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Differences in C, N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among plant functional types after a wildfire in a black spruce forest, interior Alaska

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17 **Abstract:** We measured differences in %C, %N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of plant functional types
18 (PFTs) between burned and unburned ground surfaces soon after a wildfire on a
19 north-facing slope in interior Alaska. The C and N were measured for 16 species and
20 *Sphagnum* litter. $\delta^{13}\text{C}$ differed among the PFTs and was low for trees and shrubs,
21 suggesting that woody stems slowed C dynamics or showed low water use efficiency.
22 $\delta^{15}\text{N}$ concentrations suggested that the herbaceous plants depended less on the
23 mycorrhizal associations that became weak on the burned surfaces. The shrub leaves
24 showed the lowest $\delta^{15}\text{N}$ of PFTs and showed higher $\delta^{15}\text{N}$ on the burned surface,
25 showing that N transfer from the soils to the leaves in the shrubs was slowed by the
26 wildfire. Mosses showed the highest C/N ratio. *Sphagnum* litter decomposed faster
27 on the burned surface, and %N and $\delta^{15}\text{N}$ in the litter increased from the second to third
28 year on both burned and unburned surfaces, while %C changed little. In conclusion,
29 the responses to the wildfire differed among the PFTs as characterized by their C and N
30 dynamics.

31

32 *Key words:* Burned and unburned ground surface, carbon (C) and nitrogen (N), Alaskan
33 taiga, plant functional type, stable isotope

34

35

36 Introduction

37 Wildfire changes vegetation structure and function, particularly in *Picea mariana*
38 (P. Mill.) B.S.P. forests in Alaska, USA, and Canada, because the forest regeneration is
39 dependent on wildfire (Chapin et al. 2006; Coogan et al. 2021). Wildfires are
40 becoming more intense due to global warming and will lead to changes in carbon and
41 nitrogen dynamics (Mann et al. 2012). Such intense wildfire in boreal forests changes
42 the succession of forest floor vegetation, consisting of various plant functional types
43 (PFTs), i.e., trees, shrubs, forbs, monocots and mosses (Tsuyuzaki et al. 2013).

44 Carbon (C) and nitrogen (N) status in plants differ among the PFTs, because each
45 PFT has the distinctive strategies for nutrient acquisition (Lambers *et al.* 2008).
46 Mosses represented by *Sphagnum* spp. and *Hylocomium splendens* (Hedw.) Schimp. are
47 often dominant and determine the dynamics of C and N in a peat layer on *Picea*
48 *mariana* forests (Heijmans et al. 2004). Therefore, characterizing C and N status in
49 plants and *Sphagnum* litter is important to evaluate the effects of wildfire on
50 regeneration through changing nutrient dynamics. The dynamics of C and N are
51 affected by temperature and moisture that change microbial activities in and on peat
52 (Moore et al. 2007).

53 Stable isotope analysis has various advantages in the quantification of C and N
54 cycles, represented by $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. Specifically, $\delta^{13}\text{C}$ concentrations in leaves
55 increases with increasing leaf-level intrinsic water use efficiency (WUE) in C_3 plants
56 (Dawson et al. 2002) and $\delta^{15}\text{N}$ concentrations are related to mycorrhizal associations
57 and their related N dynamics (Kwon and Tsuyuzaki 2016). These patterns imply that
58 measuring $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ could detect interactions between WUE, which is reduced by
59 changes in moisture and temperature in the underground after intensive wildfire (Volik
60 et al., 2021), and mycorrhizal associations in boreal forests (Hobbie and Hogberg 2012).
61 We also measured the relationships of decomposition rates of *Sphagnum* litter with peat
62 moisture and temperature, because this litter is a key source of C and N supply to the

63 peat. When wildfires affect litter decomposition rates, C and N dynamics in PFTs
64 might be different between the burned and unburned surfaces. In addition, in the
65 substances low in N, represented by *Sphagnum* mosses (Bengtsson et al. 2018), the C/N
66 concentration ratio is one of the predictors of litter decomposition rate (Taylor et al.
67 1989). Therefore, the litter quality was evaluated for its effect on litter decomposition
68 rate and for its effect on C and N concentrations in plants.

69 The influence of C and N dynamics on vegetation in *Picea mariana* forests from
70 increasing boreal forest wildfires is of interest. This was investigated through analysis
71 of C and N concentrations and isotopic ratios of plants from burned and unburned
72 surfaces. Peat temperature, moisture and decomposition were monitored to support
73 nutrient data. The major objectives of this study were, therefore, the characterization
74 of N, C $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in species- and PFT-based plant groups and in moss litter with its
75 decomposition rates. We examined mainly three hypotheses in relation to C and N in
76 plants and litter: 1) there are different responses of C and N properties among PFTs after
77 wildfire. 2) Mycorrhizal associations and WUE, investigated by $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$,
78 respectively, in plants were altered after wildfire. 3) burned microsites were expected to
79 undergo faster *Sphagnum* litter decomposition, because of the alteration of temperature
80 and moisture.

81

82 **Materials and methods**

83 **Study sites and field measurements**

84 The study site is Poker Flat Research Range, approximately 50 km north of
85 Fairbanks in interior Alaska (Tsuyuzaki et al. 2014). The mean annual temperature
86 was -2.0°C with the maximum and minimum monthly temperatures of 17.2°C in July
87 and -22.4°C in January during 1991 and 2020 (Japan Meteorological Agency 2021).
88 The annual precipitation was 293 mm. A huge wildfire (Boundary Fire) occurred in
89 this region from mid-June to late August 2004. Before the wildfire, the trees were

90 dominated by *Picea mariana* with *Sphagnum*-dominated forest floor. The two types of
91 vegetation developed several years after the wildfire, i.e., burned surfaces that are
92 occupied by non-*Sphagnum*s mosses, shrubs and deciduous trees, and unburned
93 surfaces are dominated by *Sphagnum* mosses (Tsuyuzaki et al. 2013).

