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Author(s)	Tsuyuzaki, Shiro; Kwon, TaeOh; Takeuchi, Fumiko; Otaki, Michiru; Sawada, Yuki
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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

Shiro Tsuyuzaki, TaeOh Kwon, Fumiko Takeuchi, Michiru Otaki, and Yuki Sawada

S. Tsuyuzaki, T. Kwon, F. Takeuchi and M. Otaki. Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060-0810 Japan.

Yuki Sawada. Faculty of Urban Management, Fukuyama City University, Fukuyama 721-0964 Japan.

Corresponding author: S. Tsuyuzaki (email: tsuyu@ees.hokudai.ac.jp).

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

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

Introduction

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

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

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

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

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

Materials and methods

Study sites and field measurements

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

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

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

Sample collection and litterbag establishment

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

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

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

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

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

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

Measurements of plant properties

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

Statistical analysis

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

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

Results

The litter environments and decomposition of *Sphagnum* mosses

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

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

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

Plant functional types

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

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

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

C and N in shrubs grown in burned and unburned substrates

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

Dominant trees

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

Discussion

Plant functional types

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

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

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

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

***Sphagnum* litter**

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

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

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

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

Behaviors of shrubs and trees

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

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

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

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

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References

- Aerts, R., Callaghan, T.V., Dorrepaal, E., van Logtestijn, P., and Cornelissen J.H.C. 2009. Seasonal climate manipulations result in species-specific changes in leaf nutrient levels and isotopic composition in a sub-arctic bog. *Funct. Ecol.* **23**: 680-688.
- Asada, T., Warneer, B., and Aravena, R. 2005. Effects of the early stage of decomposition on change in carbon and nitrogen isotopes in *Sphagnum* litter. *J. Plant Ecol.* **1**: 229-237.
- Bell, M.C., Ritson, J.P., Verhoef, A., Brazier, R.E., Templeton, M.R., Graham, N.J.D., Freeman, C., and Clark, J.M. 2018. Sensitivity of peatland litter decomposition to changes in temperature and rainfall. *Geoderma* **331**: 29-37.
- Bengtsson, F., Rydin, H., and Hajek T. 2018. Biochemical determinants of litter quality in 15 species of *Sphagnum*. *Plant and Soil* **425**: 161-176.

- 387 Bragazza, L., Buttler, A., Siegenhaler, A., and Mitchell, E.A.D. 2001. Plant litter
388 decomposition and nutrient release in peatlands. *Geophys. Monogr. Ser.* **184**:
389 99-110.
- 390 Chambers, S.D., Beringer, J., Randerson, J.T., and Chapin, F.S. III. 2005. Fire effects on
391 net radiation and energy partitioning: contrasting responses of tundra and boreal
392 forest ecosystems. *J. Geophys. Res. Atmos.* **110**: D09106.doi:10.1029/2004JD
393 005299.
- 394 Chapin III, F.S., Moilanen, L., and Kielland, K. 1993. Preferential use of organic
395 nitrogen for growth by a non-mycorrhizal arctic sedge. *Nature* **361**:150–153.
- 396 Chapin III, F.S., Oswood, M.W., van Cleve K., Viereck, L.A., and Verbyla, D.L. 2006.
397 *Alaska's changing boreal forest*. Oxford University Press, Oxford.
- 398 Coogan, S.C.P., Daniels, L.D., Boychuk, D., Burton, P.J., Flannigan, M.D., Gauthier, S.,
399 Kafka, V., Park, J.S., and Wotton, B.M. 2021. Fifty years of wildland fire science in
400 Canada. *Can. J. For. Res.* **51**: 283-302.
- 401 Coplen, T.B., Böhlenke, J.K., De Bié P., Ding T., Holden N.E., Hopple J.A., Krouse K.J.,
402 Lamberty, A., Peiser, H.S., Révész, K., Rieder, S.E., Rosman, K.J.R., Roth, E.,
403 Taylor, P.D.P., Vocke, Jr., R.D., and Xiao, Y.K. 2002. Isotope-abundance variation
404 of selected elements. *Pure Appl. Chem.* **74**: 1987-2017.
- 405 Dawson, T.E., Mambelli, S., Plamboeck, A.H., Templer, P.H., and Tu, K.P. 2002. Stable
406 isotopes in plant ecology. *Ann. Rev. Ecol. Syst.* **33**: 507-559.
- 407 Dugas, W.A., Hicks, R.A., and Gibbens, R.P. 1996. Structure and function of C₃ and C₄
408 Chihuahuan Desert plant communities. Energy balance components. *J. Arid*
409 *Environ.* **34**: 63-79.
- 410 Epron, D., Bahn, M., Derrien, D., Lattanzi, F.A., Pumpanen, J., Gessler, A., Hogberg, P.,
411 Maillard, P., Dannoura, M., Gerant, D., and Buchmann, N. 2012. Pulse-labelling
412 trees to study carbon allocation dynamics: a review of methods, current knowledge
413 and future prospects. *Tree Physiol.* **32**: 776-798.

