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Authors: Narita, Kenji, Harada, Koichiro, Saito, Kazuyuki, Sawada, Yuki, Fukuda, Masami, et al.

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Vegetation and permafrost thaw depth 10 years after a tundra fire in 2002, Seward Peninsula, Alaska

Kenji Narita[1]
Koichiro Harada[2]
Kazuyuki Saito[3]
Yuki Sawada[4]
Masami Fukuda[4] *and*
Shiro Tsuyuzaki[5]

[1]Corresponding author: Faculty of Education and Human Studies, Akita University, Akita 010-0862, Japan, knarita@ed.akita-u.ac.jp
[2]School of Food, Agricultural and Environmental Sciences, Miyagi University, Sendai 982-0215, Japan
[3]Japan Agency for Marine–Earth Science and Technology, Kanagawa 236-0001, Japan
[4]Faculty of Urban Management, Fukuyama City University, Fukuyama 721-0964, Japan
[5]Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060-0810, Japan

Abstract

The recovery of tundra vegetation and the depth of permafrost thaw were observed on the Seward Peninsula, Alaska, the site of a wildfire in 2002. The study compared the vegetation in burned and adjacent unburned tundra from 5 to 10 years post-fire. The effects of the fire on the vegetation varied between species and were spatially variable at the stand scale. The cover of evergreen shrubs, bryophytes, and lichens was still drastically decreased 5 years after the fire and had not recovered even 10 years after the fire. By contrast, the cover of graminoids, especially *Eriophorum vaginatum*, and of the deciduous shrub *Vaccinium uliginosum* increased. The depth of permafrost thaw increased, and its spatial pattern was related to vegetation structure; specifically, deeper thaw corresponded to graminoid-rich areas, and shallower thaw corresponded to shrub-rich areas. As the *E. vaginatum* cover increased, the thaw depth recovered to that of the unburned area, and the spatial variation had disappeared 10 years after the fire. Our results indicate that both the prefire vegetation structure and the differences in the regrowth properties between species play important roles in the early stage of tundra ecosystem recovery after wildfire. Our findings also show that the favorable growing conditions related to deeper thaw do not last long.

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Introduction

Arctic and subarctic ecosystems are regarded as being particularly sensitive to climate change (Watson et al., 1998; McBean et al., 2005). Climate change will probably cause large-scale changes to arctic vegetation; in particular, a further expansion of deciduous shrubs is expected with continued warming (Walker et al., 2006). Climate warming may also have important consequences for the stability of permafrost soils, which are thought to store twice as much carbon as the amount currently present in the atmosphere (Schuur et al., 2008). Permafrost warming has been observed in some arctic regions in recent decades (Osterkamp and Romanovsky, 1999), and it is expected that the thickness (Anisimov et al., 1997) and extent (Lawrence and Slater, 2005) of permafrost will decrease drastically because of climate warming. The fire regime in arctic regions, including its severity, frequency, and extent, is also expected to undergo changes due to warming (Rupp et al., 2000; Flannigan et al., 2001; McCoy and Burn, 2005). Wildfire in the tundra ecosystem may, because of the positive feedback of global and regional warming, have the severe consequence of releasing C stocks from permafrost soil (Mack et al., 2011). If warming trends cause the frequency and intensity of wildfires to increase, the successional trajectory of the tundra may change from being primarily graminoid vegetation to becoming more shrub-dominant (Higuera et al., 2008). Fire affects vegetation by killing or removing plant biomass, which increases the availability of sites for the establishment of seeds. However, the post-fire response of vegetation depends on the characteristics of the plant species, which have different degrees of susceptibility to fire and different regenerative properties. Changes to tundra vegetation as a result of fire can rapidly alter the balance of surface energy, including albedo, temperature, snow cover, and water (Viereck, 1982; McFadden et al.; 1998; Sturm et al., 2001; Chambers et al., 2005), and these changes alter the properties of the permafrost (Hinzman et al., 1991; Yoshikawa et al., 2002). For example, a decrease in plant canopy increases the insolation on the ground surface (Kasischke et al., 1995), and depletion of the insulating organic layer, or moss cover, increases the near-surface thermal conductivity of the soil (Yoshikawa et al., 2002). These effects of fire increase the thickness of the active soil layer (Heginbottom, 1971), and such alterations to the permafrost feed back to the vegetation through changes in the underground conditions for plant growth, such as temperature, nutrient supply, and soil moisture content (Woo, 1986; Waelbroeck and Monfray, 1997). Fire severity determines community composition through differences between species in regeneration strategies and root depth (Hollingsworth et al., 2013). Therefore, we can expect a relationship to exist between vegetation recovery and the temporal change in thaw depth in the course of vegetation succession after wildfire.

At a stand scale, the species composition of tundra vegetation has a spatially heterogeneous structure, and stochastic physical processes and microtopography also drive the arrangement of plant species and/or their growth pattern. Because of the heterogeneous distribution of fuels, surface water, and soil moisture content, fires burn stands at different intensities at a fine scale. Numerous studies of the post-fire succession of tundra vegetation link it to

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the thickness of the active permafrost layer (Fetcher et al., 1984; Racine et al., 2004; Bret-Harte et al., 2013), but few studies have focused on the temporal changes in the vegetation and the distribution of the permafrost after a wildfire at a stand scale. In arctic regions, vegetation structure and thaw depth correlate with certain environmental factors at a fine scale. For example, vegetation structure has been correlated with thaw depth and topography in polygon mires in the Arctic Siberian tundra (Minke et al., 2009); the effects of thawing permafrost and thermokarst affected plant species composition on a very local scale (1 m) via changes in the microclimate that accompanied ground subsidence (Schuur et al., 2007). Such fine-scale relationships may drive the regeneration of the plant community by altering plant assemblages and have consequences for the trajectory of tundra succession after wildfire. The creation of favorable patches by fire that last for longer periods may promote an increase in shrub cover for a longer duration. However, the manner in which the fine-scale spatial correlation between vegetation and permafrost thaw may change after a tundra fire is unknown. If fire creates deeper thaw areas in which plants can regenerate quickly, such favorable patches may soon disappear if the shading effect of the recovering plant is strong enough to reduce the insolation on the ground. In this paper, we present a field study of vegetation and thaw depth 5–10 years after a tundra fire on the Seward Peninsula in 2002. Our aim was to determine how plant succession and the thickness of the active permafrost layer vary spatially at a stand scale and whether these two properties simultaneously change in the 5–10 years after a tundra fire. We also aimed to assess fine-scale community assembly and successional trajectory during post-fire recovery.

Methods

STUDY AREA

We conducted a field survey in the Kougarok area in the center of the Seward Peninsula, Alaska, approximately 140 km north of Nome (65°26′28″N, 164°39′58″W at approximately 90 m a.s.l.; Fig. 1, part a). The slopes of the rolling hills support low arctic tundra dominated by open low mixed shrub-sedge tussock tundra communities (Viereck et al., 1992). The mean annual temperature is –2.4 °C; the mean January temperature is –23.1 °C, and the mean July temperature is 11.0 °C. Because of the more continental climate near the center of the Seward Peninsula, the study area is in a zone of nearly continuous permafrost with an active layer that has a mean thickness of 56 cm (Hinzman et al., 2003). The Seward Peninsula has a relatively high fire frequency compared with other tundra regions (Racine et al., 1985), and the Kougarok area has experienced three major fires in recent decades: 26 June–22 July 1971; 22 July–25 September 1997; and 4 August–10 October 2002 (Alaska Fire Service database: http://fire.ak.blm.gov/predsvcs/maps.php). However, the 1997 fire did not burn the study site, and an area between Kougarok Road and the Kougarok River has not burned since the 1940s. The 2002 fire burned the tundra vegetation with moderate to severe intensity but left behind a few unburned patches. However, in the burned area of the tussock tundra, 50% of the 14-cm organic layer was consumed by fire, which caused an increase in soil temperature, earlier freezing, and deeper thaw (Liljedahl et al., 2007). Meteorological changes and the dynamics of the active layer were monitored before and after the 2002 fire in an area approximately 1.5 km southeast of the study site and at a CALM (Circumpolar Active Layer Monitoring) site approximately 1.5 km upstream of our study site. The results from these sites may be comparable to those from our study site because of their proximity and similarity in topography.

