

Faculté des bioingénieurs

Factors influencing trace element cycling by Arctic vegetation in different habitats

A case study in Abisko, Sweden

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List of acronyms and symbols

As: Arsenic

C: Carbon

Cd: Cadmium

Cu: Copper

EF: Enrichment factor

FB: Foliar biomass

FC: Foliar concentration

Fe: Iron

FF: Foliar flux

fNPP: Foliar net primary productivity

FS: Foliar stock

ICP-MS: Inductively Coupled Plasma Mass Spectrometry

Mn: Manganese

Mo: Molybdenum

N: Nitrogen

NDVI: Normalized Difference Vegetation Index

P: Phosphorous

sp: Species

Ti: Titanium

UCLouvain: Université catholique de Louvain

V: Vanadium

Zn: Zinc

1. Introduction

Arctic and sub-Arctic regions, located at the northernmost parts of the Earth, are characterized by tundra and taiga biomes. These environments are dominated by various types of vascular plants such as sedges, forbs, deciduous and evergreen shrubs (Walker et al., 2005). The distribution and abundance of Arctic plant functional types can vary significantly based on local factors, including climate and other environmental factors such as topography, and soil conditions (Heijmans et al., 2022). Arctic and sub-Arctic ecosystems are characterized by permanently frozen ground (soil and/or rock), called permafrost, with an active upper layer that thaws seasonally (Devoie et al., 2024; French, 2007). The combination of low soil temperature and shallow active layer restricts plant growth (Jin et al., 2021).

Warming Arctic and permafrost degradation are reshaping northern ecosystems by altering microtopography, soil water dynamics, nutrient availability, and vegetation succession (Hicks Pries et al., 2013; IPCC, 2021). As permafrost thaws, it releases previously frozen pools of nutrients (Keuper et al., 2017). In nutrient-limited ecosystems, like Arctic and sub-Arctic, an increase in nutrient availability (e.g., N and P) may strongly contribute to boosting vegetation biomass and productivity, and further drive shifts in species composition (Nadelhoffer et al., 1992; Walker et al., 2005). Wetter lowlands experience a rise in sedges, whereas drier uplands show a shrub expansion (Jorgenson & Osterkamp, 2005; van der Kolk et al., 2016).

Changes in the composition and productivity of vegetation in the Arctic and sub-Arctic regions can have significant impacts on climate change feedbacks (Heijmans et al., 2022). These changes can alter the surface energy balance (Beringer et al., 2005; Meredith et al., 2019) and influence the net ecosystem carbon balance (McGuire, 2018; E. a. G. Schuur et al., 2015). Therefore, ongoing efforts to model vegetation dynamics in these areas are crucial for enhancing Earth system models and improving predictions of climate change rates (Druel et al., 2019).

A crucial aspect missing from current efforts to model vegetation dynamics is consideration of the impact of vegetation changes on nutrient cycling (Druel et al., 2019). As permafrost presence limits nutrient pools, nutrient cycling in the active layer provides a vital source of nutrients for vegetation. Stored in the soil are major elements, which include essential macro-nutrients (e.g., N, P, K) and trace elements such as micro-nutrients (e.g., Fe, Mn, Zn), non-essential nutrients (e.g., Si, Al), and trace pollutants (e.g., Pb, As; Broadley et al., 2012). As plants absorb mineral nutrients from the soil to support vital functions for growth and development, they play a central role in the biogeochemical cycling of nutrients through root uptake, seasonal leaf senescence, and litterfall. In Arctic and sub-Arctic biomes, plant residue decomposition rates are relatively low due to cold conditions, varying by plant functional types, with sedges decomposing faster than deciduous and evergreen shrubs (Hobbie, 1996; Parker et al., 2015).

Consequently, shifts in vegetation composition, such as sedge or shrub expansion, can either accelerate or decelerate litter decomposition, thereby impacting mineral nutrient recycling.

To our knowledge, numerous studies conducted across the Arctic have examined the major elements (Carey et al., 2017; Chapin et al., 1980; Chapin III et al., 1996; Hewitt et al., 2019; Jonasson, 1983; Keuper et al., 2017; Salmon et al., 2016). However, there has been relatively little attention to the impact of Arctic warming on trace element cycling (i.e., As, Cd, Cu, Fe, Mn, Mo, V, Ti, and Zn). Hence, it is essential to study the variation in mineral element distribution among Arctic cosmopolitan plant species and their cycling by vegetation. This information is crucial for enhancing simulations of vegetation dynamics in the evolving northern ecosystems (Druel et al., 2019).

This study examines how alterations in environmental conditions, such as shifts in pH, and moisture levels, affect foliar trace element concentrations. Additionally, it investigates how changes in vegetation biomass composition impact the flux of trace elements between vegetation tissues and soil litter. The research question addressed is: How do plants cycle trace elements in different Arctic habitats? One hypothesis suggests that soil concentrations, floristic composition, and rooting depth will proportionally influence foliar concentrations. These hypotheses are tested across various habitat types characterized by different environmental conditions.

2. State of the art

2.1. Arctic, northernmost region of Earth

The Earth can be divided into four domains which are characterized by broad climatic conditions (Loidi et al., 2022): cryocratic (governed by the cold), mesocratic (governed by the intermediate conditions), xerocratic (governed by aridity), and thermocratic (governed by the warmth).

Governed by the cold, the Arctic refers to the northernmost region of Earth (Figure 2-1). The region circling the Arctic, also called the circumarctic, consists of the partly ice-covered Arctic ocean and land areas of the surrounding eight Arctic states: Iceland, Denmark (including the Faroe Islands and Greenland), Norway, Sweden, Finland, Russia, Canada, and the state of Alaska from the United States of America (*The Arctic Environment — European Environment Agency*, 2017).

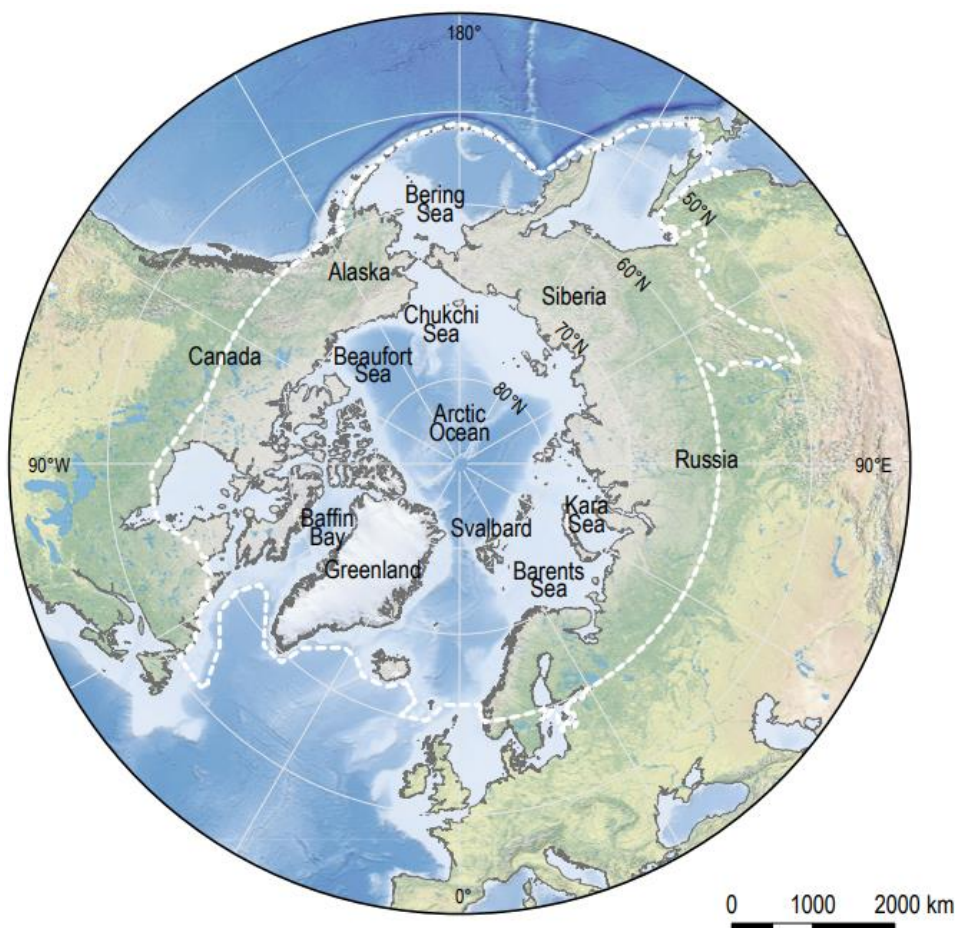


Figure 2-1: Delimitation of the Arctic polar region. Dashed lines denote approximate boundaries for the polar regions (Meredith et al., 2019).

2.2. Arctic biomes, and their climate

The Arctic is divided into tundra and taiga biomes. Biomes are determined by physiognomy or dominant life forms, regional climate or climatic zone, and ecological factors (Figure 2-2; Hunter et al., 2021).

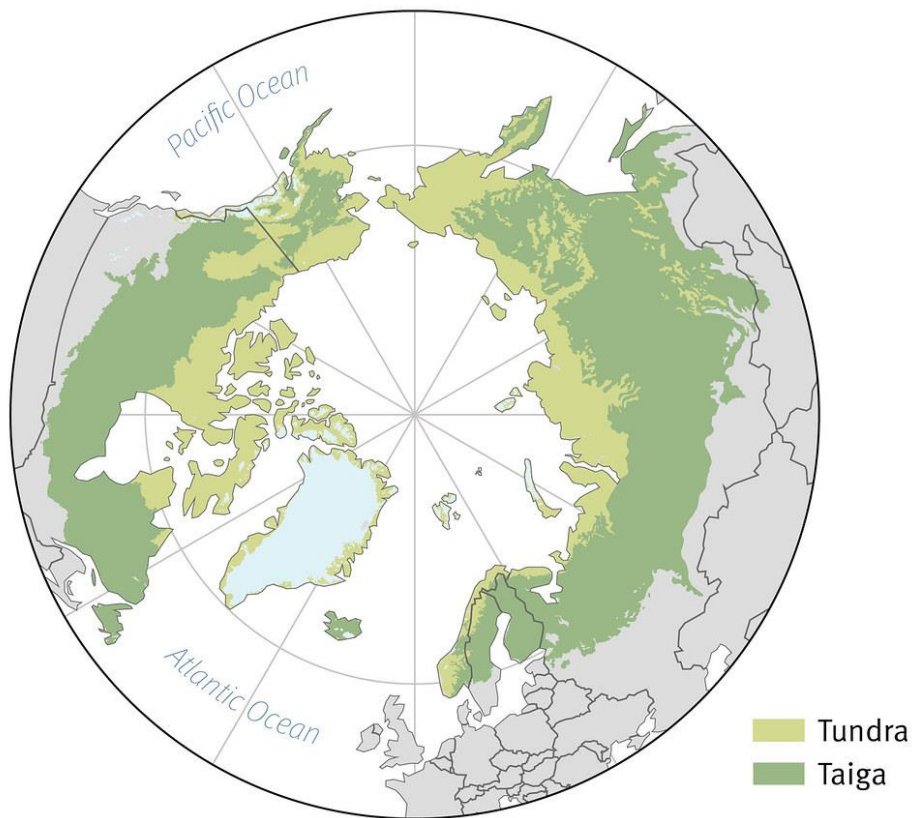


Figure 2-2: Tundra and taiga distribution in the northern hemisphere. Map from the Arctic Permafrost Atlas (Westerveld, 2023).

2.2.1. Tundra, a treeless biome

Tundra is a treeless biome and is characterized by a continuous, dense, and evergreen vegetation layer (Loidi et al., 2022). Trees cannot thrive in these conditions due to consistently low temperatures. The temperature remains below freezing (0 °C) for an extended period of six to ten months, with the warmest month averaging only 10 °C (Loidi et al., 2022).

Arctic tundra spans between the poles and a limit fluctuating within the 65° to 70° latitude range. The continentality and the marine currents influence this border, aligning more or less with the 10 °C isotherm of July in the northern hemisphere (Loidi et al., 2022). Precipitation in the Arctic tundra is low with 200 mm per year primarily in the form of snow. Wind patterns lead to uneven snow distribution and influence vegetation distribution (Loidi et al., 2022). With

the arrival of spring, the ice begins to thaw, and the short summer brings large quantities of available liquid water.

2.2.2. Taiga, the boreal forest

Taiga biome is characterized by coniferous forests, mostly evergreen but also including some deciduous broadleaved trees. Unlike the tundra, the freezing period is shorter, allowing for a frost-free season that partially thaws the soil, facilitating the establishment of trees.

The boreal taiga spans regions with higher thermal conditions and lower latitudes than the Arctic tundra, extending continuously across the northern hemisphere between 42° and 72° (Loidi et al., 2022). The climate is cold with seven to nine months where temperatures fall below 0 °C (McLaren & Turkington, 2013). Additionally, short summers range from one to three months with temperatures above 10 °C (Loidi et al., 2022). The plant growth period lasts less than six months (Loidi et al., 2022; McLaren & Turkington, 2013).