94 A time domain reflectometer (TDR) was installed in each of the burned and
95 unburned habitats to measure moisture content (v/v) in peat. The two TDR units
96 (Decagon CDC-EC5, Onset, MA, USA) were close to the center of study area.
97 Substrate moisture was measured at a 15 cm depth below living and dead mosses during
98 May 2006 and May 2007. Temperature profiles at the locations of the moisture
99 measurements were obtained by thermistor sensors (104ET-2, Semitech, Tokyo, Japan)
100 installed at 4, 8 and 15 cm in depths by thermistor sensors.

101

102 **Sample collection and litterbag establishment**

103 In total, 16 species were randomly sampled from any of 16 10 m × 10 m plots
104 established within a 200 m × 400 m study area on the north slope of Poker Flat
105 Research Range at 260-290 m elevations in summers of 2012 to 2014 (Fig. 1). Six 1
106 m × 1 m subplots were randomly established in each plot. The burned area was
107 visually estimated in each plot and each subplot at 5% intervals. Burned ground
108 surfaces comprised a mean of 66% of these 96 subplots, ranging from 0% to 100% area
109 burned (Tsuyuzaki et al. 2014). In this study, a “burned” surface means that most or
110 all of organic layer was removed by the wildfire. Subsequent sampling was conducted
111 in 0% burned or 100% burned subplots or in equivalent areas adjacent to such subplots.
112 Although the dominant species and floristic composition did not change greatly during
113 the surveyed periods (Tsuyuzaki et al. 2013), inter-annual variations in relative
114 abundance were noted.

115 All species were C₃ plants (Coplen et al. 2002), as well-known in Alaska
116 (Woodward et al. 2004), for which $\delta^{13}\text{C}$ in the leaves is expected to be related to

117 leaf-level intrinsic WUE (Dawson et al. 2002). Shrub samples were collected on
118 August 12 2014 and tree, forb, monocot and moss samples were collected on August 18
119 2012. Three samples were collected for each species from each of the burned and
120 from unburned surfaces. All sampled species were common and frequent (Tsuyuzaki
121 et al. 2013), though with 7 species collected from burned habitats, 4 from unburned
122 habitats and 5 species from both habitats, depending on the recovery and establishment
123 patterns. The sampling locations were separated by more than 5 m. For seedlings of
124 tree species less than 25 cm in height, the whole plant, including roots, was collected by
125 digging. For the other species, leaves were cut from the stems with scissors and
126 collected.

127 The species were classified into five PFTs: tree, shrub, monocots (grass, sedge and
128 cottongrass), forb and moss. Of the four shrubs, two species, *Betula nana* L. and
129 *Vaccinium uliginosum* L., are deciduous and two species, *Rhododendron groenlandicum*
130 (Oeder) Kron et Judd and *Vaccinium vitis-idaea* L., are evergreen. *Picea mariana*, one
131 of the examined tree species, is an evergreen needle-leaved species and the other two
132 species, *Populus tremuloides* Michaux and *Betula papyrifera* Marsh., are deciduous
133 broad-leaved species. The properties of C and N were measured for the leaves of all
134 species. In addition, the three parts (roots, stems and leaves) of trees were separately
135 measured to investigate differences in allocation and transport of C and N between
136 burned and unburned habitats (Dawson et al. 2002).

137 *Sphagnum* litter was cut with scissors in a plot where thick litter was accumulated
138 and collected on May 17, 2008. A total of 20 litterbags (10 cm × 15 cm) were made of
139 a polyethylene net with 1-mm pore and were filled with pre-weighted 5-6 g of moss
140 litter after the samples were freeze-dried over seven days. Ten bags were established
141 in a completely-burned plot and 10 bags were established in an unburned plot on August
142 11 2008. These two plots were close to each other to reduce topographical effects.
143 The bags were set up at about 2 m intervals at and around the western edge of the study

144 area. The bags were recovered on August 8 2009 and August 12 2010. At every
145 sampling, five bags were recovered from each of the two habitats. Then, the
146 remaining biomass was weighed soon after sampling and were freeze-dried over seven
147 days until the measurements of %C, %N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were conducted.

148

149 **Measurements of plant properties**

150 The freeze-dried samples of plants and litter for measuring stable isotope were
151 dried at 80°C in an oven for three days and weighed. Then, the samples of plants and
152 litter were finely ground in a mill with a metal blade. %C, %N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were
153 measured with a stable isotope mass spectrometer (Finnigan MAT252, Thermo Fisher
154 Scientific, Yokohama) in GSEES, Hokkaido University (Otaki and Tsuyuzaki 2019).
155 Carbon-to- nitrogen ratio (C/N) was calculated to estimate N use efficiency and
156 degradability of plants (Luo *et al.* 2017). Tree biomass was measured in three parts,
157 leaf, stem and roots, because allocation among these three parts interacts with the N and
158 C transport (Epron *et al.* 2012).

159

160 **Statistical analysis**

161 Generalized linear models (GLMs) were used to compare response variables,
162 i.e., %C, %N, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C/N, among PFTs, among the three plant parts of trees and
163 between the burned and unburned habitats of litter. The PFTs, parts and habitats are
164 used as explanatory categorical variables. Because tree regeneration was a key
165 indicator of vegetation recovery and resilience, differences were compared between
166 trees and the other PFTs and between leaf and the other parts and between burned and
167 unburned habitats. A Gaussian distribution with identity link function was assumed
168 for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C/N and a negative binomial distribution with logit link function was
169 used for %C and %N. Differences in substrate temperatures in the unburned and
170 burned peat and by peat depth were examined by generalized linear mixed-effects

171 model (GLMM) with the assumption of a Gaussian distribution with identity link
172 function and date as the random effect. Peat moisture was compared between the
173 living and dead peat deposits by GLMM as well as the temperatures except for the
174 comparison of depths. These statistical models and results are described in
175 supplementary materials (Tables S1 to S6). All statistical analyses were performed by
176 software R (ver. 3.6.1) (R Core Team 2019).

