holding capacity of organic material and the impermeability of the permafrost table, which causes increased soil moisture in the thin active layer (Woo *et al* 2008, Yi *et al* 2010, Yoshikawa *et al* 2003). It is well documented that organic horizon thickness strongly influences thaw depth in the discontinuous permafrost zone, but there is wide variation in the magnitude of change after fire (Yoshikawa *et al* 2003, Viereck *et al* 2008, O'Donnell *et al* 2011). We suggest that permafrost response to fire disturbance is modified by microclimatic and edaphic variation as we describe in detail below.

Within our study area, we found substantial differences in microclimate, attributed to both region and topography, which influenced the ground thermal regime and the sensitivity of permafrost to degradation after fire (table 1). The climate of the Yukon-Tanana Uplands ecoregion is less continental than the Yukon Flats, a tendency magnified by the higher elevation of the rocky upland sites, which causes cooler summers, warmer winters, and greater snowfall (table 1) (Jorgenson *et al* 2010). More moderate temperatures were recorded in the rocky upland sites, with lower air TDD and FDD than in the other sites. Freezing *n*-factors, which represent winter soil surface temperatures relative to local air temperatures, can be used to infer the impact of an insulating snow layer on soil temperatures in the absence of direct measurements of snow depth (Lunardini 1978, Karunaratne and Burn 2003). The rocky uplands had significantly lower freezing *n*-factors than the other landscape types, suggesting that greater snowfall in this area may have contributed to warmer winter soil surface temperatures (table 1). The sandy lowland and silty upland sites were located at low elevations in the Yukon Flats area. The greater seasonal variation in the measured values of air TDD and FDD in the Yukon Flats area reflect the strongly continental regional pattern. Within the Yukon Flats area there were climatic differences between the sandy lowland and silty upland sites, which could have been influenced by differences in topography and aspect. The sandy lowland sites had particularly high air TDD. The silty upland sites had MAAT nearly 1 °C colder than the rocky uplands and sandy lowlands. Our study area, near the northern extent of the discontinuous zone, had relatively cold MAATs (−5.2 to −6.1 °C) which helped to minimize the effects of fire. Over the broader discontinuous permafrost zone in Alaska, MAATs typically range from −2 to −6 °C (Jorgenson *et al* 2008).

In the rocky uplands affected by a moderately severe fire in 2004, mean soil volumetric moisture content was 40% lower in burned sites than unburned sites, suggesting that deep thaw into coarse-textured soils improved surface drainage (figure 3(b)). Total water storage above permafrost, however, increased 20% after fire because of the increase in the volume of thawed soil (figure 3(c)). Average MAST, which was positive even in the unburned sites with permafrost, was 2.1 °C higher in the burned sites (figure 4). The warmer winter surface soil temperatures, lower freezing *n*-factors, and low amplitude of monthly mean temperatures in the rocky uplands were likely influenced by snow insulation

