ORIGINAL PAPER

Tundra fire alters vegetation patterns more than the resultant thermokarst

Shiro Tsuyuzaki [1] · Go Iwahana [2] · Kazuyuki Saito [3]

✉ Shiro Tsuyuzaki

tsuyu@ees.hokudai.ac.jp

[1] Graduate School of Environmental Earth Science (GSEES), Hokkaido University, Sapporo 060-0810 Japan

[2] International Arctic Research (IARC), University of Alaska, Fairbanks, AK 99775-7340 USA (also in North-Eastern Federal University in Yakutsk, Sakha, Russia)

[3] Japan Agency for Marine-Earth Science and Technology (JAMSTEC), Kanagawa 236-0001 Japan

Abstract

Tundra fires are increasing their frequencies and intensities due to global warming and alter revegetation patterns through various pathways. To understand the effects of tundra fire and the resultant thermokarst on revegetation, vegetation and related environmental factors were compared between burned and unburned areas of Seward Peninsula, Alaska, using 140 50 cm × 50 cm plots. The area was burned in 2002 and surveyed in 2013. Seven vegetation types were classified by a cluster analysis and were categorized along a fire severity gradient from none to severe fire intensity. The species richness and diversity were higher in intermediately disturbed plots. Severe fire allowed the immigration of fire-favored species (e.g., *Epilobium angustifolium*, *Ceratodon purpureus*) and decreased or did not change the species diversity, indicating that species replacement occurred within the severely burned site. Although thermokarsts (ground subsidence) broadly occurred on burned sites, due to thawing, the subsidence weakly influenced vegetation patterns. These results suggest that the fire directly altered the species composition at a landscape scale between the burned and unburned sites and it indirectly altered the plant cover and diversity through the differential modification, such as thermokarst, at a small scale within the burned site.

Key words Polygonal ground · Landscape patterns · Thawing · Thermokarst · Tundra fire

Introduction

Climate change at high latitudes is inducing ecosystem changes, particularly, in the Arctic tundra region, which is the most sensitive (Jones et al. 2015). The frequency and extent of tundra fires are increasing due to global warming (Hu et al. 2015), although the effects of severe tundra fires on revegetation have not been well studied because of their low frequency and intensity (Racine et al. 2004). Tundra fire in the Arctic is accelerating global warming, because a large amount of organic carbon in the soil and permafrost is released into the atmosphere (Mack et al. 2011). Vegetation, in particular, *Sphagnum* moss cover, maintains the underground soil and ice structures by the adiabatic effects (Raynolds et al. 2008). Therefore, more focus should be given to the patterns and paces of vegetation recovery after tundra fire.

Interactions among topographical, physical and biological processes after disturbances, including tundra fire, occur at different times and have different responses and durations (Grosse et al. 2011). Tundra fires alter thermokarsts (ground subsidence) (Jones et al. 2015) that may change the vegetation patterns. The alteration occurs through various pathways (Kokelj and Jorgenson 2013). Fire removes plants from the ground surface, and creates low albedo that increases the active layer (Beringer et al. 2001, Tsuyuzaki et al. 2009). Ground subsidence occurred in a polygonal network on thawing after the 2002 tundra fire at Kougarok in the Seward Peninsula (Iwahana et al. 2016). Ice wedge degradation occurs over a decadal time scale in both continuous and discontinuous permafrost zones (Tsuyuzaki et al. 1999, Jorgenson et al. 2006). Plant establishment is affected greatly by land modifications, including thermokarst (Lloyd et al. 2003, Grosse et al. 2011). These reports suggest that fire affects vegetation structures at various spatio-temporal scales. Satellite imagery confirms that thermokarsts occur frequently in the burned areas of Kougarok where polygonal networks of high-centered polygon derived by melting ice wedges are well developed (Iwahana et al. 2016). However, no subsidence was observed in adjacent unburned sites. Therefore, we compared the vegetation development patterns between burned and unburned areas and investigated the effects of thermokarsts on vegetation within the burned area. We hypothesized that: (1) the fire had altered the vegetation (as indicated by the presence of fire-adapted species even 11 years after the last fire), (2) the effects of thermokarsts (ground subsidence) on vegetation cover and species diversity were weaker or slower than the effects of fire, because the environmental changes induced by topographic changes were not drastic as compared with the changes by fire, and (3) the fire affected the vegetation structures at landscape and habitat scales through the alterations of topography and its related factors.

Study area and methods

Study area and field methods

The study site is located in Kougarok, Seward Peninsula (65^{o}26’’N, 164^{o}39’W, 90 m elevation) in northwestern Alaska (Fig. 1). The region is located in a transitional area between discontinuous and continuous permafrost zones, and it is underlain locally by a thin (15-50 m) continuous permafrost (> 90% areal cover) (Brown et al. 1997). The characteristics of climate in this region are as follows (Liljedahl et al. 2007): The annual mean air temperature during 2000 and 2006 was between -2.7^{o}C and -5.9^{o}C. Summer rainfall from June to August averaged 94 mm during the seven years. Winter precipitation for the seven years averaged 80 mm, as estimated by the snow water equivalent in early May. The study site suffered from a tundra fire during 4 August and 10 October 10 2002. In an area close to our study site, the fire intensity was moderate to severe and consumed 50% of organic layer (Liljedahl et al. 2007). Thermokarsts were observed firstly on the burned area in 2006 (Iwahana et al. 2016). The soil profiles had peat sediments or mixed layers of peat and silty mineral soils. Peaty soil profiles contained few or thin ice lenses, while mineral soil particles did thick ones.