177

178 **Results**

179 **The litter environments and decomposition of *Sphagnum* mosses**

180 The maximum and minimum temperatures were 21.2°C and -12.6 °C, both of which
181 were recorded at 4 cm deep in the dead moss (Fig. 2). Temperature decreased with
182 increasing peat depths (GLMM, $p < 0.01$). The dead moss showed a higher
183 temperature than the living moss ($p < 0.01$). In total, therefore, the temperature was
184 higher at shallow layers in burned habitats. An interaction between the depths and
185 habitats was detected ($p < 0.01$). Peat moisture ranged from 8.8% to 19.6% and was
186 lower, i.e., drier, in the dead moss ($p < 0.01$).

187 *Sphagnum* litter showed 78.8% and 78.3% mass remaining after one and two years
188 on average. The amount remaining was greater on the unburned surface (GLM, $p <$
189 0.01) (Fig. 3), showing that the litter decomposition was faster on the burned
190 surface. %C in litter samples did not change over the two years ($p > 0.05$) and %N
191 increased from 1.5% to 3.5% ($p < 0.01$). $\delta^{13}\text{C}$ was higher on the burned surface than
192 on the unburned surface, independent of the years ($p < 0.01$), showing that C release
193 from litter was greater on the burned surfaces, as indicated by fast litter decomposition
194 on the burned surfaces. $\delta^{15}\text{N}$ increased with time ($p < 0.01$) and did not differ between
195 the habitats ($p > 0.05$), showing that the wildfire did not affect N dynamics in the litter.
196 C/N ratios decreased slightly from 58.0 to 56.0 and 51.0 on the burned and unburned
197 surfaces, respectively, over one year. C/N decreased greatly to 12.9 and 12.5 on

198 burned and unburned habitats, respectively, after two years. C/N differed between the
 199 years of 2009 and 2010, while C/N was not significantly different between the habitats
 200 overall ($p < 0.01$).

201

202 **Plant functional types**

203 Of the three tree species, the evergreen, needle-leaved tree, *Picea mariana*,
 204 established on both habitats and the other two deciduous, broad-leaved trees, *Populus*
 205 *tremuloides* and *Betula neoalaskana*, established only on the burned surface (Fig. 4).
 206 All the four shrub species established in both habitats. The examined two forbs,
 207 *Polygonum alaskanum* W. Wight ex Hultén and *Epilobium angustifolium* L., established
 208 well on the burned surface while the two monocot species, *Carex bigelowii* Torr. ex
 209 Schwein. and *Eriophorum vaginatum* L., established mostly on the unburned surface.
 210 The four mosses were classified into two types based on the habitat preferences; viz.
 211 *Sphagnum fuscum* (Schimp.) H. Klinggr. and *Hylocomium splendens* (Hedw.) Schimp.
 212 were found only on the unburned surface while *Ceratodon purpureus* (Hedw.) Brid. and
 213 *Polytrichum commune* Hedw. established only on the burned surface.

214 The %C, %N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in leaves varied among the five PFTs (Fig. 4), while
 215 these did not differ between burned and unburned surfaces. As compared to the trees,
 216 the monocots and mosses showed lower %C and shrub had higher %C (GLM, $p < 0.01$).
 217 The mosses showed lower %N than the trees ($p < 0.01$) and therefore, showed higher
 218 C/N than the trees with C/N of four mosses higher than 40, reflecting low values of %N.
 219 C/N ratios ranged from 20 to 60 for all the examined vascular plants except for
 220 *Epilobium angustifolium*, of which C/N ratio was 90. $\delta^{13}\text{C}$ ranged from -33.5‰ to
 221 -25.3‰ for all the examined species. The trees showed the lowest $\delta^{13}\text{C}$ of the five
 222 PFTs and the monocots showed the highest value ($p < 0.01$). $\delta^{15}\text{N}$ showed remarkable
 223 differences among the examined PFTs, i.e., the shrubs showed the lowest $\delta^{15}\text{N}$
 224 (-4.894‰ in average) and herbs (monocots and forbs) showed the highest $\delta^{15}\text{N}$ (5.987‰

225 and 3.950%, respectively) ($p > 0.05$).

226

227 **C and N in shrubs grown in burned and unburned substrates**

228 % C was higher in *Rhododendron groenlandicum* and *Vaccinium vitis-idaea* leaves
229 than in *Betula nana*, while it was lower in *Vaccinium uliginosum* than in *Betula nana*
230 (GLM, $p < 0.01$) (Fig. 5). % N was lower in *Rhododendron groenlandicum* and
231 *Vaccinium vitis-idaea* than in *Betula nana* ($p < 0.01$). Except for high $\delta^{13}C$ in
232 *Rhododendron groenlandicum*, $\delta^{13}C$ did not differ among the other three shrub species
233 ($p > 0.05$). $\delta^{15}N$ was higher in *Vaccinium uliginosum* than in *Betula nana* ($p < 0.05$).
234 $\delta^{15}N$ and $\delta^{13}C$ in the shrub leaves was higher on the burned surface than on the
235 unburned surface (GLM, $p = 0.01$ and 0.04 , respectively), while the % C , % N , C/N did
236 not differ between the two habitats (Fig. 5).

237

238 **Dominant trees**

239 % C in all the three examined tree species did not differ among the three parts, leaf,
240 stem and root (GLM, $p > 0.05$) (Table 1). % N also did not differ among the three tree
241 species ($p > 0.05$). However, % N was higher in leaves than in stems or roots for *Picea*
242 *mariana* on the unburned surface and *Betula papyrifera* on the burned surface ($p < 0.01$).
243 $\delta^{13}C$ in *Picea mariana* was higher in the roots than in the leaves ($p < 0.01$).
244 Furthermore, it was higher on the unburned surface than on the burned surface ($p <$
245 0.01). *Populus tremuloides* showed the highest $\delta^{13}C$ of the tree species on the burned
246 surface ($p < 0.01$). $\delta^{15}N$ did not differ among tree species and among the three parts (p
247 > 0.05). C/N was higher in stems on *Picea mariana* and *Betula papyrifera* on the
248 burned surface ($p < 0.01$).