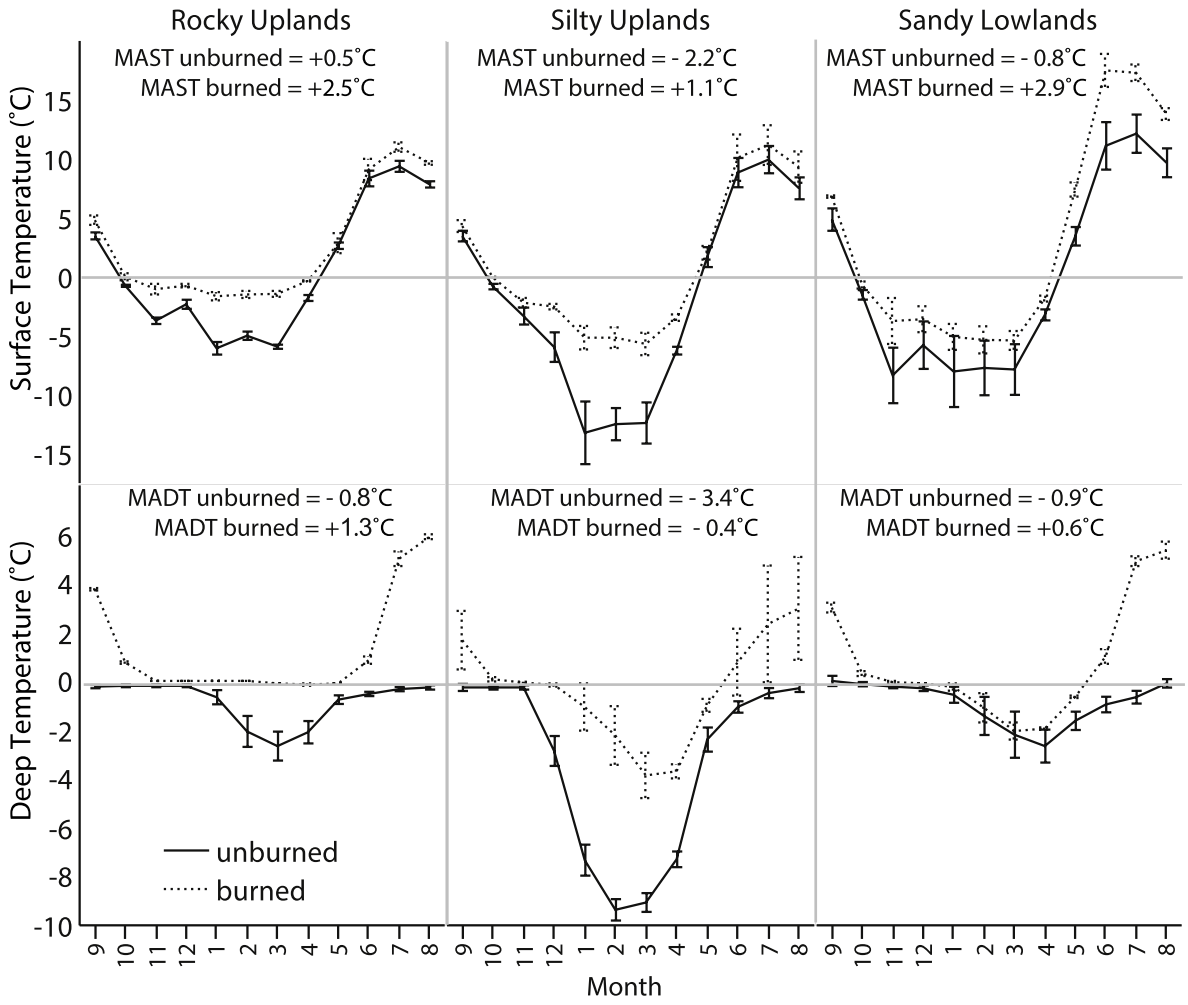


Figure 4. Monthly mean (±SE) soil temperatures at the surface (5 cm) and at depth (100 cm) for unburned (solid line) and burned (dotted line) sites by landscape type from September 2011 to August 2012 ($n = 17$). Note, one outlier from a low-severity burn in the rocky uplands was excluded. Mean annual surface temperatures (MAST) and mean annual deep temperatures (MADT) are displayed in text boxes.

from greater regional snowfall and higher elevations (table 1, figure 4). Average MADT also increased by 2.1 °C after fire (figure 4). Winter temperatures at 1 m depth in the burned sites were constrained at 0 °C, indicating the persistence of unfrozen water throughout the winter and the development of a talik, a perennially unfrozen layer situated between the seasonally frozen layer and permafrost. In the burned sites, permafrost thawed below the 1 m depth of observation in the rocky soil, whereas in unburned sites mean thaw depth was 49 cm (figure 3(d)). Seasonal heat input increased 67% after fire (figure 3(d)). Heat input after fire was lower than in the other landscapes, but was still high enough to thaw permafrost beyond the depth of seasonal frost.

In the silty uplands affected by a fire in 2009, mean volumetric moisture content showed little difference between burned and unburned sites as soils remained near saturation (figure 3(b)), but water storage in the active layer increased more than two-fold with the deepening of the active layer (figure 3(c)). Average MAST was 3.3 °C higher in burned sites compared to the unburned sites and average MADT was 3.8 °C higher (figure 4). The relatively cold winter temperatures at 1 m depth suggest complete refreezing of the deepened active layer. The increase in MADT after fire was greatest in the silty uplands, yet MADT remained the coldest of all soil landscapes after fire. Mean thaw depths were two-fold higher in burned (125 cm) than in unburned sites (59 cm) (figure 3(d)). Soil heat input was nearly three-fold higher in the burned sites compared to unburned sites (figure 3(e)). Despite these large changes in soil temperature, heat input, and thaw depth, there was no evidence of talik development after fire. Soil heat loss was likely exacerbated by the cold air temperatures, low snowfall, and high thermal conductivity of the active layer during winter associated with the high moisture content.

