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Mineral element recycling in topsoil following permafrost degradation and a vegetation shift in sub-Arctic tundra

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ABSTRACT

Climate change affects the Arctic and sub-Arctic regions by exposing previously frozen permafrost to thaw, unlocking soil nutrients, changing hydrological processes, and boosting plant growth. As a result, sub-Arctic tundra is subject to a shrub expansion, called "shrubification", at the expense of sedge species. Depending on the intrinsic foliar properties of these plant species, changes in foliar mineral element fluxes with shrubification in the context of permafrost degradation may influence topsoil mineral element composition. Despite the potential implications of changes in topsoil mineral element concentrations for the fate of organic carbon, this remains poorly quantified. Here, we investigate vegetation foliar and topsoil mineral element composition (Si, K, Ca, P, Mn, Zn, Cu, Mo, V) across a natural gradient of permafrost degradation at a typical sub-Arctic tundra at Eight Mile Lake (Alaska, USA). Results show that foliar mineral element concentrations are higher (up to 9 times; Si, K, Mo for all species, and for some species Zn) or lower (up to 2 times; Ca, P, Mn, Cu, V for all species, and for some species Zn) in sedge than in shrub species. As a result, a vegetation shift over ~40 years has resulted in lower topsoil concentrations in Si, K, Zn, and Mo (respectively of 52, 24, 20, and 51%) in highly degraded permafrost sites compared to poorly degraded permafrost sites due to lower foliar fluxes of these elements. For other elements (Ca, P, Mn, Cu, and V), the vegetation shift has not induced a marked change in topsoil concentrations at this current stage of permafrost degradation. A modeled amplified shrubification associated with a further permafrost degradation is expected to increase foliar Ca, P, Mn, Cu, and V fluxes, which will likely change these element concentrations in topsoil. These data can serve as a first estimate to assess the influence of other shifts in vegetation in Arctic and sub-Arctic tundra such as sedge expansion under wetter soil conditions.

1. Introduction

Permafrost (i.e., ground that remains below 0 °C for at least two consecutive years) is thawing upon climate change (IPCC, 2021; Schuur et al., 2015; Van Everdingen, 1998). This is leading to a release of carbon (C) into the atmosphere with decomposition of organic C estimated at 120–195 Pg by 2100 (Hugelius et al., 2014; IPCC, 2021; Schuur et al., 2015). The release of C into the atmosphere as greenhouse gases (CO_2 and CH_4) that increase air temperature contributes to a positive feedback effect on warming and deeper permafrost degradation (Koven et al., 2011; Schuur et al., 2015). Another consequence of climate change and permafrost degradation is the shift in vegetation in Arctic and sub-arctic tundra (7.11×10^6 km^2; Walker et al., 2005) that is primarily dominated by shrubs, sedges, forbs, mosses, and lichens (Bliss et al., 1973). The nutrients released by permafrost degradation, the increasing air temperature and the drier conditions in the long term promote the growth of shrubs and decrease the biomass of sedges due to competition (Heijmans et al., 2022; Mekonnen et al., 2021). Thus, we are facing a shift in vegetation from sedges (mainly *Eriophorum* spp. and *Carex* spp.; Crawford, 2013) to shrubs, called "shrubification", resulting from permafrost degradation (Sturm et al., 2001). However, permafrost degradation and the resulting changes in air temperature, soil moisture, and soil nutrients are not the only drivers of vegetation change in Arctic and sub-Arctic tundra. Other processes like wildfires can promote the

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expansion of sedges (Heijmans et al., 2022; Mekonnen et al., 2021).

Shifts in vegetation can influence organic C decomposition in topsoil, mainly composed of plant residues, changing CO_2 and CH_4 emissions, which could enhance permafrost degradation (Berg and McClaugherty, 2020; Heijmans et al., 2022). Indeed, shrub expansion increases soil temperature by accumulating a thicker snow cover that insulates the soil. In addition, the presence of tall shrubs growing above the snowpack reduces the albedo. Together, these factors associated with shrub expansion contributes to speed up topsoil organic C decomposition (Heijmans et al., 2022; Marsh et al., 2010; Myers-Smith and Hik, 2013). Moreover, shrubrification leads to a higher biomass production which can promote the priming effect and increase organic C decomposition rate (Mekonnen et al., 2021). Conversely, woody species have a lower organic C decomposition rate than sedge species, that limits the effects which accelerate decomposition (Hobbie, 1996). Other factors, depending or not on plant biomass and plant community, affect topsoil decomposition, including organic matter quality (carbon-to-nitrogen ratio), physical and chemical protection of the organic C (Waldrop et al., 2010), microbial biomass and community, soil conditions (temperature and moisture; Bracho et al., 2016), and the mineral element concentrations (Schmidt et al., 2011).

Some mineral elements, such as silicon (Si), calcium (Ca), potassium (K), phosphorus (P), manganese (Mn), zinc (Zn), copper (Cu), molybdenum (Mo), and vanadium (V) influence organic C decomposition in topsoil: these elements can act on the growth (Qualls and Richardson, 2000; Schaller and Struyf, 2013) or the environment (Lovett et al., 2016) of decomposers (microorganisms and fungus); and some of these elements (such as Ca and Mn) can create complexes with organic C through organo-mineral associations, thereby limiting organic C decomposition (Keiluweit et al., 2015; Li et al., 2021). Furthermore, these mineral elements are nutrients for plants and are more specifically essential macroelements (Ca, K, and P), essential microelements (Mn, Zn, Cu, and Mo) and beneficial elements (Si and V) (Marschner, 2011). These mineral elements promote plant growth, improve protection against stress (Si, K, and Cu; Greger et al., 2011; Marschner, 2011), regulate the osmotic potential (K; Clarkson & Hanson, 1980), are involved in the redox reactions during photosynthesis (Mn, Cu, and V; Graham et al., 1988), are structural elements (Ca and P; White & Broadley, 2003), are involved in the fixation of atmospheric N (Mo and V; Schwarz et al., 2009) or in DNA replication (Zn; Broadley et al., 2007). However, the influence of vegetation shift on the recycling of these mineral element and their concentrations in topsoil in the context of permafrost degradation remain poorly quantified. This includes considering the relationship between changes in soil temperature and soil moisture associated with permafrost degradation and mineral element recycling by vegetation.

Here, our main objective is to quantify the influence of the widely observed shrubification upon permafrost degradation on topsoil mineral element concentrations (Si, K, Ca, P, Mn, Zn, Cu, Mo, and V). The shrubification following permafrost degradation at Eight Mile Lake (Alaska, USA) is used as a case study to explore consequences of different shifts in Arctic tundra vegetation such as sedge expansion under wetter soil conditions. To reach our main objective, our specific goals are: (1) quantifying the foliar concentrations of these mineral elements in the main sedge and shrub species of sub-Arctic tundra; (2) estimating the foliar fluxes of these mineral elements that return to topsoil; and (3) measuring topsoil concentrations of these mineral elements along a permafrost degradation gradient.

2. Materials and methods

2.1. Study area

The field campaign was conducted in August – September 2019 in Alaska (USA), at Eight Mile Lake (63°52′42.1″N, 149°15′12.9″W), approximately 14 km west of Healy (Fig. 1, Vogel et al., 2009). The area is a moist acidic tundra at an elevation of 700 m a.s.l. on a northeast-facing slope (4%). The mean annual temperature in Healy was −1.3 °C between 1976 and 2005 with extreme temperature in December (−16 °C) and in July (15 °C), the mean annual precipitation (rain and snow) is 378 mm, and the snow cover present from mid-September to mid-May is on average 52 cm thick (Natali et al., 2012; Osterkamp et al.,