The present surveys were conducted during 7 to 12 August 2013, 11 years after the 2002 fire. The study area is distributed in a zone of nearly continuous permafrost of which active layer averaged 56 cm, because of the continental climate near the center of Seward Peninsula (Hinzman et al. 2003). On a southwest facing slope, seven transects were set up randomly within a 250 m × 100 m area (Fig. 1). The field investigations confirmed that the landscape was broadly homogenous in any slope direction (Iwahana et al. 2016) if fires did not occur for long term (Narita et al. 2015). Three transects were set up in the burned site, and the other three transects were set up in the unburned site. All the transects in the burned site were established on areas where thermokarsts were observed. The distance from subsidence was recorded on each plot. On each transect, 50 cm

× 50 cm plots were set up at 1-m intervals. The lengths of the transects were between 11 m and 19 m. A total number of plots was 140.

Plant cover was visually estimated by overlying a 50 cm × 50 cm frame, which was subdivided into 25 10 cm × 10 cm cells by strings on each plot. The total number of cells occupied by each plant species was counted when the plant cover was higher than 4% (= 1 cell). When the cover was less than 4%, the cover intervals became narrowed. The litter cover was estimated, as well as plant cover, and litter thickness was measured using a ruler. The litter amount was evaluated as the cover multiplied by the average thickness. The relative longitudes, latitudes and elevations of the four corners of each plot were determined by an RTK differential GPS system with a base station (GS15 VIVA, Leica Geosystems, Norcross, GA) and a rover (GS14 GNSS Receiver, Leica). The horizontal and vertical measurement errors were less than 10 mm and 20 mm, respectively. In addition, the maximum and minimum elevations were measured in each plot. Therefore, a total of six geographical positions were measured on each plot. At the six points, the thaw depth and peat moisture were measured. The peat moisture (%, v/v) was measured by a time domain reflectometry (TDR) (Hydrosense, Campbell Scientific, Logan) with 12-cm probes. Based on the positioning data, the slope gradient and aspect were calculated. The standard deviation of the elevations of the six positions measured in each plot were calculated and used as a surrogate for ground surface roughness (Tsuyuzaki et al. 1999).

Statistical analysis

The total plant cover, species richness, species diversity (*H*') and evenness (*J*') were calculated on each 50 cm × 50 cm plot. Based on the cover of each species in each plot, a two-way indicator species analysis (TWINSPAN) was performed to recognize vegetation types. A feature of TWINSPAN is that vegetation is classified based on considering the balance between frequency and abundance of species. Pseudo-species is used to retain the quantitative information (Jongman et al. 1995). Steel-Dwass test, a non-parametric multiple comparison procedure, was used for *post-hoc* multiple comparisons to compare differences in the species composition characteristics and measured environmental factors between the cluster groups when the non-parametric Kruskal-Wallis one-way analysis of variance (ANOVA) was significant (Underwood 1997). For all the analyses, the number of samples (*n*) was the 140 plots.

Non-metric multidimensional scaling (NMDS) was conducted to investigate the relationships between environmental factors and vegetation types and between environmental factors and species (McCune and Grace 2002). The stress was referred to decide the effectiveness of the non-metric of NMDS. The biplots of NMDS were made for plot-environment and species-environment relationships. All statistical analyses except for TWINSPAN were conducted with the statistical package vegan on the program R (version 3.4.0) (R Core Team 2017). TWINSPAN was conducted with the software CANOCO version 4.5 (ter Braak & Smilauer 2002).

Results

Vegetation patterns

In total, 30 species were recorded in the 140 plots. Seven cluster groups (hereafter, groups A to G) were recognized by the TWINSPAN cluster analysis (Fig. 2). At the first cluster division, the plant communities were divided into two groups by the dominance of *Betula nana*, *Vaccinium vitis-idaea* and *Vaccinium uliginosum* (A to D) and by the dominance of *Polytrichum commune* and *Calamagrostis canadensis* (E to G). Group D (*Eriophorum* vegetation type) was separated from groups A to C by the dominance of *C. canadensis*, *Eriophorum vaginatum* and *Polytrichum commune*. Group A (*Vaccinium*) was separated from groups B and C by the establishment of *Sphagnum fuscum*. The presence of *Cladonia* sp. separated group B from group C (*Carex*). Group B (*Ledum*) also showed high cover of *Ledum groenlandicum*. Among groups E through G, group G (*Calamagrostis-Ceratodon*) was separated by the presence of *Ceratodon purpureus*. Groups E and G showed high frequency and cover of *C. canadensis* and *P. commune*. Group E (*Calamagrostis-Polytrichum*) was separated from group F (*Polytrichum-Calamagrostis*) by the presence of *Carex bigelowii*, *Epilobium angustifolium* and *Rubus chamaemorus*. Few seedlings were observed in all the plots.

The highest cover and frequency were obtained by a tussock-forming cottongrass, *E. vaginatum* whose mean cover and occurrence frequency were 21% and 89%, respectively. *L groenlandicum* occurred with the second highest frequency (82%) in the plots (Table 1), followed by *R.*

chamaemorus (63%), *V. vitis-idaea* (61%) and *V. uliginosum* (61%), all of which showed more than 10% in cover. Because all of these four species, except for *R. chamaemorus* (perennial herb), were shrubs, the plant communities were categorized as tussock-shrub tundra.

There were significant differences in the total plant cover (Kruskal-Wallis test, χ^2 = 20.098, *P* = 0.003), species richness (χ^2 = 13.79, *P* = 0.032) and diversity (χ^2 = 16.197, P = 0.013) among the vegetation groups. Evenness did not show differences among the groups (χ^2 = 11.700, *P* = 0.069). The average total plant cover exceeded 100% in all the vegetation groups (Table 1). Plot cover was 20-40% higher in groups C and E than in group B (Steel-Dwass test, $t > 2.82$, $P < 0.05$). The species richness in each plot ranged from 4 to 10, and it was higher in groups C and D than in group G ($t > 2.24$, $P < 0.05$). The species diversity was higher in groups C than in groups E through G ($t > 2.79$, $P < 0.05$). Thus, species richness and diversity tended to be higher in groups C and D, and it was low in group G. The evenness did not differ among the seven groups ($t < 2.19$, $P > 0.05$).