Precipitation varies between 250 mm and over 1000 mm, particularly in coastal areas (McLaren & Turkington, 2013). Most of the precipitation occurs in the summer, coupled with the snowmelt in spring, ensuring there is no drought in the summer season (Loidi et al., 2022).

2.3. Arctic vegetation

2.3.1. Vegetation composition

Tundra, domination of vascular plants

Arctic tundra vegetation is mainly composed of short-statured vegetation, sorted into different plant functional types according to their morphological and physiological characteristics (Chapin III et al., 1996). Specifically, tundra ecosystems are mainly characterized by vascular plants like sedges (which are part of the graminoid group), forbs, deciduous and evergreen shrubs, and non-vascular plants such as mosses, along with non-plant organisms like lichens (Figure 2-3 & Figure 2-4; Walker et al., 2005).

The distribution and abundance of these species can vary significantly based on local factors, including climate and other environmental factors such as topography, soil composition, and active layer thickness (Heijmans et al., 2022). The active layer plays a critical role in the life of tundra plants, serving as the layer where roots can access nutrients and water from the soil during the summer months (Iversen et al., 2015; Keuper et al., 2012). More precisely, the combination of low soil temperature and shallow active layer restricts plant growth. However, frozen grounds favor organic matter accumulation in the active layer because of low decomposition rates (Jin et al., 2021).

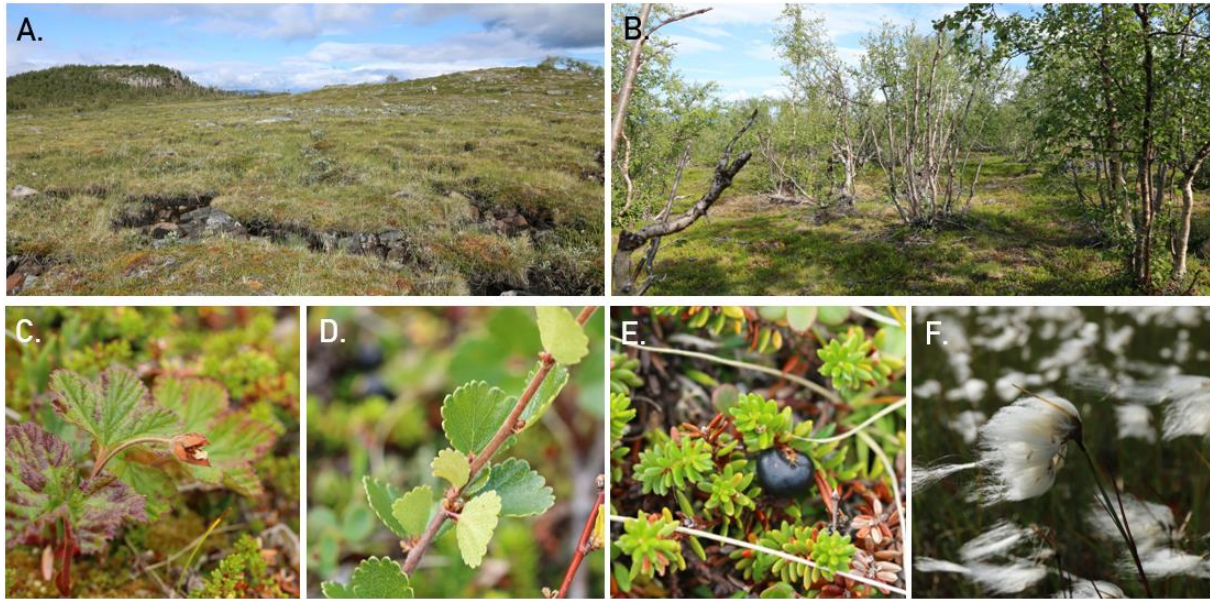


Figure 2-3: Photographies of a tundra (A) and a taiga (B) ecosystems near Abisko Research Station, northern Sweden; Close-up photographs of the ground-level vegetation: C. *Rubus chamaemorus*, forb; D. *Betula nana*, deciduous shrub; E. *Empetrum nigrum*, evergreen shrub; F. *Eriophorum* sp., sedge.

Taiga, domination of conifer stands

Taiga vegetation is composed of a canopy layer dominated mainly by conifers (Figure 2-3 & Figure 2-4; McLaren & Turkington, 2013). The pattern of canopy composition is the product of complex interactions involving terrain factors, regeneration process, and succession following disturbance events (Andison & Kimmins, 1999; Chen & Popadiouk, 2002).

Under the canopy, mosses and lichens are more prevalent than vascular plants in terms of abundance and diversity. Mosses thrive in mesic and moist locations, while lichens predominantly occupy drier sites, especially beneath a layer of pine trees (Majasalmi & Rautiainen, 2020; McLaren & Turkington, 2013). Understory species composition is influenced by seven environmental variables (Chávez & Macdonald, 2010): soil moisture, soil temperature, total light during the leaf-off period, cover of coarse and fine downed woody material, and availability of NH_4^+ and Ca^{2+} .

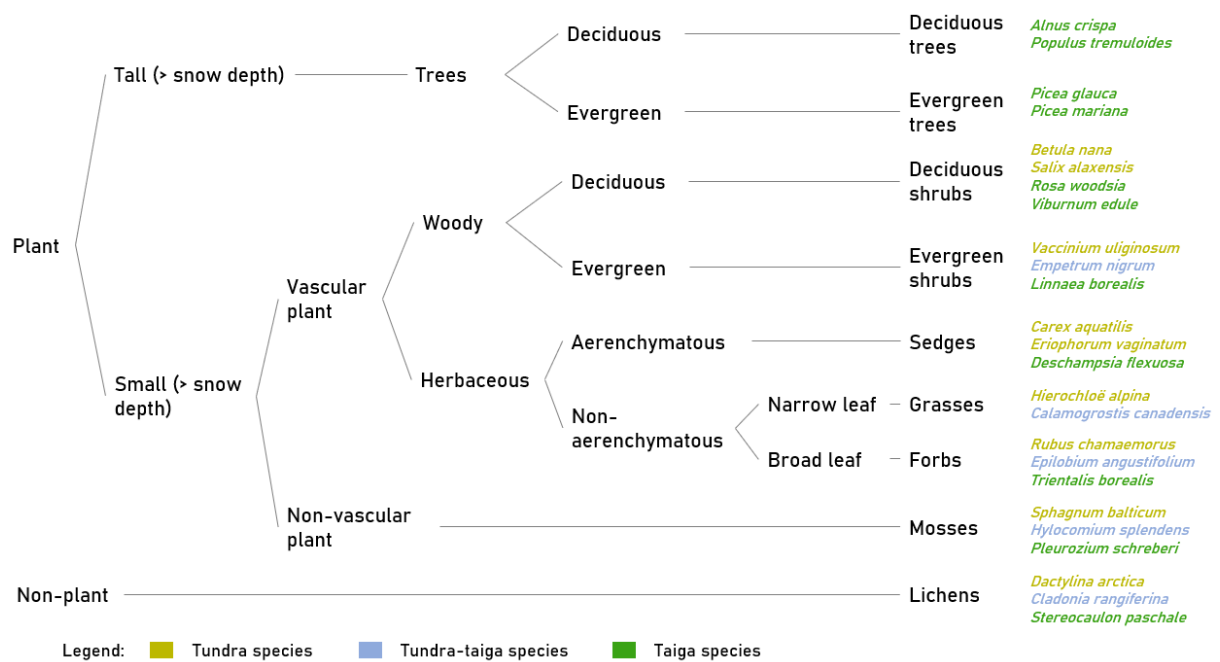


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2.3.2. Plant nutrition

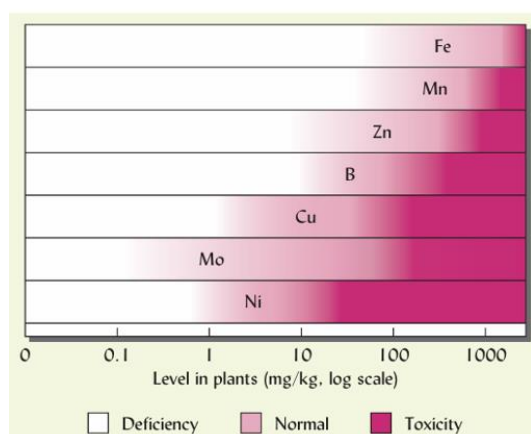
Plant nutrients

Plants require nutrients for normal growth. Arnon and Stout (1939) described an essential plant element based on criteria. These are (Mengel et al., 2001): (1) A deficiency of the element makes it impossible for the plant to complete its life cycle; (2) The deficiency is specific to the element in question; (3) The element is directly involved in the nutrition of the plant, as a constituent of an essential metabolite or required for the action of an enzyme system. Thus, several chemical elements were identified as essential for higher plants. They all support multiple physiological functions in plant tissues (Table 2-1). Required in relatively large amounts for plant nutrition, macro-nutrients are divided into two groups: non-mineral (C, H, O) and mineral (N, P, K, Ca, Mg, S). Micro-nutrients (e.g., Zn, Fe, Mn, Mo, Cu) are required in smaller quantities (Figure 2-5A). Beneficial elements (e.g., Na, Si, Al, V) are non-essential for plant growth but facilitate and improve plant development. There are also trace pollutants (e.g., Pb, Cd, As). In this master's thesis, only trace elements will be considered: As, Cd, Cu, Fe, Mn, Mo, Ti, V, and Zn.

Table 2-1: Functions of several micro-nutrients in plant tissues.

Mineral nutrient	Element form for plant absorption	Examples of functions in plant tissues	References
Cu	Cu^{2+}	Constituent of proteins, important in photosynthesis, respiration, C and N metabolism, lignification	(Broadley et al., 2012; Daniels, 2016)
Fe	Fe^{2+} (all species except grasses), Fe^{3+} (grasses)	Constituent of heme proteins, Fe-S proteins, redox reaction with enzymes	(Broadley et al., 2012)
Mn	Mn^{2+}	Constituent of enzymes, enzyme activation, cell division, and extension	(Broadley et al., 2012)
Mo	MoO_4^{2-}	Present in nitrogenase (nitrogen fixation) and nitrate reductase enzymes; essential for nitrogen fixation and nitrogen assimilation.	(Daniels, 2016)
Zn	Zn^{2+}	Constituent of enzymes, enzyme activation, protein synthesis	(Broadley et al., 2012)

A.



B.

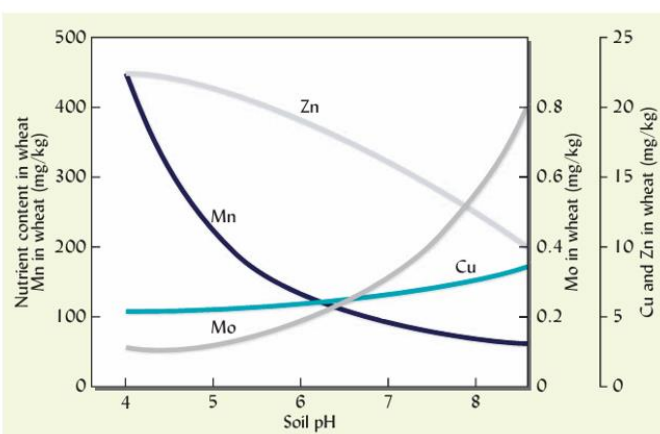


Figure 2-5: A. Deficiency, normal, and toxicity levels in plants for seven micro-nutrients on a logarithmic scale. It is important to keep in mind the remarkable differences in the ability of different plant species to accumulate and tolerate different levels of micro-nutrients. (Diagram courtesy of Ray R. Weil, based on data from many sources; Daniels, 2016); B. Effect of soil pH on Mn, Zn, Cu, and Mo concentrations in wheat plants. The plants were grown in soils from different countries around the world. (Drawn from data in Sillanpa, 1982; Daniels, 2016)

Sources for plant nutrient uptake

Plants cover their carbon needs by assimilating CO_2 from the atmosphere, while they acquire most of their mineral nutrients from the soil. In the soil, these nutrients exist mainly in inorganic form, either as free cations or as anions (Table 2-1). Nutrient availability in the soil is the sum of mineral nutrients that can be removed from the soil solution and exchangeable reserves. It is the result of dynamic interactions between various soil processes (Mauclet, 2022). As plants

absorb nutrients from the soil solution, reactions occur to restore the solution, including exchanges between the soil solution and exchange sites, nutrient desorption, mineral weathering, and organic matter turnover (Chapin et al., 1980; Mauclet, 2022).