- Gatica, M.G., Aranibar, J.N., and Pucheta, E. 2017. Environmental and species-specific controls on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in dominant woody plants from central-western Argentinian drylands. *Austral Ecol.* **42**: 533-543.
- Glime, J.M. 2017. Chapter 7-1. Water relations: conducting structures. *In*: Glime, J.M. Bryophyte ecology. Vol. 1. Michigan Technology University, Houghton. 7-1-1 - 7-1-28.
- Golluscio, R.A., and Oesterheld, M. 2007. Water use efficiency of twenty-five co-existing Patagonian species growing under different soil water availability. *Oecologia* **154**: 207-217.
- Granath, G., Moore, P.A., Lukenbach, M.C., and Waddington, J.M. 2016. Mitigating wildfire carbon loss in managed northern peatlands through restoration. *Scientific Rep.* **6**: 28498, doi: 10.1038/srep28498.
- Hajek, T. 2009. Habitat and species controls on *Sphagnum* production and decomposition in a mountain raised bog. *Boreal Env. Res.* **14**: 947-958.
- Heijmans, M.M.P.D., Arp, W.J., and Chapin III, S. 2004. Controls on moss evaporation in a boreal black spruce forest. *Global Biogeochem. Cycles* **18**: GB2004, doi: 10.1029/2003BG002128.
- Hobbie, E.A., and Hogberg, P. 2012. Nitrogen isotopes link mycorrhizal fungi and plants to nitrogen dynamics. *New Phytol.* **196**: 367-382.
- Hobbie, J.E., Hobbie, E.A., Drossman, H., Conte, M., Weber, J.C., Shamhart, J., and Weinrobe M. 2009. Mycorrhizal fungi supply nitrogen to host plants in Arctic tundra and boreal forests: ^{15}N is the key signal. *Can. J. Microbiol.* **55**: 84-94.
- Hobbie, S.E. 1996. Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecol. Monogr.* **66**: 503-522.
- Hobbie, S.E., and Agerer, R. 2010. Nitrogen isotopes in ectomycorrhizal sporocarps correspond to belowground exploration types. *Plant Soil* **327**: 71-83.
- Japan Meteorological Agency. 2021. ClimatView. Fairbanks, AK. <https://www.data.jma>.

go.jp/gmd/cpd/monitor/climatview/graph_mkhtml.php?n=70261&y=2013&m=8&s
=3&r=4&e=3&k=0&d=0

Kwon, T., and Tsuyuzaki, S. 2016. Differences in nitrogen redistribution between early
and late plant colonizers through ectomycorrhizal fungi on the volcano Mount
Koma. *Ecol. Res.* **31**: 557-567.

Lambers, H., Chapin, III F.S., and Pons, T.L. 2008. *Plant physiological ecology (2nd
edition)*. Springer, Berlin.

Lovett Doust, J., and Lovett Doust, L. 1990. *Plant reproductive ecology: patterns and
strategies*. Oxford University Press, Oxford.

Luo, W., Li, M.-H., Sardans, J., Lu, X.-T., Wang, C., Penuelas, J., Wang, Z., Han, X.-G.,
and Jiang, Y. 2017. Carbon and nitrogen allocation shifts in plants and soils along
aridity and fertility gradients in grasslands of China. *Ecol. Evol.* **7**: 6927-6934.

Mack, M.C. 2007. Biomass %N, %C, natural abundance ¹⁵N and ¹³C isotopic signatures
for common and rare under-and overstory plants in long unburned and burned
(1999) boreal forest stands, Caribou-Poker Creek and Delta Junction, Bonanza
Creek LTER. UAF, Fairbanks. <https://www.lter.uaf.edu/data/data-detail/id/522>
(unpublished data).

Mann, D.H., Rupp, T.S., Olson, M.A., and Duffy P.A. 2012. Is Alaska's boreal forest
now crossing a major ecological threshold? *Arct. Antarct. Alp. Res.* **44**: 319-331.