Environmental characteristics

The ratio of plots measured in the burned sites increased from groups A to G (Table 2). None of the plots in group A (*Vaccinium* type) received fire damage in the last fire, and they were therefore used as a benchmark. Group A was characterized by high shrub covers, represented by *Vaccinium* species, and *S. fuscum* establishment (Table 1). Groups B to D were established on both unburned and burned sites (Table 2). Groups E to G were established only on burned sites and they were the first to separate from the other groups on TWINSPAN (Fig. 2), demonstrating that groups E to G possessed specific vegetation. The trace of charcoal still remained in the plots on the burned sites. These three groups were characterized by the fire-favored species, *P. commune* and *C. canadnesis*. Therefore, the seven vegetation types varied along a fire-severity gradient.

On burned sites in groups D and E, *S. fuscum* survived vegetatively in a few plots possessing ground subsidence and surface water flow (Table 1). The distance from subsidence was the longest in groups A and B, which received the least fire (Table 2), demonstrating that thawing occurred least on the unburned sites. Since the subsidence did not occur on the unburned sites, the distance from subsidence was significantly different between the burned and unburned sites (Kruskal-Wallis test, χ^2 = 63.175, $P < 0.001$; Steel-Dwass test, $t > 3.319$, $P < 0.05$). On the burned sites, however, the vegetation patterns were not related to ground subsidence, i.e., the distance from ground subsidence was not different among the cluster groups C to G. The thaw depth ranged from 23 cm to 61 cm and did not differ among the vegetation groups or between the burned and unburned sites (Kruskal-Wallis test, χ^2 = 7.322, P = 0.292).

The litter amount was higher in groups E and G than in group B (Kruskal-Wallis test, χ^2 = 18.704, P = 0.005, Steel-Dwass test, t > 2.928, P < 0.05) (Table 2). Group B was distributed mostly in unburned sites, and groups E and G were distributed among burned sites, demonstrating that the litter amount tended to be the highest on burned sites. The litter was mostly composed of tussock-forming monocotyledons (e.g., *C. canadensis*, *C. bigelowii* and *E. vaginatum*). The plots where *C. canadensis* had high cover (i.e., in groups E and G; Table 1) possessed a great amount of litter, indicating that litter accumulation was promoted by the dominance of this species in the area.

The ground-surface roughness was the highest in groups B and D, and it was the lowest in groups A and G (Kruskal-Wallis test, χ^2 = 21.279, P = 0.001; Steel-Dwass test , t > 2.63, P < 0.05) (Table 2). The high roughness was derived from induced thermokarsts, tussock development and/or different burning of organic layer. The mean peat moisture ranged from 52 in group F to 77 in group C, and it was higher in groups A and G than in group F (Kruskal-Wallis test, χ^2 = 18.569, P = 0.005; Steel-Dwass test , t > 2.932, P < 0.05). Group A was located in an unburned site, and group G was located in a burned site, implying that peat moisture was distributed heterogeneously at a small scale, irrespective of fire.

The slope gradient ranged from 0^o to 29^o, and it did not differ among the vegetation types (Kruskal-Wallis test, χ^2 = 11.311, P = 0.079). The steep gradient was mostly derived from thermokarsts. Aspect showed a wide range and did not differ among groups (Kruskal-Wallis test, χ^2 = 5.080, P = 0.534). Because the slope gradient and aspect were mostly determined by thermokarsts, these two topographical characteristics had little effect on the differentiation of vegetation types.

Relationships between plant community and topography

Coefficients of determination on NMDS indicated that the distance from subsidence and litter amount significantly explained the ordination patterns (test of random data permutations, r^2 > 0.071,

$P < 0.01$) and peat moisture and ground-surface roughness ($P < 0.05$). Thaw depth, slope and aspect were not significantly related to the first two axes ($r^2 < 0.037$, $P > 0.075$). The stress was 0.258 and the non-metric fit was significant ($r^2 = 0.934$).

The vegetation groups A to G were ordered from the highest to the lowest scores along the axis I of NMDS (Fig. 3). The scores of groups E to G, which were all burned plots, did not overlap the scores of groups A to D, and group G was separated clearly from groups E and F. This trend was supported by TWINSPAN (Fig. 2) and the ratio of burned plots (Table 2). Because the unburned site did not develop thermokarsts, the distance from subsidence was a surrogate for the damages caused by the 2002 tundra fire. Therefore, the vegetation groups that were established along axis I represented a fire severity gradient.

Axis II was significantly related to peat moisture and surface roughness (Fig. 3). These two factors were significantly different among the cluster groups (Table 2). On axis II, group C showed lower scores than groups F and G. Group F tended to show higher scores than group G (Fig. 3). These results indicated that peat moisture and surface roughness differentiated the vegetation types within the burned site.

With respect to species scores on NMDS (Fig. 4), *C. purpureus* and *E. angustifolium*, *P. commune* and *C. canadensis* showed the lowest scores along axis I. *C. purpureus* and *E. angustifolium* established only on burned plots, and *P. commune* and *C. canadensis* established less often on unburned plots, indicating that these four species preferred to establish after the tundra fire. In addition, these species established mostly on the burned site, but species richness did not differ between groups A and B and groups E and F (Table 1), indicating that species replacement occurred in groups E and F after the tundra fire. *E. vaginatum* and *V. uliginosum* showed high scores along axis II, and *C. bigelowii* and *E. angustifolium* showed low scores. Because axis II reflected peat moisture and surface roughness, the former two species established more frequently on wet and/or rough-surface sites and the latter two were more prevalent on dry and/or smooth-surface sites.