Soil mineralogy mainly influences the concentrations of mineral elements within the soil. On the other hand, the pH and redox potential of the soil also greatly affect its elemental composition (Figure 2-5B; Daniels, 2016). In strongly acidic environments, cations are prevalent, whereas anions like Mo are predominantly found in high pH conditions. Soil moisture levels significantly affect redox potential pe , thus influencing trace element availability (Figure 2-6; Blume et al., 2016; Sparks et al., 2022). When a large water input saturates the soil pore spaces, oxygen levels rapidly drop to near zero within a few hours to a few days. As a result, the soil becomes suboxic, then anoxic, leading to a decrease in redox potential. Under suboxic conditions, microbial activity reduces NO_3^- as an alternative electron acceptor to oxygen (Blume et al., 2016). When O_2 and NO_3^- are depleted and the soil becomes anoxic, anaerobic bacteria turn to oxidized metal species as electron acceptors. This leads to the reduction of Mn(IV/III) and Fe(III) oxides and hydroxides, resulting in increased Mn^{2+} and Fe^{2+} concentrations in the soil solution (Sparks et al., 2022). The reductive dissolution of manganese and iron oxide minerals indirectly triggers the mobilization of trace elements such as As, Mo, Cd, Pb, Cu, and Zn (Blume et al., 2016).

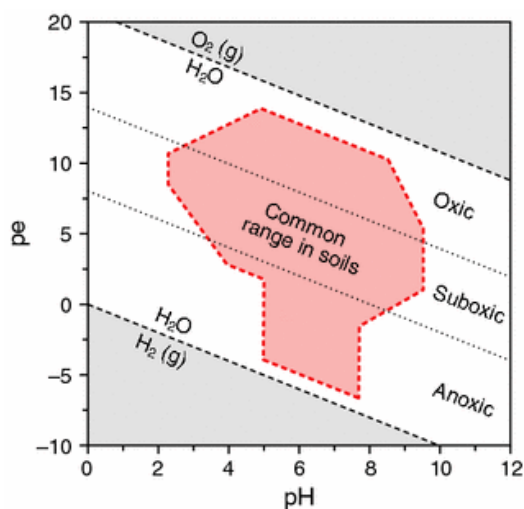


Figure 2-6: Theoretically possible pe -pH range in water environmental systems (white area) and common pe -pH range in soils (red area). The pe -pH range is divided into an oxic ($pe + pH > 14$), a suboxic ($9 < pe + pH < 14$), and an anoxic range ($pe + pH < 9$). The upper and lower limits are given by the water stability equations. (from Blume et al., 2016)

Plant nutrient cycling

Plant nutrient cycling is essential to sustain plant growth and development. Nutrient cycling follows the successive steps (Figure 2-7): (1) plant nutrient uptake by roots; (2) seasonal transfer of the mineral elements from plant tissues to soil litter reservoir during seasonal litterfall; and (3) microbial decomposition.

The seasonal transfer of mineral elements is influenced by plant physiology, through leaf longevity. The life cycle of leaf tissue varies between deciduous and evergreen species. Deciduous shrubs and sedges undergo annual leaf turnover, while evergreen shrubs maintain their leaves for several years (Grant, 2015; Grant et al., 2011). Mosses and lichens are categorized as semi-deciduous with partial annual tissue turnover (Grant, 2015; Grant et al., 2011).

When senescent plant tissue is incorporated into the soil litter reservoir, a dynamic interaction between temperature, moisture, and litter substrate quality occurs, exerting control over microbial activity, organic matter decomposition, and nutrient mineralization (Chapin et al., 1980). In the Arctic, due to moisture-saturated soil conditions and low oxygen content, the decomposition rate is low, and thus, soil litter accumulates (Nadelhoffer et al., 1992).

Ultimately, the uptake and cycling of nutrients by plants can significantly impact the vertical distribution of mineral elements in the soil. Vertical leaching moves nutrients downward, redistributing them to deeper layers, whereas plant cycling tends to concentrate nutrients near the soil surface while depleting them in the root zone (Jobbágy & Jackson, 2001).

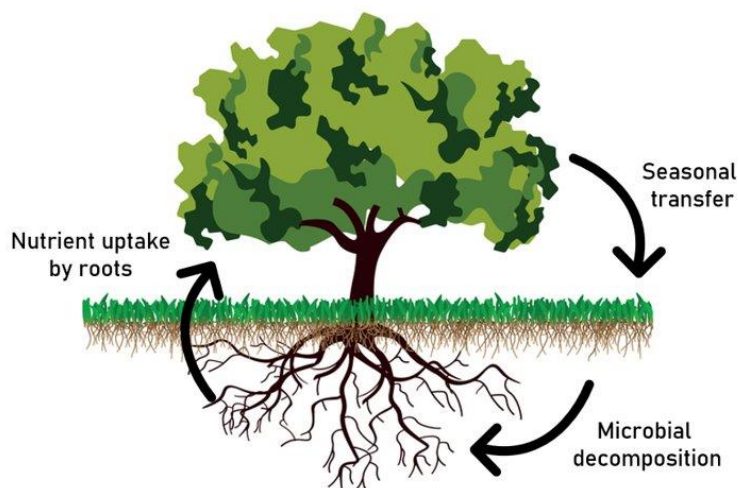


Figure 2-7: Nutrient cycling in three steps. Arrows represent nutrient movements from stocks to others: soil to plant tissues, plant tissues to soil litter, and soil litter to soil.

2.4. Permafrost, permanently frozen ground limiting plant nutrient cycling

Arctic and sub-Arctic ecosystems are characterized by permafrost (Mauclet et al., 2022). Permafrost is ground material (e.g., soil, rock...) that remains at or below 0 °C for at least two consecutive years (Devoie et al., 2024; French, 2007). Worldwide, permafrost covers about 25% of the Earth's terrestrial parts (Anisimov & Nelson, 1996; French, 2007; Zhang et al., 2008).

It is classified according to its areal extent. Four categories are described (Figure 2-8; Bockheim, 2015): continuous where permafrost covers > 90% of the surface, discontinuous where it

occupies between 50 and 90%, sporadic where it occupies 10-50%, and isolated where the surface covered is less than 10%.

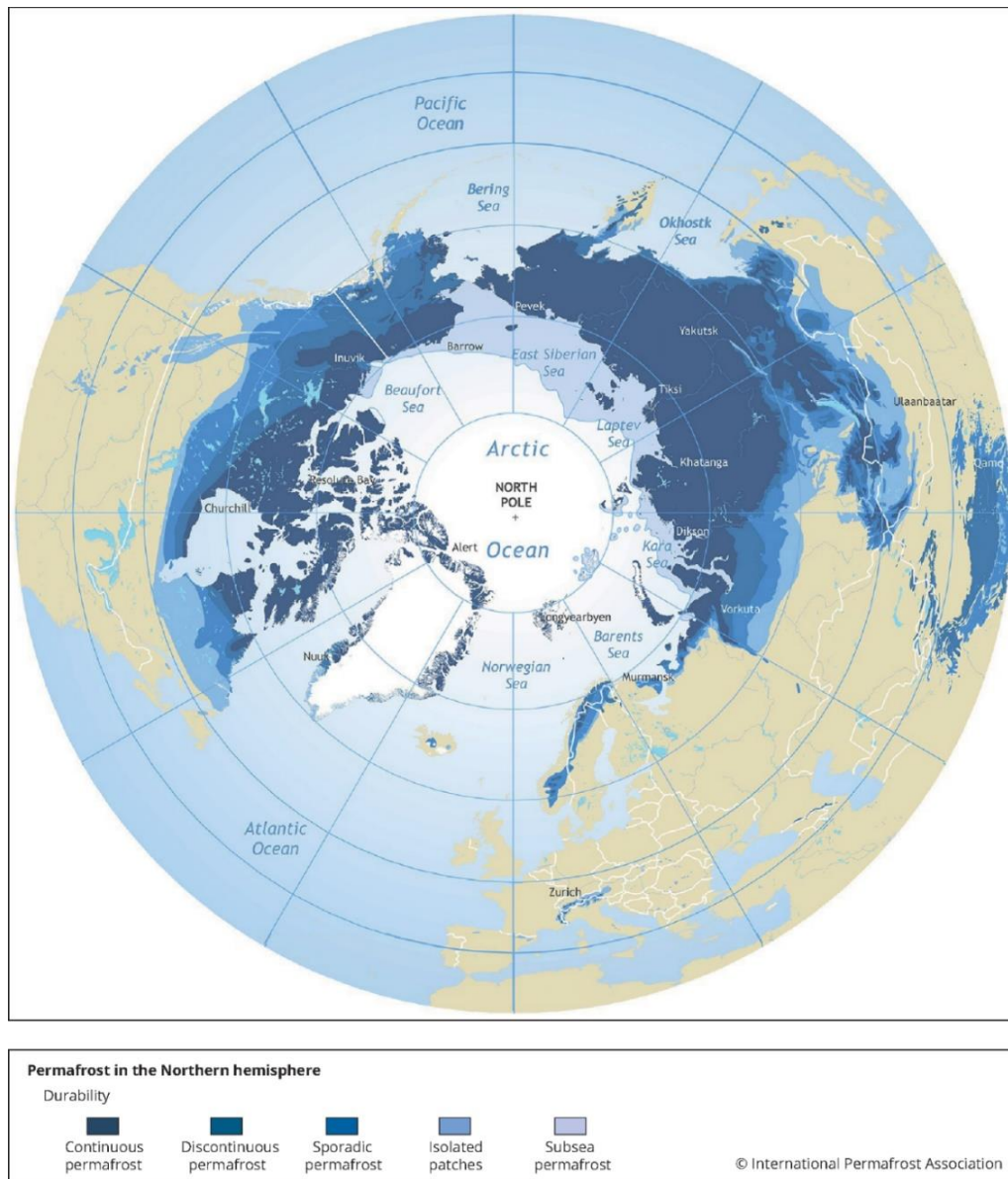


Figure 2-8: Permafrost in the northern hemisphere with terrestrial and subsea parts. Shades of blue indicate the areal extent of the terrestrial permafrost: continuous (> 90%), discontinuous (50-90%), sporadic (10-50%), and isolated (< 10%). Map realized by International Permafrost Association (The Arctic Environment — European Environment Agency, 2017).

The active layer is the uppermost part of the permafrost that thaws and refreezes seasonally. At the transition between the base of the active layer and the upper part of permafrost, is the transient layer which thaws only in years with exceptionally hot summers (French, 2007; Shur et al., 2005). Thanks to its high and quasi-uniform ice content, this layer acts as a buffer essential for permafrost stability (Shur et al., 2005). Influenced by climate and local factors, active layer thickness varies from < 0.5 m in vegetated land to > 10 m in exposed rock zones.

Most biological and hydrological activities in Arctic soils are restricted to this seasonal thaw layer (Hinzman et al., 2005).

2.5. Warming Arctic

During the period 1880-2012, the global average temperature (combined over land and ocean) increased by about 0.85 °C, mainly attributed to anthropogenic forcing (IPCC, 2021). Warming accelerated after the 1970s even if the warming is not equal in all regions. Specifically, Arctic surface air temperatures have risen more than twice as fast as the global average over the past two decades (Figure 2-9; IPCC, 2021; Meredith et al., 2019).

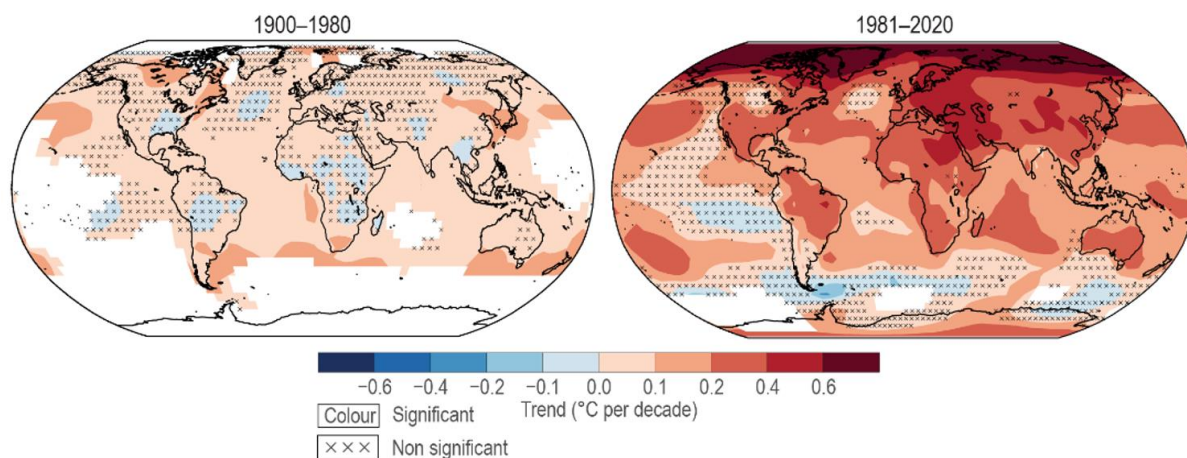


Figure 2-9: Evolution of air temperatures over 1900-1980, and 1981-2020 (IPCC, 2021)

Warming Arctic has several impacts: early melting of snow cover, ice cover reduction, and permafrost degradation. In addition, melting snow cover leads to a reduction in albedo, intensifying permafrost degradation (Meredith et al., 2019; van der Kolk et al., 2016). One of the main concerns associated with thawing permafrost is the exposure of large amounts of frozen carbon, which is subject to microbial decomposition, resulting in the emission of greenhouse gases (CO₂ and CH₄) into the atmosphere (McGuire, 2018). This process creates a positive feedback loop that exacerbates global warming. In addition, thawing permafrost leads to an increase in nitrogen availability for plants around the thaw front (Keuper et al., 2017). Furthermore, permafrost degradation also alters topography and soil moisture (Hicks Pries et al., 2013).