249

250 **Discussion**

251 **Plant functional types**

252 The mosses with high C/N tended to show lower %C and %N than the vascular
253 plants (Fig. 1), indicating that the mosses stored N less so than the vascular plants.
254 Because %N did not differ among the vascular species, differences in C/N among them
255 were determined mostly by %C. N concentration averages 2.1% and 1.0% for 49
256 boreal vascular plant species on burned and unburned surfaces, respectively, and 1.8%
257 and 0.7% for mosses, soon after a wildfire (Mack 2007). Because mosses, including
258 four species examined in this study (Fig. 4), generally have low N concentrations with a
259 narrow range (Zechmeister et al. 2008), as compared with vascular plants, the difference
260 between the vascular plants and mosses became more than among the vascular
261 plants. %C, %N, $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and C/N ratio did not differ between the burned and
262 unburned habitats, probably because all the PFTs except for shrubs were restricted to
263 one habitat. On the shrub species, all of which were sampled from burned and
264 unburned habitats, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were different between the two habitats. These
265 suggested that C and N dynamics were altered after wildfire when they survived on
266 burned surfaces.

267 The $\delta^{13}\text{C}$ of examined plants, all of which were C_3 plants, showed a wide range
268 among the species, depending on PFTs (Fig. 4). These results suggested that WUE
269 differed greatly among the PFTs, also found in arid regions (Dugas et al. 1996; Peng et
270 al. 2007) and in tropical forests (Wright et al. 2021). $\delta^{13}\text{C}$ was lower in the woody
271 plants (trees and shrubs) than in the herbaceous plants (monocots and forbs). $\delta^{13}\text{C}$ in
272 *Picea mariana*, of the trees, was reduced by the wildfire (Table 1), suggesting that *Picea*
273 *mariana* reduced WUE after wildfire in boreal forests. Soil scarification increases
274 WUE for *Picea mariana* in boreal forests (Wotherspoon et al. 2020), while
275 paludification does not alter WUE for *Picea mariana* in boreal peatlands while
276 decreasing the growth rate (Beaulne et al. 2021). These results showed that the
277 responses of WUE on *Picea mariana* vary with the characteristics of disturbances or
278 habitats. However, the estimation of WUE by $\delta^{13}\text{C}$ must be made with caution

279 because the highest WUE occurs during the driest years and does not always hold true
280 (Golluscio and Oesterheld 2007; Medlyn et al. 2017).

281 Three monocot species showed the highest $\delta^{15}\text{N}$ (Fig. 4). Of the monocots, *Carex*
282 *bigelowii* and *Eriophorum vaginatum*, are non-mycorrhizal plants (Hobbie et al. 2009,
283 Ruotsalainen and Aikio 2011). When plants are non-mycorrhizal, $\delta^{15}\text{N}$ becomes high
284 and stable because there is no fractionation of N isotopes (Hobbie and Agerer 2010).
285 Therefore, $\delta^{15}\text{N}$ of *Carex bigelowii* and *Eriophorum vaginatum* can be used as the
286 benchmark to investigate the dependence of plants on mycorrhizal fungi. Another
287 monocot, *Calamagrostis canadensis*, showed high $\delta^{15}\text{N}$, as well. The development of
288 mycorrhizal fungi in *Calamagrosits canadensis* roots might be expected to be low after
289 disturbance by wildfire. Although the mycorrhizal association of *Polygonum*
290 *alaskanum*, a forb, is unknown, a phylogenetically and morphologically similar species,
291 *Polygonum sachalinense*, is non- or less- arbuscular mycorrhizal (Obase et al. 2008).
292 Low $\delta^{15}\text{N}$ in the leaves also suggested that mycorrhizal associations are low for the
293 monocots and forbs. $\delta^{15}\text{N}$ of shrubs was higher on the burned surfaces. $\delta^{15}\text{N}$ varies
294 among species and PFTs, corresponding with mycorrhizal association in the plant roots
295 (Aerts et al. 2009). Three of the four shrubs, showing low $\delta^{15}\text{N}$, develop ericoid
296 mycorrhizae (Hbobie et al. 2009). Furthermore, all of these shrubs tended to show
297 higher $\delta^{15}\text{N}$ on the burned habitat (Fig. 5), suggesting that the mycorrhizal associations
298 were weakened by the wildfire. Short-term environmental factors may interact with
299 species- or PFT-specific plant traits related to water and N use strategies and override
300 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Gatica et al. 2017).

301

302 ***Sphagnum* litter**

303 The *Sphagnum* litter decomposed faster on the burned surface (Fig. 3). The
304 albedo is higher on dead or burned *Sphagnum* mosses than on the unburned, living
305 mosses (Chambers et al. 2005, Tsuyuzaki et al. 2009). The peat moisture decreased

306 with increasing temperature on the burned surface, probably due to evaporation. In
307 addition, high evaporation of living mosses induces cooling effects on the temperature
308 in peat in a boreal black spruce forest (Heijmans et al. 2004). Litter decomposition
309 increases with increasing temperature and rainfall due to microbial activities in various
310 wetlands (Bell et al. 2018). These relationships suggest that intensive wildfires change
311 nutrient dynamics in the ground by accelerating litter decomposition, due probably to
312 high temperature and low water content in the burned ground (Fig. 2). Low water
313 content in peat results in great aeration and opportunities for aerobic decomposition
314 (Granath et al. 2016).

315 N loss was influenced less by the wildfire, as shown by no differences of %N and
316 $\delta^{15}\text{N}$ between burned and unburned habitats. %N increased drastically from 2009 to
317 2010, probably because N immobilization in *Sphagnum* litter was absent during the first
318 year and then occurs (Bragazza et al. 2001). C/N decreased drastically in the second
319 year, due mostly to an increase in %N that was 4-6 times higher in 2010 than in
320 2009. %C did not change with time. These results suggested that the wildfire
321 enhanced the loss of N-unbounded components more in the second year. C-use
322 efficiency in litter increases when the litter is N-poor, as shown in the initial stage of
323 litter decomposition in this study because the decomposers are initially N-limited
324 (Manzoni 2017). The decomposition of *Sphagnum* litter, which is made mostly of
325 cellulose, is limited in lignin or phenolic compounds as well as the N availability of the
326 microbes (Hajek 2009).