Discussion

Effects of tundra fire on vegetation

Because shrubs, represented by *L. groenlandicum*, *V. vitis-idaea* and *V. uliginosum*, were dominant, the overall plant communities were categorized as tussock-shrub tundra (Viereck et al. 1992). The tundra fire affected the overall vegetation patterns. The revegetation patterns suggested that the 2002 tundra fire burned the ground surface in a heterogeneous and patchy manner. The recovery of ecosystems occurs slowly after a severe disturbance, and more rapidly after a mild disturbance (Tsuyuzaki et al. 2013). The plant cover and albedo returned to the original status by the third plant-growing season after the 2007 Anaktuvuk River fire in tundra (Rocha and Shaver 2011). The net primary productivity returned to the pre-fire status but the biomass was still reduced four years after the 2007 fire (Bret-Harte et al. 2013).

Species richness and/or diversity were relatively high in moderately-burned plots (groups C and D). The species composition changed with the establishment of fire-favored species on burned plots. Intermediate disturbance hypothesis could explain that (Wilson and Tilman 2002). Although fire-favored plants, such as *E. angustifolium* and *C. purpureus*, establish soon after tundra fires (Racine et al. 2004), these fire-favored plants did not become dominant in Kougarok (Narita et al. 2015). These patterns showed that these fire-favored species persisted with low cover for a long time. Therefore, the effects of tundra fire long-lived.

Effects of fire on plant life forms

Lichens were less frequent on burned sites than on unburned sites, although the lichen cover was low even on unburned sites. The recovery of lichens takes longer than vascular plant recovery after wildfires (Jandt et al. 2008).

Shrubs except for *L. groenladicum* showed lower cover on burned sites, particularly, in groups E to G. Since seedlings were few in the plots, vegetative reproduction had an important role on the persistence and revegetation. However, most shrubs did not increase their cover. In contrast, shrubs, including *L. groenladicum* and *Vaccinium* species, recover quickly by vegetative reproduction (as sprouters) when they survive a fire on post-burned forest floor, which is dominated by *Sphagnum* mosses, in a *Picea mariana* forest (Tsuyuzaki et al. 2013). These recovery paces should be related to their climates, i.e., the climate is more stressful in tundra. In addition, the tundra fire in 2002 was more severe than usual and had prolonged effects on the vegetation, although the effects were spatially heterogeneous. In Arctic tundra that does not experience disturbances (such as fires), global warming typically shifts the vascular plant biomass from monocotyledon-dominated tundra to shrub-dominated tundra (Walker et al. 2006; Shuur et al. 2007). The persistence of sprouters and the limited availability of soil nitrogen seem to promote the development of mixed shrub/sedge tussock tundra after severe fire along the Anaktuvuk River, Alaska, unless the permafrost thaws (Bret-Harte *et al.* 2013). The vegetation structures were still different between the burned and unburned sites even 11 years after the tundra fire. To understand the revegetation mechanisms, the behaviors of sprouters, e.g., *Vaccinium*, *Ledum* and *Calamagrostis*, should be mentioned more.

Microtopography derived by thermokarst

Thermokarst was observed only on the burned area. The development of thermokarst after the fire is confirmed by the temporal changes in satellite imagery (Iwahana et al. 2016). However, the thermokarst development did not affect significantly the vegetation patterns in the study sites. These results showed that the fire primarily induced the ground subsidence. Various microenvironments are changed with the development of thermokarsts (Rocha and Shaver 2011; Kokelj and Jorgenson 2013). The post-fire ecosystem increased its thaw depth in non-polygonal areas for 11 years after the tundra fire in the Seward Peninsula, where a deep thaw depth was associated with the monocotyledon-rich areas and a shallow thaw depth was associated with shrub-rich areas (Narita et al. 2015). In contrast, no clear changes in thaw depth were observed within thermokarsts in the polygonal network. One cause should be that the subsidence occurred behind the tundra fire and therefore affected the vegetation patterns later than the fire. In addition, the species composition consisted mostly of perennial shrubs and herbs. The responses of these plants to the gradual environmental changes are often slow due to the vegetative habits (Cotto et al. 2017). However, tall shrub thickets develop rapidly on retrogressive thaw slumps and following tundra fires in ice-rich tundra (Lantz et al. 2010, Jones et al. 2013). The responses of vegetation to tundra fire may be site-or region-specific.

The peat moisture did not differ greatly between the burned and unburned sites for 11 years after the tundra fire, while the peat moisture increased in the burned tussock site in the Seward Peninsula soon after the 2002 fire (Liljedahl et al. 2007). These suggested that the peat moisture recovered rapidly in the burned sites. In addition, the peat moisture was related to the vegetation differentiation in the burned sites. Groups F (*Polytricum*-*Calamagrostis* type) and G (*Calamagrostis*-*Ceratodon*) experienced severe fire within burned sites showed high and low levels of peat moisture, respectively. The peat moisture was affected more by topographical characteristics, such as thermokarsts, than by fire-driven effects after a severe tundra fire, and such topographical characteristics differentiated groups F and G independent of the fire.

The ground surface roughness was higher in group D (*Eriophorum*) and lower in group G on the burned site, and it was higher in group B (*Ledum*) and lower in group A (*Vaccinium*) on the unburned site. The 2002 tundra fire in Kougarok left tussocks and increased surface roughness for a short period of time until 2006 (Liljedahl et al. 2007). *E. vaginatum* was widespread in both the burned and the unburned sites, and it formed tussocks well in Group D where the species richness was high. *E. vaginatum* increases the cover soon after a tundra fire by vegetative reproduction (Narita et al. 2015). *E. vagiantum* seemed to survive through the fire and had facilitative effects in the tundra, as well as in the *Sphagnum* peatland. The tussocks formed by *E. vaginatum* provided litter that facilitated the establishment of cohabitants by ameliorating harsh environments of the *Sphagnum* peatland, except for instances of extreme weather (Koyama and Tsuyuzaki 2013).