The increase in temperature, nitrogen availability, and the change in soil moisture lead to vegetation shifts in the Arctic region. Initially, sedges, which have a greater capacity for root elongation, extend their roots to the permafrost thaw front. In contrast, shrubs are unable to do so, with their roots remaining primarily near the surface. As a result, sedges would accumulate a higher N concentration in their tissues, stimulating their growth (Hewitt et al., 2019). Moreover, the initial water saturation of the soil during permafrost thawing provides even greater advantages for sedges. However, in the long term, as temperature rises, humidity

changes, and nitrogen is added, shrub growth is also stimulated. Even if the environment meets the ecological requirements of sedges, the increase in shrub biomass creates competition with a shading effect that excludes all heliophile species, which explains the gradual disappearance of sedges (Salmon et al., 2019).

As a result, permafrost degradation initially leads to an increase in sedge biomass, followed by an increase in shrub and forb biomass at the expense of sedges. Therefore, shrubs are more widespread in well-drained or dry soils. Although sedges tolerate very wet environments where shrubs cannot thrive, shrubs seem to dominate these habitats due to increased drainage (E. A. G. Schuur et al., 2007; van der Kolk et al., 2016). Several Earth observation satellites have confirmed the increase in shrub cover and growth in certain parts of the Arctic (Mekonnen et al., 2021). The summer Normalized Difference Vegetation Index (NDVI) has increased significantly (spectral greening) and decreased locally (spectral browning) over recent decades in the Arctic (Figure 2-10). The spectral greening detected by these satellites is associated with an increase in shrub cover.

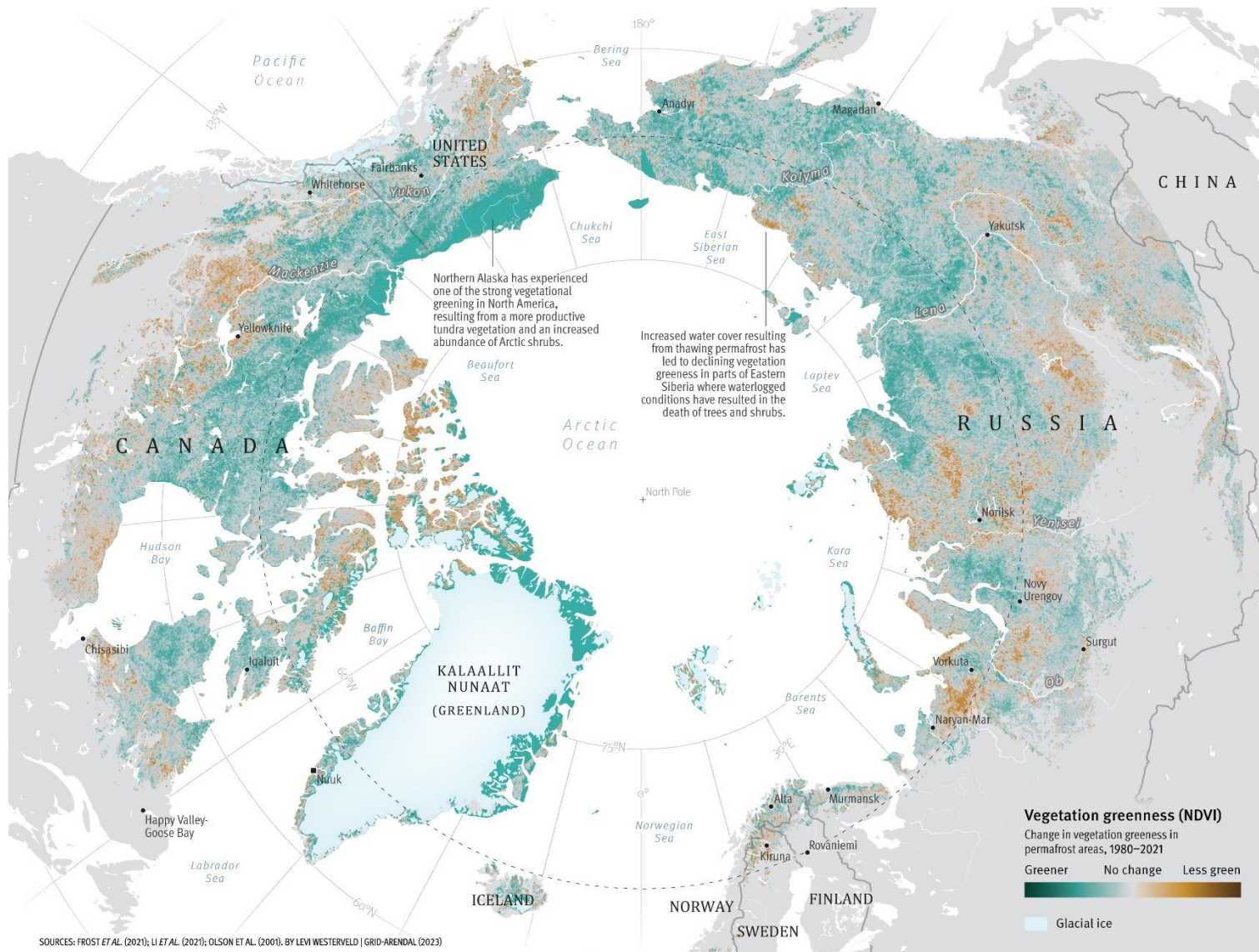


Figure 2-10: Observed changes in vegetation greenness in permafrost areas between 1980-2021. (Westerveld, 2023)

This increase in shrubs has repercussions on the environment, particularly on permafrost degradation via feedback mechanisms (Figure 2-11). Shrubs can trap a thicker layer of snow on the ground in winter, insulating the soil from low temperatures and exacerbating permafrost degradation (Myers-Smith et al., 2015). In addition, shrub albedo is lower than the one of sedges, further increasing soil temperatures (Marsh et al., 2010).

Microbial activity is significantly impacted by changes in soil temperature and moisture. Extreme soil moisture conditions impede or slow microbial decomposition while warmer and drier soil conditions enhance microbial activity and organic matter decomposition (Schimel et al., 1999). Furthermore, shrub increasing, which raises soil temperatures, intensifies this decomposition process. However, evergreen shrubs, having a slower decomposition rate compared to sedges, forbs, and deciduous shrubs, slow down the organic matter decomposition processes (Hobbie, 1996).

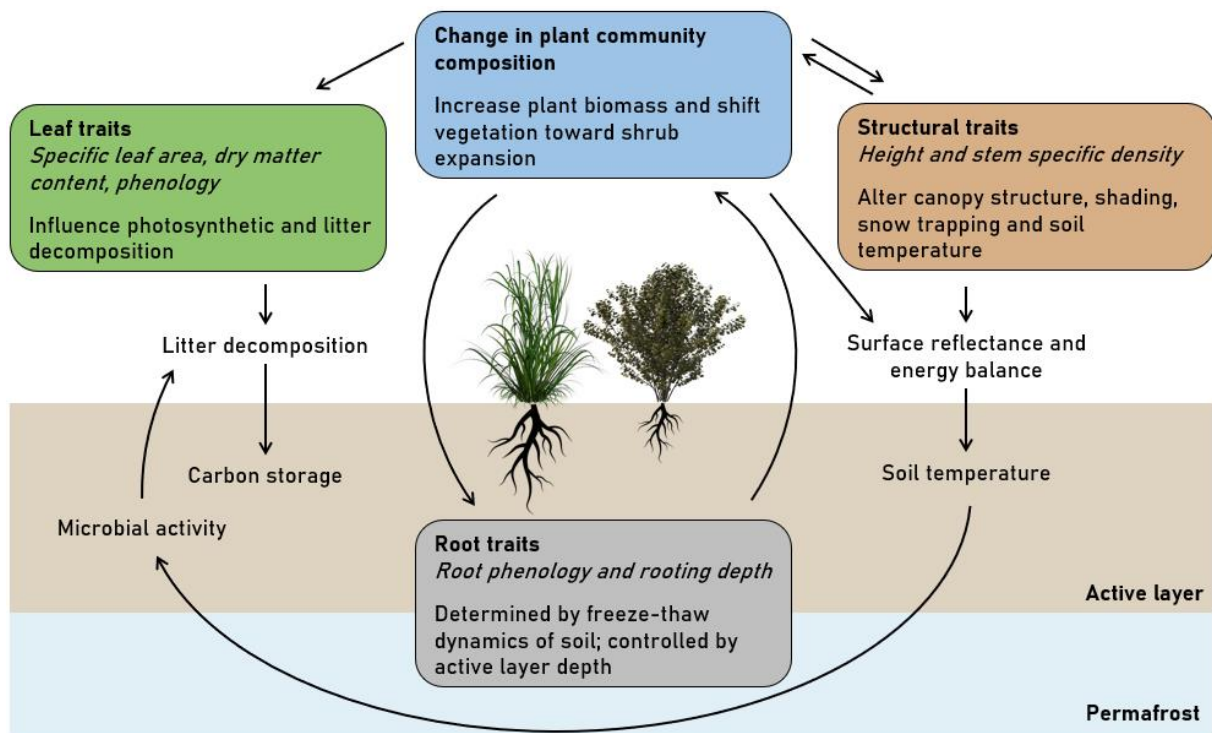


Figure 2-11: Influence of changes in plant traits on ecosystem functions such as surface albedo, energy balance, soil temperature, biogeochemical cycling, and carbon storage. Changes in these key ecosystem functions could create feedback to the global climate system, whose direction and magnitude remain currently uncertain. Further data and analyses have the potential to fill in the gaps in ecological data syntheses and Earth system models to improve the quantification of the ecological feedback of Arctic ecosystem change (adapted from Myers-Smith et al., 2019).

Many studies have examined the effects of Arctic warming on the plant element cycle, focusing mainly on macro-nutrients, C, N, or P (Carey et al., 2017; Chapin et al., 1980; Chapin III et al., 1996; Hewitt et al., 2019; Jonasson, 1983; Keuper et al., 2017; Salmon et al., 2016). However, there is a notable gap in research concerning its impact on trace elements cycling. It is therefore important to study the variation in trace element content among Arctic cosmopolitan plant

species and their cycle in vegetation. Understanding the effect of Arctic warming on nutrient cycling is crucial for improving simulations of vegetation dynamics in evolving northern ecosystems (Druel et al., 2019).

3. Objectives and general approach

This master's thesis aims to understand the factors influencing plant nutrient uptake and their consequences on seasonal transfer in Arctic ecosystems. This research will improve the understanding of the response of vegetation to variations in environmental conditions. More specifically, this master's thesis will answer the following research question:

“How do plants cycle trace elements in different Arctic habitats?”

To answer this question, we will study the foliar and soil trace element concentrations in two study sites in Abisko, Sweden: a peatland mire and a heathland, showing contrasting environmental conditions. We will focus on As, Cd, Cu, Fe, Mn, Mo, V, Ti, and Zn, which show contrasting concentrations between different plant species.

To answer the research question, the following sub-objectives are set (Figure 3-1).

Sub-objective 1: What factors influence plant nutrient uptake in the different Arctic habitats?

This research considers nine cosmopolitan Arctic plant species with different rooting depths, most present in both sites. Foliar element concentrations are compared between all species. It allows to test the following hypotheses: (1) species present in different ecosystems have similar element concentrations, and (2) species with deeper rooting depths have a higher element concentration. Finally, foliar element concentrations are compared with the soil element concentrations. To do this, enrichment factors are calculated between the plant and the mineral horizon. The comparison enables to highlight whether the concentrations in the soil influence those in the plant.

Sub-objective 2: How does plant biomass composition influence foliar element stocks and fluxes?

The biomass of the nine Arctic plant species is sorted and weighted in each habitat. Foliar stocks and fluxes are calculated for trace elements and compared between habitats. It enables to determine how changes in plant biomass composition influence the flux of trace elements between plant tissues and soil litter.