327 It should also be noted that C/N ratios are diverse among *Sphagnum* species. The
328 initial litter of *Sphagnum angustifolium* showed C/N ratios of 25-30 two years after
329 installing litterbags in a peat bog in northeastern Hungary (Peli et al. 2016). The initial
330 C/N of *S. balticum* C/N was 66 in an Alaskan tundra habitat (Hobbie 1996).
331 *Sphagnum fuscum* litter had C/N values of more than 100 in a peatland-forest complex,
332 British Columbia, Canada, even two in two years after setting up litterbags (Asada et al.

2005). The decomposition of *Sphagnum* litter may be more species-specific than previously thought because differences in litter decomposition rates are related to carbon quality more than to nitrogen concentration (Hobbie 1996). Of the four moss species, *Polytrichum commune* showed the highest $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Fig. 4). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values as measured for *Polytrichum juniperinum* on unburned surfaces in an interior Alaska were -28.8‰ and 3.0‰, respectively (Mack, 2007). These results may reflect the fact that *Polytrichum* mosses develop water-conducting tissue (Glime 2017), which probably accounts for the stable isotope signatures.

341

342 **Behaviors of shrubs and trees**

343 The shrubs established in both burned and unburned habitats and did not show
344 significant differences in the properties of C and N among them, except for $\delta^{15}\text{N}$ (Fig.
345 5). Six shrub species, including *Vaccinium vitis-idaea* and *Rhododendron*
346 *groenlandicum*, had been previously shown to have higher %N on unburned surfaces
347 (Mack 2007), as found in this study. These shrubs regenerated mostly by vegetative
348 reproduction on the two habitats (Tsuyuzaki et al. 2013). Vegetative reproduction
349 often alleviates resource limitation through below-ground nutrient transport under
350 stressful conditions or in disturbed habitats (Lovett Doust and Lovett Doust 1990).
351 Their capabilities to adapt to various habitats, particularly on the burned surface via
352 vegetative reproduction, should facilitate their establishment and growth and
353 consequently did not show the significant differences of chemical properties between
354 the two habitats due to belowground nutrient transport.

355 On the burned surfaces, *Picea mariana* allocated to the aboveground biomass more
356 than *Betula papyrifera* and to the height growth more than *Populus tremuloides* (Fig. 6).
357 These two broad-leaved tree species, which are pioneer trees after wildfire (Chapin et al.
358 2006), do not establish on the unburned surfaces while they establish well on the burned
359 surfaces (Tsuyuzaki et al. 2014). However, *Picea mariana* grows in height much more

360 slowly than do the broad-leaved trees (Tsuyuzaki et al. 2014).

361 In conclusion, the Boundary Wildfire, which altered the temperature and water
362 content in peat, greatly affected C dynamics, particularly through the *Sphagnum* litter
363 and *Picea mariana* shoots. The N dynamics were characterized well by the
364 combination of PFTs (in particular, differences among woody, herbaceous and moss
365 species), burned vs. unburned habitats and mycorrhizal associations.

366

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373

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509 indicative value for nitrogen deposition patterns and source allocation on a
510 nationwide scale. *Environ. Sci. Technol.* **42**: 8661-8667.

511 **Table 1.** Carbon content (%), nitrogen content (%), $\delta^{13}\text{C}$ (‰), $\delta^{15}\text{N}$ (‰) and C/N ratio in three tree species established on burned or
 512 unburned habitats. Each cell shows mean with standard deviation. For statistical differences, see appendix (Table S5).