Tundra fire reduced soil organic layer, including peat. The trace of charcoal still remained patchily on the ground surface. This reduction has both positive and negative roles on seedling emergence. For example, the reduction assists the seedling emergence of broad-leaved trees and disturbs that of black spruce after a wildfire in a boreal forest (Tsuyuzaki et al. 2014). Since there were few seedlings even on the unburned surface, the effects of organic layer on seedlings seemed to be weak for 11 years after the fire.

Spatio-temporal vegetation patterns

The tundra fire altered the vegetation and topography for a decade at various spatial scales. The vegetation patterns were explained by scale-dependent environmental factors (Tsuyuzaki et al. 2004; Turner et al. 2003). Fire firstly determined the vegetation structure at large scale and then differentiated the vegetation within the burned area through the manipulation of microenvironments.

Remote sensing combined with field monitoring will provide insights into the dynamics of Arctic landscapes, where plant cover varies over short distances due to microtopographic effects (Panda et al. 2010, Gamon et al. 2012). The present study provided evidence that diverse vegetation developed due to a tundra fire because the fire intensity was spatially heterogeneous, such that areas that were affected by severe and moderate fire developed different vegetation patterns.

Acknowledgements The authors thank K. Harada for field assistance. We also thank the staff members of IARC (International Arctic Research Center, University of Alaska at Fairbanks) for various support, including discussion and English improvement. This work was partly supported by IARC-JAXA and JSPS.

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Table 1. Vegetation patterns classified by TWINSPAN in 140 plots on burned and unburned sites, Seward Peninsula, Alaska. The species used as pseudo-species, shown in Fig. 2, are shown. Pseudo-species classified by TWINSPAN are enclosed by frames. Diversity variables and plot cover are shown as the mean and standard deviation. Multiple comparisons in richness, diversity, evenness and cover were performed by the Steel-Dwass test when the ANOVA was significant at $P < 0.05$. The significance of ANOVA is indicated by asterisks on the names of parameters. **: significant at $P < 0.01$. *: significant at $P < 0.05$. NS: not significant. The different letters indicate that the medians are significantly different at $P < 0.05$ using the Steel-Dwass test. Mean cover of each species is shown with frequency in parentheses. +: less than 1%. .: not observed.

Cluster group	A	B	C	D	E	F	G	Total
Number of plots	12	32	14	49	15	10	8	140
Species richness *	6.5 ± 1.4	6.9 ± 1.2	7.5 ± 1.5	7.0 ± 1.2	6.5 ± 0.9	6.2 ± 1.0	5.6 ± 1.4	6.7 ± 1.3
			a	a			b	
Species diversity *	1.47 ± 0.37	1.53 ± 0.21	1.64 ± 0.16	1.47 ± 0.25	1.45 ± 0.18	1.42 ± 0.11	1.19 ± 0.46	1.48 ± 1.28
			a		b	b	b	
Evenness NS	0.79 ± 0.17	0.80 ± 0.08	0.83 ± 0.05	0.76 ± 0.10	0.78 ± 0.09	0.79 ± 0.09	0.68 ± 0.22	0.77 ± 0.11
Species								
Betula nana L.	9 (75)	17 (91)	12 (57)	15 (63)	4 (33)	.	2 (25)	12 (60)
Vaccinium vitis-idaea L.	15 (92)	8 (94)	10 (86)	4 (49)	1 (20)	5 (40)	+ (12)	6 (61)
Vaccinium uliginosum L.	26 (100)	13 (59)	28 (79)	15 (65)	7 (27)	8 (50)	1 (38)	15 (61)
Polytrichum commune Hedw.	+ (8)	.	2 (43)	8 (55)	36 (100)	30 (100)	38 (88)	11 (47)
Calamaglostis canadensis (Michx.) Beauv.	.	+ (6)	4 (29)	3 (63)	38 (100)	27 (100)	44 (100)	10 (50)
Carex bigelowii Torr.	6 (67)	7 (78)	17 (100)	1 (12)	15 (73)	1 (10)	2 (12)	6 (47)
Eriophorum vaginatum L.	22 (75)	15 (97)	9 (93)	32 (98)	11 (80)	32 (90)	4 (38)	21 (89)
Ceratodon purpureus (Hedw.) Brid.	.	.	1 (14)	+ (2)	.	+ (10)	14 (100)	1 (9)
Rubus chamaemorus L.	1 (25)	8 (75)	17 (86)	6 (65)	3 (60)	1 (30)	2 (62)	6 (63)
Ledum groenlandicum Oeder	8 (67)	33 (97)	25 (86)	22 (88)	14 (67)	8 (80)	6 (38)	21 (82)
Sphagnum fuscum (Schimp.) Klinger	9 (58)	+ (3)	.	+ (6)	.	.	.	1 (8)
Epilobium angustifolium L.	.	.	.	+ (8)	5 (60)	+ (10)	.	1 (10)
Cladonia spp.	.	1 (31)	.	+ (2)	.	+ (10)	.	+ (9)
Total plant cover (%) **	110 ± 21	103 ± 18	128 ± 28	115 ± 25	139 ± 33	119 ± 11	115 ± 29	116 ± 26
		a	b		b			

Other species recorded from the plots: *Hylocomium splendens* (Hedw.) Schimp., *Poaceae* sp., *Sphagnum* spp., *Polytrichum formosum* Hedw., *Empetrum* *nigrum* L. ssp. hermaphroditum (Lange ex Hagerup) Bocher, Bryophytes spp. (three species), *Marchantia polymorpha* L., *Umbilicaria* sp., *Peltigera leucophlebia* (Nyl.) Gyelnik, *Betula nana* L., *Calamagrostis canadensis* (Michx.) Beauv., *Polemonium acutiflorum* Willd., *Petasites frigidus* (L.) Franch., *Salix lanata* L., *Salix pulchra* Cham., *Salix* sp., *Cetraria* spp.