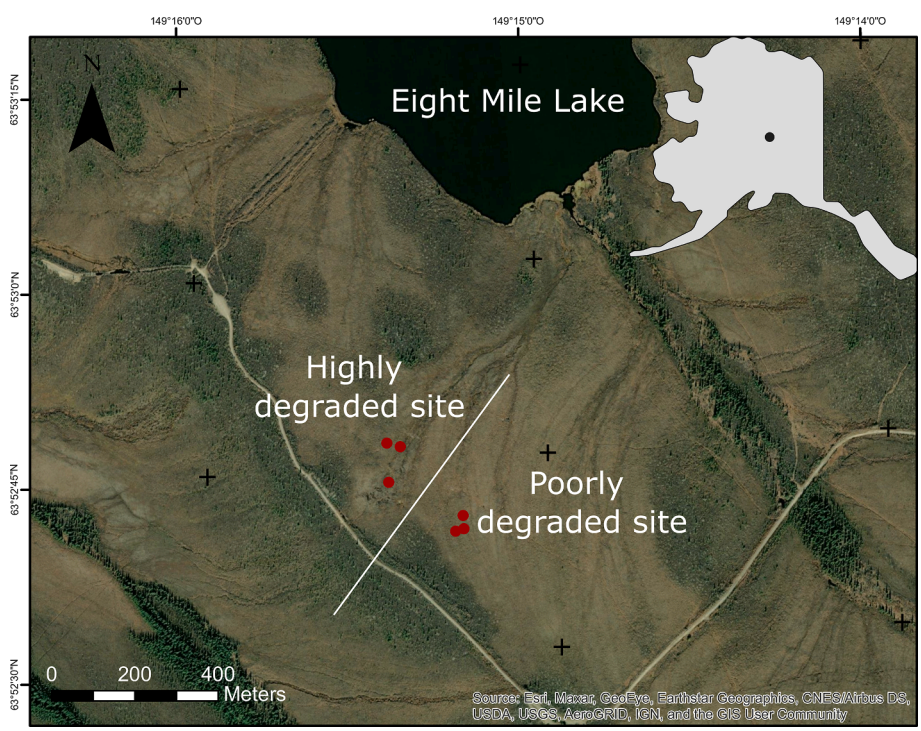

Fig. 1. Location of the study area Eight Mile Lake in Interior Alaska (USA) with sampling plots (red points) in poorly degraded site (dominated by sedges) and highly degraded site (dominated by shrubs).

2009; Vogel et al., 2009).

Soils are classified as Cryosols (WRB soil classification) or Gelisols (USDA soil taxonomy) with an organic layer of 45–65 cm thick (>20% organic C) which covers cryoturbated mineral soil (<20% organic C) that is a mixture of glacial till (small stones and cobbles) and windblown loess, and an active layer thickness between 50 and 120 cm (Kelley et al., 2021; Natali et al., 2011). Soil pH_{water} increases in depth from around 3 to 7.

The tussock-forming sedge, *Eriophorum vaginatum*, and the deciduous shrub, *Vaccinium uliginosum*, dominate Eight Mile Lake (Schuur et al., 2007). Other common vascular plants contribute to the vegetation like *Carex bigelowii*, *Betula nana*, *Rubus chamaemorus*, *Empetrum nigrum*, *Rhododendron subarcticum*, *Vaccinium vitis-idaea*, *Andromeda polifolia*, and *Oxycoccus microcarpus*. Nonvascular plant cover is dominated by feather mosses (primarily *Sphagnum* spp. but also *Aulacomnium* spp., *Polytrichum* spp., *Pleurozium* spp., *Dicranum* spp., etc.), as well as several lichen species (primarily *Cladonia* spp.). Species composition in this area has been observed to be shifting from sedge- to shrub-dominated tundra with permafrost degradation and thermokarst formation (Schuur et al., 2007; Vogel et al., 2009).

The Eight Mile Lake watershed includes two sites along a permafrost degradation gradient monitored since the mid to late 1980s (Schuur et al., 2007): (1) moderately disturbed moist tussock tundra, where the vegetation is dominated by sedges (site hereafter called "poorly degraded site"); and (2) a site with a more pronounced permafrost degradation and deeper thermokarst depressions, where the vegetation is dominated by shrubs (site hereafter called "highly degraded site"). The difference of permafrost degradation gradient has led to a shift in vegetation from sedges to shrubs over a period of ~ 40 years (Schuur et al., 2007; Vogel et al., 2009).

2.2. Vegetation and topsoil sampling

The sampling campaign took place between August and September 2019 at the late growing season period. Samples of vegetation (foliar tissues samples) and topsoil (the first 5 cm of the soil) were collected at three replicate plots on each site (Fig. 1). Plots representative of spatial heterogeneity of permafrost degradation (Siewert et al., 2021) were selected by choosing three replicates dominated by sedges that we considered as poorly degraded sites and three replicates dominated by shrubs that we considered as highly degraded sites following the shrubification upon permafrost degradation (Table 1). For foliar tissues samples (n = 24), the four most common vascular species that recycle their biomass in topsoil each year were considered: two sedges (*Eriophorum vaginatum* and *Carex bigelowii*) and two deciduous shrubs (*Betula nana* and *Vaccinium uliginosum*). We collected senescent leaves of each species with a pruning shears over an area of 5 m^2 around each topsoil sample to represent the chemical composition in leaves falling on topsoil. Topsoils (n = 6) were collected using a knife on a 20 cm^2.

Topsoil samples were dried at ambient temperature in a ventilated and thermoregulated room during two weeks and foliar samples were dried at 60 °C for 24 h. Then, both types of samples were ground at 2 mm.

Table 1
Main characteristics of the sampling plots: location, active layer depth, and depth of the organo-mineral transition.

Site dominated by:	Plot	Latitude	Longitude	Active layer depth (cm)	Organo-mineral transition (cm)
Sedges	1	63°52′40.4″N	149°15′18.0″W	50	45
	2	63°52′39.6″N	149°15′19.4″W	88	10
	3	63°52′39.7″N	149°15′17.6″W	75	20
Shrubs	1	63°52′43.7″N	149°15′28.7″W	48	40
	2	63°52′46.1″N	149°15′26.3″W	96	20
	3	63°52′46.6″N	149°15′27.8″W	65	30

2.3. Mineral element concentration measurements

The concentrations in Si, K, Ca, P, Mn, and Zn in foliar vegetation (n = 24; Mauclet et al., 2021) and in topsoil (n = 6) were determined using the non-destructive portable X-ray fluorescence (pXRF) device *Niton xl3t Goldd+* (Thermo Fisher 220 Scientific). For the measurement, a transparent film (prolene 4 μm) was fixed at the base of a circular plastic cap, in which we deposited a ~1 cm thick foliar or topsoil powder sample. We conducted the analyses in laboratory conditions, using a lead stand to protect the operator from X-rays emission. To ensure trueness, this method was calibrated with some of the samples measured with an inductively coupled plasma - optical emission spectrometer (ICP-OES, iCAP 6500 ThermoFisher Scientific).

For trace elements undetected by the pXRF method (Cu, Mo, and V), foliar (n = 8, selecting foliar samples from one sampling plot per site for the four plant species considered) and topsoil (n = 6) concentrations were determined using an inductively coupled plasma - mass spectrometer (ICP-MS, ICAPQ Thermo Fisher Scientific). Samples were first dissolved by acid digestion using a mix of acid (HF, HNO_3) and H_2O_2 reacting under series of heat (90 °C) and evaporating (40 °C) conditions in a clean room (ISO 6) and under hood (ISO 5). Recovery was assessed using the reference material Lichen IAEA-336: 92% for Cu, 71% for Mo, and 105% for V. Concentrations below the detection limit (DL; < 0.02 mg kg^{-1} for Cu, < 0.002 mg kg^{-1} for Mo, and <0.0006 mg kg^{-1} for V) were replaced by $\frac{DL}{2}$. Blank values of Cu, Mo, and V represent respectively 1.38, 0.584 and 0.803% of the mean of the concentrations measured on the different samples.

2.4. Data treatment and statistical analysis

We determined the foliar fluxes (FF) of the studied mineral elements that return to topsoil using the foliar mineral element concentrations (FC) measured (Section 2.3) following the same approach reported in Mauclet et al (2021). At an annual time-scale, we assumed that the sub-Arctic tundra reached its equilibrium and that the annually produced biomass (net primary productivity, NPP) is equivalent to the senescing biomass returning to topsoil. Therefore, the estimation of annual foliar fluxes (FF) was calculated using the following equation (Mauclet et al., 2021):

$$FF = FC \times fNPP \times \frac{1}{1000} \quad (1)$$

With FF, foliar mineral element flux (mg m^{-2} a^{-1}), FC, foliar mineral element concentration (mg kg^{-1}) and fNPP, foliar NPP (g m^{-2} a^{-1}).