The Mauze Gulch passes through the center of the study area (Fig. 1, part b) and divides the northwest- and southeast-facing slopes. Plant cover was continuous, with more than 95% total coverage, and the height of the vegetation was approximately 30–60 cm in the unburned area. The meadow vegetation, which extended along the gulch to a width of 10–20 m, consisted of tall willows, dwarf birch, and grasses 1.5 m high. Kougarok Road runs northwest-southeast and forms a boundary between the burned and unburned areas resulting from the 2002 fire. The study area consisted of four sites: a burned southeast-facing slope (BS), a burned northwest-facing slope (BN), an unburned southeast-facing slope (US), and an unburned northwest-facing slope (UN). The two unburned sites were used as a proxy for the prefire vegetation for each corresponding burned slope.

FIELD MEASUREMENTS

To study the effects of fire on the structure of the vegetation, we established a series of permanent plots in 2007. At each site, we set a 100-m transect perpendicular to the Mauze Gulch and established eleven 1 × 1 m permanent quadrats at 10-m intervals. Four lines were established at distances of approximately 100 m from the road to eliminate the unwanted influence of the roadside vegetation. Before beginning our field observations, we searched for fire scars (such as charred plants and soil) in the large unburned area, but we found no signs of combustion. We set the first quadrat (quadrat number 0) approximately 1 m from the edge of the stream; the quadrat numbers indicate their approximate distances from the gulch. Because the species composition of the meadow vegetation was quite different from the adjacent tundra vegetation and showed no signs of combustion, we omitted from the analysis the data from two quadrats (numbers 0 and 10) in the burned sites and one quadrat (number 0) in the unburned sites. Of the remaining quadrats, 9 and 10 were in the burned and unburned sites, respectively.

Visual estimates of cover were made for all species in each of the 1 × 1 m quadrats, of which all four corners were permanently marked by plastic or metal stakes. Species cover was estimated as a percent of the area inside a quadrat. We divided each quadrat into four 50 × 50 cm subquadrats and then estimated plant cover to 1% accuracy (10 × 10 cm) using a 50 × 50 cm plastic frame with a 1-cm scale and a 1-m ruler to improve precision. The 4% cover values were summed to estimate absolute percent cover in the quadrats, and all coverage estimates were made by the same person to reduce observer error. Site measurements were repeated in 2007, 2009, 2010, and 2012 in the burned area and in 2007, 2009, and 2012 in the unburned area. We also measured thaw depth by inserting a metal probe at three points in each quadrat in 2007, 2008, 2009, 2010, and 2012. All measurements were performed from mid- to late August.

STATISTICAL ANALYSES

The species diversity in each quadrat was estimated using the Shannon-Wiener indices, after which one-way analysis of variance (ANOVA) was performed to identify differences in species diversity between the four sites and years. Post hoc tests were performed using the Bonferroni procedure.

We performed one-way repeated measures ANOVAs to compare species and growth form cover between years and

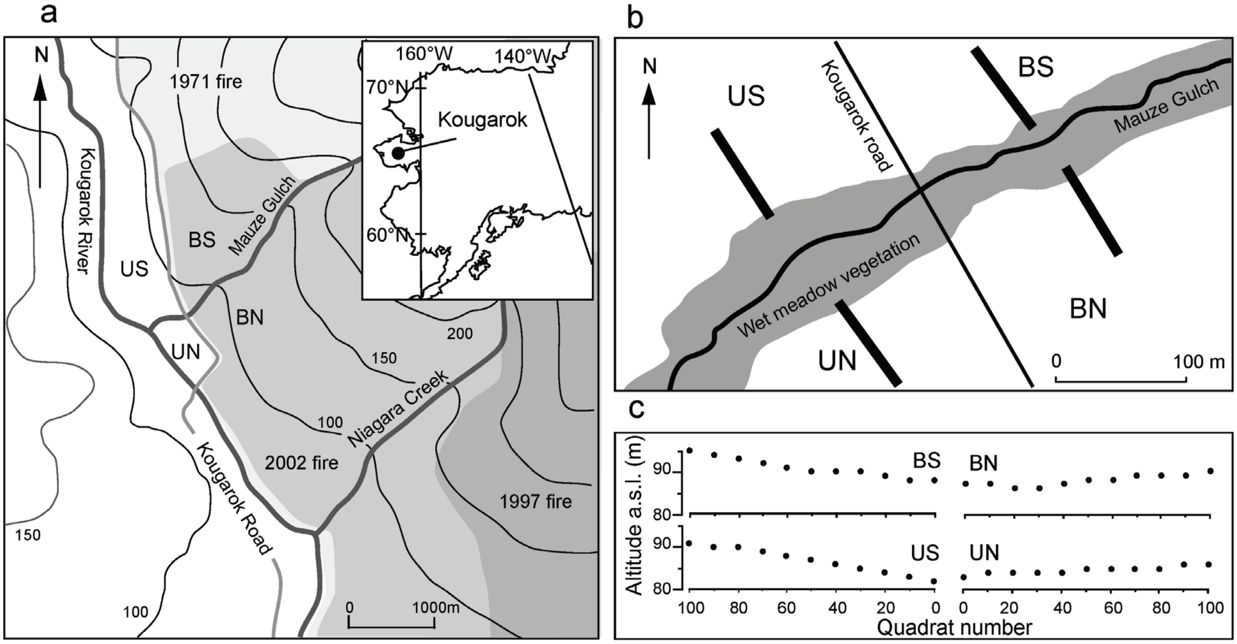

FIGURE 1. (a) Location of the study area. The four study sites are located in the Kougarok area (65°25′N, 164°38′W) in the center of the Seward Peninsula, Alaska. Kougarok Road and Mauze Gulch form boundaries between the four experimental sites: BN (burned northwest-facing slope), BS (burned southeast-facing slope), UN (unburned northwest-facing slope), and US (unburned southeast-facing slope). The gray area shows the burned zones from the 1971, 1997, and 2002 fires. (b) A line transect was established at each of the four sites, and eleven 1 × 1 m quadrats were set at a 10 m interval along each transect. (c) The profile of each site is shown along with each of the four transects.

sites. If the assumption of sphericity was not met as assessed by Mauchly's test, we applied a Greenhouse and Geisser correction (Greenhouse and Geisser, 1959). Because the data set was unbalanced, we performed one-way ANOVA to compare the cover of plant growth forms and thaw depth between sites between years, and post hoc tests were performed using the Bonferroni procedure. All plant species cover values were ranked using the average of the tied ranks prior to ANOVA. We performed Spearman's rank correlation analysis to identify relationships between the dominant species after merging the two slopes for the burned and unburned areas.

To explore the most important correlations, a principal components analysis (PCA) of the variance was performed on 11 dominant species belonging to each growth form in 2007, 2009, and 2012 to analyze the effect of wildfire on the vegetation. Detrended component analysis (DCA) by segments and nonlinear rescaling was conducted to estimate the underlying gradient length. In DCA, if the gradient length is less than 4 SD (standard deviation), the variation in the species assemblage is within a relatively narrow range; hence, the linear PCA approach is appropriate. If the gradient length is 4 or more SD, the variation in the assemblage occurs over a larger range, and the unimodal approach is appropriate (ter Braak and Prentice, 1988). The suitability of PCA was also assessed prior to analysis by the Kaiser-Meyer-Olkin (KMO) measure (Kaiser, 1974) and Bartlett's test of sphericity. Spearman's rank correlation analysis was performed to analyze the correlations between species and between the PCA axes and thaw depth. These analyses were performed with SPSS 22.0.0 (IBM Corporation, 2011) software and PC-ORD 6 (MJM). The floristic nomenclature follows that defined by Hulten (1968).

Results

GENERAL SPECIES COMPOSITION

The changes in plant composition over the five years of observation are shown in Table 1. The vegetation in the unburned area in 2007 was mixed shrub-sedge tussock tundra with some mosses and lichens. Plant cover was continuous, with more than 95% total coverage, and the vegetation height was approximately 30–60 cm. The vegetation on the unburned northwest-facing slope was dominated by *Ledum palustre* (38.4%), followed by *Betula nana* (23.4%), *Vaccinium vitis-idaea* (15.0%), *Eriophorum vaginatum* (14.2%), *Vaccinium uliginosum* (13.7%), and *Carex bigelowii* (8.0%). The southeast-facing slope had nearly the same components; the dominant species were *L. palustre* (27.5%), followed by *V. vitis-idaea* (20.8%), *V. uliginosum* (20.8%), *E. vaginatum* (17.6%), and *B. nana* (16.0%). Sphagnum mosses and lichens covered 15.3% and 7.5% of the ground surface, respectively. The northwest-facing slope had lower evergreen shrub cover and higher graminoid cover than the southeast-facing slope, but the difference was negligible.