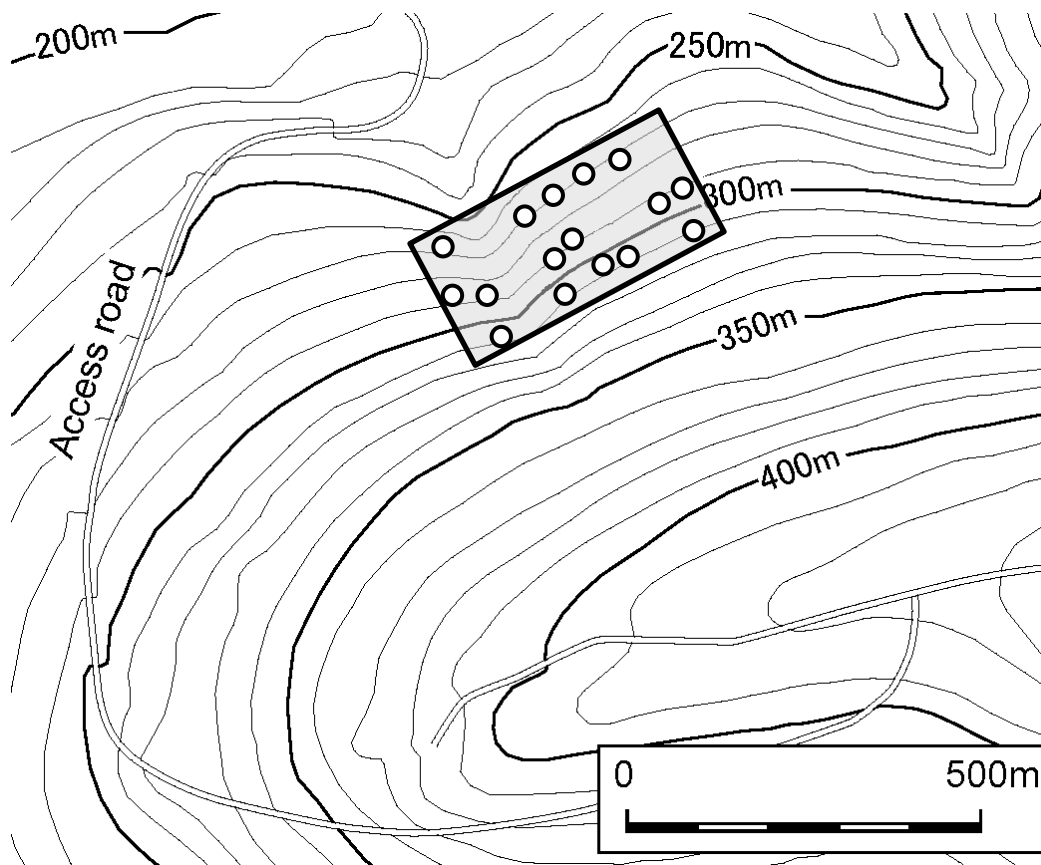
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Habitat	Species	Tissue	Carbon (%)	Nitrogen (%)	C/N	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
Unburned	<i>Picea mariana</i>	Leaf	48.9 ± 1.7	1.57 ± 0.35	32.0 ± 6.6	-31.4 ± 0.2	0.49 ± 2.09
		Stem	52.4 ± 0.9	0.84 ± 0.17	64.5 ± 14.3	-30.3 ± 0.4	-3.22 ± 1.43
		Root	49.7 ± 1.4	1.37 ± 0.05	36.2 ± 2.0	-29.1 ± 0.7	-1.20 ± 0.77
Burned	<i>Picea mariana</i>	Leaf	49.5 ± 0.6	1.03 ± 0.12	48.6 ± 5.7	-31.7 ± 0.8	-0.01 ± 2.09
		Stem	49.0 ± 3.6	0.63 ± 0.17	81.4 ± 20.9	-31.5 ± 1.0	-1.74 ± 1.85
		Root	47.9 ± 2.2	1.29 ± 0.29	38.5 ± 8.1	-30.9 ± 0.2	2.25 ± 1.10
	<i>Betula neoalaskana</i>	Leaf	47.4 ± 0.8	1.24 ± 0.16	38.6 ± 5.3	-30.5 ± 0.9	0.83 ± 2.67
		Stem	51.6 ± 1.9	0.74 ± 0.11	70.8 ± 12.1	-30.7 ± 0.8	0.11 ± 2.87
		Root	48.0 ± 0.9	0.94 ± 0.18	59.4 ± 5.9	-30.4 ± 0.3	1.07 ± 1.95
	<i>Populus tremuloides</i>	Leaf	50.5 ± 1.2	1.71 ± 0.35	30.4 ± 5.0	-30.5 ± 0.1.2	0.68 ± 1.98
		Stem	49.4 ± 1.9	0.75 ± 0.24	73.1 ± 28.2	-30.1 ± 1.4	-0.68 ± 1.77
		Root	47.3 ± 1.6	0.94 ± 0.18	52.0 ± 10.4	-29.0 ± 0.4	0.37 ± 1.66

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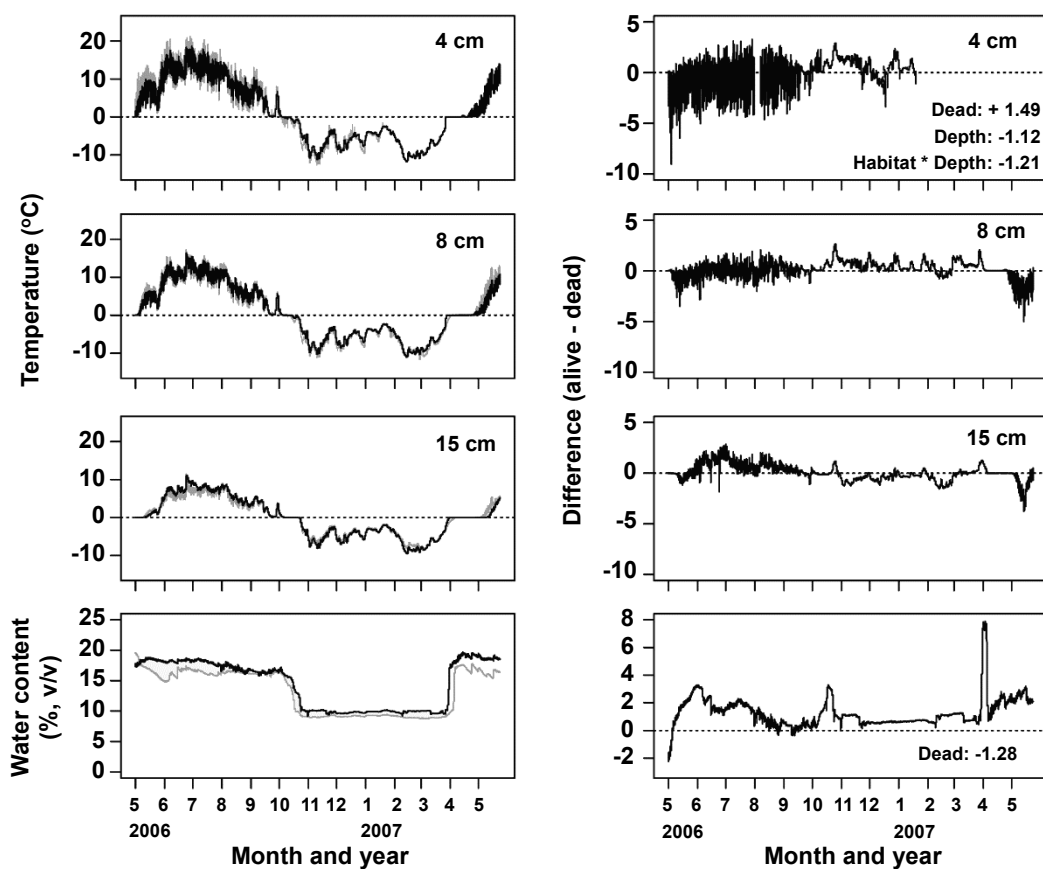
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519 **Fig. 1.** Study area (+65.12, -147.46), shown by a gray square, in Poker Flat Research
520 Range, interior Alaska. Open circles indicate the locations of 16 10 m × 10 m plots for
521 surveying revegetation patterns after the 2004 wildfire. North is upward on the map.
522 The coordinates are confirmed by GoogleEarth.