In Equation (1), the foliar NPP (fNPP) can be obtained from variables available at our study site using the following equation (Mauclet et al., 2021):

$$fNPP = r_1 \times AB \times r_2 \times \frac{1}{1000} \quad (2)$$

with r_1, ratio between fNPP and aboveground NPP (unitless; available in Salmon et al., 2016), r_2, ratio between aboveground NPP and aboveground biomass (a^{-1}; available in Schuur et al., 2007), and AB, aboveground biomass (g m^{-2}; available in Jasinski et al., 2018a).

We calculated standard deviations of annual foliar fluxes (Δ FF) determined from the standard deviation of foliar mineral element concentration (Δ FC) using the following equation:

$$\Delta FF = \Delta FC \times fNPP \times \frac{1}{1000} \quad (3)$$

All statistics were performed using R 4.0.2 (RStudio Inc., Boston, Massachusetts, USA) and plots using the ggplot2 package. The significant differences in mineral element fluxes and concentrations between species or between sites were evaluated using a one-way analysis of

variance (ANOVA) and a Tukey's honestly significant difference (HSD) post-hoc test. The 95% confidence intervals of the statistic were used to test for a significant difference between values, which is equivalent to a p-value cutoff of 0.05.

2.5. Shift in vegetation modeling

Shrub growth strongly responds to recent warming at Arctic sites and is not limited to warmer tundra regions, suggesting that a further permafrost degradation caused by air warming will strengthen shrub expansion (Weijers et al., 2018). In order to understand the influence of a further permafrost degradation on topsoil composition, we estimated the foliar mineral element fluxes at a modeled amplified shrubification, i.e., with even more shrub biomass and even less sedge biomass. This change in aboveground biomass directly affects the fNPP (Equation (2)) that influences the foliar mineral element fluxes (Equation (1)).

Considering the foliar biomass at the poorly and highly degraded sites (Jasinski et al., 2018b), we calculated v, the rate of change in foliar biomass over ~ 40 years at the highly degraded site relative to the poorly degraded site.

$$\text{Where, } v = \frac{AB_{highly\ degraded\ site}}{AB_{poorly\ degraded\ site}} \tag{4}$$

We modeled the hypothetical foliar biomass for each species at a further permafrost degradation, i.e., a more intense shrub biomass ($AB_{\text{modeled highly degraded site}}$) by transposing the rate of change in leaf biomass (factor v) to the biomass species at the highly degraded site ($AB_{\text{highly degraded site}}$) according to evidence from the literature for strengthening of shrub expansion (Weijers et al., 2018):

$$AB_{modeled\ highly\ degraded\ site} = AB_{highly\ degraded\ site} \times v \tag{5}$$

We used this predicted $AB_{\text{modeled highly degraded site}}$ to estimate foliar fluxes in a theoretical more advanced permafrost degradation situation, called "modeled highly degraded site" ($FF_{\text{modeled highly degraded site}}$).

3. Results and discussion

3.1. Foliar mineral element concentrations in sedges and shrubs

The least concentrated element in foliar samples of all species is V (on average 0.070 ± 0.062 mg kg^{-1}) and the most concentrated element is Ca in shrub species (5870 ± 612 mg kg^{-1}) and Si in sedge species (7045 ± 5046 mg kg^{-1}). The foliar concentration in sedges ranks as follows from the least to the most concentrated element: V < Mo < Cu < Zn < Mn < P < Ca < K < Si (Fig. 2; Supplementary material). Sedge species (*Carex bigelowii* and *Eriophorum vaginatum*) have on average higher foliar concentrations of Mo (~9 times), Si (~8 times), and K (~2 times) than shrubs (*Betula nana* and *Vaccinium uliginosum*). The higher foliar Si concentration in sedges than in shrubs can be attributed to the higher ability of sedge roots to take up Si (Ma and Takahashi, 2002). In contrast, sedges have lower foliar Ca (~2 times), P (~2 times), Mn (~2 times), and V (~3 times) concentrations than shrubs. Calcium is often located in cell walls and lower foliar Ca concentration in sedges than in shrubs is due to their low concentration in cell wall pectate (White and Broadley, 2003). The foliar concentration of Cu was similar between sedges and shrubs. The foliar concentration of Zn shows different trends between the sedges and the two shrubs: both sedges have a lower Zn concentration than *Betula nana* (*Betula* spp. is known to accumulate Zn; Gosz et al., 1973), but have a higher Zn concentration than *Vaccinium uliginosum*. Within sedges, *Eriophorum vaginatum* presents lower foliar Si (~4 times), Ca (~2 times) and Mo (~2 times) concentration than *Carex bigelowii*. These differences can be related to the duration of the leaf exsertion, elongation, and senescence (Shaver and Laundre, 1997). Indeed, these processes take place rapidly at the start of the growing season in *Carex bigelowii*, unlike *Eriophorum vaginatum* for which this is more gradual (Shaver and Laundre, 1997). Overall, the difference in the foliar mineral element concentrations by species between the poorly and the highly degraded sites is low (~11.3%).

According to these observations, foliar mineral element concentrations are presented by grouping data for the poorly and highly degraded sites for all the sedge species (*Eriophorum vaginatum* and *Carex bigelowii*) and for all the shrub species (*Betula nana* and *Vaccinium uliginosum*; Fig. 3). This representation shows a significant difference in foliar Si, K, Ca, P, Mn, Zn, and Mo concentrations between sedge and shrub species (p-value < 0.05) and a tendency towards lower Cu and V concentrations of 11% and 68% respectively in sedge relative to shrub species.

In literature, foliar concentrations in Si (Engström et al., 2008), K (Chapin et al., 1975), and Mo (Garmo et al., 1986) are up to 8-times higher in sedge species than in shrub species, which is comparable to our data that is up to 9-times higher for these elements. The reported foliar Ca and P (Jasinski et al., 2018b), Mn and Zn (Alexeeva-Popova and Drozdova, 2013) concentrations are consistently lower in sedge species than in shrub species, i.e., up to 3-times lower which is comparable to our data that is up to 2-times lower for these elements. For foliar Cu concentration, the reported difference in foliar concentration between sedge and shrub species is less clear than for other elements (1.1-times higher in sedge species than in shrub species; Alexeeva-Popova & Drozdova, 2013). A smaller difference in foliar Cu concentration between sedge and shrub species was also observed in our data but in the opposite direction (1.1-times lower in sedge than in shrub species). These data suggest that foliar Cu concentration is less variable than other foliar element concentrations between sedge and shrub species.

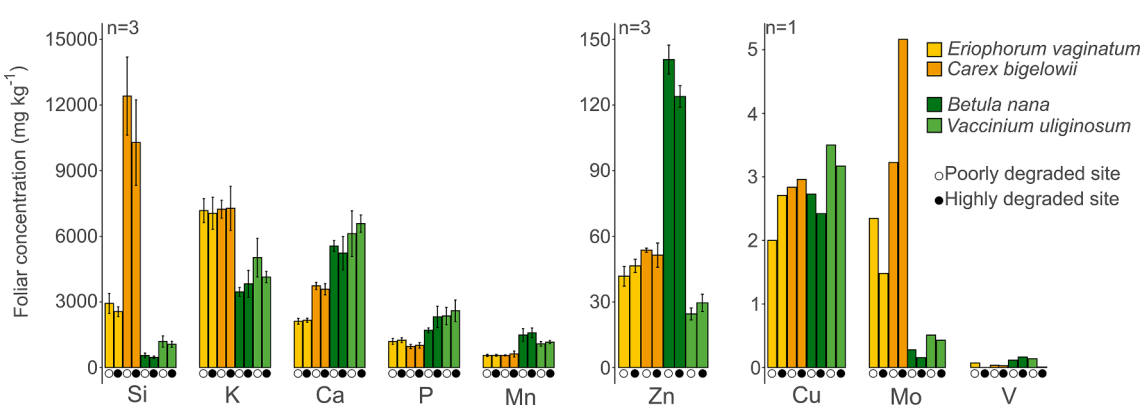

Fig. 2. Foliar mineral element concentrations in *Eriophorum vaginatum*, *Carex bigelowii* (sedges in yellow), *Betula nana*, and *Vaccinium uliginosum* (shrubs in green) at the end of the growing season (August – September 2019). Concentrations were measured at the "poorly degraded site" dominated by sedges (open symbols below the bar chart) and "highly degraded site" dominated by shrubs (full symbols). Concentrations in Si, K, Ca, P, Mn, and Zn are the mean of three replicates with their standard deviation, and Cu, Mo, and V concentrations are measured on one foliar sample of each species.