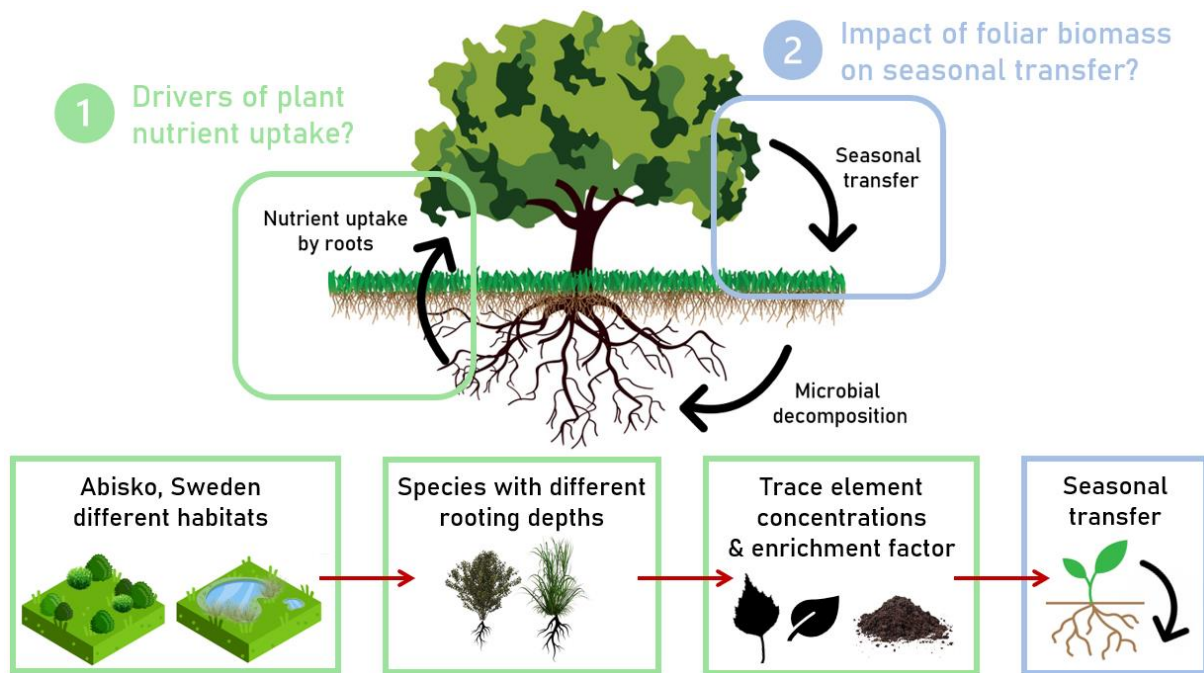


Figure 3-1: Master's thesis's general approach in which successive steps aim to answer two sub-objectives. From two sites in Abisko, Sweden, nine cosmopolitan Arctic plant species with different rooting depths are considered. Then, foliar trace element concentrations are compared between all species. Afterward, foliar element concentrations are compared with the soil element concentrations for each species by calculating enrichment factors. Finally, foliar element stocks and fluxes are calculated to determine the impact of plant biomass composition on seasonal transfer.

4. Materials and methods

4.1. Study site

Situated at Abisko, northern Sweden, the study area includes various Arctic environments (Figure 4-1A). Abisko is characterized by a subarctic climate (Dfc in Köppen and Geiger classification), meaning the coldest month has a mean temperature inferior to 0 °C and the warmest month has a mean temperature above 10 °C (Strand et al., 2021). From 1985 to 2010, the mean annual air temperature at Abisko was 0.02 °C and the mean annual precipitation was 330 mm (Schmidt, 2012).

Two study sites were considered (Figure 4-1B; Table 4-1): a peatland mire and a heathland. Located on the southern shore of Lake Torneträsk, the first site was a permafrost peatland mire called Storflaket (68°34'N, 18°97'E; 360 m a.s.l, ~5 ha). The mire was in a zone of discontinuous permafrost, with a peat layer of 50-90 cm thick underlined by glacial silty sediments and an active layer thickness around 60 cm (Olid et al., 2020). The second site was a heathland ecosystem southwest of the Báddosdievvá hill (68°31'N, 18°86'E; 600 m a.s.l, ~25 ha). It was characterized by shallow soils on top of metamorphic bedrock (Agnan et al., 2019).

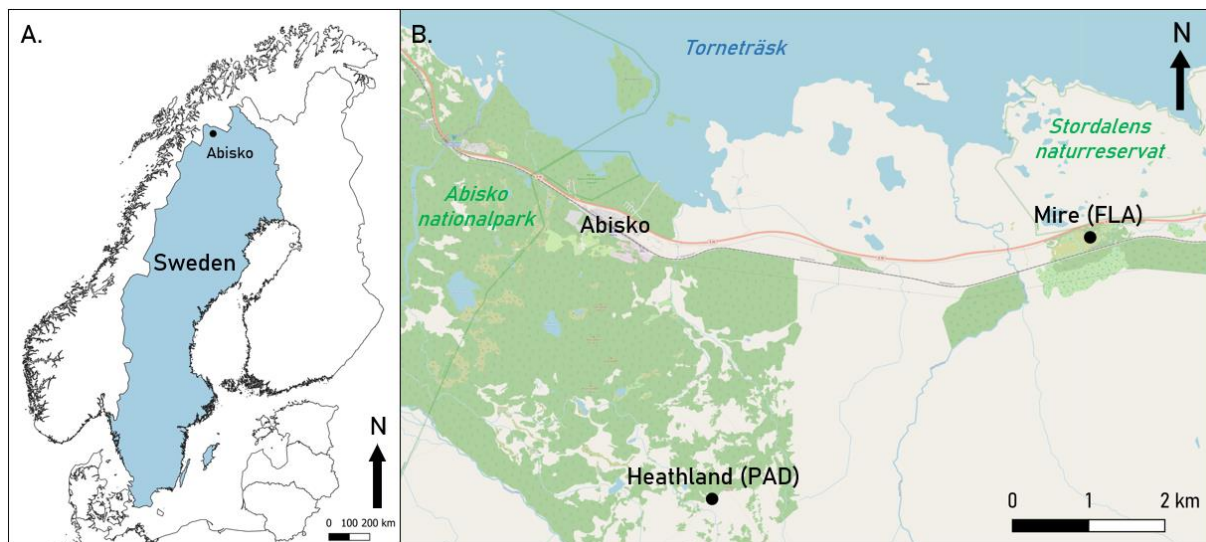


Figure 4-1: Geographical context of the Abisko region and location of the sampling site. A. Northern Europe; B. Abisko area. Two sites were studied: one was a permafrost peatland mire called Storflaket and the other was a heathland. The base map is the OpenStreetMap tile from QGIS.

Table 4-1: Environmental characteristics of the two study sites (Agnan et al., 2019; Olid et al., 2020).

	Mire (FLA)	Heathland (PAD)
Latitude, longitude	68°34'N, 18°97'E	68°31'N, 18°86'E
Elevation (m a.s.l.) ^a	360	600
Slope aspect/steepness		SW/~1 °
Bedrock	Glacial sedimentary deposits	Calc-silicate rocks
Soil type	Histosol	Histosol
Soil pH (range) ^b		
Organic horizons		3.9-4.9
Mineral horizons		4.9-5.8
Active layer thickness (cm)	60-80	60-80

In August 2021 and 2022, a field trip was led in Abisko by Sorbonne Université and UCLouvain. This expedition was part of the research project “Interactions between Cycles in Ecosystems across Permafrost in Transition – INCEPTION” led by Marie Alexis from Sorbonne Université, Paris. The INCEPTION project focused on understanding the biogeochemical cycles, specifically the nitrogen cycle, in rapidly warming Arctic and subarctic ecosystems.

During the expedition, vegetation composition was characterized, and vegetation and soil samples were collected in both ecosystems (i.e., mire and heathland). For this purpose, both ecosystems were divided into several sub-sites corresponding to the different habitats.

Each site was subdivided into different habitats, based on vegetation composition, micro-topography, and the presence of free water. The mire ecosystem was divided into three habitats: (1) a palsa, the highest part of the mire and dominated by dwarf shrubs including *Betula nana*, *Empetrum nigrum*, *Vaccinium uliginosum*, and by patches of *Rubus chamaemorus*, a forb species; (2) a bog, series of hollows in the palsa, filled with stagnant water and presenting a cover of *Sphagnum* sp. and *Eriophorum vaginatum*; and (3) a fen, lowest part of the mire, characterized by free water and dominated by large aquatic graminoid species such as *Carex rostrata* and *Eriophorum angustifolium*.

Alike, the heathland ecosystem was subdivided into three habitats: (1) a humid-heath habitat dominated by dwarf shrubs and mosses; (2) a dry-heath habitat presenting a dominance of dwarf shrubs like *Betula nana*, *Empetrum nigrum*, and *Vaccinium uliginosum*; and (3) a birch forest habitat with similar shrubs to the dry-heath habitat, with additional *Vaccinium vitis-idaea*.

^a Based on a 10 m national DEM (*geonorge.no*).

^b pH_{CaCl₂ 0.25mM}

4.2. Sampling

4.2.1. Vegetation sampling

Within each ecosystem (i.e., mire and heathland), vegetation floristic composition was determined in 1 m × 1 m quadrats, randomly distributed across the different habitats (Figure 4-2). A code was attributed to each quadrat, called sub-site (Table 4-2).

In the mire, four quadrats were distributed between the palsa, bog, and fen habitats. While, in the heathland ecosystem, four quadrats were positioned in each habitat (i.e., humid-heath, and dry-heath) and two quadrats were placed in the birch forest. The forest composition was determined with 10 m × 10 m quadrats to cover its larger geographical extent.

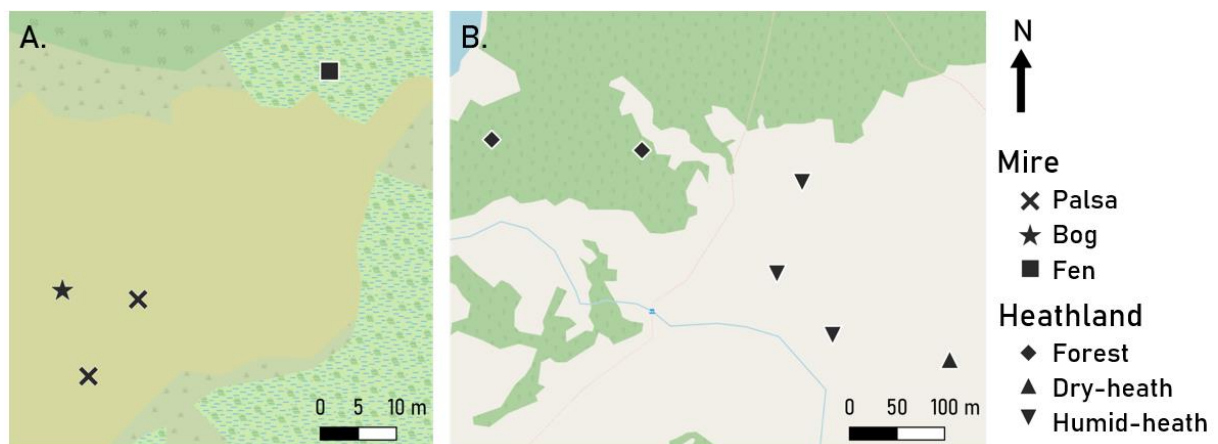


Figure 4-2: Localisation of the different quadrats in the six habitats. The base map is the OpenStreetMap tile from QGIS. A. In the mire: two quadrats in palsa, one in bog, and one in fen; B. In the heathland: two quadrats in the birch forest, one in dry-heath, and three in humid-heath.

Table 4-2: Codes associated with each sub-site and the habitat associated.

Site	Habitat	Sub-site code
Mire (FLA)	Palsa	FLA-1
		FLA-2
	Bog	FLA-7
	Fen	FLA-11
Heathland (PAD)	Humid-heath	PAD-A2
		PAD-B2
		PAD-C1
	Dry-heath	PAD-D4
	Forest	PAD-F1
		PAD-F8

In each quadrat, the cover percentage of each species was estimated visually (Daubenmire, 1959), and aboveground biomass was collected and dried at 60 °C for at least 48 h.

4.2.2. Soil sampling

Soil samples were collected as close to each vegetation quadrat as possible using a stainless-steel auger and a knife (Figure 4-2). Sampling covered the entire soil depth in the heathland ecosystem (from 10 cm in the dry-heath to 60 cm in the humid-heath), but was limited to the active layer in the mire (from 45 cm in the palsa to 1 m deep in the bog). Due to a water table level higher than ground level, sampling in the fen was not possible. Two horizon types were identified and sampled separately based on visual inspection: (1) an "organic" horizon with partially decomposed organic matter, including litter and vegetation belowground biomass; and (2) a "mineral" horizon with well-decomposed organic matter (for saturated soils) and a higher proportion of coarse mineral particles (for drier soils), and little to no belowground biomass.

4.3. Sample preparation

4.3.1. Vegetation sample preparation

For this research, nine cosmopolitan Arctic species with different rooting depths were considered. In the deciduous shrubs category, were selected *Betula nana* and *Vaccinium uliginosum*. *Vaccinium vitis-idaea* and *Empetrum nigrum* were part of evergreen shrubs. In the sedges, *Carex rostrata*, *Eriophorum angustifolium*, *Eriophorum scheuchzeri*, and *Eriophorum vaginatum* were chosen. *Rubus chamaemorus* was the only forb species selected. Most of the selected species were present in both sites. Table 4-3 presents the cover percentage of each species in the different sub-sites.