Manzoni, S. 2017. Flexible carbon-use efficiency across litter types and during
decomposition partly compensates nutrient imbalances-results from analytical
stoichiometric models. *Front. Microbiol.* **26**: Article 661. doi: 10.3389/fmicb.
2017.00661.

Medlyn, B.E., De Kauwe, M.G., Lin, Y.-S., Knauer, J., Duursma, R.A., Williams, C.A.,
Arneth, A., Clement, R., Isaac, P., Limousin, J.-M. 2017. How do leaf and
ecosystem measures of water-use efficiency compare? *New Phytol.* **216**: 758-770.

Moore, T.R., Bubier, J.L., and Bledzki, L. 2007. Litter decomposition in temperate

peatland ecosystems: the effect of substrate and site. *Ecosystems* 10: 979-963.

Obase, K., Tamai, Y., Yajima, T., and Miyamoto, T. 2008. Mycorrhizal colonization status of plant species established in an exposed area following the 2000 eruption of Mt. Usu, Hokkaido, Japan. *Landscape Ecol. Eng.* 4: 57-61.

Otaki, M., and Tsuyuzaki, S. 2019. Succession of litter-decomposing microbial organisms in deciduous birch and oak forests, northern Japan. *Acta Oecol.* 101, 103485.

Peli, E.R., Nagy, J., and Cserhalmi, D. 2016. Decomposition rate, and carbon and nitrogen dynamics of Sphagnum litter: lessons from a peat bog. *Pol. J. Ecol.* 64: 231-240.

Peng, Y., Jiang, G.M., Liu, X.H., Niu, S.L., Liu, M.Z., and Biswas, D.K. 2007. Photosynthesis, transpiration and water use efficiency of four plant species with grazing intensities in Hunshandak Sandland, China. *J. Arid Environ.* 70: 304-315.

R Core Team. 2019. R: *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ruotsalainen, A.L., and Aikio, S. 2011. Mycorrhizal inoculum and performance of nonmycorrhizal *Carex bigelowii* and mycorrhizal *Trientalis europaea*. *Canad. J. Bot.* 82: 443-449.

Taylor, B.R., Parkinson, D., and Parsons, W.F.J. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70: 97-104.

Tsuyuzaki, S., Kushida, K., and Kodama, Y. 2009. Recovery of surface albedo and plant cover after wildfire in a *Picea mariana* forest in interior Alaska. *Clim. Change* 93: 517-525.

Tsuyuzaki, S., Narita, K., Sawada, Y., and Harada K. 2013. Recovery of forest-floor vegetation after a wildfire in a *Picea mariana* forest. *Ecol. Res.* 28: 1061-1068.

Tsuyuzaki, S., Narita, K., Sawada, Y., and Kushida, K. 2014. The establishment patterns of tree seedlings are determined immediately after wildfire in a black spruce (*Picea*

- 495 *mariana*) forest. Plant Ecol. **215**: 327-337.
- 496 Volik, O., Petrone, R., Kessel, E., Green, A., and Price, J. 2021. Understanding the peak
497 growing season ecosystem water-use efficiency at four fens in the Athabasca oil
498 sands region. Hydrol. Proc. **35**: e14323.
- 499 Woodward, F.I., Lomas, M.R., and Kelly, C.K. 2004. Global climate and the distribution
500 of plant biomes. Proc. Royal Soc. B **359**: 1465-1476.
- 501 Wotherspoon, A., Thiffault, N., and Bradley, R.L. 2020. Resource availability and
502 physiological response of black spruce to scarification in two climatic regions of
503 Québec (Canada). Silva Fennica **54**: 10375. doi: 10.14214/sf.10375.
- 504 Wright, C.L., de Lima, A.L.A., de Souza, E.S., West, J.B., and Wilcox, B.P. 2021. Plant
505 functional types broadly describe water use strategies in the Caatinga, a seasonally
506 dry tropical forest in northeast Brazil. Ecol Evol. **11**: 11808-11825.
- 507 Zechmeister, H.G., richter, A., Smidt, S., Hohenwallner, D.H., Order, I., Maringer, S.,
508 and Wanek, W. 2008. Total nitrogen content and $\delta^{15}\text{N}$ signatures in moss tissue:
509 indicative value for nitrogen deposition patterns and source allocation on a
510 nationwide scale. Environ. Sci. Technol. **42**: 8661-8667.

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 unburned habitats. Each cell shows mean with standard deviation. For statistical differences, see appendix (Table S5).