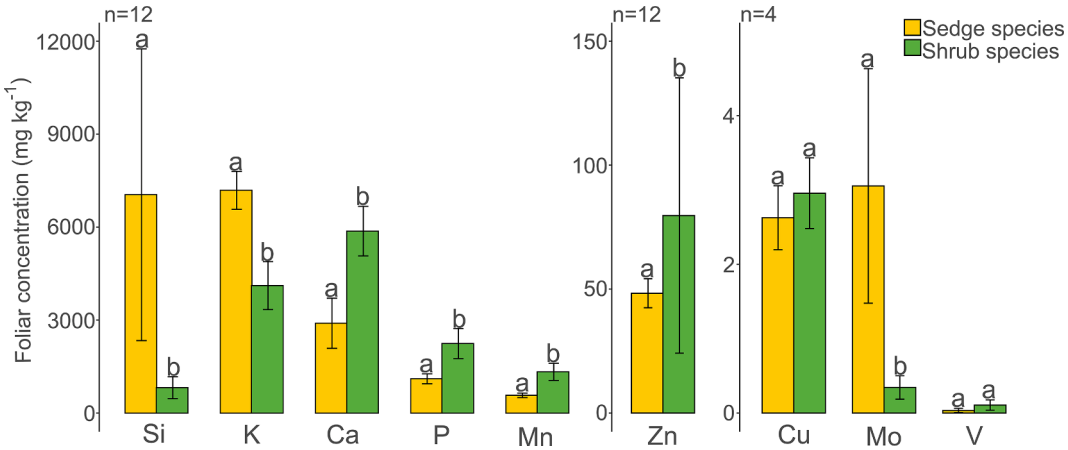

Fig. 3. Foliar mineral element concentrations in sedge and shrub species at the end of the growing season (August – September 2019). Concentrations are the mean of 12 samples (for Si, K, Ca, P, Mn, Zn) and 4 samples (for Cu, Mo, V) with their standard deviation from the different sites (poorly and highly degraded sites) for the sedge species (in yellow: *Eriophorum vaginatum* and *Carex bigelowii*), and for the shrub species (in green: *Betula nana* and *Vaccinium uliginosum*). Letters correspond to one-way ANOVA test and Tukey's HSD post-hoc test and compare variables between different species (sedges and shrubs): two different letters mean significantly different concentrations (p-value < 0.05).

3.2. *Influence of permafrost degradation on foliar mineral element fluxes*

The total Si, K, and Zn foliar fluxes are significantly lower (by nearly twice) in the highly degraded site than in the poorly degraded site (Fig. 4; p-value < 0.05). There is also a trend towards lower foliar Mo flux (47% lower) in the highly degraded site compared to the poorly degraded site. This can be explained by the higher shrub contribution of mineral element fluxes to topsoil of 87% (on average) at the highly degraded site relative to the poorly degraded site, related to the increase in shrub biomass and the decrease in sedge biomass (Schuur et al., 2007) (Fig. 4). These changes in biomass and the higher foliar Si, K, Zn, and Mo concentrations in sedge species than in shrub species (Fig. 3; for the shrub *Vaccinium uliginosum* for Zn, Fig. 2) can explain the differences in foliar Si, K, Zn, and Mo fluxes induced by permafrost degradation, i.e., between the highly and the poorly degraded sites.

For Ca, P, Mn, Cu, and V, the total foliar fluxes are not higher in the highly degraded site than in the poorly degraded sites despite the higher concentrations of these elements in shrub species relative to sedge species, and despite the increase in shrub biomass in the highly degraded sites (Fig. 4). This is likely related to the relative difference in biomass between the two sites: the difference in sedge biomass (loss of 100.3 g m^{-2}) is higher than the difference of shrub biomass (gain of 50.43 g m^{-2}) from highly to poorly degraded sites (Jasinski et al., 2018a). Therefore, the shrub expansion at Eight Mile Lake is still at an early stage of vegetation shift, the influence of foliar fluxes in elements more concentrated in shrub species is not detected and the net foliar flux is not being changed.

Relative to the current gradient of permafrost degradation at the study site from poorly to highly degraded sites (observations), we estimated the mineral element fluxes associated with a modeled amplified shrubification upon a further permafrost degradation (modeled highly degraded site). Foliar Si, K, Zn and Mo fluxes are not significantly different between the highly degraded site and the modeled highly degraded site (p-value > 0.05), showing that these fluxes do not linearly decrease with permafrost degradation and reach a plateau (Fig. 4). Conversely, the total foliar Ca and Mn fluxes are significantly higher in the modeled highly degraded site relative to the poorly degraded site (p-value < 0.05). There is also a trend towards higher foliar P (44%), Cu (29%), and V (40%) fluxes in the modeled highly degraded site compared to the highly degraded site. At this higher level of permafrost

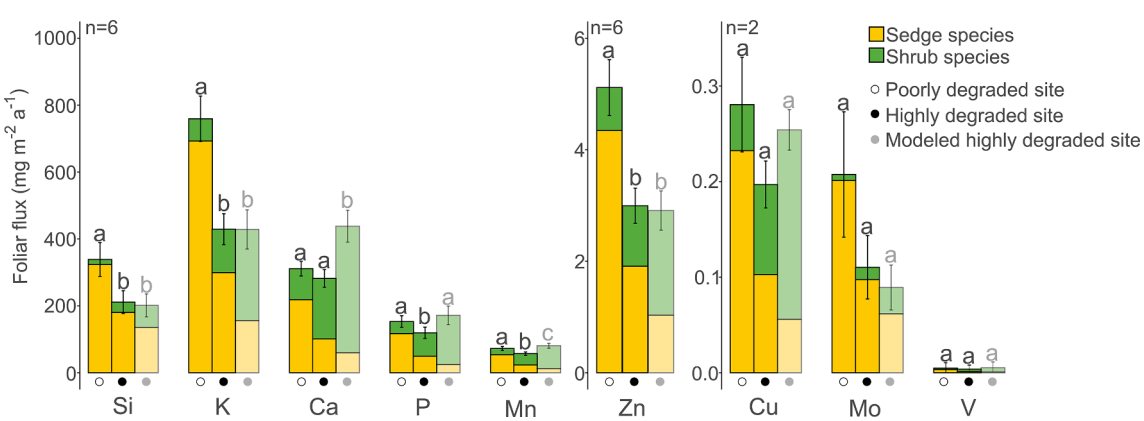

Fig. 4. Annual foliar fluxes of mineral elements at the end of the growing season (August – September 2019) at the "poorly degraded site" dominated by sedges (open symbol) and the "highly degraded site" dominated by shrubs (full symbol), and for one "modeled highly degraded site" showing a further permafrost degradation and shrubification (transparency, gray symbol). Fluxes are the sum of *Eriophorum vaginatum* and *Carex bigelowii* fluxes for sedge species (yellow) and *Betula nana* and *Vaccinium uliginosum* fluxes for shrub species (green) at poorly, highly, and modeled highly degraded sites, respectively (with their standard deviation). Foliar mineral element concentrations used to calculate foliar fluxes were obtained from the mean of six (for Si, K, Ca, P, Mn, Zn) or two (for Cu, Mo, V) foliar concentrations that gather foliar concentration from the poorly and highly degraded sites. Letters correspond to one-way ANOVA test and Tukey's HSD post-hoc test and compare variables between different species (sedges and shrubs): two different letters mean significantly different concentrations (p-value < 0.05).

degradation, foliar mineral element fluxes are thus increasing or remaining constant.

The observed changes in foliar mineral element fluxes suggest that permafrost degradation related to vegetation shift, from sedge to shrub species, is directly affecting the mineral element recycling to topsoil. According to the estimated current foliar fluxes and upon a further permafrost degradation, the chemical composition of the topsoil could be enriched in Ca, P, Mn, Cu, and V, and depleted in Si, K, Zn, and Mo from a poorly degraded site to a highly degraded site.