In the sandy lowlands after severe fires in 2004 and 2010, mean soil volumetric moisture content was 27% lower in burned than unburned sites (figure 3(b)). Accompanying a nearly two-fold increase in thaw depth between unburned (109 cm) and burned (196 cm) sites (figure 3(d)) was a 29% increase in mean water storage after fire (figure 3(c)). This landscape was unusual with its lower moisture contents and greater thaw depths, likely due to the sandy soils beneath the thin loess caps and the aridity of the climate. Average MAST was 3.7 °C higher in burned than unburned sites, which

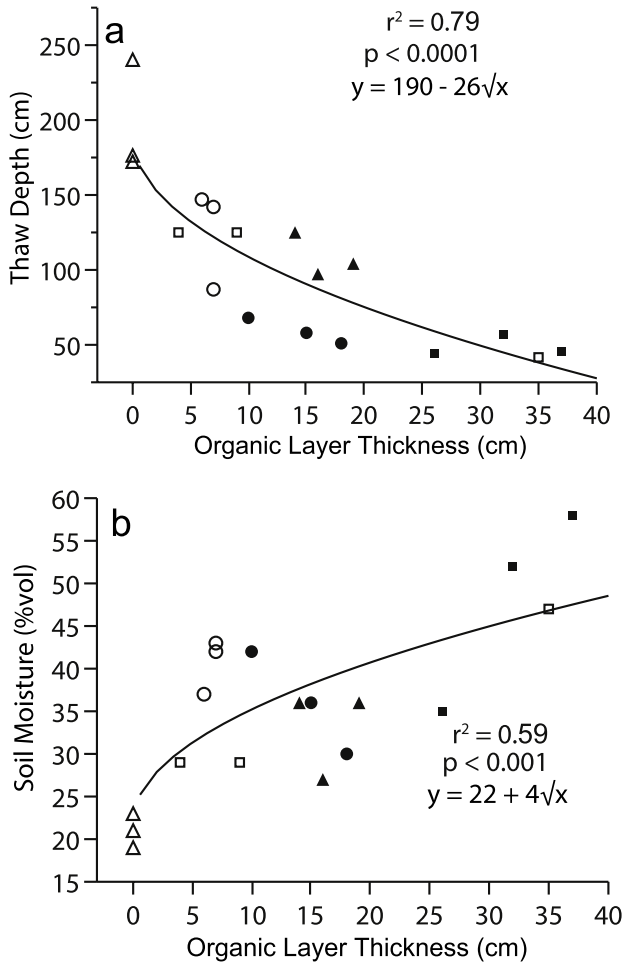


Figure 5. Relationships between surface organic thickness and thaw depth (a) and surface organic thickness and volumetric soil moisture (b) across all sites ($n = 18$). Solid markers represent unburned sites, open markers represent burned sites. Triangles = sandy lowlands; circles = silty uplands; squares = rocky uplands.

had the highest surface temperatures of the study (figure 4). The magnitude of increase in summer surface temperatures after fire was greatest in this landscape, which we attribute to the severity of the fires, exposure of mineral soils, and low soil moisture. Average MADTs were 1.5 °C higher in the burned sites, due mostly to warmer summer temperatures (figure 4). Mean soil heat input after the fires increased by 86% (figure 3(e)). Although the winter temperatures at 1 m depth in the burned sites were below 0 °C, observations of seasonal frost above underlying unfrozen soil, and deep thaw depths, indicate that thin taliks developed at two, and possibly three, of the burned sites.

These findings suggest that the underlying mineral soil texture mediates the soil moisture regime after fire-initiated permafrost thaw, thus influencing the vulnerability of permafrost to long-term degradation. The sensitivity of permafrost to fire disturbance is further modified by landscape position, which controls microclimate. The recovery of permafrost is likely impacted by the rate of thaw in relation to the recovery of vegetation. The ecosystem response to changing climatic and fire regimes will be largely impacted by the response of permafrost. Because boreal forest soils function as an important terrestrial carbon sink, changes in carbon cycling in this region are of particular significance to global climate (McGuire *et al* 2009, Grosse *et al* 2011, O'Donnell *et al* 2011, Yuan *et al* 2012). Decomposition, nutrient cycling, and productivity are largely temperature and moisture dependent (Chapin *et al* 2010); thus, the differential response in soil thermal and moisture regimes to fire will likely mediate the impact of changing climatic and fire regimes on carbon cycling throughout the discontinuous permafrost zone.