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

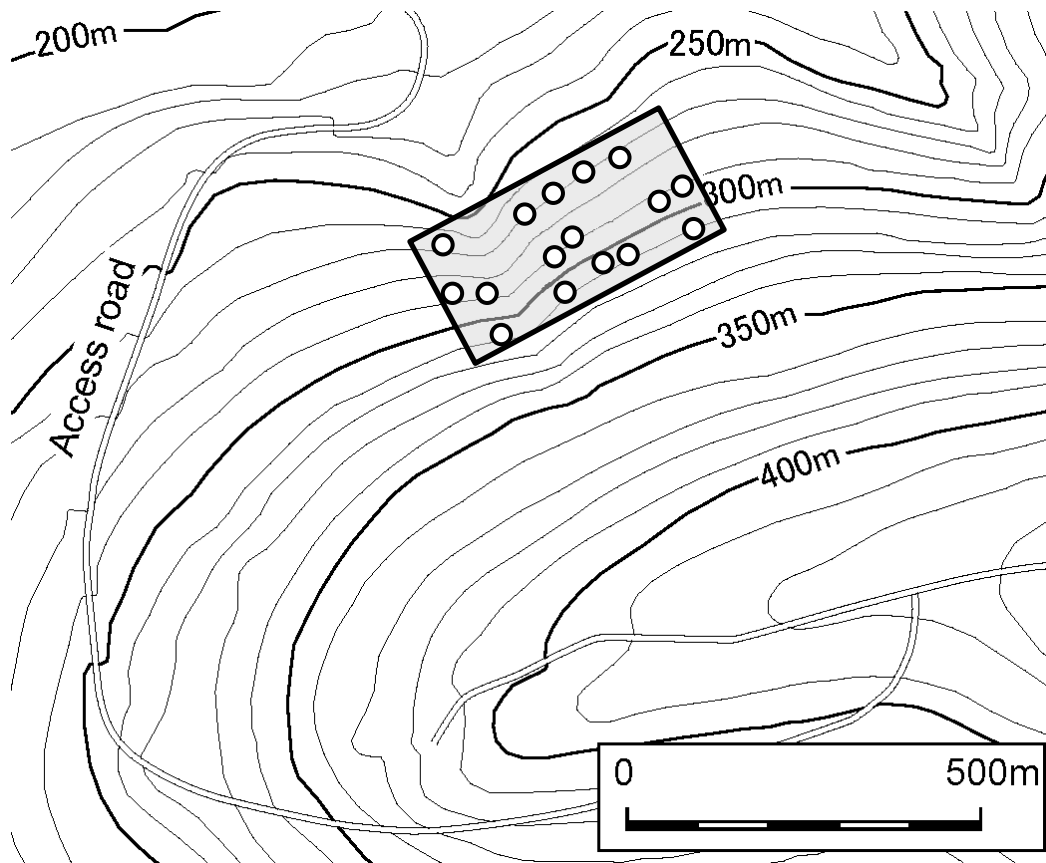


Fig. 1. Study area (+65.12, -147.46), shown by a gray square, in Poker Flat Research Range, interior Alaska. Open circles indicate the locations of 16 10 m × 10 m plots for surveying revegetation patterns after the 2004 wildfire. North is upward on the map. The coordinates are confirmed by GoogleEarth.