3.3. Influence of permafrost degradation on topsoil mineral element concentrations

We investigated the difference in mineral element concentrations in the topsoil between the poorly and the highly degraded sites, resulting from a ~ 40 years old vegetation shift at Eight Mile Lake (Osterkamp et al., 2009) with a quantified decrease in sedge biomass and a quantified increase in shrub biomass (Schuur et al., 2007). The mineral elements have the same order of abundance in topsoil than in foliar samples (Section 3.1), except that topsoil Mo concentration is lower than topsoil V concentration (Mo < V < Cu < Zn < Mn < P < Ca < K < Si; Fig. 5; Supplementary material). Our data indicate a trend towards lower topsoil concentrations in Si, K, Zn, and Mo (of 52, 24, 20, and 51%, respectively) from poorly to highly degraded sites. Conversely, topsoil concentrations in Ca, P, Mn, Cu, and V remain constant between both sites.

Different reasons may explain the absence of difference in topsoil mineral element concentrations between the poorly and highly degraded sites (for Ca, P, Mn, Cu, and V), even if the change in plant biomass is confirmed. Firstly, changes in net foliar Ca, P, Mn, Cu, and V fluxes are not detected at this current stage of permafrost degradation even if there is a change in shrub foliar fluxes (Section 3.2). This can contribute to limit the current change in topsoil mineral element concentrations. Secondly, the difference in plant biomass composition between the two sites results from a permafrost degradation over a ~ 40-year time span (Osterkamp et al., 2009), that may be too recent to observe a change in topsoil mineral element composition. Indeed, soil samples analyzed (i.e., 5-cm thickness) are aged under 170 years (Hutchings et al., 2019). Thereby, this topsoil layer not only represents the ~ 40 years of vegetation shift between the poorly and highly degraded sites but also vegetation accumulation before the monitored change. The contribution of mineral elements from previously non-degraded soils across the site may mask any difference observed over the last 40 years of permafrost degradation. Thirdly, topsoil mineral element composition not only results from biomass input but also from other (a-)biotic factors (Berg and McClaugherty, 2020). For example, topsoil trace element concentrations may change with the acidic condition that solubilized and leached mineral elements such as Mn (Gautam et al., 2019). The more easily leached elements need a longer time to accumulate in the topsoil relative to the other elements (Hagen-Thorn et al., 2006). Fourthly, topsoil mineral element composition can be influenced by atmospheric deposition (Binkley and Högberg, 1997).

3.4. Implications of a change in topsoil composition related to permafrost degradation

In the future, changes in topsoil mineral element composition could have a larger impact on the nutrient dynamics (Marschner, 2011). Indeed, changing topsoil concentrations of the studied mineral elements (Si, K, Ca, P, Mn, Zn, Cu, Mo, V), which are crucial plant nutrients, may influence their availability for vegetation. This could lead to an amplification loop: permafrost degradation releases nutrients which leads to shrubification, in turn influences the nutrients in topsoil that can be taken up by the vegetation. For example, decreasing the Mo concentration for vegetation in topsoil could lead to chlorosis and necrosis along the mains veins of mature leaves (Bussler, 1970). On the contrary, increasing Cu and V concentrations for vegetation in topsoil can promote plant growth (Basiouny, 1984; Hänsch and Mendel, 2009).

Furthermore, upon permafrost degradation, a change in mineral element composition of topsoil and shift in vegetation could have an influence on organic C decomposition. A lower topsoil Mo concentration could lead to a decrease in organic C decomposition rate due to the role of Mo as a co-factor for nitrogenase during nitrogen fixation, thereby decreasing N recycled in topsoil by N-fixing plant species (Darnajoux et al., 2019; Jean et al., 2013). However, a higher topsoil V concentration can reverse the trend given that V can replace Mo as a co-factor of the nitrogenase (Barron et al., 2009; Bellenger et al., 2008; Pourhassan et al., 2016). Conversely, a higher topsoil Cu concentration may alter the structure of microorganisms and fungi communities, being toxic for the decomposers and thereby may decrease organic C decomposition rate (Duarte et al., 2008). In that case, studying more precisely dissolved organic carbon (DOC) in the context of shrubification upon permafrost degradation would allow to test the influence of changes in topsoil mineral element concentrations on the C cycle.

Climate change and more specifically warmer air temperatures that have risen 0.6 °C per decade over the last 30 years in high latitudes regions (Fig. 6, step 1), leads to permafrost thaw (Fig. 6, step 2; IPCC, 2013). Shrubification caused by a long-term (at decadal time scale) increase in air temperature (Fig. 6, step 1), permafrost thaw (Fig. 6, step 2), nutrient release (Fig. 6, step 3), and drier soil conditions due to the

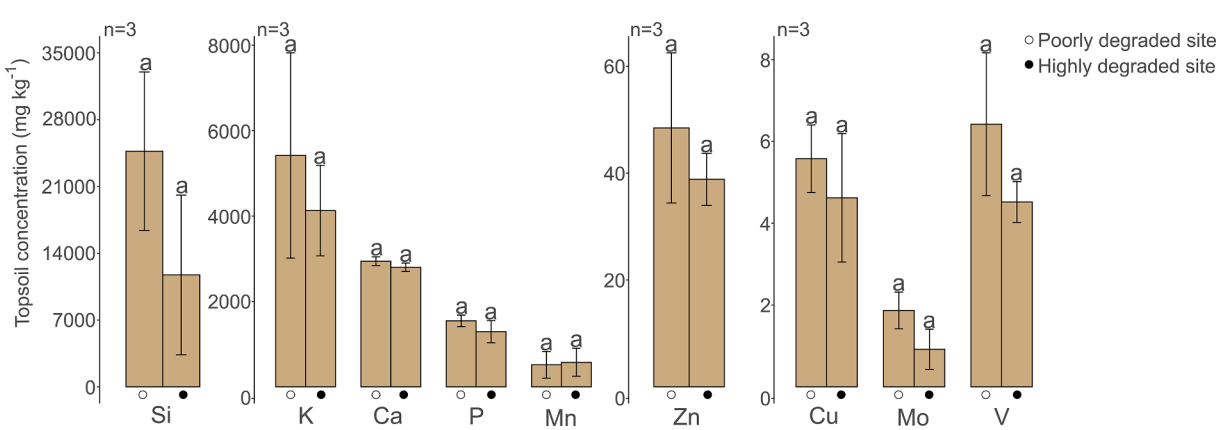

Fig. 5. Topsoil mineral element concentrations at the end of the growing season (August – September 2019) at the "poorly degraded site" dominated by sedges and at the "highly degraded site" dominated by shrubs. Concentrations are the mean with standard deviation of three concentrations measured and letters correspond to one-way ANOVA test and Tukey's HSD post-hoc test and compare variables between different sites (poorly and highly degraded sites): two different letters mean significantly different concentrations (p-value < 0.05).

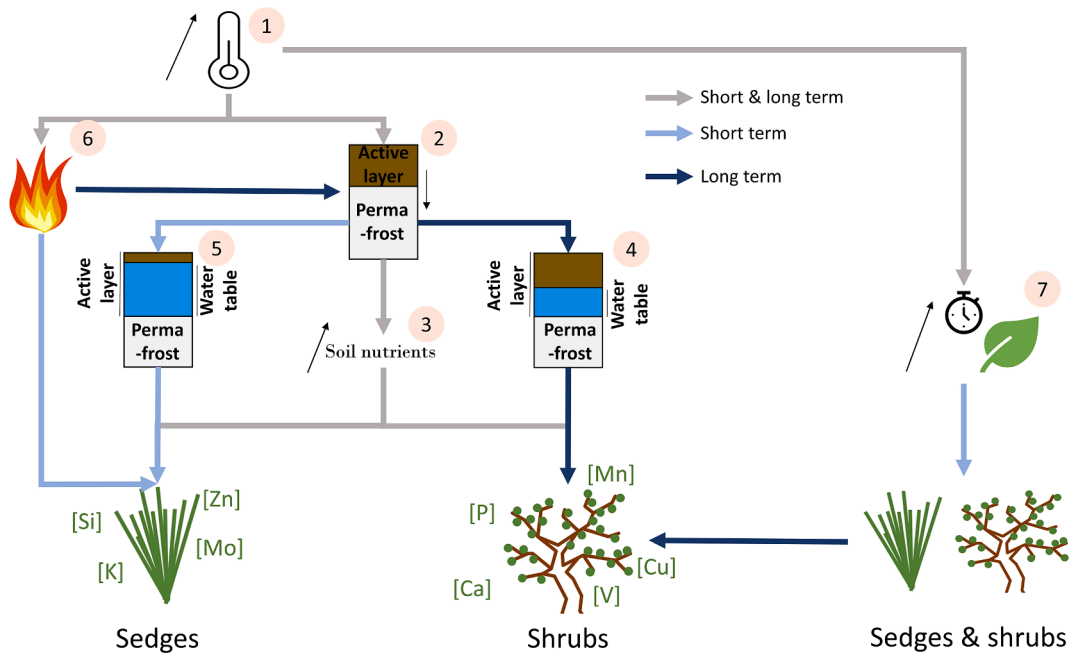

Fig. 6. Conceptual representation of different shifts in vegetation caused by climate change and permafrost degradation that lead to sedge, shrub or sedge and shrub expansion according to the time scale (adapted from Mekonnen et al., 2021). See Section 3.4 for the description of steps (1) to (7) included in cascade processes.