The burned area was also composed of mixed shrub-sedge tussock tundra vegetation; the cover of evergreen and deciduous shrubs was lower, and the cover values for graminoids and bryophytes were more than double those of the unburned sites. The most dominant vascular species on the burned northwest-facing slope was *E. vaginatum* (50.2%), followed by *L. palustre* (17.1%), *B. nana* (10.6%), *Calamagrostis canadensis* (8.8%), and *V. uliginosum* (7.6%). Bryophytes, such as *Ceratodon purpureus* (27.7%) and *Polytrichum* spp. (7.3%), which were rare in the unburned sites, were abundant in some quadrats. A decrease in shrubs and an increase in graminoids after the fire were also observed on the burned southeast-facing slope. The dominant species was *E. vagi-*

TABLE 1

Total cover of species during observation (2007 - 2012) (mean ± SD, 9 quadrats in burned area, and 10 quadrats in control area). Repeated measures ANOVAs were performed to test differnces between years at each of the 4 sites.

	BN				BS				UN			US		
growth forms / species	2007	2009	2010	2012	2007	2009	2010	2012	2007	2009	2012	2007	2009	2012
Evergreen Shrubs	19.3 ± 9.6	19.6 ± 9.1	19.3 ± 9.2	22.6 ± 10.7*	10.3 ± 15.2	10.7 ± 12.8	9.9 ± 11.6	15.0 ± 14.5*	55.4 ± 24.7	56 ± 25.0	62.6 ± 29.3	50.8 ± 25.4	50.4 ± 21.3	60.0 ± 24.0
Ledum palustre	17.1 ± 8.3	16.8 ± 7.4	16.6 ± 7.5	18.7 ± 8.6	9.2 ± 14.1	9.4 ± 11.8	8.3 ± 10.4	12.2 ± 12.6*	38.4 ± 21.5	38 ± 20.6	42.4 ± 21.8	27.5 ± 18.0	26.5 ± 15.2	32.9 ± 19.6
Vaccinium vitis-idaea	2.2 ± 1.9	2.8 ± 2.8	2.8 ± 2.6	3.9 ± 3.1*	1.1 ± 1.5	1.2 ± 1.5	1.7 ± 1.8	2.8 ± 3.2**	15.0 ± 8.3	17 ± 9.3	17.9 ± 11.2	18.0 ± 8.2	20.1 ± 10.2	22.5 ± 4.9
Empetrum nigrum	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	2.0 ± 3.9	1.3 ± 3.1	2.3 ± 4.6	5.3 ± 12.5	3.8 ± 7.8	4.6 ± 8.9
Deciduous Shrubs	26.4 ± 25.6	27.9 ± 24.7	27.7 ± 22.3	32.2 ± 22.9	21.5 ± 17.7	27.0 ± 26.6	29.1 ± 28.5	39.0 ± 25.3**	45.5 ± 15.7	42 ± 16.8	38.0 ± 14.5**	46.5 ± 19.2	44.9 ± 17.0	45.6 ± 16.8
Vaccinium uliginosum	7.6 ± 11.4	9.4 ± 12.1	9.0 ± 11.0	10.8 ± 12.1*	12.8 ± 15.9	18.4 ± 25.3	19.9 ± 27.5	21.3 ± 25.0**	13.7 ± 13.7	14.2 ± 13.3	13.4 ± 11.7	20.8 ± 12.9	22.1 ± 9.7	23.4 ± 10.6
Betula nana	10.6 ± 12.0	12.2 ± 14.0	12.4 ± 13.5	14.4 ± 12.4	3.6 ± 7.0	4.8 ± 8.1	5.1 ± 8.5	10.6 ± 11.3**	23.4 ± 15.5	21 ± 14.1	17.0 ± 9.8*	16.0 ± 7.5	14.7 ± 7.4	14.7 ± 6.4
Rubus chamaemorus	5.1 ± 6.3	3.1 ± 5.0	3.6 ± 5.3	3.3 ± 3.9*	3.3 ± 1.9	1.2 ± 1.1	0.7 ± 0.8	1.8 ± 1.7**	4.5 ± 4.2	2.9 ± 2.9	3.3 ± 3.6*	2.6 ± 2.6	1.3 ± 1.8	1.7 ± 1.6
Arctostaphylos alpina	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.8 ± 2.3	0.9 ± 2.7	1.7 ± 5.0*	0.1 ± 0.3	0.0 ± 0.0	0.1 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Salix pulchra	3.2 ± 5.1	3.1 ± 4.5	2.7 ± 2.9	3.7 ± 4.4	1.8 ± 3.5	1.8 ± 4.3	2.5 ± 5.9	3.6 ± 6.4**	3.8 ± 10.0	3.5 ± 9.4	4.2 ± 10.9	6.7 ± 14.2	6.8 ± 14.5	5.8 ± 11.5
Salix sp 1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 1.3	0.0 ± 0.0	0.0 ± 0.0
Graminoids	72.4 ± 23.4	74.5 ± 26.2	69.4 ± 20.8	79.6 ± 17.8	66.2 ± 29.7	67.5 ± 36.6	73.0 ± 34.8	72.9 ± 32.7	23.0 ± 20.6	26.9 ± 22.6	32.6 ± 22.9**	30.4 ± 17.8	27.5 ± 15.8	34.1 ± 16.3*
Eriophorum vaginatum	50.2 ± 22.1	57.8 ± 24.4	57.6 ± 19.4	61.1 ± 17.1	37.9 ± 24.5	50.0 ± 36.0	52.8 ± 37.8	53.0 ± 36.3	14.2 ± 21.9	15.3 ± 22.9	16.9 ± 25.3	17.6 ± 20.0	15.4 ± 15.2	18.7 ± 16.5
Calamagrostis canadensis	8.8 ± 9.8	6.7 ± 8.4	3.1 ± 3.6	7.6 ± 9.0**	20.7 ± 18.6	10.9 ± 7.1	11.2 ± 14.0	10.8 ± 14.2**	0.8 ± 1.2	1.1 ± 1.6	1.1 ± 2.1	0.8 ± 1.0	0.3 ± 0.7	1.5 ± 1.6
Carex bigelowii	5.8 ± 11.4	6.0 ± 11.1	7.0 ± 8.7	8.8 ± 9.2*	7.7 ± 11.1	6.6 ± 5.5	7.9 ± 7.4	8.7 ± 8.3	8.0 ± 4.5	10.5 ± 5.8	14.6 ± 7.6*	11.2 ± 5.9	10.9 ± 5.7	13.9 ± 6.4
Eriophorum angustifolium	7.2 ± 11.8	3.6 ± 7.8	1.4 ± 1.7	2.1 ± 3.2	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 1.0	0.3 ± 1.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
unknown	0.4 ± 0.7	0.4 ± 0.9	0.3 ± 1.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.8 ± 1.4	0.1 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.8 ± 2.5	0.8 ± 2.5	0.0 ± 0.0
Forbs	0.7 ± 1.4	0.6 ± 1.1	0.7 ± 1.7	1.6 ± 3.1	0.2 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.7	0.0 ± 0.0	0.1 ± 0.3	0.3 ± 0.7	0.1 ± 0.3	0.1 ± 0.3
Epilobium angustifolium	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
Petasites frigidus	0.7 ± 1.4	0.6 ± 1.1	0.7 ± 1.7	1.6 ± 3.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.3 ± 0.7	0.0 ± 0.0	0.1 ± 0.3	0.3 ± 0.7	0.1 ± 0.3	0.1 ± 0.3
Bryophytes	36.3 ± 28.2	14.1 ± 12.5	7.8 ± 9.4	3.7 ± 2.6***	40.7 ± 21.8	29.1 ± 15.5	20.9 ± 23.6	18.6 ± 21.9**	14.5 ± 19.8	9.1 ± 14.2	10.2 ± 14.4	16.7 ± 18.4	17.1 ± 20.5	17.1 ± 21.0
Polytrichum spp.	7.3 ± 9.7	4.9 ± 7.1	1.6 ± 1.1	2.4 ± 2.3*	21.7 ± 23.6	19.6 ± 15.3	19.1 ± 24.1	17.8 ± 21.8	0.1 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.4 ± 0.5	0.1 ± 0.1	0.2 ± 0.3
Ceratodon purpureus	27.7 ± 25.2	7.1 ± 7.9	4.9 ± 7.3	0.3 ± 0.7***	18.9 ± 14.0	9.1 ± 8.8	1.7 ± 2.4	0.8 ± 1.7***	0.0 ± 0.0	0.0 ± 0.0	0.2 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.3
Sphagnum spp.	0.6 ± 0.9	0.6 ± 0.9	0.5 ± 1.3	0.4 ± 0.7	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	11.6 ± 18.8	6.7 ± 14.2	8.2 ± 13.7*	15.3 ± 18.8	13.8 ± 19.5	15.0 ± 19.1
Marchantia polymorpha	0.7 ± 1.1	0.3 ± 1.0	0.0 ± 0.0	0.0 ± 0*	0.1 ± 0.3	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
other mosses	0.0 ± 0.0	1.2 ± 3.3	0.8 ± 2.0	0.6 ± 0.8*	0.0 ± 0.0	0.4 ± 0.7	0.0 ± 0.1	0.0 ± 0.0	2.8 ± 3.6	2.5 ± 3.8	1.9 ± 3.1	1.0 ± 1.3	3.2 ± 3.3	1.8 ± 3.1
Lichens	2.7 ± 5.8	0.3 ± 0.4	0.0 ± 0.1	0.5 ± 1.3	1.0 ± 1.0	0.2 ± 0.3	0.0 ± 0.0	0.1 ± 0.1**	6.3 ± 5.8	3.8 ± 4.3	3.5 ± 4.6*	7.5 ± 10.2	4.3 ± 9.2	6.2 ± 8.8*
foliose lichens	2.7 ± 5.8	0.2 ± 0.3	0.0 ± 0.0	0.5 ± 1.3	1.0 ± 1.0	0.2 ± 0.3	0.0 ± 0.0	0.0 ± 0.1**	2.4 ± 3.0	1.4 ± 1.9	0.0 ± 0.0*	2.0 ± 2.6	1.1 ± 1.3	2.2 ± 2.3
fruticose lichens	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.0 ± 0.1	3.9 ± 5.2	2.4 ± 3.3	3.5 ± 4.6	5.5 ± 10.1	3.1 ± 9.4	4.0 ± 8.3