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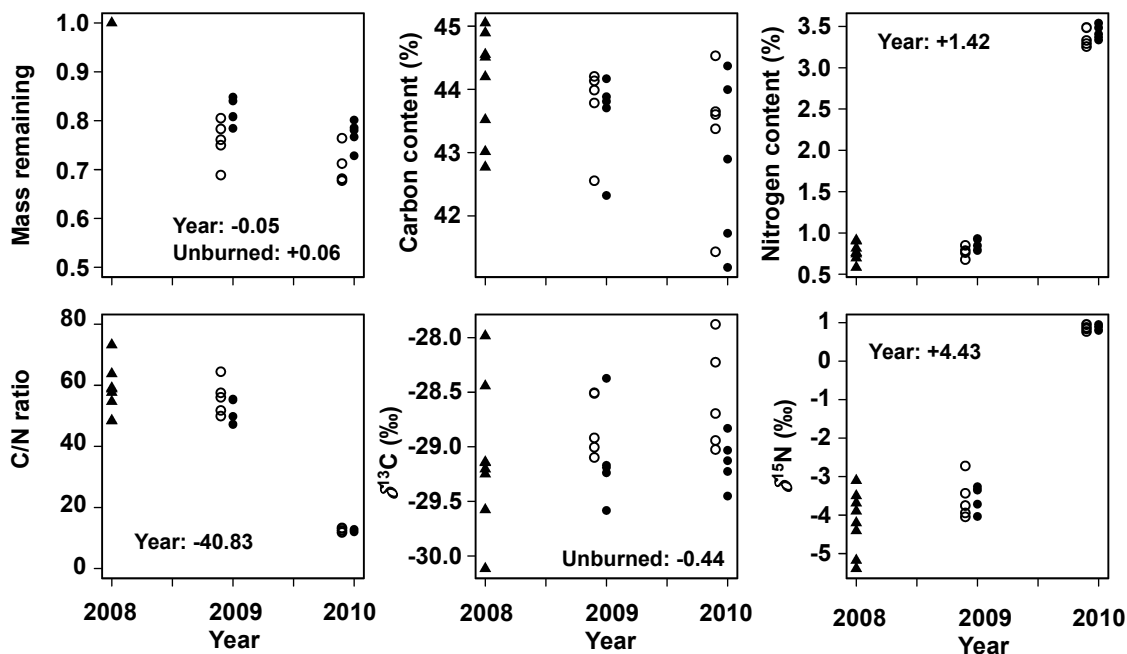
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530 **Fig. 2.** Fluctuations of temperature and water content at 4, 8 and 15 cm in
 531 living and dead *Sphagnum* mats. Left panels: black and grey lines show living and
 532 dead *Sphagnum* mats, respectively. Right panels: differences between the living and
 533 dead mats (living minus dead mats). The overall differences are confirmed statistically
 534 by GLMM ($p < 0.001$). Temperature at 4 cm depth in the living moss is absent after
 535 January 2007, because of data logger breakdown.
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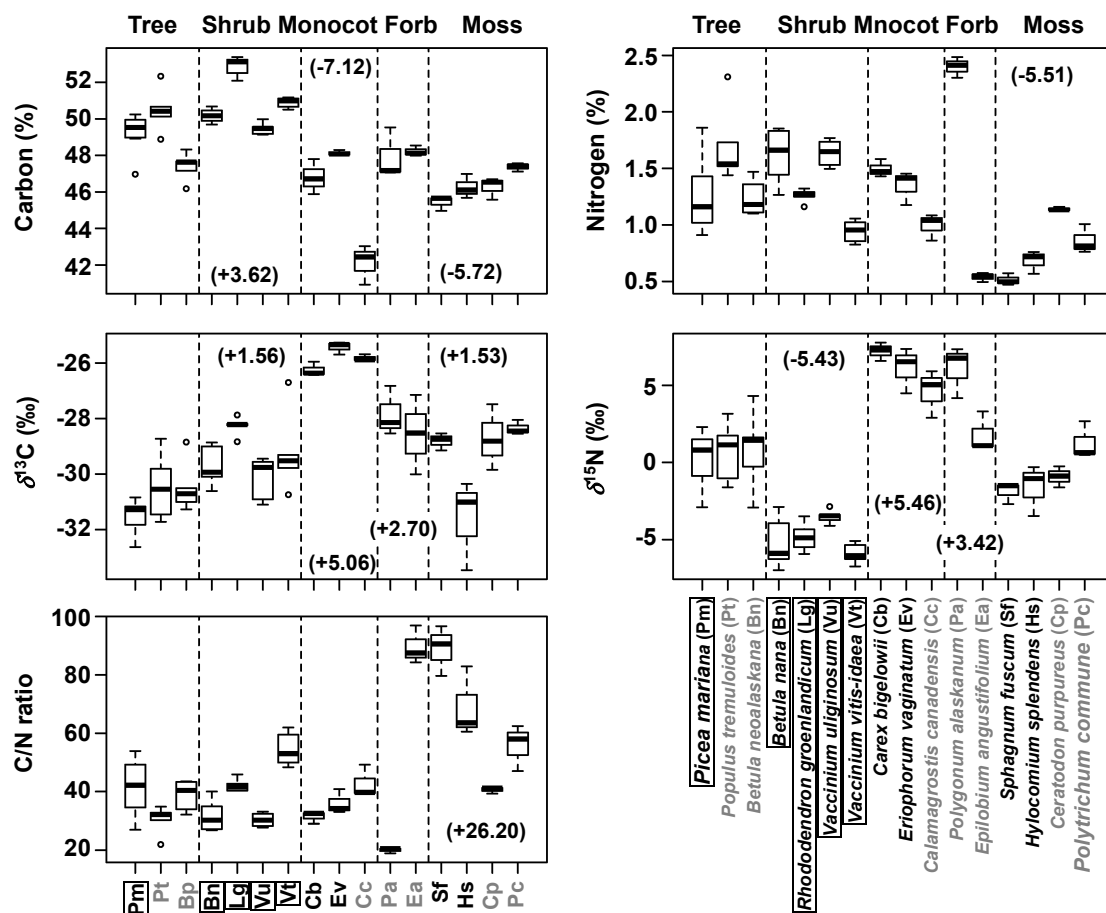
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540 **Fig 3.** Yearly fluctuations of chemical properties (mass remaining, carbon content,
 541 nitrogen content, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in *Sphagnum* litter on the burned (open circles) and
 542 unburned (closed circles) habitats. Triangles indicate the initial status prior to setting
 543 the litterbags up in the field. Differences among the years and between the habitats are
 544 examined by GLM ($p < 0.01$). The litterbags were set up in the summer of 2008.
 545 When the estimates are significantly different, the difference in estimates is indicated in
 546 each panel.