loss of previously frozen water stock in soil (Fig. 6, step 4) could lead to change in topsoil mineral element composition (Section 3.2; Heijmans et al., 2022; Mekonnen et al., 2021). According to our observations, we can infer a change in topsoil mineral element composition associated to other shifts in vegetation at spatial and temporal scales other than those of our study. On the short-term (on annual time scale), permafrost degradation leads to wetter conditions with the presence of thawed water, previously frozen in the permafrost (Fig. 6, step 5; Schuur et al., 2007). Given that sedges can better adapt in wet conditions unlike shrubs, this leads to a sedge expansion (van der Kolk et al., 2016). In that scenario, the associated change in topsoil mineral element composition is in the opposite direction than upon shrubification with an enrichment of Si, K, Zn, and Mo and a depletion in Ca, P, Mn, Cu, and V in topsoil. Climate change with higher air temperatures can also lead to wildfires (Fig. 6, step 6), creating bare spaces that sedges colonize faster than the shrubs (Mekonnen et al., 2021). However, wildfires induce the removal of an insulating surface litter and alter soil temperature that increases permafrost degradation and leads to a shrub expansion on the long term (Jiang et al., 2015; Michaelides et al., 2019). In that scenario, the mineral element composition of topsoil would evolve in the same direction than the influence of shrubification on the long term with an enrichment of Ca, P, Mn, Cu, and V and a depletion of Si, K, Zn, and Mo. At Eight Mile Lake, according to the Fig. 6, the observed permafrost degradation and the lack of wildfire reinforces the idea that shrubs are dominating this site. We could imagine a sedge expansion if wildfires appear with a drier soil and a larger increase in temperature but in the long term, shrubs would be the dominant plant type at Eight Mile Lake.

Finally, both sedge and shrub growth can be stimulated. Indeed, climate change increases the length of the growth season leading to a higher productivity of all the vegetation (Xu et al., 2013). The gain in length of the growing season is estimated at >3 days per decade since the 1980s (Xu et al., 2013). In that scenario, there is an increase in the concentrations of all mineral elements in topsoil (Fig. 6, step 7). However, the growth of shrubs, which have a greater height and leaf area than sedges, can lead to competition for light resulting in shrubs dominating the tundra (Hudson et al., 2011).

More locally, shifts in vegetation can be observed following soil collapse with permafrost degradation: the associated change in topography and hydrological conditions can lead to the extension of shrub or sedge species (Mekonnen et al., 2021; Sulman et al., 2021). Upon these cascade processes with vegetation shifts between sedges and shrubs, the resulting impact on the topsoil mineral element composition is likely to follow the same trend as the one reported for changes between sedge and shrub species in this study.

4. Conclusions

This study quantifies the influence of permafrost degradation associated with a vegetation shift from sedges to shrubs on topsoil and plant mineral element concentrations (Si, K, Ca, P, Zn, Mn, Cu, Mo, and V) in sub-Arctic tundra soils. The observation data support lower foliar Si, K, Zn, and Mo fluxes and a no change in Ca, P, Mn, Cu, and V fluxes upon permafrost degradation from the poorly degraded site to the highly degraded site. This results in a lower topsoil Si, K, Zn, and Mo concentrations (of 52, 24, 20, and 51%, respectively), and no change in Ca, P, Mn, Cu, and V concentrations in topsoil upon the current permafrost degradation. Upon amplified shrubification associated with further permafrost degradation, here modeled by transposing observed foliar biomass changes, foliar Ca, P, Mn, Cu, and V fluxes are higher, which will likely change these element concentrations in topsoil. This study provides a first estimate to assess the influence of shifts in vegetation in sub-Arctic tundra (shrubification, sedge expansion with wetter conditions, etc.) on topsoil mineral element composition, i.e., for mineral elements that are key players for the rate of organic C decomposition and nutrient availability for vegetation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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References

Alexeeva-Popova, N.V., Drozdova, I.V., 2013. Micronutrient composition of plants in the Polar Urals under contrasting geochemical conditions. Russ. J. Ecol. 44, 100–107. https://doi.org/10.1134/S1067413613020033.

Barron, A.R., Wurzburger, N., Bellenger, J.P., Wright, S.J., Kraepiel, A.M.L., Hedin, L.O., 2009. Molybdenum limitation of asymbiotic nitrogen fixation in tropical forest soils. Nat. Geosci. 2, 42–45. https://doi.org/10.1038/ngeo366.

Basiouny, F.M., 1984. Distribution of vanadium and its influence on chlorophyll formation and iron metabolism in tomato plants. J. Plant Nutr. 7, 1059–1073. https://doi.org/10.1080/01904168409363265.

Bellenger, J.P., Wichard, T., Kustka, A.B., Kraepiel, A.M.L., 2008. Uptake of molybdenum and vanadium by a nitrogen-fixing soil bacterium using siderophores. Nat. Geosci. 1, 243–246. https://doi.org/10.1038/ngeo161.

Berg, B., McClaugherty, C., 2020. Plant Litter: Decomposition, Humus Formation, Carbon Sequestration. Springer International Publishing, Cham. doi: 10.1007/978-3-030-59631-6.

Binkley, D., Högberg, P., 1997. Does atmospheric deposition of nitrogen threaten Swedish forests? For. Ecol. Manag. 92, 119–152. https://doi.org/10.1016/S0378-1127(96)03920-5.

Bliss, L.C., Courtin, G.M., Pattie, D.L., Riewe, R.R., Whitfield, D.W.A., Widden, P., 1973. Arctic Tundra Ecosystems. Annu. Rev. Ecol. Syst. 4, 359–399. https://doi.org/10.1146/annurev.es.04.110173.002043.

Bracho, R., Natali, S., Pegoraro, E., Crummer, K.G., Schädel, C., Celis, G., Hale, L., Wu, L., Yin, H., Tiedje, J.M., Konstantinidis, K.T., Luo, Y., Zhou, J., Schuur, E.A.G., 2016. Temperature sensitivity of organic matter decomposition of permafrost-region soils during laboratory incubations. Soil Biol. Biochem. 97, 1–14. https://doi.org/10.1016/j.soilbio.2016.02.008.

Broadley, M.R., White, P.J., Hammond, J.P., Zelko, I., Lux, A., 2007. Zinc in plants. New Phytol. 173, 677–702. https://doi.org/10.1111/j.1469-8137.2007.01996.x.

Bussler, W., 1970. Die Entwicklung der Mo-Mangelsymptome an Blumenkohl. Z. Für Pflanzenernähr. Bodenkd. 125, 36–50. https://doi.org/10.1002/jpln.19701250105.

Chapin, F.S., Cleve, K.V., Tieszen, L.L., 1975. Seasonal nutrient dynamics of tundra vegetation at Barrow, Alaska. Arct. Alp. Res. 7, 209. https://doi.org/10.2307/1549997.

Clarkson, D.T., Hanson, J.B., 1980. The mineral nutrition of higher plants. Annu. Rev. Plant Physiol. 31, 239–298. https://doi.org/10.1146/annurev. pp.31.060180.001323.

Crawford, R.M.M., 2013. Tundra-Taiga Biology. Oxford University Press.