Level of significance between years: * P < 0.05, ** P < 0.01, *** P < 0.001. Other differences are not statistically significant.

natum (37.9%), followed by *Calamagrostis canadensis* (20.7%), *V. uliginosum* (12.8%), *L. palustre* (9.2%), and *Carex bigelowii* (7.7%). Higher coverage by *Polytrichum* spp. (23.3%) and *Ceratodon purpureus* (18.9%) was also observed. The southeast-facing slope had lower shrub cover and higher cover by *C. canadensis* and *Polytrichum* spp. than the northwest-facing slope. There were no signs of new establishment or expansion of willows and shrub birch as reported in other tundra fire studies (Racine et al., 2004; Landhausser and Wein, 1993).

Across all four sites, we encountered 16 vascular and 7 nonvascular plant species and families. Average Shannon-Wiener index values were 2.48 ± 0.52, 2.26 ± 0.33, 2.58 ± 0.35, and 2.79 ± 0.21 for burned northwest, burned southeast, unburned northwest, and unburned southeast-facing slopes, respectively. Diversity varied significantly between the four sites (one-way ANOVA, $F_{102,3} = 9.856$, $P < 0.001$); the diversity of the burned area was lower than that of the unburned area (Bonferroni post hoc; $P = 0.012$ for burned northwest vs. unburned southeast, and $P = 0.010$ and $P < 0.001$ for burned southeast vs. unburned northwest and burned south vs. unburned southeast-facing slopes, respectively). There was no significant annual variation between years at any of the sites ($F_{102,2} = 1.003$, $P = 0.370$).

TEMPORAL CHANGES IN VEGETATION COVER AND THAW DEPTH

One-way ANOVA of growth form cover across sites revealed differences across sites and changes in cover during the observation period. The analysis of vascular plant cover indicated an obvious difference in the amount of graminoids between the burned and unburned sites and a decline in evergreen shrubs after the fire (Fig. 2 and Table 2). Evergreen shrub cover in the burned areas was less than half that in the unburned areas throughout the study. By contrast, the graminoids in the burned areas were more common than in the unburned areas throughout the study period. Deciduous shrub cover was lower in the burned area than in the unburned area in 2007 but was not significantly different between the burned and unburned areas afterward. No differences in the cover of shrubs and graminoids were observed

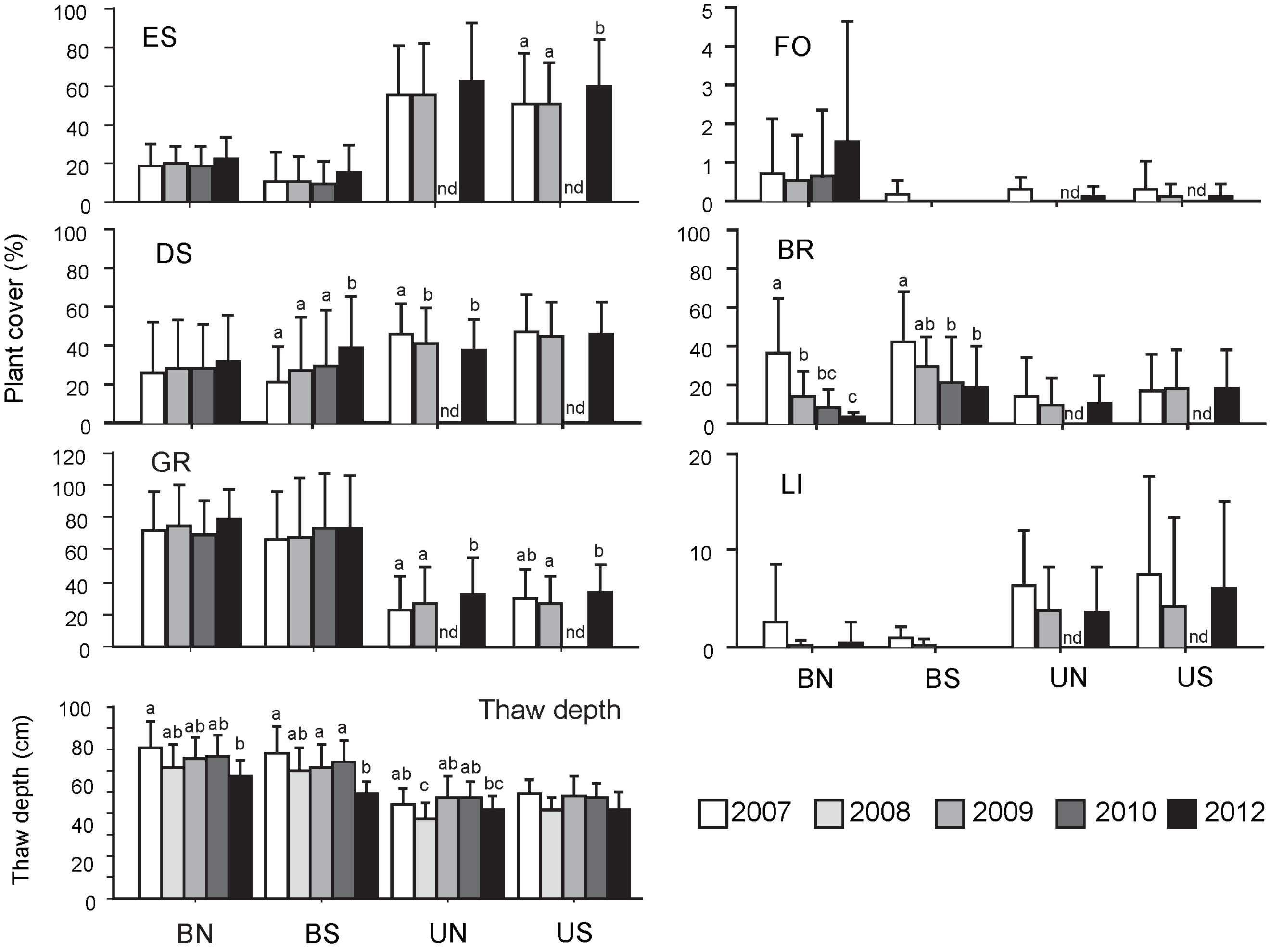

FIGURE 2. The amount of cover of six plant growth forms (ES: evergreen shrubs, DS: deciduous shrubs, GR: graminoids, FO: forbs, BR: bryophytes, LI: lichens) and the depth of permafrost thaw (mean ± SD). Different letters denote significant pairwise differences between years (Bonferroni $P < 0.05$) within a growth form at each of the four sites. Growth forms without letters did not differ significantly between years. The thaw depth on the unburned southeast-facing slope varied significantly, but pairwise analysis did not reveal any significant differences. nd: no data available.