Table 4-3: Cover percentage (%) of the considered species in the different sub-sites. The underlined numbers correspond to the species sorted and used for the following analysis.

Functional groups	Species	Cover percentage (%)									
		FLA-1	FLA-2	FLA-7	FLA-11	PAD-A2	PAD-B2	PAD-C1	PAD-D4	PAD-F1	PAD-F8
Evergreen shrub	<i>Vaccinium vitis-idaea</i>	0	0	0	0	0	0	<u>1</u>	<u>1</u>	<u>25</u>	<u>2</u>
	<i>Empetrum nigrum</i>	<u>25</u>	<u>20</u>	0	0	0	<u>20</u>	<u>30</u>	<u>30</u>	<u>25</u>	<u>35</u>
Deciduous shrub	<i>Vaccinium uliginosum</i>	<u>10</u>	<u>10</u>	0	0	0	<u>5</u>	<u>10</u>	<u>5</u>	0	<u>4</u>
	<i>Betula nana</i>	<u>10</u>	<u>1</u>	0	0	0	<u>1</u>	<u>5</u>	<u>20</u>	<u>2</u>	0
Sedge	<i>Carex rostrata</i>	0	0	1	<u>25</u>	<u>20</u>	0	0	0	0	0
	<i>Eriophorum angustifolium</i>	0	0	0	<u>75</u>	0	0	0	0	0	0
	<i>Eriophorum vaginatum</i>	0	0	<u>30</u>	0	<u>46</u>	0	0	0	0	0
	<i>Eriophorum scheuchzeri</i>	<u>30</u>	<u>5</u>	0	0	0	0	0	0	0	0
Forb	<i>Rubus chamaemorus</i>	<u>15</u>	<u>25</u>	0	0	0	<u>1</u>	<u>1</u>	0	0	1

Considered species were sorted from the bulk quadrat to isolate enough material for mineral element analysis by species (n = 34; Figure 4-3).



Figure 4-3: Sorting stage of the dried biomass: A-B. Biomass of each quadrat is disposed on a craft paper.; C. Selected species are sorted (i.e., *Betula nana*); D. and placed into a plastic vial.

Individually, these 34 samples were ground with liquid nitrogen (Figure 4-4).

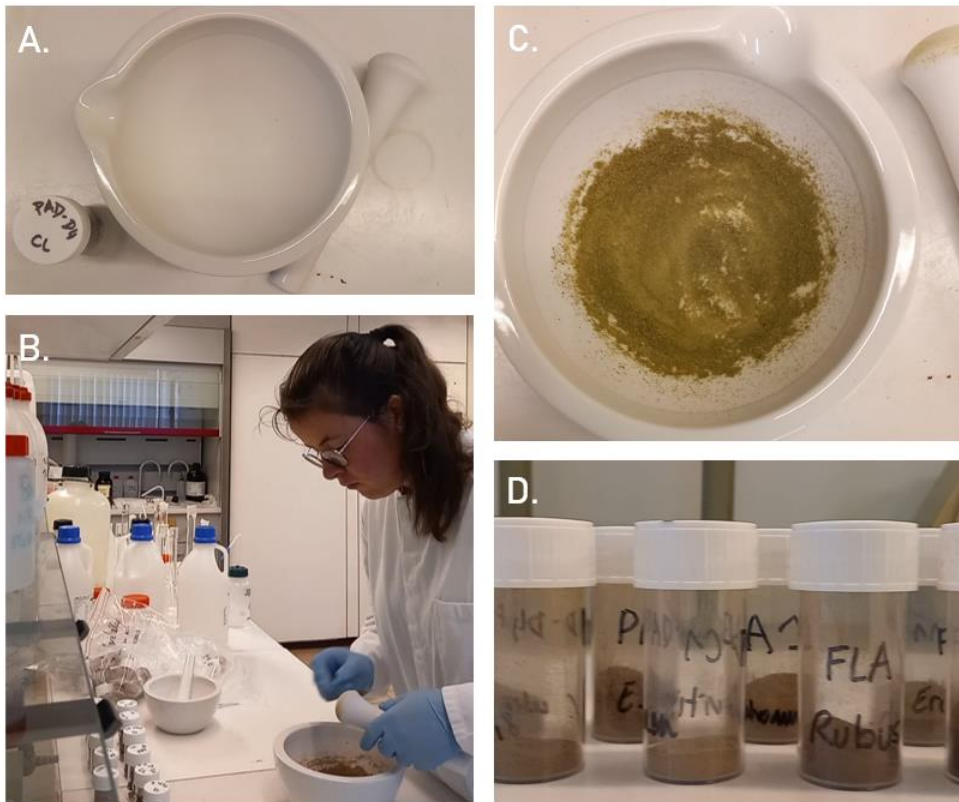


Figure 4-4: Stage of sample reduction to powder: A. A mortar and a pestle are used to ground the samples.; B. Liquid nitrogen is added to the samples.; C. The result of this stage is the transformation of the sample into a powder.; D. which is transferred into a plastic vial.

4.4. Mineral element analysis

Trace element concentrations were determined after the acid dissolution of the various plant matrices studied.

4.4.1. Acid dissolution

For each ground plant sample, 100 mg were weighed and placed in a Teflon vial (Savillex Purillex® PFA Vial). In addition, a blank and a sample of reference lichen (IAEA-336) were analyzed to evaluate measurement accuracy. Successive steps were followed (Figure 4-5):

1. 0.5 mL of nitric acid (HNO_3) 65% and 0.5 mL of fluoridric acid (HF) were added to each sample. They were ultrasonic homogenized for 3×3 min. For half a day, vials were left half-opened at room temperature for a degassing step. Samples were heated at 90°C for two days, then solutions were evaporated at 40°C .
2. 1 mL of hydrogen peroxide (H_2O_2) was added, and each sample was ultrasonic homogenized during 3×3 min. A degassing step lasted for half a day with the cap ajar. Then, solutions were evaporated at 40°C .
3. 1 mL of aqua regia (0.8 mL of hydrochloric acid (HCl) 37% and 0.2 mL HNO_3 65%) were added. Samples were ultrasonic homogenized for 3×3 min. They were heated at 90°C for one day, then solutions were evaporated at 40°C .
4. 1 mL of HNO_3 65% was finally added. Samples were ultrasonic homogenized during 3×3 min, and heated at 90°C for one day.

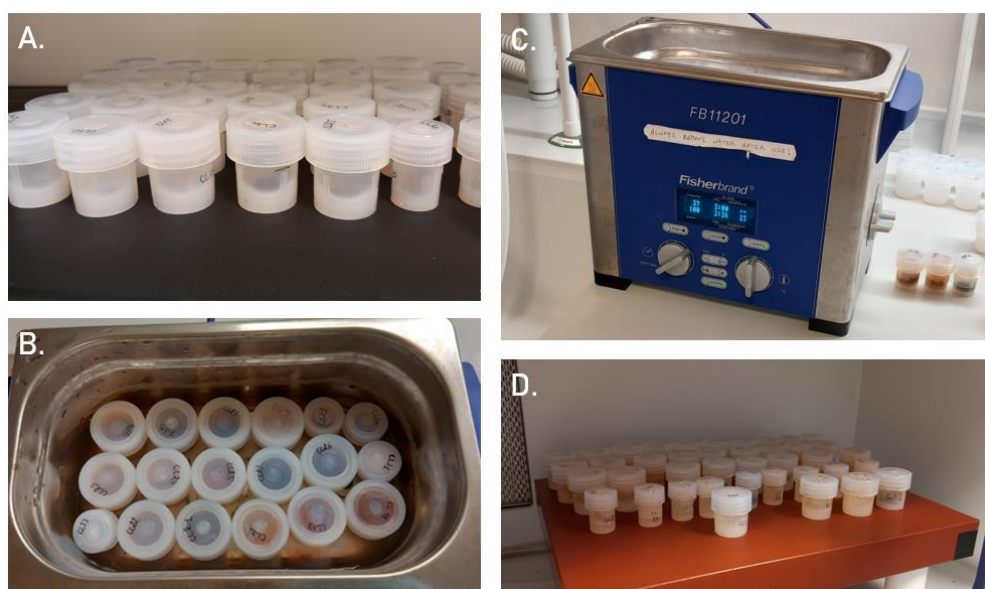


Figure 4-5: Stage of acid dissolution: A. Weighted samples in Savillex; B-C. Ultrasonic homogenization; D. Samples on a heating plate at step 4 of the acid dissolution.

Trace element contents were determined in HNO₃ 2% diluted samples by Inductively Coupled Plasma Mass Spectrometry (ICP-MS).

4.4.2. Analysis by Inductively Coupled Plasma Mass Spectrometry

Trace element concentrations were determined by ICP-MS. This analysis method was based on the separation, detection, and quantification of ions according to their charge-to-mass ratio (Menet, 2011; Telgmann et al., 2017). To correct the eventual drift of the instrument, three elements (i.e., Ru, In, Re) were injected into the analyzed solutions.

The analyzed elements were the following: As, Cd, Cu, Fe, Mn, Mo, Ti, V, and Zn.

Data quality: accuracy of measurement

The recoveries were calculated as the ratio between the measured concentrations of the reference lichen (IAEA-336) and the certified values (Equation 4-1; Table 4-4). In most cases, the coverage was slightly below 100% attesting to the accuracy of the methods and measurements. Only Cu and Mo were below 80%. Mo had a low recovery of 35%.

$$Recovery = \frac{C_{measured}}{C_{reference}} \times 100 (\%) \quad (4-1)$$

Table 4-4: Recovery (%) obtained from reference lichen (IAEA-336). There are no reference values for Mo and Ti, the used values are the accepted laboratories' means.

Sample	Recovery (%)								
	As	Cd	Cu	Fe	Mn	Mo	Ti	V	Zn
Lichen	89	81	79	88	87	35	94	89	88

Analytical blanks

One analytical blank was run during acid dissolution to ensure the absence of contamination. The ratio between the analytical blanks and the average of the results obtained for acid dissolution showed values of less than 3% for most of the elements present in the plants except for As and Ti (Table 4-5).

Table 4-5: Ratio (%) between the analytical blanks and the average of the samples for acid dissolution.

Matrix	Ratio (%)								
	As	Cd	Cu	Fe	Mn	Mo	Ti	V	Zn
Plants	8	-5	<1	3	<1	2	6	1	3

Limits of quantification and detection

The limits of detection (LOD) and quantification (LOQ) were given by the ICP-MS (Table 4-6). They varied between elements but were always inferior to 0.3 µg/L for LOD and 1 µg/L for LOQ.

Table 4-6: Limits of detection (LOD) and quantification (LOQ) ($\mu\text{g/L}$) obtained for the samples of the acid dissolution

	As	Cd	Cu	Fe	Mn
LOD ($\mu\text{g/L}$)	5.90×10^{-4}	2.10×10^{-3}	3.90×10^{-3}	1.78×10^{-2}	4.91×10^{-3}
LOQ ($\mu\text{g/L}$)	1.97×10^{-3}	7.00×10^{-3}	1.29×10^{-2}	5.94×10^{-2}	1.64×10^{-2}
	Mo	Ti	V	Zn	
LOD ($\mu\text{g/L}$)	1.04×10^{-3}	2.35×10^{-2}	7.67×10^{-4}	2.34×10^{-2}	
LOQ ($\mu\text{g/L}$)	3.47×10^{-3}	7.82×10^{-2}	2.55×10^{-3}	7.81×10^{-2}	

4.5. Available data for Abisko

Thanks to different investigations performed by Hugo Potier (PhD student at Sorbonne Université), supplementary data were available.

The soil of the different sub-sites was described by giving each horizon (i.e., organic or mineral) different information such as mass humidity or horizon depth (Appendix 1).

For each habitat (i.e., Palsa, Bog, Forest, Dry-heath, and Humid-heath), soil element concentrations were obtained with ICP-OES after an acid dissolution with HF. Concentrations were available for Al, As, Ba, Cd, Co, Cr, Cu, Fe, Mn, Mo, Ni, Pb, Se, Sr, Ti, V, and Zn (Appendix 2).

4.6. Data treatment

Tela Botanica for biotope description

Tela Botanica network is the result of collaboration between botanists and the public. This example of collaborative science led to the development of an electronic flora, eFlore, which provides information on the floral species of France and several French-speaking regions (www.tela-botanica.org; Heaton et al., 2010). This flora describes the species, including its geographical distribution and ecology (climatic and soil characteristics) with Ellenberg indicators. These data were used to describe the environmental characteristics of habitats in the first section of “Results & discussion”.