Darnajoux, R., Magain, N., Renaudin, M., Lutzoni, F., Bellenger, J.P., Zhang, X., 2019. Molybdenum threshold for ecosystem scale alternative vanadium nitrogenase activity in boreal forests. Proc. Natl. Acad. Sci. 116, 24682–24688. https://doi.org/10.1073/pnas.1913314116.

Duarte, S., Pascoal, C., Alves, A., Correia, A., Cássio, F., 2008. Copper and zinc mixtures induce shifts in microbial communities and reduce leaf litter decomposition in streams. Freshw. Biol. 53, 91–101. https://doi.org/10.1111/j.1365-2427.2007.01869.x.

Engström, E., Rodushkin, I., Öhlander, B., Ingri, J., Baxter, D.C., 2008. Silicon isotopic composition of boreal forest vegetation in Northern Sweden. Chem. Geol. 257, 247–256. https://doi.org/10.1016/j.chemgeo.2008.10.004.

Garmo, T.H., Fr∅slie, A., H∅ie, R., 1986. Levels of copper, molybdenum, sulphur, zinc, selenium, iron and manganese in native pasture plants from a mountain area in Southern Norway. Acta Agriculturae Scandinavica 36 (2), 147–161.

Gautam, M.K., Lee, K.-S., Berg, B., Song, B.-Y., Yeon, J.-Y., 2019. Trends of major, minor and rare earth elements in decomposing litter in a cool temperate ecosystem, South Korea. Chemosphere 222, 214–226. https://doi.org/10.1016/j.chemosphere.2019.01.114.

Gosz, J.R., Likens, G.E., Bormann, F.H., 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest, New Hampshire. Ecol. Monogr. 43, 173–191. https://doi.org/10.2307/1942193.

Graham, R.D., Hannam, R.J., Uren, N.C., 1988. Manganese in Soils and Plants: Proceedings of the International Symposium on 'Manganese in Soils and Plants' held at the Waite Agricultural Research Institute, The University of Adelaide, Glen Osmond, South Australia,. Springer Science & Business Media.

Greger, M., Landberg, T., Vaculik, M., Lux, A., 2011. Silicon influences nutrient status in plants (abstract). Proceedings of The 5th International Conference on Silicon in Agriculture, China.

Hagen-Thorn, A., Varnagiryte, I., Nihlgård, B., Armolaitis, K., 2006. Autumn nutrient resorption and losses in four deciduous forest tree species. For. Ecol. Manag. 228, 33–39. https://doi.org/10.1016/j.foreco.2006.02.021.

Hänsch, R., Mendel, R.R., 2009. Physiological functions of mineral micronutrients (Cu, Zn, Mn, Fe, Ni, Mo, B, Cl). Curr. Opin. Plant Biol. Physiol. Metabolism 12, 259–266. https://doi.org/10.1016/j.pbi.2009.05.006.

Heijmans, M.M.P.D., Magnússon, R.Í., Lara, M.J., Frost, G.V., Myers-Smith, I.H., van Huissteden, J., Jorgenson, M.T., Fedorov, A.N., Epstein, H.E., Lawrence, D.M., Limpens, J., 2022. Tundra vegetation change and impacts on permafrost. Nat. Rev. Earth Environ. 3, 68–84. https://doi.org/10.1038/s43017-021-00233-0.

Hobbie, S.E., 1996. Temperature and plant species control over litter decomposition in Alaskan Tundra. Ecol. Monogr. 66, 503–522. https://doi.org/10.2307/2963492.

Hudson, J.M.G., Henry, G.H.R., Cornwell, W.K., 2011. Taller and larger: shifts in Arctic tundra leaf traits after 16 years of experimental warming. Glob. Change Biol. 17, 1013–1021. https://doi.org/10.1111/j.1365-2486.2010.02294.x.

Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J.W., Schuur, E.A.G., Ping, C.-L., Schirrmeister, L., Grosse, G., Michaelson, G.J., Koven, C.D., O'Donnell, J.A., Elberling, B., Mishra, U., Camill, P., Yu, Z., Palmtag, J., Kuhry, P., 2014. Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. Biogeosciences 11, 6573–6593. https://doi.org/10.5194/bg-11-6573-2014.

Hutchings, J.A., Bianchi, T.S., Kaufman, D.S., Kholodov, A.L., Vaughn, D.R., Schuur, E.A.G., 2019. Millennial-scale carbon accumulation and molecular transformation in a permafrost core from Interior Alaska. Geochim. Cosmochim. Acta 253, 231–248. https://doi.org/10.1016/j.gca.2019.03.028.

IPCC, 2021. AR6 Climate change 2021: the physical science basis.

IPCC, 2013. Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.

Jasinski, B., Schuur, E.A.G., Mack, M.C., 2018a. Eight Mile Lake Research Watershed, Thaw Gradient: peak growing season aboveground biomass 2017. Bonanza Creek LTER.

Jasinski, B., Schuur, E.A.G., Mack, M.C., 2018b. Eight Mile Lake Research Watershed, Thaw Gradient: leaf SLA, C, N, P, Ca, Mg, delta-13C, delta-15N at peak biomass, 2017, Bonanza Creek LTER - University of Alaska Fairbanks BNZ:706. https://doi.org/doi:10.6073/pasta/f8a89e7b8545105b6aeff28449411d80.

Jean, M.-E., Phalyvong, K., Forest-Drolet, J., Bellenger, J.P., 2013. Molybdenum and phosphorus limitation of asymbiotic nitrogen fixation in forests of Eastern Canada: Influence of vegetative cover and seasonal variability. Soil Biol. Biochem. 67, 140–146. https://doi.org/10.1016/j.soilbio.2013.08.018.

Jiang, Y., Rocha, A.V., O'Donnell, J.A., Drysdale, J.A., Rastetter, E.B., Shaver, G.R., Zhuang, Q., 2015. Contrasting soil thermal responses to fire in Alaskan tundra and boreal forest. J. Geophys. Res. Earth Surf. 120, 363–378. https://doi.org/10.1002/2014JF003180.

Keiluweit, M., Nico, P., Harmon, M.E., Mao, J., Pett-Ridge, J., Kleber, M., 2015. Long-term litter decomposition controlled by manganese redox cycling. Proc. Natl. Acad. Sci. 112, E5253–E5260. https://doi.org/10.1073/pnas.1508945112.

Kelley, A.K., Pegoraro, E., Mauritz, M., Hutchings, J.A., Natali, S., Hicks-Pries, C.E., Schuur, E.A.G., 2021. Eight Mile Lake Research Watershed, Thaw Gradient : Seasonal thaw depth 2004-2020. Bonanza Creek LTER. https://doi.org/10.6073/PASTA/BEB6635175CBCE79C9F83DDF657075EE.

Koven, C.D., Ringeval, B., Friedlingstein, P., Ciais, P., Cadule, P., Khvorostyanov, D., Krinner, G., Tarnocai, C., 2011. Permafrost carbon-climate feedbacks accelerate global warming. Proc. Natl. Acad. Sci. 108, 14769–14774. https://doi.org/10.1073/pnas.1103910108.

Li, H., Santos, F., Butler, K., Herndon, E., 2021. A Critical Review on the Multiple Roles of Manganese in Stabilizing and Destabilizing Soil Organic Matter. Environ. Sci. Technol. 55, 12136–12152. https://doi.org/10.1021/acs.est.1c00299.

Lovett, G.M., Arthur, M.A., Crowley, K.F., 2016. Effects of Calcium on the Rate and Extent of Litter Decomposition in a Northern Hardwood Forest. Ecosystems 19, 87–97. https://doi.org/10.1007/s10021-015-9919-0.

Ma, J.F., Takahashi, E., 2002. Soil, Fertilizer, and Plant Silicon Research in Japan. Elsevier.

Marschner, H., 2011. Marschner's Mineral Nutrition of Higher Plants. Academic Press.

Marsh, P., Bartlett, P., MacKay, M., Pohl, S., Lantz, T., 2010. Snowmelt energetics at a shrub tundra site in the western Canadian Arctic. Hydrol. Process. 24, 3603–3620. https://doi.org/10.1002/hyp.7786.