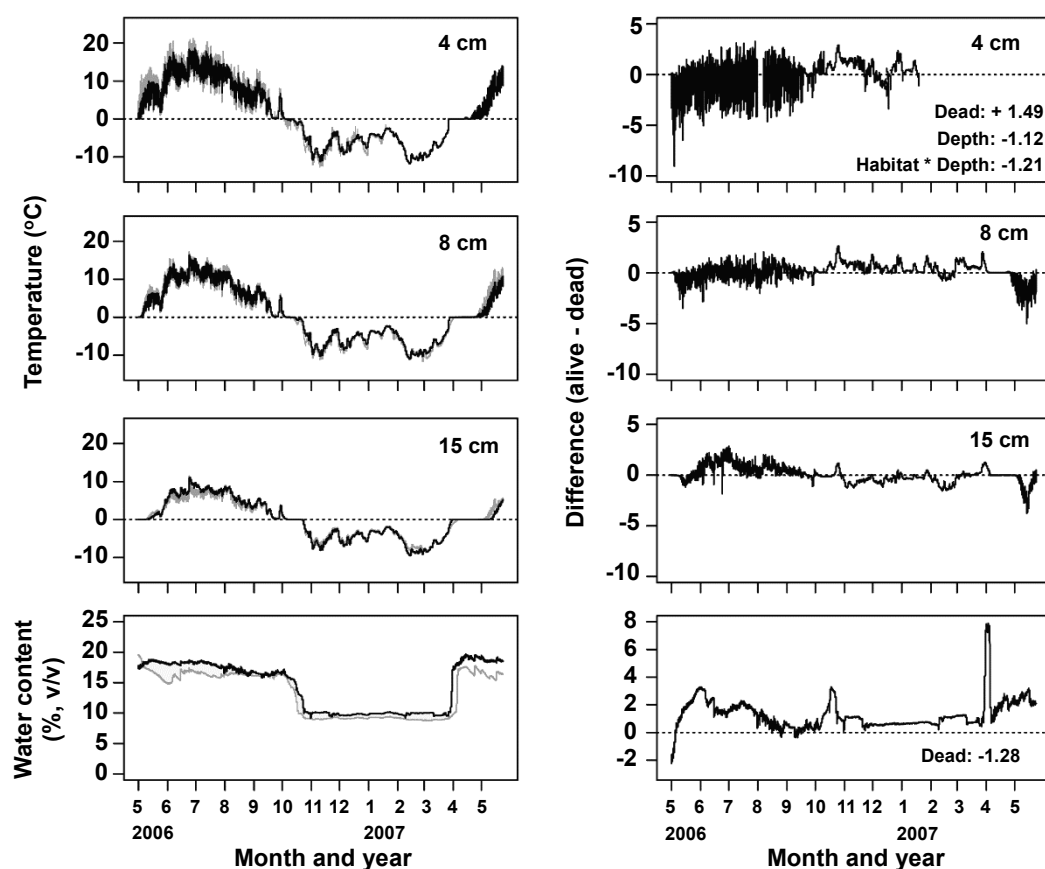


Fig. 2. Fluctuations of temperature and water content at 4, 8 and 15 cm depths in living and dead *Sphagnum* mats. Left panels: black and grey lines show living and dead *Sphagnum* mats, respectively. Right panels: differences between the living and dead mats (living minus dead mats). The overall differences are confirmed statistically by GLMM ($p < 0.001$). Temperature at 4 cm depth in the living moss is absent after January 2007, because of data logger breakdown.