TABLE 2

Results of one-way ANOVA for between-site differences in plant cover by growth form and thaw depth. Plant covers were ranked using the average of tied rank prior to ANOVA. Results of forbs could not be analyzed because they were observed in only a few quadrats.

		factor				
		site				
Growth form	Years	Ndf	Ddf	*F*	*P*	post-hoc
Evergreen shrubs	2007	3	34	16.115	**<0.001**	BNa, BSa < UNb, USb
	2009	3	34	18.707	**<0.001**	BNa, BSa < UNb, USb
	2012	3	34	19.401	**<0.001**	BNa, BSa < UNb, USb
Deciduous shrubs	2007	3	34	3.985	**0.016**	
	2009	3	34	1.787	0.168	
	2012	3	34	0.596	0.662	
Graminoids	2007	3	34	12.71	**<0.001**	BNa, BSa > UNb, USb
	2009	3	34	9.839	**<0.001**	BNa, BSa > UNb, USb
	2012	3	34	11.336	**<0.001**	BNa, BSa > UNb, USb
Bryophytes	2007	3	34	4.474	**0.009**	BNab, BSa > UNb, USab
	2009	3	34	3.766	**0.020**	BNab, BSa > UNb, USab
	2012	3	34	1.437	0.249	
Lichens	2007	3	34	2.959	**0.046**	
	2009	3	34	3.364	**0.030**	
	2012	3	34	12.063	**<0.001**	BNa, BSa < UNb, USb
Thaw depth	2007	3	34	14.078	**<0.001**	BNa, BSa > UNb, USb
	2008	3	34	18.018	**<0.001**	BNa, BSa > UNb, USb
	2009	3	34	6.381	**<0.001**	BNa, BSab > UNb, USb
	2010	3	34	12.773	**<0.001**	BNa, BSa > UNb, USb
	2012	3	34	10.139	**<0.001**	BNa > BSb, UNb, USb

Notes: Ndf, numerator degrees of freedom; Ddf, denominator degrees of freedom; BN, burned northwest; BS, burned southeast; UN, unburned northwest; US, unburned southeast Treatments that share the same lower case letter were not significantly different in post-hoc tests (Bonferroni/Dunn) performed when site was significant at $P < 0.05$ (bold).

between slopes in either the burned or unburned areas. For nonvascular plants, the burned areas had a higher incidence of bryophytes than the unburned areas in 2007 and 2009, but no difference between the two areas was detected in 2012. Lichens showed very low cover in the burned area and did not recover. Repeated measures ANOVA for growth forms also showed annual variations within the sites; no notable temporal trends were detected for either evergreen shrubs or graminoids, but gradual increases were observed in deciduous shrubs on the southeast-facing slope of the burned area (Fig. 2). This result was due to the vital resprouting of *V. uliginosum*. Similarly, a trend of rapid decrease was observed for bryophytes that was due mainly to the disappearance of *Ceratodon purpureus*, which was abundant in the burned area, over the five-year observation period.

Thaw depths were significantly greater in the burned areas than in the unburned areas during the five years and showed similar annual shifts at all four sites (Fig. 2). The thaw depth averaged 70.7 ± 13.5 cm (mean ± SD) on the burned northwest-facing slope, 68.3 ± 12.5 cm on the burned southeast-facing slope, 43.9 ± 8.0 cm on the unburned northwest-facing slope, and 49.4 ± 7.3 cm on the unburned southeast-facing slope in 2007. There were significant decreasing annual trends, and the thaw on the burned southeast-facing slope (48.9 ± 5.7 cm) was shallower than that on the burned northwest-facing slope (57.4 ± 7.9 cm) (post hoc $P = 0.005$), but it was the same as that in the unburned areas (41.7 ± 6.5 cm for northwest-facing and 42.1 ± 7.5 cm for southeast-facing slopes) in 2012. In the unburned area, the northwest-facing slope exhibited a slightly greater temporal change than the southeast-facing slope.

SPATIAL VARIATION IN THE VEGETATION AND THAW DEPTH

The changes in cover of the nine dominant species along the transects are shown in Figure 3. Two evergreen shrubs (*L. palustre*

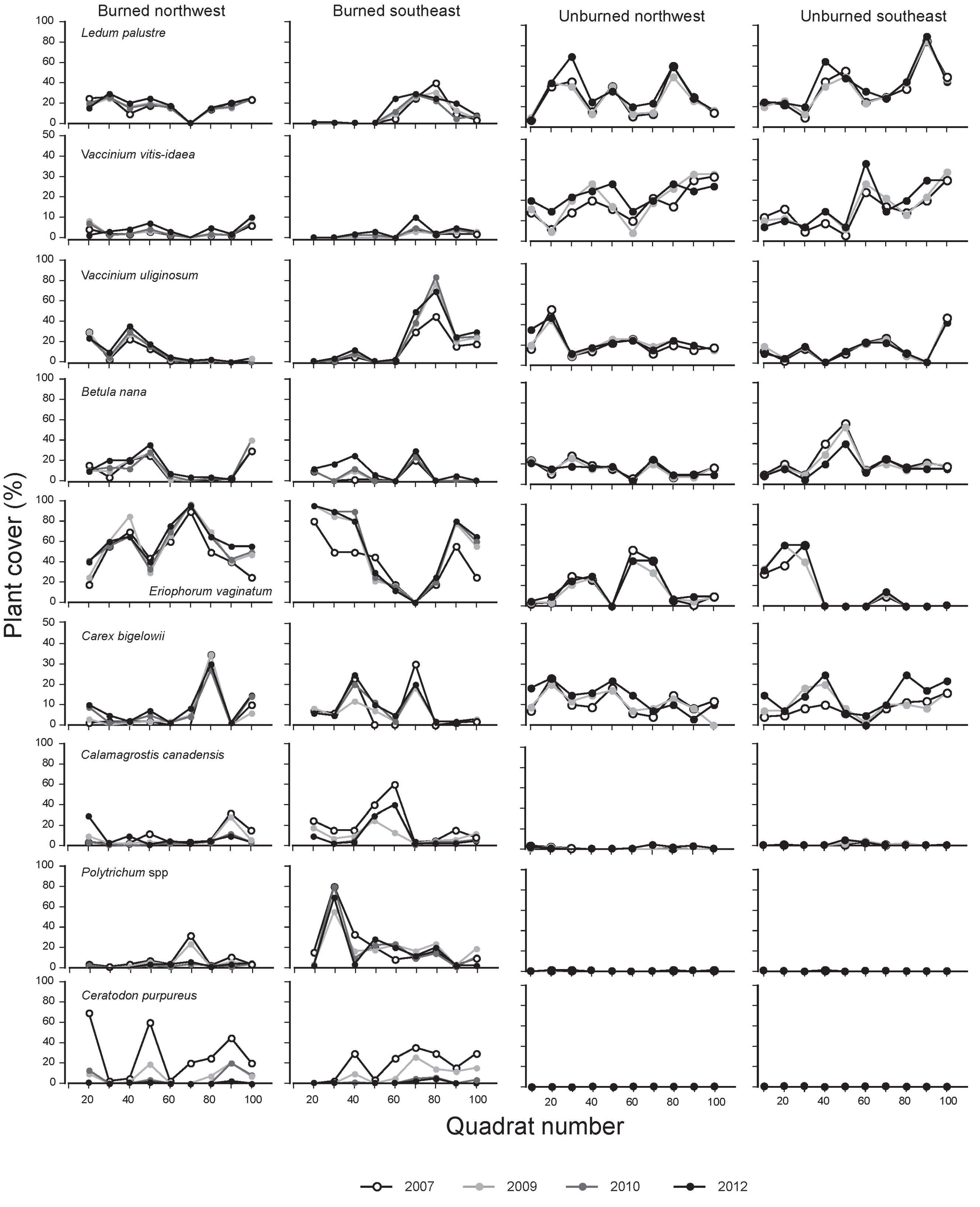

FIGURE 3. **Spatial and temporal patterns of nine dominant species along a 100 m line transect in the four study sites. The data from quadrats 0 and 10 in the burned sites and quadrat 0 from the unburned sites were not used. Note that the vertical scales for *Vaccinium vitis-idaea* and *Carex bigelowii* are half of those for other species.**

and *V. vitis-idaea*) showed lower means and spatial variation on both slopes in the burned area than those in the unburned areas during the study period (F-test; $P > 0.05$). In particular, *V. vitis-idaea* cover was consistently very low (<10%) and did not recover in any of the burned quadrats. By contrast, a deciduous shrub, *V. uliginosum*, showed a higher degree of spatial variation in the burned area than in the unburned area. On the northwest-facing slope, the cover showed the same variance in both the burned and unburned areas in 2007, but as they increased notably in a few quadrats, the variances became higher in the burned areas than in the unburned areas in 2009 (F-test; $F_{8,9} = 6.877$, $P = 0.011$) and 2012 ($F_{8,9} = 5.552$, $P = 0.022$). The regrowth of *V. uliginosum* was restricted to quadrats where its cover was relatively high in 2007, suggesting that regrowth depended on the plants that remained after the fire.