Mauclet, E., Agnan, Y., Hirst, C., Monhonval, A., Pereira, B., Vandeuren, A., Villani, M., Ledman, J., Taylor, M., Jasinski, B.L., Schuur, E.A.G., Opfergelt, S., 2021. Changing sub-Arctic tundra vegetation upon permafrost degradation: impact on foliar mineral element cycling. Biogeosci. Discuss. 1–34 https://doi.org/10.5194/bg-2021-263.

Mekonnen, Z.A., Riley, W.J., Berner, L.T., Bouskill, N.J., Torn, M.S., Iwahana, G.o., Breen, A.L., Myers-Smith, I.H., Criado, M.G., Liu, Y., Euskirchen, E.S., Goetz, S.J., Mack, M.C., Grant, R.F., 2021. Arctic tundra shrubification: a review of mechanisms and impacts on ecosystem carbon balance. Environ. Res. Lett. 16 (5), 053001.

Michaelides, R.J., Schaefer, K., Zebker, H.A., Parsekian, A., Liu, L., Chen, J., Natali, S., Ludwig, S., Schaefer, S.R., 2019. Inference of the impact of wildfire on permafrost and active layer thickness in a discontinuous permafrost region using the remotely sensed active layer thickness (ReSALT) algorithm. Environ. Res. Lett. 14, 035007 https://doi.org/10.1088/1748-9326/aaf932.

Myers-Smith, I.H., Hik, D.S., 2013. Shrub canopies influence soil temperatures but not nutrient dynamics: an experimental test of tundra snow–shrub interactions. Ecol. Evol. 3, 3683–3700. https://doi.org/10.1002/ece3.710.

Natali, S., Schuur, E.A.G., Rubin, R.L., 2012. Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. J. Ecol. 100, 488–498. https://doi.org/10.1111/j.1365-2745.2011.01925.x.

Natali, S., Schuur, E.A.G., Trucco, C., Hicks Pries, C.E., Crummer, K.G., Baron Lopez, A. F., 2011. Effects of experimental warming of air, soil and permafrost on carbon balance in Alaskan tundra. Glob. Change Biol. 17, 1394–1407. https://doi.org/10.1111/j.1365-2486.2010.02303.x.

Osterkamp, T.E., Jorgenson, M.T., Schuur, E.A.G., Shur, Y.L., Kanevskiy, M.Z., Vogel, J. G., Tumskoy, V.E., 2009. Physical and ecological changes associated with warming permafrost and thermokarst in Interior Alaska. Permafr. Periglac. Process. 20, 235–256. https://doi.org/10.1002/ppp.656.

Pourhassan, N., Bruno, S., Jewell, M.D., Shipley, B., Roy, S., Bellenger, J.P., 2016. Phosphorus and micronutrient dynamics during gymnosperm and angiosperm litters decomposition in temperate cold forest from Eastern Canada. Geoderma 273, 25–31. https://doi.org/10.1016/j.geoderma.2016.03.018.

Qualls, R.G., Richardson, C.J., 2000. Phosphorus enrichment affects litter decomposition, immobilization, and soil microbial phosphorus in wetland mesocosms. Soil Sci. Soc. Am. J. 64, 799–808. https://doi.org/10.2136/sssaj2000.642799x.

Salmon, V.G., Soucy, P., Mauritz, M., Celis, G., Natali, S., Mack, M.C., Schuur, E.A.G., 2016. Nitrogen availability increases in a tundra ecosystem during five years of experimental permafrost thaw. Glob. Change Biol. 22, 1927–1941. https://doi.org/10.1111/gcb.13204.

Schaller, J., Struyf, E., 2013. Silicon controls microbial decay and nutrient release of grass litter during aquatic decomposition. Hydrobiologia 709, 201–212. https://doi.org/10.1007/s10750-013-1449-1.

Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56. https://doi.org/10.1038/nature10386.

Schuur, E.A.G., Crummer, K.G., Vogel, J.G., Mack, M.C., 2007. Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan Tundra. Ecosystems 10, 280–292. https://doi.org/10.1007/s10021-007-9024-0.

Schuur, E.A.G., McGuire, A.D., Schädel, C., Grosse, G., Harden, J.W., Hayes, D.J., Hugelius, G., Koven, C.D., Kuhry, P., Lawrence, D.M., Natali, S., Olefeldt, D., Romanovsky, V.E., Schaefer, K., Turetsky, M.R., Treat, C.C., Vonk, J.E., 2015. Climate change and the permafrost carbon feedback. Nature 520, 171–179. https://doi.org/10.1038/nature14338.

Schwarz, G., Mendel, R.R., Ribbe, M.W., 2009. Molybdenum cofactors, enzymes and pathways. Nature 460, 839–847. https://doi.org/10.1038/nature08302.

Shaver, G.R., Laundre, J., 1997. Exsertion, elongation, and senescence of leaves of Eriophorum vaginatum and Carex bigelowii in Northern Alaska. Glob. Change Biol. 3, 146–157. https://doi.org/10.1111/j.1365-2486.1997.gcb141.x.

Siewert, M.B., Lantuit, H., Richter, A., Hugelius, G., 2021. Permafrost causes unique fine-scale spatial variability across tundra soils. e2020GB006659 Glob. Biogeochem. Cycles 35. https://doi.org/10.1029/2020GB006659.

Sturm, M., Racine, C., Tape, K., 2001. Increasing shrub abundance in the Arctic. Nature 411, 546–547. https://doi.org/10.1038/35079180.

Sulman, B.N., Salmon, V.G., Iversen, C.M., Breen, A.L., Yuan, F., Thornton, P.E., 2021. Integrating Arctic plant functional types in a land surface model using above- and belowground field observations. e2020MS002396 J. Adv. Model. Earth Syst. 13. https://doi.org/10.1029/2020MS002396.

van der Kolk, H.-J., Heijmans, M.M.P.D., van Huissteden, J., Pullens, J.W.M., Berendse, F., 2016. Potential Arctic tundra vegetation shifts in response to changing temperature, precipitation and permafrost thaw. Biogeosciences 13, 6229–6245. https://doi.org/10.5194/bg-13-6229-2016.

Van Everdingen, R.O., 1998. Multi-language glossary of permafrost and related ground-ice terms in chinese, english, french, german..., Arctic Inst. of North America University of Calgary. ed.

Vogel, J., Schuur, E.A.G., Trucco, C., Lee, H., 2009. Response of CO2 exchange in a tussock tundra ecosystem to permafrost thaw and thermokarst development. J. Geophys. Res. Biogeosciences 114. https://doi.org/10.1029/2008JG000901.

Waldrop, M.P., Wickland, K.P., White Iii, R., Berhe, A.A., Harden, J.W., Romanovsky, V. E., 2010. Molecular investigations into a globally important carbon pool: permafrost-protected carbon in Alaskan soils. Glob. Change Biol. 16, 2543–2554. https://doi.org/10.1111/j.1365-2486.2009.02141.x.

Walker, D.A., Raynolds, M.K., Daniëls, F.J.A., Einarsson, E., Elvebakk, A., Gould, W.A., Katenin, A.E., Kholod, S.S., Markon, C.J., Melnikov, E.S., Moskalenko, N.G., Talbot, S.S., Yurtsev, B.A.(†), Team, T. other members of the C., 2005. The Circumpolar Arctic vegetation map. J. Veg. Sci. 16, 267–282. https://doi.org/10.1111/j.1654-1103.2005.tb02365.x.

Weijers, S., Myers-Smith, I.H., Löffler, J., 2018. A warmer and greener cold world: summer warming increases shrub growth in the alpine and high Arctic Tundra. Erdkunde 72, 63–85.

White, P.J., Broadley, M.R., 2003. Calcium in plants. Ann. Bot. 92, 487–511. https://doi.org/10.1093/aob/mcg164.

Xu, L., Myneni, R.B., Chapin, F.S., Callaghan, T.V., Pinzon, J.E., Tucker, C.J., Zhu, Z., Bi, J., Ciais, P., Tømmervik, H., Euskirchen, E.S., Forbes, B.C., Piao, S.L., Anderson, B.T., Ganguly, S., Nemani, R.R., Goetz, S.J., Beck, P.S.A., Bunn, A.G., Cao, C., Stroeve, J.C., 2013. Temperature and vegetation seasonality diminishment over northern lands. Nat. Clim. Change 3, 581–586. https://doi.org/10.1038/nclimate1836.