Table 2. The characteristics of environmental factors examined in seven vegetation types, A to G, classified by TWINSPAN on burned and unburned sites in Seward Peninsula, Alaska. Each numeral indicates the mean and standard deviation. Multiple comparisons were conducted by the Steel-Dwass test when the Kruskal-Wallis ANOVA was significant. The significance of ANOVA is indicated by asterisks on the names of parameters. **: significant at $P < 0.01$. NS: non-significant. The different letters indicate that the medians are significantly different at $P < 0.05$ using the Steel-Dwass test. Number of plots, see Table 1.

Cluster group	A	B	C	D	E	F	G	Total
Burned plots (%)	0.0	15.6	85.7	98.0	100.0	100.0	100.0	70.0
Distance from subsidence (m) **	14.9 ± 0.7 a	12.4 ± 5.1 a	2.7 ± 5.7 b	3.3 ± 4.0 b	1.7 ± 1.0 b	2.9 ± 2.1 b	3.0 ± 1.8 b	6.1 ± 6.1
Litter amount **	0.73 ± 0.51	0.50 ± 0.38 a	0.69 ± 0.38	0.67 ± 0.56	1.01 ± 0.50 b	0.85 ± 0.47	1.20 ± 0.72 b	0.72 ± 0.52
Thaw depth (cm) NS	38.8 ± 8.8	38.2 ± 7.7	34.7 ± 7.7	37.0 ± 5.4	36.1 ± 3.7	37.8 ± 2.8	39.1 ± 3.6	37. 3 ± 6.3
Ground surface roughness **	6.1 ± 2.4 a	8.8 ± 2.2 b	8.6 ± 3.0	8.7 ± 3.3 b	7.3 ± 3.1	7.2 ± 3.2	5.0 ± 1.4 a	8.0 ± 3.0
Peat moisture (%) **	72 ± 17 a	60 ± 14	77 ± 21	68 ± 18	62 ± 8	69 ± 9 a	52 ± 9 b	66 ± 17
Slope gradient (^{o}) NS	8.3 ± 4.2	11.2 ± 5.7	10.2 ± 5.9	9.9 ± 6.8	8.2 ± 6.4	9.5 ± 6.5	4.2 ± 2.1	9.6 ± 6.1
Aspect (^{o}) NS	18 ± 44	16 ± 57	0 ± 58	22 ± 55	41 ± 50	32 ± 55	19 ± 73	21 ± 55

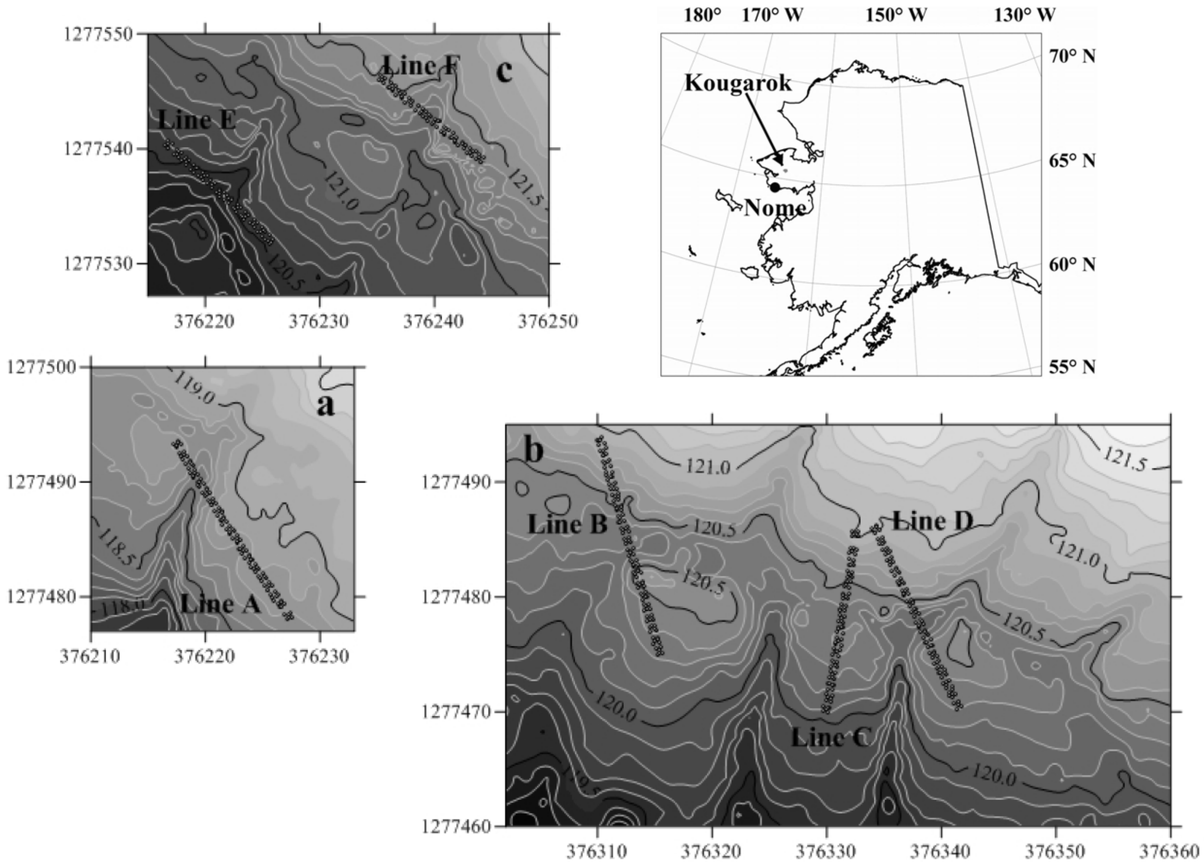

Fig. 1. Topological maps (a-c) shown with the locations of transects A-F, determined by differential GPS survey. Major counter lines are 0.5 m intervals. The coordinate system is given in meters. The right-top map indicates the location of study area (Kougarok) in Alaska.