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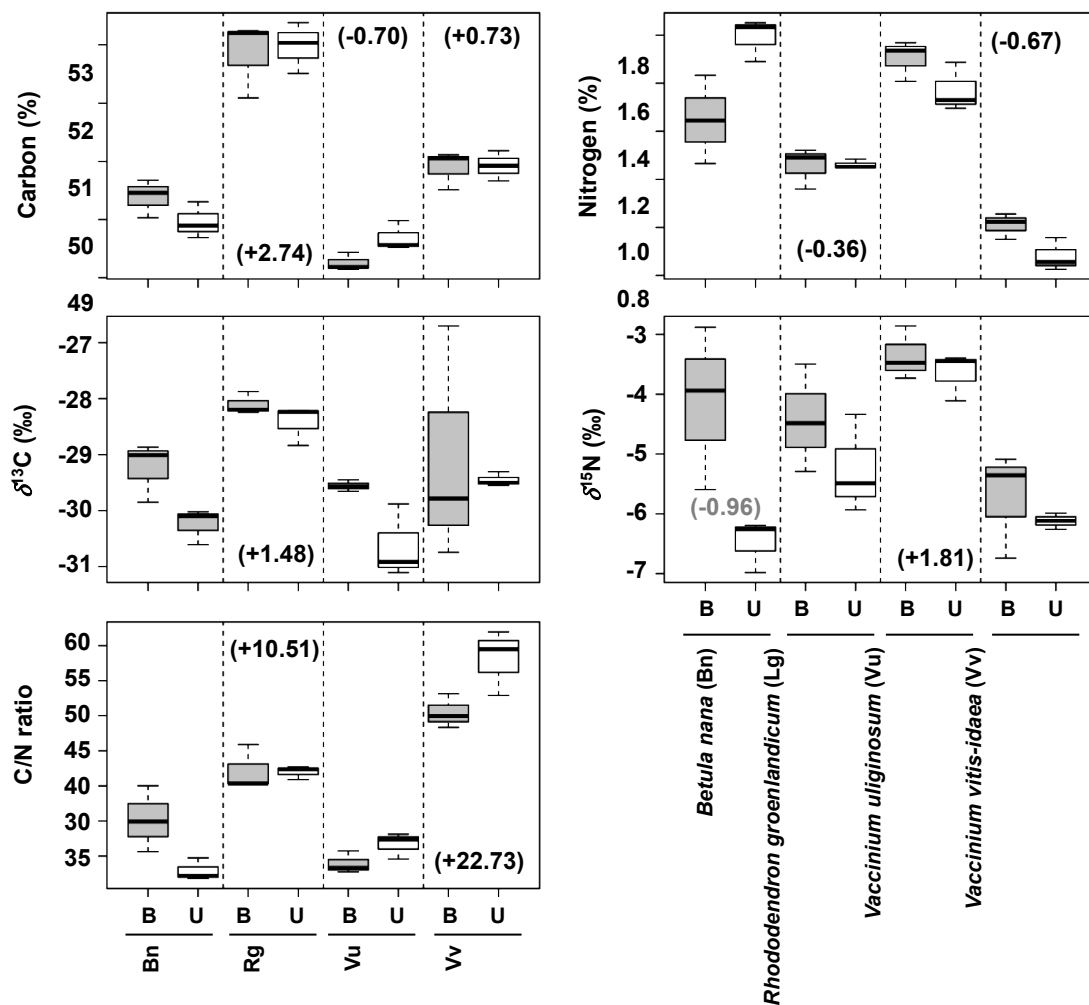
552 **Fig. 4.** Carbon content (%), nitrogen content (%), $\delta^{13}\text{C}$ (‰), $\delta^{15}\text{N}$ (‰) and C/N ratio in
 553 the leaves of 16 boreal plant species. The species are classified into five plant
 554 functional types (PFTs). Black, grey and enclosed letters indicate the samples
 555 collected from the unburned, burned and both habitats. Differences between each PFT
 556 and trees and between burned and unburned surfaces were examined by GLM ($p < 0.01$).
 557 The differences between the burned and unburned surfaces are not significant at $p >$
 558 0.05 for all the response variables. When the estimates are significantly different, the
 559 difference in estimates is shown in the parentheses.

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567 **Fig. 5.** Chemical properties, carbon content (%), nitrogen content (%), $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and
 568 C/N ratio in the leaves of shrubs, collected in 2014 from burned (B) and unburned (U)
 569 surfaces. The differences between the two habitats and among species were examined
 570 by GLM ($p < 0.01$). When the estimates are significantly different, the difference in
 571 estimates is shown in parentheses. The comparisons by GLMs were conducted
 572 between burned to unburned habitats (shown on each species in black letters) and
 573 between *Betula nana* to the other shrub species. See also, Fig. 2.