E. vaginatum showed a highly variable spatial distribution along the transects at all four sites, but the vigorous recovery of the burned southeast-facing slope resulted in a higher spatial variance than that of the unburned southeast-facing slope ($F_{8,9} = 5.595$, $P = 0.021$ and $F_{8,9} = 4.835$, $P = 0.033$ in 2009 and 2012, respectively). The regrowth of this species was also restricted to quadrats that had relatively high cover in 2007. *C. bigelowii* also showed a patchy distribution and a weak relationship with the other two graminoids, and *C. canadensis* tended to be abundant in areas where the cover of both *E. vaginatum* and *V. uliginosum* was low. Two nonvascular pioneer species, *Polytrichum* spp. and *C. purpureus*, also showed a high degree of spatial variation, although their spatial patterns did not show a clear relationship with those of the dominant species.

The three shrub species tended to show the same distributions, and *E. vaginatum* was abundant in the burned area where shrub incidence was low. There were statistically significant or marginally positive correlations during the years of observation between *L. palustre* and *V. vitis-idaea* (Spearman's rho = 0.794, $P < 0.001$; rho = 0.680, $P = 0.006$; rho = 0.639, $P = 0.008$, and rho = 0.498, $P = 0.045$ for 2007, 2009, 2010, and 2012, respectively) and *L. palustre* and *V. uliginosum* (rho = 0.463, $P = 0.056$; rho = 0.616, $P = 0.011$; rho = 0.540, $P = 0.026$, and rho = 0.447, $P = 0.065$ for 2007, 2009, 2010, and 2012, respectively), but there was a significant negative relationship between *L. palustre* and *E. vaginatum* (rho = –0.473, $P = 0.040$; rho = –0.530, $P = 0.029$; rho = –0.657, $P = 0.006$; and rho = –0.596, $P = 0.010$ for 2007, 2009, 2010, and 2012, respectively). In the unburned area, a consistent relationship was detected only between *L. palustre* and *E. vaginatum* (rho = –0.608, $P = 0.008$; rho = –0.564, $P = 0.010$; and rho = –0.571, $P = 0.008$ for 2007, 2009, and 2012, respectively). The three graminoids also tended to appear in the same quadrats, but their relationships were not statistically significant or consistent. This resulted in two distinctive patterns of vegetation, one shrub-dominated and the other graminoid-dominated, at a 10-m scale in the burned area, that was more distinct on the southeast-facing slope. Owing to the slow shrub regeneration rate, this spatial structure was maintained during the five years.

The thaw depth profiles were spatially variable along transects, and the difference between the deepest and shallowest quadrats was nearly double in 2007 (86 cm vs. 48 cm and 87 cm vs. 49 cm in the northwest- and southeast-facing slopes, respectively) (Fig. 4). The thaw depth profile across the slopes changed annually but maintained a consistent spatial pattern over the five years. The shallowest depths were observed near quadrats 70 to 90 on the burned southeast-facing slope and near quadrat 30 on the burned northwest-facing slope. The variance in depth among the quadrats gradually decreased in the burned area. The coefficients of variation for thaw depth among quadrats gradually declined from 2007 to 2012 in both slopes, but a statistically significant difference was detected only for the burned southeast-facing slope (between 2007 and 2012, $F_{8,9} = 4.696$, $P = 0.042$; between 2009 and 2012, $F_{8,9} = 6.897$, $P = 0.001$; and between 2009 and 2012, $F_{8,9} = 4.494$, $P = 0.048$).

The PCA results for the vegetation composition data for 2007, 2009, and 2012 are shown in Figure 5. We added lichens and sphagnum mosses to the analysis because they are important

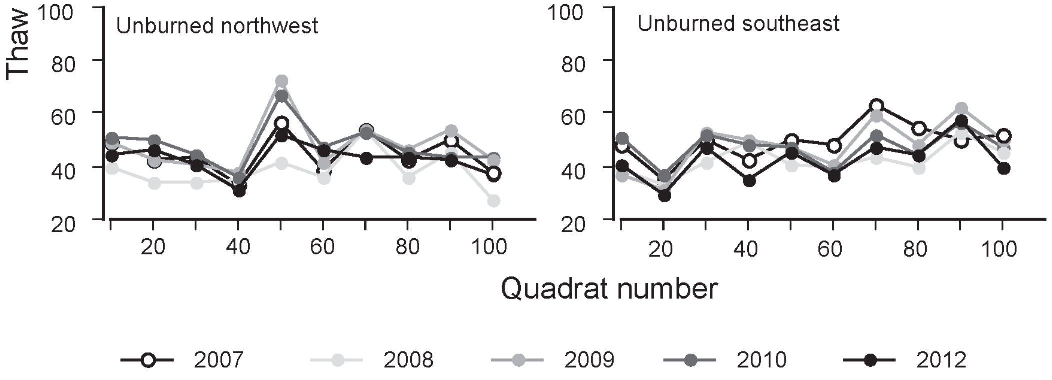

FIGURE 4. **Spatial and temporal pattern of permafrost thaw depth from 2007 to 2012. Data were not collected in 2011.**