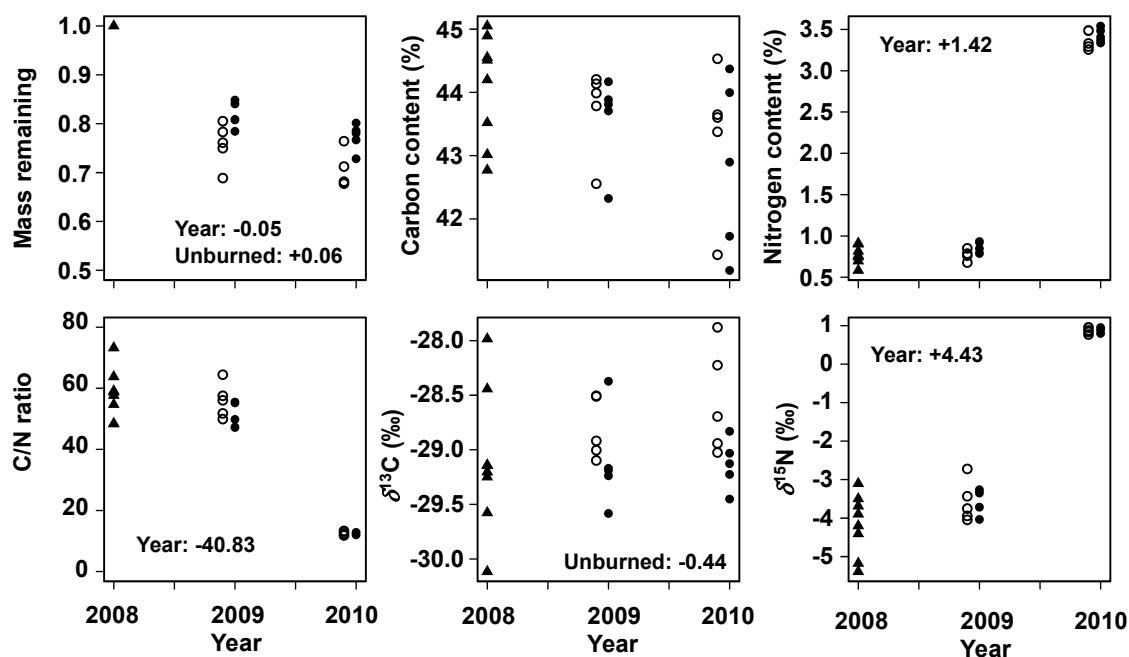


Fig 3. Yearly fluctuations of chemical properties (mass remaining, carbon content, nitrogen content, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in *Sphagnum* litter on the burned (open circles) and unburned (closed circles) habitats. Triangles indicate the initial status prior to setting the litterbags up in the field. Differences among the years and between the habitats are examined by GLM ($p < 0.01$). The litterbags were set up in the summer of 2008. When the estimates are significantly different, the difference in estimates is indicated in each panel.

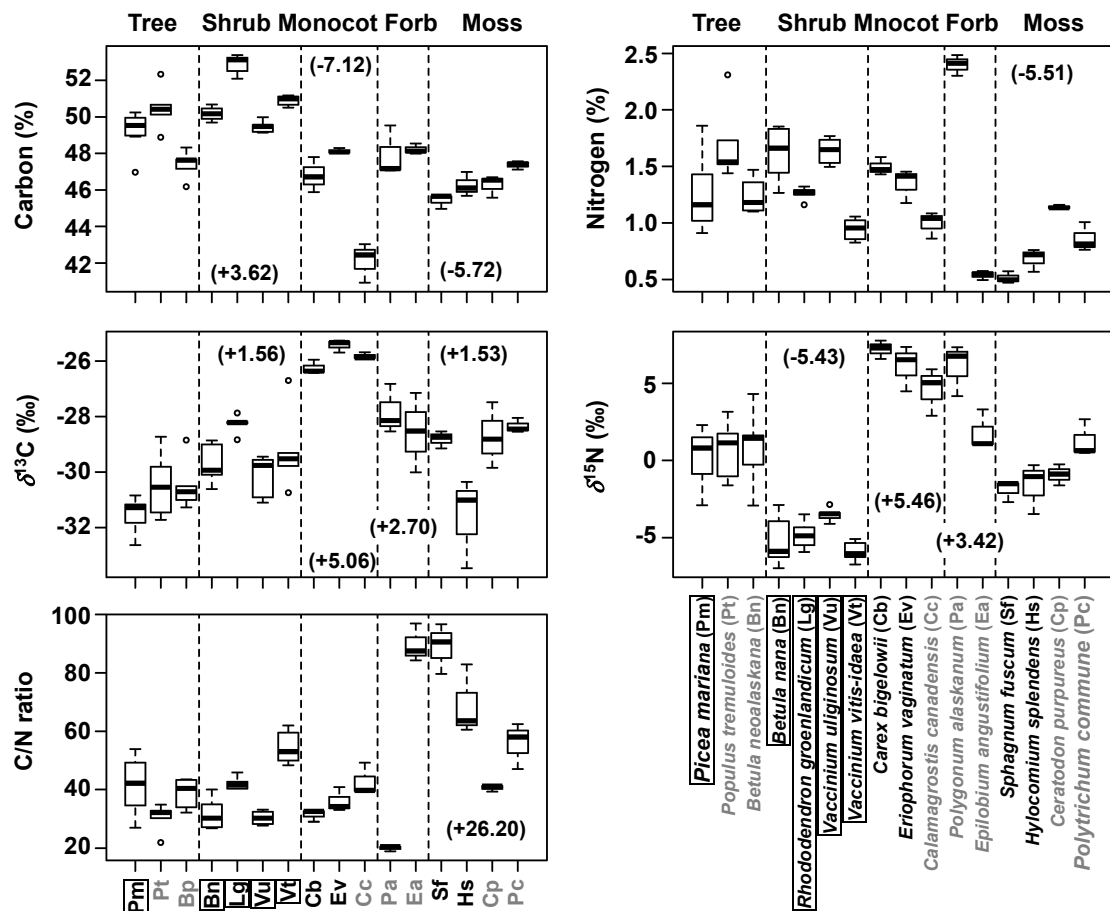


Fig. 4. Carbon content (%), nitrogen content (%), $\delta^{13}\text{C}$ (‰), $\delta^{15}\text{N}$ (‰) and C/N ratio in the leaves of 16 boreal plant species. The species are classified into five plant functional types (PFTs). Black, grey and enclosed letters indicate the samples collected from the unburned,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



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