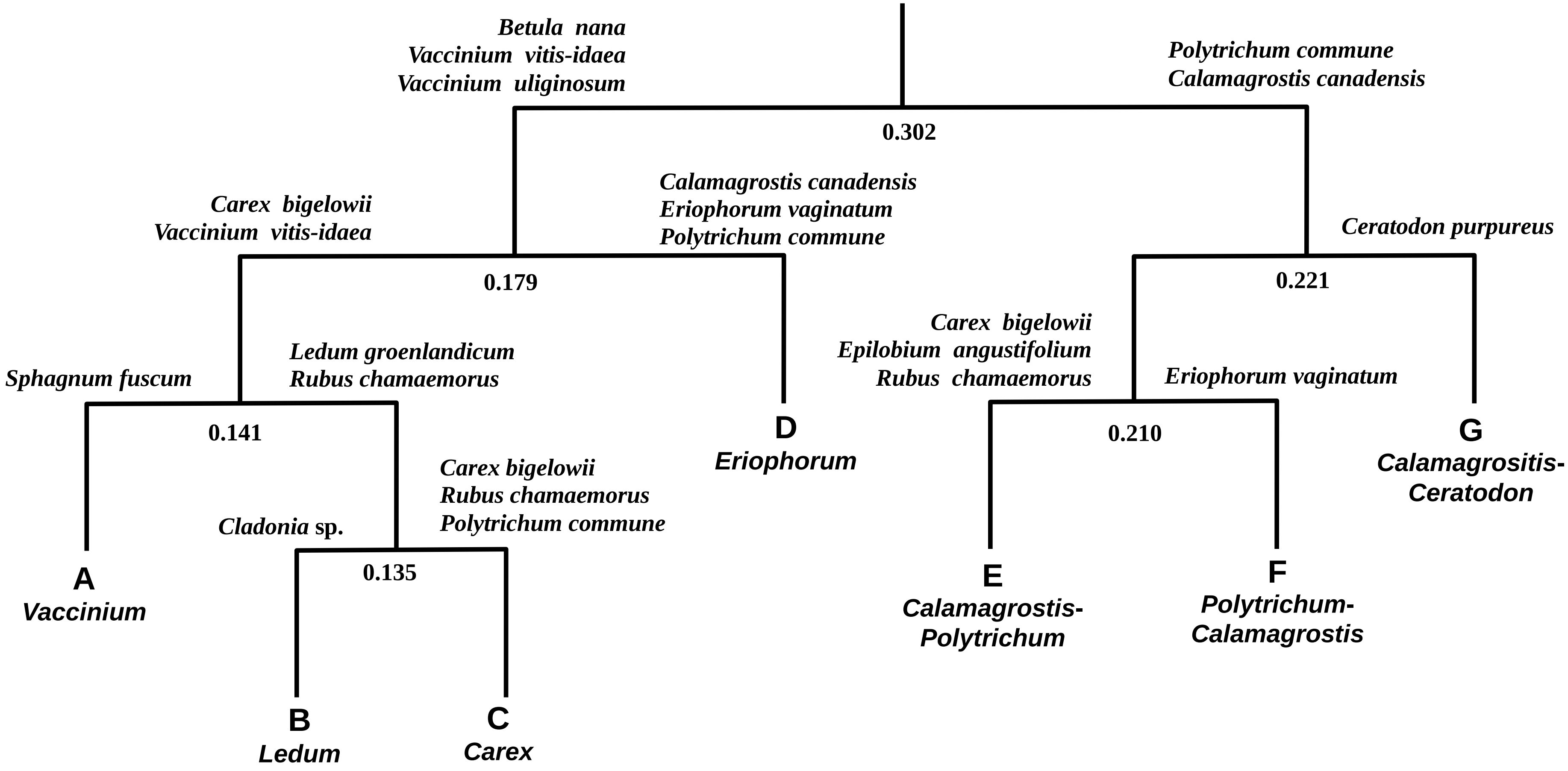

Fig. 2. Vegetation development patterns examined by TWINSPAN using 140 plots in burned and unburned sites, Seward Peninsula, Alaska. Each number indicates an eigenvalue at the division point. The group names, shown below codes A-G, are labelled by the genera of frequently-occurring species. The indicator species that were used for the divisions are shown on the left and right sides of the cluster branches. Refer to Table 1.