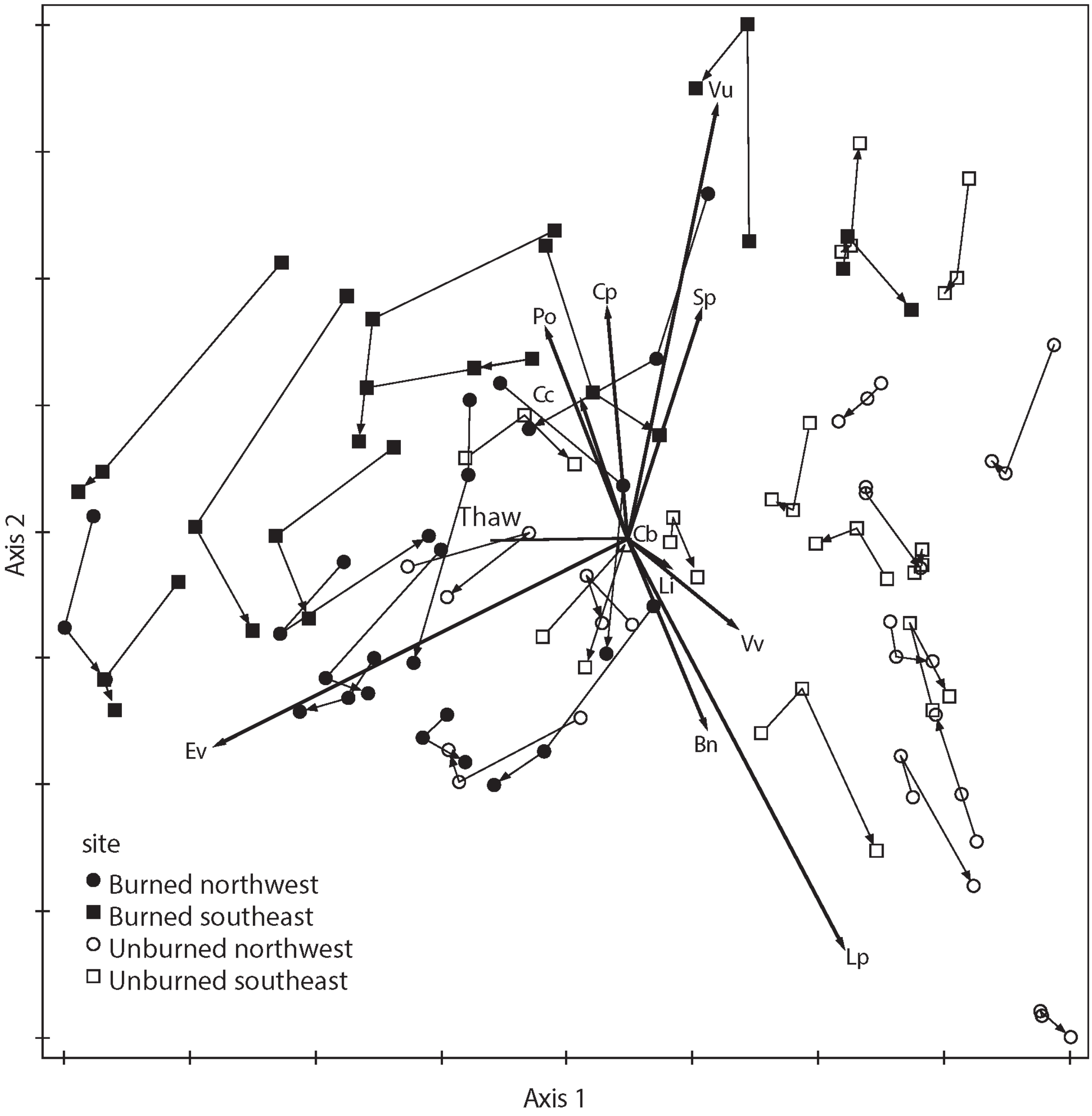

FIGURE 5. Principal component analysis (PCA) ordination diagram of the quadrat scores for 114 quadrats (38 quadrats × 3 years) surveyed in 2007, 2009, and 2012. We used the data for eight dominant vascular plant species (Ls, *Ledum palustre*; Vv, *Vaccinium vitis-idaea*; Vu, *Vaccinium uliginosum*; Bn, *Betula nana*; Ev, *Eriophorum vaginatum*; Cc, *Calamagrostis canadensis*, and Cb, *Carex bigelowii*) and four nonvascular plants and plant growth forms (Cp, *Ceratodon purpureus*; Po, *Polytrichum* spp.; Sp, sphagnum mosses; and Li, lichens). The connected lines and arrows indicate quadrats surveyed continuously from 2007 to 2012.

components of the tundra vegetation. Because the gradient length calculated by DCA was 2.8 SD, which suggests a linear species distribution along the gradients, we adopted a PCA approach. The overall Kaiser-Meyer-Olkin (KMO) measure was 0.650, a “mediocre” rating according to Kaiser (1974). Bartlett’s test of sphericity was also statistically significant (χ^2 [55] = 241.097, $P < 0.001$), indicating that the data were likely appropriate for the analysis. The PCA coefficients of determination indicated that these 11 species significantly explained the ordination patterns; the first PCA axis explained 50.6% of the total variance of the data set, the second axis explained 11.3%, and the third explained 10.2%. The first two axes were examined further, and among these species, *L. palustre*, *E. vaginatum*, and *V. uliginosum* were the primary species determining vegetation structure (Fig. 5). Axis 1 had a strong positive relationship to *L. palustre* and a negative correlation with *E. vaginatum* in both the burned and unburned areas over the three years. *V. vitis-idaea* and an early successional nonvascular species, *C. purpureus*, were positively but weakly correlated with axis 1 only in the burned areas. The second axis was positively correlated with *V. uliginosum* in both areas, but the relationship was relatively stronger in the unburned area. The second axis was also negatively related to *E. vaginatum* in the burned area and *L. palustre* in the unburned area over the three years. Sphagnum mosses were also positively correlated with the second axis in the unburned area.

Quadrat PCA scores showed different patterns between the burned and unburned areas, with some exceptions (Fig. 5). Quadrats in the unburned area had high scores on axis 1, and the burned quadrats had low scores, reflecting the rich cover of *E. vaginatum*. However, the quadrat scores for the two areas were not clearly divided, which suggested that the burned area consisted of patches with a species composition similar to that in the unburned area. For example, burned area quadrat scores(BS-70 and BS-80) in the upper right indicated relatively higher cover of *L. palustre* and *V. uliginosum* and less cover of *E. vaginatum*.

The annual fluctuations in the PCA quadrat scores became larger in the burned areas over time, and the shift to lower values on both axes showed that the major causes of the fluctuation patterns were the regeneration of *E. vaginatum* and the decline of early successional species (*C. canadensis*, *C. purpureus*, and *Polytrichum* spp.) in the burned area. The quadrats in the unburned area fluctuated less on axis 2, which reflected the yearly changes in an evergreen shrub, *L. palustre*, and a deciduous shrub, *V. uliginosum*. The difference in species composition and the yearly fluctuations among quadrats in the burned area indicated that the trajectory of regeneration varies spatially and reflected the initial species composition soon after the fire.

The correlation between the PCA axes and thaw depth indicated an important relationship between vegetation composition and permafrost dynamics. The first axis, which negatively correlated with *E. vaginatum* and positively correlated with the shrub species and the nonvascular pioneer species, *C. purpureus*, was significantly negatively correlated with thaw depth (Spearman's rho = –0.607, $P < 0.001$, $n = 38$; Table 3) in 2007, but no relationships were detected in 2009 and 2012. By contrast, no such relationships were detected in the unburned areas throughout the study period, which supports the results of the co-occurrence of species and thaw depth distribution (Figs. 3 and 4).

Discussion

We found clear evidence of spatial variation in recovering vegetation and permafrost thaw depth at the stand level, and there was an association between the two factors for five years after wildfire in the arctic tundra vegetation of the Seward Peninsula. The spatially variable regeneration observed among quadrats indicates that the presence of surviving plants on and below the ground is a principal determinant of post-fire vegetation communities, as regeneration occurred primarily in resprouting plants.

Overall, the post-fire vegetation recovery observed at our study sites followed a pattern of early-stage tundra revegetation similar to that observed after another tundra fire on Nimrod Hill, located approximately 40 km northeast of our site (Racine et al., 2004). This pattern was characterized by rapid invasion followed by a decrease in early successional species, a rapid increase in graminoids and deciduous shrubs, a slow recovery of evergreen shrubs, and the disappearance of lichens and the *Sphagnum* moss layer. Among the evergreen shrub species, the most notable change after the fire was observed in *L. palustre*, which decreased to less than half that in the unburned areas 5 years after the fire and had not recovered 10 years after the fire. In other studies, the aboveground primary productivity of *L. palustre* was observed to recover or even exceed that of an unburned area (Racine et al., 2004; Jandt et al., 2008; Bret-Harte et al., 2013), but its cover did not recover markedly in almost all the quadrats during the 5 years of our study. This was possibly due to the few remaining plants of this species in most quadrats soon after the fire. The rapid increase in *E. vaginatum* has been reported as starting 1 year after a wildfire and being maintained throughout the development of new stems and leaves from the remaining tussock bases and the germination of dispersed seeds (Racine, 1981). In contrast, *C. canadensis*, an early successional graminoid, can invade a burned area through seeds but cannot persist in later successional stages due to changing soil conditions and/or competition with other graminoids, especially *E. vaginatum* (Viereck and Schandelmeier, 1980). The newly established nonvascular species at our study sites were *Epilobium angustifolium, Ceratodon purpureus, Polytrichum* spp., and *Marchantia polymorpha*, which are generally observed at early stages of succession and become established through seeds or spores after a wildfire in tundra and boreal forests (Ruokolainen and Salo, 2009). The establishment of numerous willows from seeds 6 to 10 years after the fire was observed on Nimrod Hill (Racine et al., 2004), but we did not observe such an increase or invasion by deciduous shrubs despite the proximity of willow-dominated meadow vegetation. Shrub expansion has been documented during the past 50 years throughout Alaskan arctic landscapes that lack fire (Sturm et al., 2001). Climate warming models predict that increases in temperature will lead to a vegetation succession from tundra to deciduous forest in the Seward Peninsula (Rupp et al., 2000; Higuera et al., 2008), but another study using the ALFRESCO model predicted that partial replacement of tundra by graminoids may occur 17 years after a fire (Barrett et al., 2012).