3.3. Thaw settlement

The resilience of permafrost in the silty uplands was further assessed through monitoring changes in thaw depths and surface elevations along transects encompassing different disturbance regimes (figure 6). Transect 1 was located in an area that burned around 1925 (previously considered 'unburned'), and Transect 2 was located in the 2009 burn. Both transects were partially affected by a fire in 1967, which resulted in an increase in deciduous tree cover. The 1967 fire left a legacy of deeper thaw in both of the transects, but the persistence of near-surface permafrost indicates stability and resilience to fire.

From 2010 to 2012, changes in the ground surface and permafrost table in the combined 1925 and 1967 burns were negligible. At the 1925 burn, declines in surface and permafrost elevation along a portion of the transect near a meteorological tower site were attributed to trampling of the thick mossy organic mat by researchers. Compaction was visually observed along this portion of the transect. Transect 2 was less vulnerable to compaction due to the thin residual surface organic layer (~0–10 cm) and the minimal use by researchers. The 2009 fire lowered the permafrost table throughout the transect and caused thaw settlement in the portion of the transect that had shallow active layers in 2010. The effects of the 2009 fire on the permafrost table and thaw settlement were most pronounced between the first and second year after fire. By the third year after fire, the permafrost table had largely stabilized. From 2010 to 2012, the permafrost table at the 2009 fire (only) was lowered by an average of 41 cm (max. 75 cm). Ground surface elevations declined on average by 9 cm (max. 39 cm), which is consistent with the expected thaw settlement due to the degradation of ice-rich permafrost. Along the portion of this transect that had previously burned in 1967, the permafrost table was lowered by an average of 25 cm (max. 35 cm) with no detectable thaw settlement, suggesting that the ice-rich intermediate layer of the upper permafrost had degraded as a result of the 1967 fire and had not recovered in the ~45 years of succession after the fire.

Overall, these results indicate that permafrost in the silty uplands was resilient to fire, as the fires of 1925, 1967, and 2009 did not result in a talik indicative of significant degradation. We attribute this to the ability of the active layer to adjust and absorb the additional soil heat flux after fire due to its high moisture content, the recovery of vegetation that