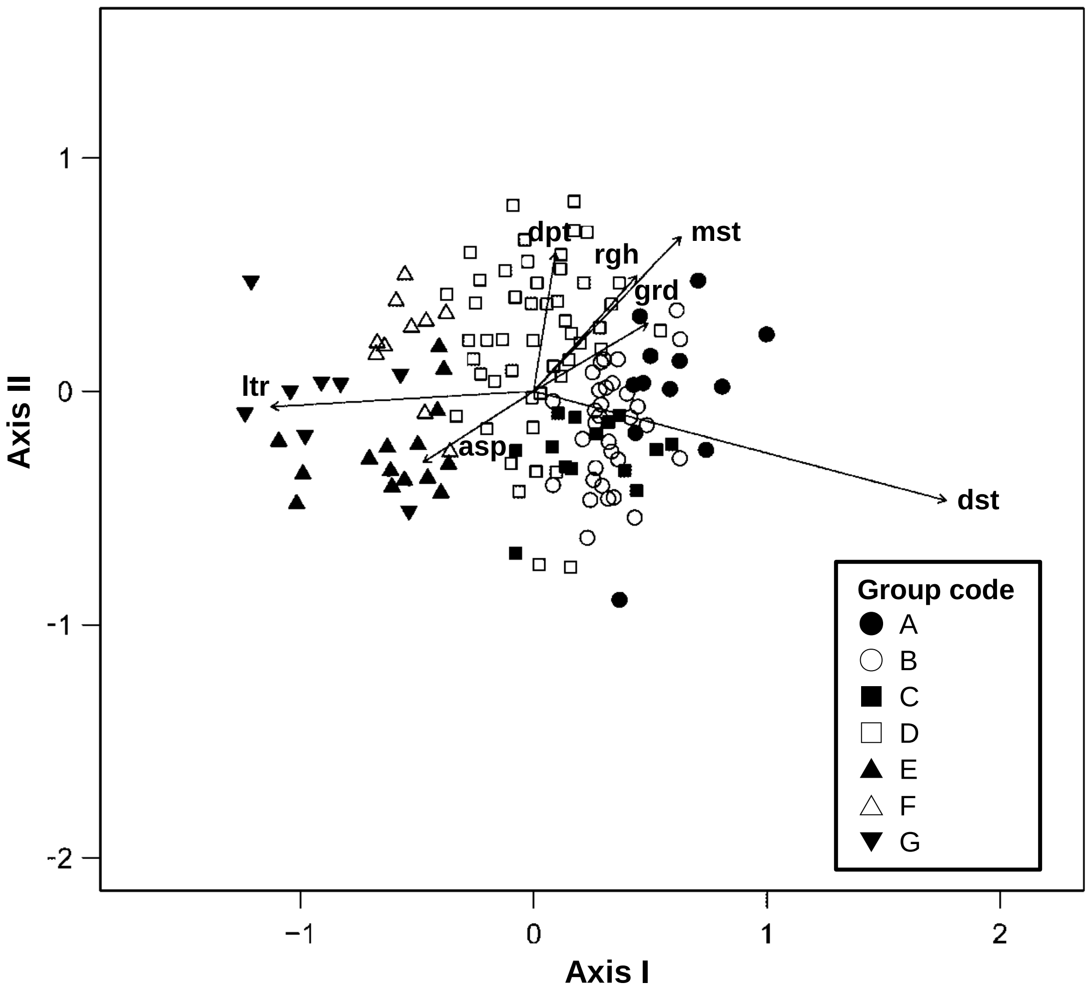

Fig. 3. NMDS ordination diagram on plot scores in 140 50 cm × 50 cm plots surveyed in Seward Peninsula after the 2002 tundra fire. Environmental factors: dst = distance from subsidence, mst = peat moisture, grd = slope gradient, rgh = surface roughness, dpt = thaw depth, ltr = litter amount. See also, Table 1.

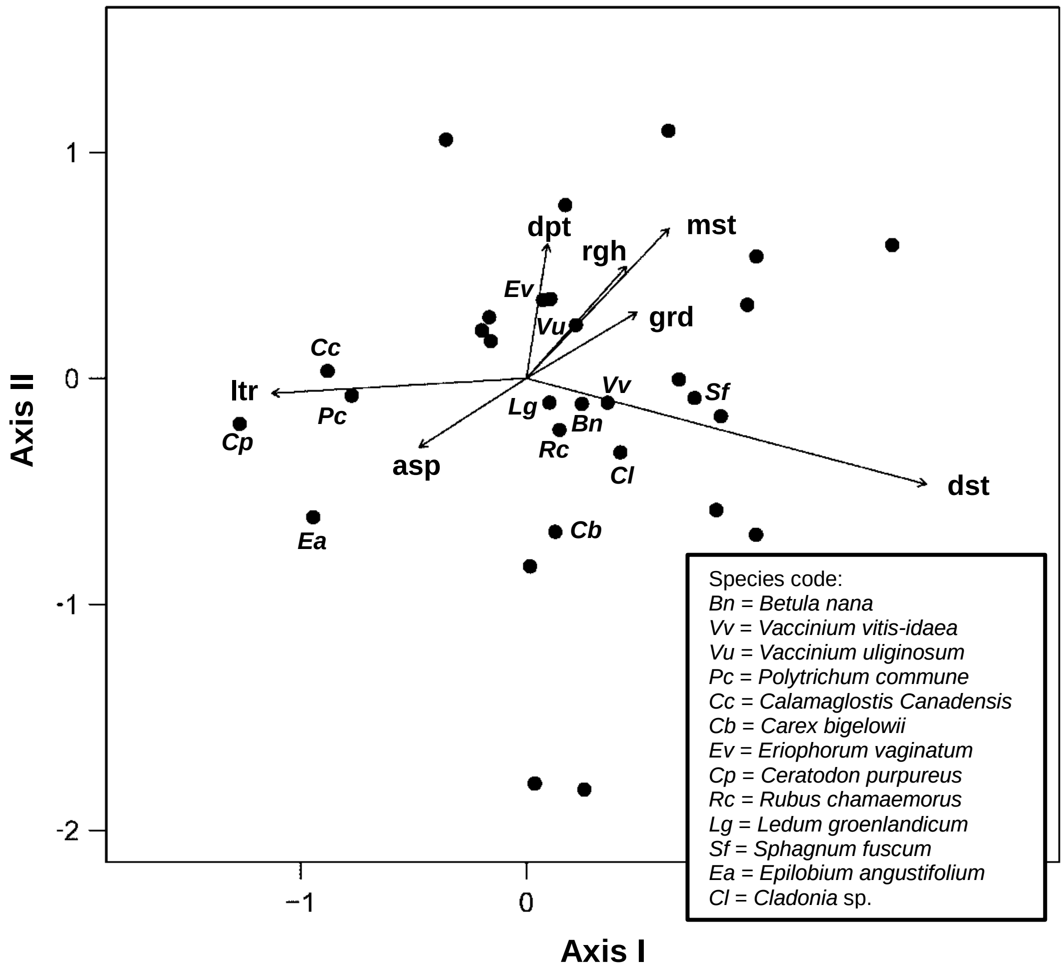

Fig. 4. NMDS ordination diagram on species scores in 140 50 cm × 50 cm plots surveyed in Seward Peninsula after the 2002 tundra fire. The codes of environmental factors, see the same as in Fig. 3.