Enrichment factor

The enrichment factor (EF; Bern et al., 2019) was calculated for each trace element (X) in the plant (Equation 4-2) using Ti, a lithogenic element, to normalize. The mineral horizon class samples were the reference material. It was decided not to consider the organic horizon, as the species mainly absorb nutrients from this horizon due to their shallow root systems (Iversen et al., 2015).

$$EF = \frac{(X/Ti)_{plant}}{(X/Ti)_{mineral}} \quad (4-2)$$

Foliar stocks and fluxes

For both sites (i.e., mire and heathland in 2021), datasets of vegetation aboveground biomass were obtained at the sorting stage. For vascular plant species, aboveground biomasses were converted to foliar biomasses using species-specific ratios (r ; Appendix 5; Potier et al., 2024). The foliar biomass (FB) was calculated as follows (Equation 4-3):

$$FB = AB \times r \text{ (g m}^{-2}\text{)} \quad (4-3)$$

With FB, foliar biomass (g m⁻²), AB, aboveground biomass (g m⁻²), and r , the ratio between foliar biomass and aboveground biomass (-). Data are presented in Appendix 6.

The estimation of foliar element stocks (FS) was calculated using the following equation (Equation 4-4):

$$FS = FC \times FB \times \frac{1}{1000} \text{ (mg m}^{-2}\text{)} \quad (4-4)$$

With FS, foliar element stock (mg m⁻²), FC, foliar element concentration (mg kg⁻¹), and FB, foliar biomass (g m⁻²). The standard deviation (σ_{FS}) was further calculated to assess the heterogeneity of foliar element stocks among species and across the different habitats with Equation 4-5:

$$\sigma_{FS} = [\sigma_{FB} \times FC + \sigma_{FC} \times FB] \times \frac{1}{1000} \quad (4-5)$$

With σ_{FB} , standard deviation of the foliar biomass, and σ_{FC} , standard deviation of the foliar concentration. Data for FC and σ_{FC} are presented in Appendix 9 while data for FS and σ_{FS} are presented in Appendix 10.

For the estimation of foliar fluxes (FF) at an annual time scale, we considered that the vegetation was at its equilibrium, with the annually produced biomass (net primary productivity, NPP) equivalent to the senescing biomass (biomass returning to the soil litter). The estimation of annual foliar fluxes (FF) of mineral elements from standing leaf to foliar litter was calculated using the following equation (Equation 4-6):

$$FF = FC \times fNPP \times \frac{1}{1000} \text{ (mg m}^{-2} \text{ a}^{-1}\text{)} \quad (4-6)$$

With FF, foliar element flux (mg m⁻² a⁻¹), and fNPP, foliar net primary productivity (g m⁻² a⁻¹). In 2017, fNPP was evaluated for five species (*Vaccinium uliginosum*, *Betula nana*, *Carex bigelowii*, *Eriophorum vaginatum*, *Rubus chamaemorus*) at the CiPEHR site in Eight Mile Lake, Alaska (Appendix 11; Mauclet et al., 2022). In this study, the values from CiPEHR were used. Foliar NPP for *Carex bigelowii* was used for *Carex rostrata* and fNPP for *Eriophorum vaginatum* was used

to determine *Eriophorum* sp. with a ratio between plant height aboveground (www.telabotanica.org) and fNPP. Therefore, *Eriophorum angustifolium* and *Eriophorum scheuchzeri* had an estimated fNPP of 157 g m⁻² a⁻¹ and 87 g m⁻² a⁻¹ respectively. As foliar fluxes (FF) were estimated at an annual time scale, evergreen species were not considered. Data are presented in Appendix 12.

Standard deviations of annual foliar fluxes (σ_{FF}) were calculated using Equation 4-7:

$$\sigma_{FF} = \sigma_{FC} \times fNPP \times \frac{1}{1000} \quad (4-7)$$

5. Results & discussion

5.1. Environmental description of habitats

This first section investigates the available variables to provide a comprehensive description of the different habitats selected for this study. Each habitat hosts different species depending on local environmental conditions. The ecological characteristics of each species are used to determine the environmental characteristics of the habitats.

Species in the same functional group have similar ecological characteristics (Appendix 3). Shrubs generally prefer more acidic soils than sedges, except for *Eriophorum vaginatum* and *Eriophorum scheuchzeri*, which grow in the same pH range as shrubs ($4 < \text{pH} < 4.5$). Evergreen shrubs are generally found on drier soils, ranging from mesoxerophilic to mesohydric conditions, as are deciduous shrubs, which occupy mesohydric to mesohygrophilic soils. Sedges, on the other hand, occupy wetter soils, with *Eriophorum* species being hygrophilic and *Carex rostrata* hydrophilic. *Rubus chamaemorus*, a forb species, inhabits habitats that are generally wet and acidic (Åboliņa et al., 2023). All nine species are distributed in nutrient-poor soils, under hyperoligotrophic (e.g., *Eriophorum vaginatum*) or oligotrophic (e.g., *Vaccinium vitis-idaea*, *Vaccinium uliginosum*, and *Carex rostrata*) conditions.

By aggregating the ecological parameters of each species within the same habitat, it can be concluded that habitats within the same site follow a gradient of abiotic conditions, such as pH and humidity (Figure 5-1). For instance, within the mire, humidity increases from Palsa to Fen, influencing the species composition. Habitats like Palsa, Forest, and Dry-heath, characterized by drier and more acidic conditions, are predominantly populated by forbs and shrubs. Even in the wetter conditions of Humid-heath, forbs and shrubs are still present. Sedges are typically found in habitats with higher moisture levels such as Bog, Fen, or Humid-heath. However, only *Eriophorum scheuchzeri*, a type of sedge, is found in the drier habitat of Palsa because, unlike other sedges, it grows in a more acidic environment ($4 < \text{pH} < 4.5$).

This finding underlines the fact that the local distribution of Arctic vegetation depends primarily on variations in soil moisture (Heijmans et al., 2022; Peterson & Billings, 1980). Specifically, areas with high soil moisture tend to support graminoid vegetation, while drier regions are often dominated by shrubs (Walker et al., 2005). Although shrubs thrive in moist soil conditions (Frost et al., 2014), they struggle in waterlogged environments, unlike sedges, which possess adaptations that enable them to withstand both anaerobic and waterlogged conditions.

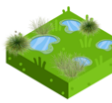
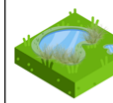
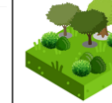
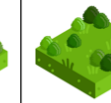
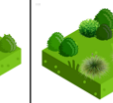
		Mire (FLA)			Heathland (PAD)		
		pH  Humidity 			pH  Humidity 		
		Palsa	Bog	Fen	Forest	Dry-heath	Humid-heath
							
Deciduous Evergreen shrub	SPECIES						
	<i>Vaccinium vitis-idaea</i>				x	x	x
	<i>Empetrum nigrum</i>	x			x	x	x
	<i>Vaccinium uliginosum</i>	x			x	x	x
shrub	<i>Betula nana</i>	x			x	x	x
	<i>Carex rostrata</i>		x	x			x
	<i>Eriophorum angustifolium</i>			x			
	<i>Eriophorum vaginatum</i>		x				x
Sedge	<i>Eriophorum scheuchzeri</i>	x					
	<i>Rubus chamaemorus</i>	x			x		x
Forb							

Figure 5-1: Environmental description of the two sites (i.e., mire and heathland). Each habitat (i.e., Palsa, Bog, Fen, Forest, Dry-heath, and Humid-heath) is characterized by abiotic conditions such as pH, and humidity. The pH and humidity indications come from the Ellenberg indicators provided by the electronic flora, eFlore, from Tela Botanica (www.tela-botanica.org). These conditions favor establishing some species (marked by a cross in the table), grouped by functional groups (written on the left of the figure). In the figure, the habitats are sorted by following a gradient in abiotic conditions.

5.2. Factors influencing foliar nutrient concentrations

The first objective of this master's thesis is to understand and identify the factors influencing foliar nutrient concentrations in different Arctic habitats. This section is divided into several parts, each of them examining the influence of a possible factor such as soil concentrations, floristic composition of habitat, and rooting depth.

Average foliar element concentrations, measured in mg kg^{-1} , are presented for each habitat (Figure 5-2A). The foliar element concentration of a habitat $FC_{avg,habitat}$ is the average of the element concentrations of a sub-site, which is the sum of the element concentrations of the species present, weighted by the species biomass proportion in the sub-site (Equation 5-1). Weighting takes into account the proportion of species present. A more present species will have a greater influence on the overall element concentration of a habitat.

$$FC_{avg,habitat} = \frac{1}{n} \sum_{i=1}^n \left[\sum_{j=1}^k \left(FC_{i,j} \times \frac{biomass_{i,j}}{biomass_i} \right) \right] \text{ with } i = 1, \dots, n \text{ and } j = 1, \dots, k \quad (5-1)$$

With n , the number of sub-sites in the habitat; k , the number of species in the sub-site i ; $FC_{i,j}$, the foliar element concentrations in the species j from the sub-site i ; $biomass_{i,j}$, the foliar

biomass in the species j from the sub-site i ; $biomass_i$, the total foliar biomass of the sub-site i . Data for $biomass_{i,j}$ and $FC_{i,j}$ are presented in Appendixes 6 and 7 respectively.

Within the mire, Palsa, Bog, and Fen are represented in different shades of brown, while within the heathland site, Forest, Dry-heath, and Humid-heath are shown in shades of green (Figure 5-2). The color gradient, from lighter to darker tones, reflects the gradient of abiotic conditions such as pH, and humidity, as illustrated in Figure 5-1.

The most concentrated element in foliar samples is Mn for almost every habitat (in Palsa 5170 mg kg⁻¹) and the least concentrated micro-nutrient is V (in Forest 0.569 mg kg⁻¹). The foliar element concentrations in a habitat follow from the most to the least concentrated element: Mn > Fe > Zn > Ti > Cu > Mo > V > Cd > As (Figure 5-2A). This order follows the order of nutrient requirements except that Mn concentrations are higher than Fe ones (Figure 2-5A; Daniels, 2016). On average, across all habitats, Palsa has the highest foliar element concentrations, except for Cu, Cd, and Ti. On the other hand, Forest and Bog have the lowest foliar element concentrations.

There is an additional point to mention concerning these data. The averages (Equation 5-1) are calculated for two sub-sites in Palsa, two in Forest, and three in Humid-heath (Table 4-3). For the other habitat, there is only one sub-site studied. The variability in foliar element concentrations reflects the heterogeneity in foliar concentration between sub-sites within similar habitats. Humid-heath, for example, is made up of three sub-sites, one with sedge species and the other two with shrubs and forbs. This heterogeneity explains the high variability of this habitat.

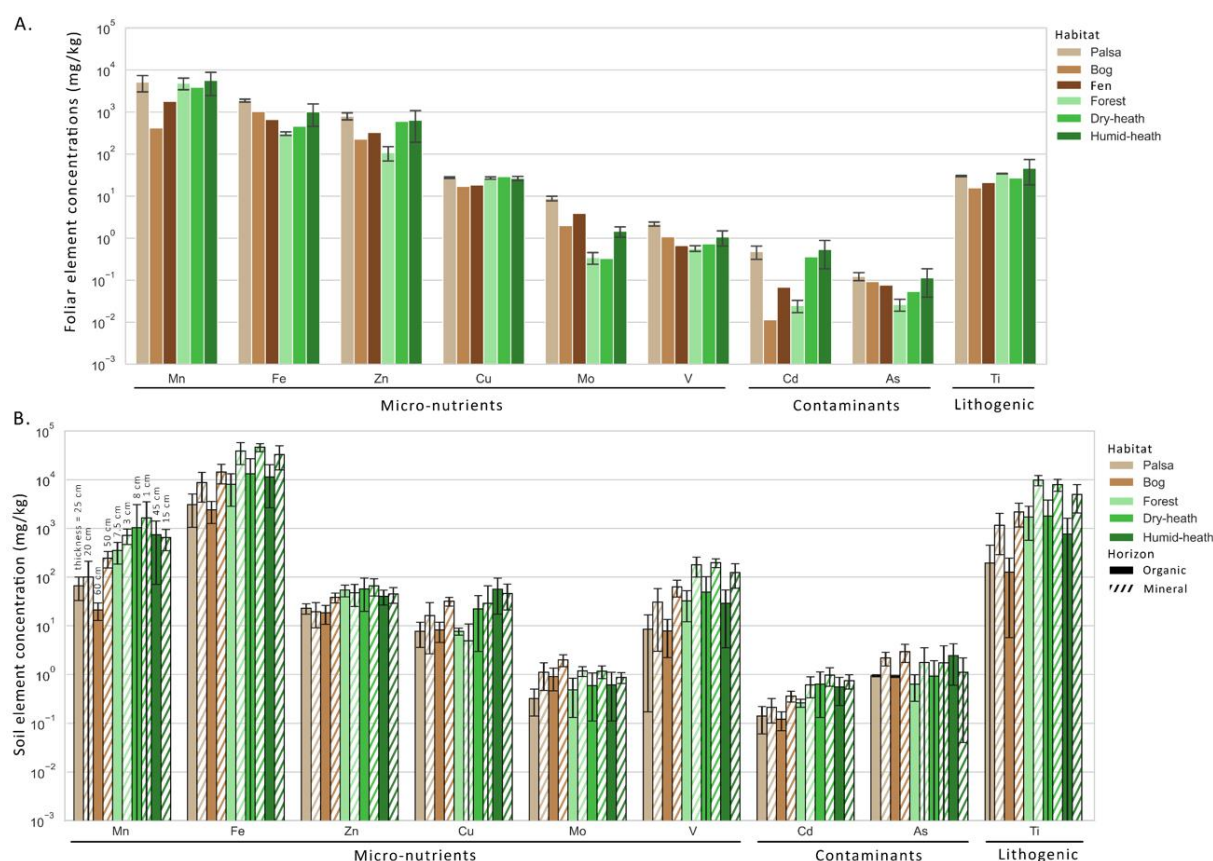


Figure 5-2: Trace element concentrations per habitat (mg kg^{-1}). Elements are divided into three categories: micro-nutrients necessary for plant growth, contaminants, and lithogenic. Habitats are sorted by site and follow a gradient of abiotic conditions. A. Foliar element concentrations per habitat. Species concentrations were obtained from ICP-MS, and then a biomass-weighted average for each species was used to obtain the average for a given habitat. Standard deviations represent variations between sub-sites of the same habitat. Bog, Fen, and Dry-heath have no standard deviation value because there is only one sub-site in this habitat.; B. Soil element concentrations per habitat. Concentrations in the organic horizon are shown in plain color, while those in the mineral horizon are represented by colored lines. Standard deviations represent variations between sub-site horizons of the same habitat. The thicknesses of the horizons collected are shown above the bar graphs. Those data are from Hugo Potier's research (Potier et al., 2024). Concentrations for Fen were not available.