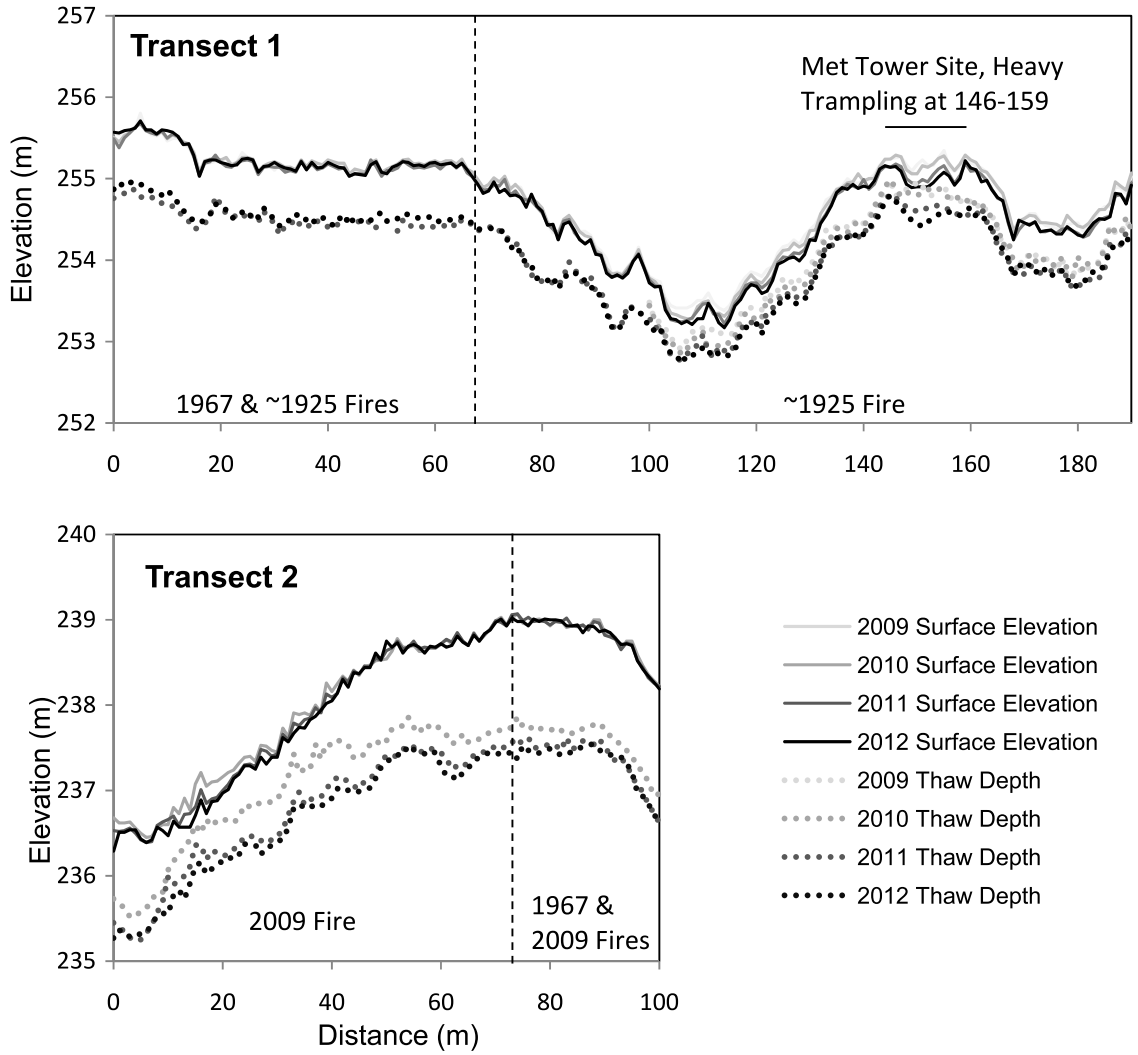


Figure 6. Cross-sectional profile of the elevation of the ground surface and permafrost surface along two transects in the silty uplands under different disturbance regimes from 2009 to 2012. Transect 1 burned around 1925 and a portion of it re-burned in 1967. Transect 2 burned in 2009, and a portion of it had previously burned in 1967. Note that the organic mat was compacted by human disturbance in Transect 1, with heavy trampling near a meteorological tower site.

reduces soil heat flux, and the high latent heat contents of the ice-rich permafrost that slows surface thawing.

4. Conclusions

Regional climate and topography interacted to create microclimates that influenced the ground thermal regime and permafrost, but this effect was strongly mediated by surface and subsurface conditions, which are products of disturbance history, ecological succession, and substrate. Successional patterns varied depending on fire severity and pre-fire species composition, which influence the recovery of the surface organic layer. Surface organic layer thickness was an important variable controlling the ground thermal regime and thaw depth. The reduction of the surface organic layer through moderate to severe burning caused the warming and thawing of upper permafrost across all soil landscapes, but talik initiation was observed only in the rocky uplands and sandy lowlands. The sensitivity of the rocky uplands and sandy lowlands was influenced by soil texture, whereby increased thaw depths after fire resulted in a reduction in soil moisture contents, as well as by greater snowfall at high elevations in the rocky uplands. Permafrost in the silty uplands was resilient to fire because of the high moisture content of the active layer and the high latent heat associated with the ground ice, which slows thaw and allows the deeper active layer to absorb more heat while vegetation recovery changes surface characteristics. Long-term permafrost degradation after fire is more likely in areas of the discontinuous permafrost zone with warmer climates and greater snowfall, whereas cold areas and continental climates in the northern portion of the discontinuous permafrost zone can allow permafrost to persist even after severe fire. A warming climate alone is expected to cause widespread permafrost degradation in the discontinuous permafrost zone (Grosse *et al* 2011, Jafarov *et al* 2012), and the impact of fire could hasten such degradation (Shur and Jorgenson 2007, Jorgenson *et al* 2010, Jiang *et al* 2012), though response will vary considerably depending on

complex interactions of climate, topography, soil properties, vegetation, and fire severity.

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