We found that the composition of dominant species and its recovery was highly variable at a 10 m scale along transects in the burned area, and the burned study site consisted of shrub- and graminoid-dominated mosaics during the observation period. Evergreen shrubs recovered only in quadrats where plant cover was relatively abundant in 2007, and no germinated seedlings were observed in any of the quadrats, indicating that newly established shrubs were rare at this point in time. Furthermore, deciduous shrubs, especially *V. uliginosum,* recovered only in shrub mosaics, whereas *E. vaginatum* recovered in many quadrats, although mainly inside graminoid mosaics; it could not invade the shrub mosaics. These results suggest that both the different regeneration abilities of plants and the distribution of surviving plants soon after a fire play a role in the reconstruction of a community assemblage 10 years after the fire. Graminoids produce wind-dispersed seeds, whereas shrubs produce seeds dispersed by sap fruits, and the different dispersal strategies may partly determine the rate of species establishment and, thus, the structure of tundra vegetation communities after wildfires. Community structure after a disturbance is highly affected by the relative success of the different regeneration strategies (Hollingsworth et al., 2013).

An increase in *V. uliginosum* offset the poorer recovery of *E. vaginatum* in the shrub mosaic, which suggests that favorable conditions, such as nutrient enrichment, warm temperatures, and adequate water supply, were created by the fire in both mosaics. Variations in fire characteristics can play a dominant role in determining community composition, even within boreal forest communities that are highly structured by environmental gradients (Hollingsworth et al., 2013). However, we could not detect such clear, fine-scale effects of the spatial variation in fire characteristics on the plant assembly at our burned site, because no fire-severity data were collected. Based on the slow recovery rate of evergreen shrubs, the community assembly observed in this study partly reflected the structure of the prefire community. The PCA result that some quadrats in the shrub mosaics in the burned area had a similar composition to those in the unburned area also supports this speculation. However, quadrats with high incidences of early-establishing nonvascular species, particularly *Polytrichum* spp., were thought to have burned at relatively higher intensities because the two bryophytes can colonize only compacted layers of charred humus or exposed mineral soils (Schimmel and Granström, 1996). The pattern of distribution did not always coincide with graminoid- or shrub-dominated mosaics, which suggests that spatial variation in fire intensity cannot directly explain the community assembly in the burned area.

The fire thawed the permafrost to a greater depth than in the unburned area, but the difference gradually decreased and was almost nonexistent 10 years after the fire. This is a relatively shorter interval than that observed after other tundra fires (Rocha et al., 2012) but is similar to the result from the Nimrod Hill study (Racine et al., 2004). The deepening of the active layer after a wildfire could have important implications for water retention, nutrient availability, and the decomposition rate (Weintraub and Schimel, 2005). The difference in recovery between species is partly the result of different responses to the availability of soil nutrients, and the experimental addition of nutrients increased the biomass and productivity of deciduous shrubs but reduced the growth of evergreen shrubs in moist tussock tundra (Chapin et al., 1995). Graminoids and deciduous shrubs responded positively to nutrient addition, but evergreen shrubs responded negatively (Chapin and Shaver, 1996). However, the favorable conditions created by fire may be transient and hence available only to the species that survive or to those that can disperse seeds over a wide area soon after a fire. In this study, the low rate of shrub recovery in the area with a deeper thaw may have been restricted by the rapid expansion of *E. vaginatum*, as tundra species tend to reduce their productivity under experimental light attenuation (Chapin et al., 1995). These results suggested that the spatial heterogeneity of the thaw may limit community assembly throughout succession. The thaw depth profiles along the transects showed spatially variable patterns and were related to the aboveground plant assemblages in the burned area in 2007. However, such spatial variation and the relationship between thaw depth and vegetation gradually diminished thereafter, possibly as a result of increasing shading by *E. vaginatum*. As the plant cover recovered, the shading effect increased and the thaw gradually became shallower. The positive effect of deeper permafrost thaw on plant growth declined with the increase in the shading effect of the aboveground plant cover, which acted as negative feedback on thaw depth. Our results predict that the short fire interval on the Seward Peninsula may permit graminoids to dominate for longer periods, which is consistent with a result from a theoretical model in which short-term extremes in temperature and precipitation cause the establishment and persistence of drought-resistant grassland steppe vegetation (Rupp et al., 2000). This may be the case for the Seward Peninsula because its fire rotation time is considerably shorter than that in other areas in northern Alaska (Racine et al., 1985), and this is expected to become more common in other tundra ecosystems as fire frequency gradually increases owing to global warming (Rupp et al., 2000; Flannigan et al., 2001; McCoy and Burn, 2005). However, short-term plant responses are poor predictors of long-term changes in community composition because compensatory physiological responses, species interactions, and different time lags between physiological and demographic traits buffer plant growth and successional processes (Chapin et al., 1995).

In contrast to the burned area, no relationship between thaw depth and any of the component plants was detected in the unburned areas. The spatial variation in thaw depth in the unburned areas suggests that microtopography possibly influences the variation in thaw depth in our study area. Fine-scale topography affects

TABLE 3

Spearman's correlations of species and groups, and thaw depth for PCA Axes 1 and 2.

	Axis 1						Axis 2					
	Burned site (N = 18)			Unburned site (N = 20)			Burned site (N = 18)			Unburned site (N = 20)		
Species and group	2007	2009	2012	2007	2009	2012	2007	2009	2012	2007	2009	2012
Ledum palustre	**0.785** ***	**0.722** **	**0.724** **	**0.848** ***	**0.828** ***	**0.829** ***	0.010	0.035	–0.019	**–0.469** *	**–0.515** *	**–0.542** *
Vaccinium vitis-idaea	**0.750** ***	**0.564** *	0.385	0.086	0.231	**0.463** *	0.077	0.125	–0.13	0.179	0.108	0.068
Vaccinium uliginosum	**0.513** *	0.438	0.414	0.093	0.164	0.046	**0.546** *	0.384	**0.468** *	**0.826** ***	**0.743** ***	**0.812** ***
Betula nana	0.251	0.217	0.069	0.209	0.293	0.283	–0.018	–0.413	–0.271	–0.318	–0.296	–0.105
Eriophorum vaginatum	**–0.884** ***	**–0.956** ***	**–0.961** ***	**–0.857** ***	**–0.864** ***	**–0.881** ***	**–0.718** **	**–0.602** **	**–0.513** *	0.097	0.103	0.062
Calamagrostis canadensis	–0.106	0.016	0.049	0.31	**0.742** ***	0.118	0.187	0.331	0.128	0.307	0.137	0.189
Carex bigelowii	0.005	–0.157	0.099	**0.618** **	0.354	0.402	–0.123	0.053	–0.01	0.149	0.079	0.103
Polytrichum spp.	–0.341	0.035	0.093	0.21	0.047	0.266	0.391	**0.622** **	0.366	–0.07	0.157	0.324
Ceratodon purpureus	**0.650** **	**0.599** **	**0.502** *	.	.	**–0.459** *	**0.662** **	0.489	0.42	.	.	0.127
Sphagnum mosses	0.259	0.234	0.387	–0.102	–0.194	–0.188	–0.126	–0.353	–0.269	**0.663** **	**0.535** *	**0.539** *
Lichens	0.275	0.311	0.301	0.085	–0.178	0.076	0.32	0.173	0.009	**–0.495** *	–0.208	–0.324
Thaw depth	**–0.606** **	–0.145	–0.225	–0.047	0.096	–0.158	–0.205	–0.237	–0.466	–0.304	–0.388	–0.365

Notes: Significance ($P < 0.05$) is bold. Level of significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. Other differences are not statistically significant.

thaw depth through many physical surface properties, for example, soil moisture and temperature, snow thickness, and solar radiation (Price, 1971; Nelson et al., 1997; Schuur et al., 2007; Minke et al., 2009). Although both slopes in our study area were relatively flat and no noticeable concave depressions were observed, the effect of microtopography on thaw depth is undeniable, suggesting that the observed spatial pattern in thaw depth is governed by traits not measured in this study.

In conclusion, the recovery of vegetation after a fire burned a large portion of the Kougarok area in 2002 is similar to the early stage of regeneration that was observed after the 1972 tundra fire on Nimrod Hill, with the exception of the invasion of large deciduous shrubs. Vegetation recovery and thaw depth after the tundra fire were spatially variable within a stand and changed simultaneously over 5 to 10 years. The community structure was possibly determined by both the distribution of the remaining plants and the differences in regeneration ability between plant species. Although fire may play a role in redistribution dynamics by thawing permafrost to a greater depth in the early stage of plant succession, the effect did not last long because the more deeply thawed areas disappeared as a result of the rapid increase in sedge cover. Increasing fire severity and frequency may shift the succession of tundra vegetation from shrub-dominated to graminoid-dominated tussocks by reducing both the abundance of the remaining plants and the opportunity for shrubs to regenerate, thereby enabling graminoids to persistently dominate.

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