5.2.1. Influence of soil concentrations

Concentrations of elements measured in soil organic and mineral horizon classes are compared between different habitats, expressed in mg kg^{-1} (Figure 5-2B). On average, soil element concentrations follow from the most to the least concentrated element: $\text{Fe} > \text{Ti} > \text{Mn} > \text{V} > \text{Zn} > \text{Cu} > \text{As} > \text{Mo} > \text{Cd}$. Average element concentrations in both horizons are consistent with soil element concentration ranges from a study conducted in Abisko in 2019 (Agnan et al., 2019).

For many elements, mineral horizon concentrations are higher than in the organic horizon. For example, Fe, V, and Ti are present in each habitat at concentrations at least 65% higher in the mineral horizon classes. It is generally related to a lithogenic origin, directly inherited from the parent material (Agnan et al., 2019; Kabata-Pendias, 1993), and to a smaller extent to leaching

(Jobbágy & Jackson, 2001). Similarly, Mo and Cd concentrations are at least 25% higher in the mineral horizon classes. The lithogenic factor may be less important in this case, and the Cd dependence on atmospheric deposition may explain its abundance in the surface horizon (Agnan et al., 2019; Halbach et al., 2017). Zn and Cu show slight differences between horizons, and even higher concentrations in organic horizons, with up to 56% more Cu in Forest. Recycling of elements on the surface may be more important than lithogenic input at depth (Jobbágy & Jackson, 2001).

Soil properties govern sorption and desorption processes. The main properties are pH, redox potential, Fe, Mn, and Al oxyhydroxides, cation exchange capacity (CEC), clay fraction ($\mu < 0.02$ mm), and soil organic matter content (Shaheen et al., 2013). In this study, only information on pH and moisture content, provided by Tela Botanica, is available for habitats.

Element sorption is directly related to soil pH. As soil pH increases, the retention of trace element cations at the soil surface increases, making them unavailable to vegetation (Figure 2-5B ; Daniels, 2016; Shaheen et al., 2013). In other words, in the soil, cation concentrations decrease with an increase in pH when anion concentrations increase. For the mire in the organic horizons, from Palsa to Fen, there is a decrease in Mn, Fe, and Zn, and an increase in Mo. Copper is a little affected by the pH (Daniels, 2016). The pH influence is not observed in the heathland.

Soil moisture levels significantly affect redox potential, thus influencing trace element availability (Blume et al., 2016; Sparks et al., 2022). Under anoxic conditions in the soil, Mn(IV/III) and Fe(III) oxides and hydroxides are reduced, resulting in increased Mn^{2+} and Fe^{2+} concentrations in the soil solution. The reductive dissolution of manganese and iron oxide minerals indirectly triggers the mobilization of trace elements such as As, Mo, Cd, Pb, Cu, and Zn. We therefore expect to observe in a wetter habitat higher concentrations of Mn, Fe, and cations that were associated with Mn and Fe oxides. Looking at the element concentrations in the organic horizon, there is an increase in Mn, Cu, Cd, and As from Forest to Humid- heath. In the mire, from Palsa to Fen, we see an increase in Mo. However, Mn and Fe decrease from Palsa to Fen, which is not what is expected.

Another hypothesis is that soil element concentration depends on soil depth. The thickness of the active layer influences the elements present in the soil. Permafrost thawing releases nutrients, which are now available in the soil solution (Keuper et al., 2017). In those study sites, the active layer thickness was not measured but was estimated at 60-80 cm (Agnan et al., 2019; Olid et al., 2020). It is therefore not possible to explain the variation in soil concentrations as a function of the variation in active layer thickness. The horizons of each habitat were sampled and measured, but there is no link between thicker soil and higher concentrations (Figure 5-2B).

To resume, variations between soil element concentrations are partly explained by pH and soil moisture levels.

To investigate the hypothesis of the influence of soil concentrations on foliar concentrations, foliar and soil concentrations are compared in the same habitat (Figures 5-2A & 5-2B). The assumption that high foliar concentrations correspond to high soil concentrations is true for all micro-nutrients except Mn and V. Foliar Mn concentrations are the highest when it is not the case for soil Mn concentrations. We expected foliar Mn concentrations lower than Fe concentrations to follow the nutrient requirement order in plants (Daniels, 2016). If this was the case, the high foliar concentrations would correspond to high soil concentrations. The high foliar Mn concentrations are caused by the presence of shrubs and forbs in most habitats, which accumulate this element more than Fe (Mauclet et al., 2022). Contrary to Mn, foliar V concentrations are the lowest nutrient concentrations while soil V concentrations are not the lowest. Although V increases metabolic activity in various plants, many studies prove levels above 2 mg kg⁻¹ are dangerous to plant growth (Hanus-Fajerska et al., 2021; Imtiaz et al., 2015). Vanadium toxicity explains why foliar V concentrations are generally inferior to this level.

To compare concentrations between habitats, the enrichment factor (EF) is calculated for each species. If habitats have an EF greater than 2, the reference value (Agnan et al., 2019), it means an enrichment. Average EFs are displayed per habitat and the reference value is represented by a red dashed line (Figure 5-3). The EF of a habitat $EF_{avg,habitat}$ is the average of the EFs of a sub-site, which is the sum of the EFs of the species present, weighted by the species biomass proportion in the sub-site (Equation 5-2). Weighting takes into account the proportion of species present. A more present species will have a greater influence on the overall EF of a habitat.

$$EF_{avg,habitat} = \frac{1}{n} \sum_{i=1}^n \left[\sum_{j=1}^k \left(EF_{i,j} \times \frac{biomass_{i,j}}{biomass_i} \right) \right] \text{ with } i = 1, \dots, n \text{ and } j = 1, \dots, k \quad (5-2)$$

With n , the number of sub-sites in the habitat; k , the number of species in the sub-site i ; $EF_{i,j}$, the EF in the species j from the sub-site i ; $biomass_{i,j}$, the foliar biomass in the species j from the sub-site i ; $biomass_i$, the total foliar biomass of the sub-site i . Data for $biomass_{i,j}$ and $EF_{i,j}$ are presented in Appendixes 6 and 8, respectively.

By comparing EFs between habitats, only V (in Forest, Dry-heath, and Humid-heath) presents a depletion. This is because soil V concentrations are superior to foliar ones. The lowest EF values are observed in the mire (i.e., Palsa and Bog) with slight V enrichment ($EF < 3$). Heathland (i.e., Forest, Dry-heath, and Humid-heath) shows a small enrichment in Fe ($2 < EF < 5$). The low EF values for V and Fe are due to higher concentrations in the soil than in the plant. The highest EF values are found in the Forest for Mn ($EF > 2500$) and Cu ($EF > 1800$). Additionally, Palsa and Humid-heath also display high EF values for Mn ($EF > 1500$), and Dry-heath shows high values for Zn ($EF > 2000$). Average EF values are a function of the EF of species growing in the habitat. As habitats are composed of different species, we should look at the influence of species on the foliar element concentrations.

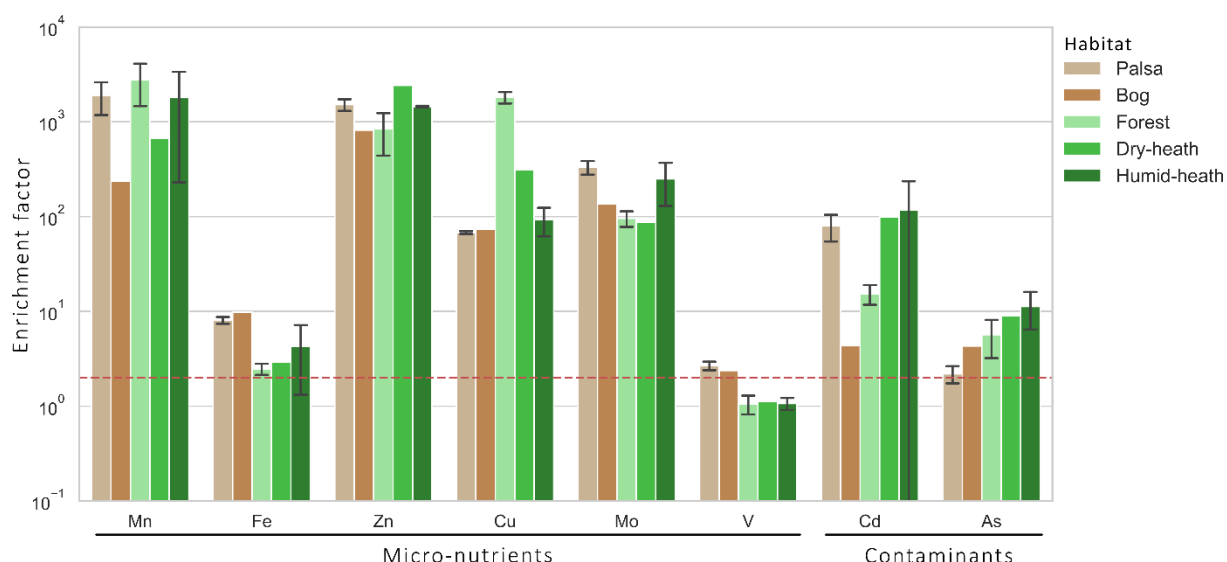


Figure 5-3: Enrichment factor in habitat normalized to Ti and mineral soil horizons of the same study sites. Elements are divided into two categories: micro-nutrients necessary for plant growth, and contaminants. Habitats are sorted by site and follow a gradient of abiotic conditions. The dashed red line represents the threshold at which the habitat is enriched. The threshold is set at 2 (Agnan et al., 2019). Standard deviations represent variations between sub-sites of the same habitat. Bog and Dry-heath have no standard deviation value because there is only one sub-site in this habitat.

5.2.2. Influence of the floristic composition of a habitat

The second studied factor is the influence of the floristic composition of a habitat. The environmental description of the habitats shows that species composition varies according to abiotic conditions (Figure 5-1). Shrubs and forbs predominate in drier habitats such as Palsa and Forest. Wetter habitats mainly host sedges like Bog or Fen. This subsection aims to investigate the influence of those species on the foliar element concentrations.

To test this hypothesis, foliar element concentrations are represented by habitat, where the concentration in a habitat is subdivided into concentrations in the species (Figure 5-4). The elemental concentration of a species in a habitat is the average of the foliar concentrations of that species in that habitat (Appendix 7). It should first be noted that the contribution of species to the foliar concentrations in a habitat varies from one element to another.

Firstly, several elements display relatively similar concentrations across different species. For example, each species contributes equally to Cu concentrations, except in sedge-only habitats such as Bog and Fen. Mn, As, and Ti are other good examples of this trend, but with slightly higher concentrations for *Betula nana*, *Empetrum nigrum*, and *Rubus chamaemorus*.

Secondly, when considering Fe, Mo, and V, *Rubus chamaemorus* exhibits notably higher concentrations than other species. This species accounts for more than 30% of the total foliar concentration in a given habitat. Moreover, total concentrations in Humid-heath and Palsa

habitats, which host this species, are at least 1.5-times and 3-times higher, respectively, than in habitats where this species is absent.

Finally, certain species exhibit high concentrations of specific elements. For example, *Betula nana* displays the highest Zn concentrations, while *Vaccinium uliginosum* has elevated Cd concentrations compared to other species. *Betula nana* is known for its ability to accumulate Zn (Gosz et al., 1973). Additionally, *Vaccinium uliginosum* is known to tolerate high levels of trace elements in the soil, particularly Cd, as demonstrated in a previous study (Belanovic & Beloica, 2013). Sedge species generally have lower concentrations except for *Eriophorum scheuchzeri*. Those results confirm that foliar element concentrations are species-specific (Mauclet et al., 2022).

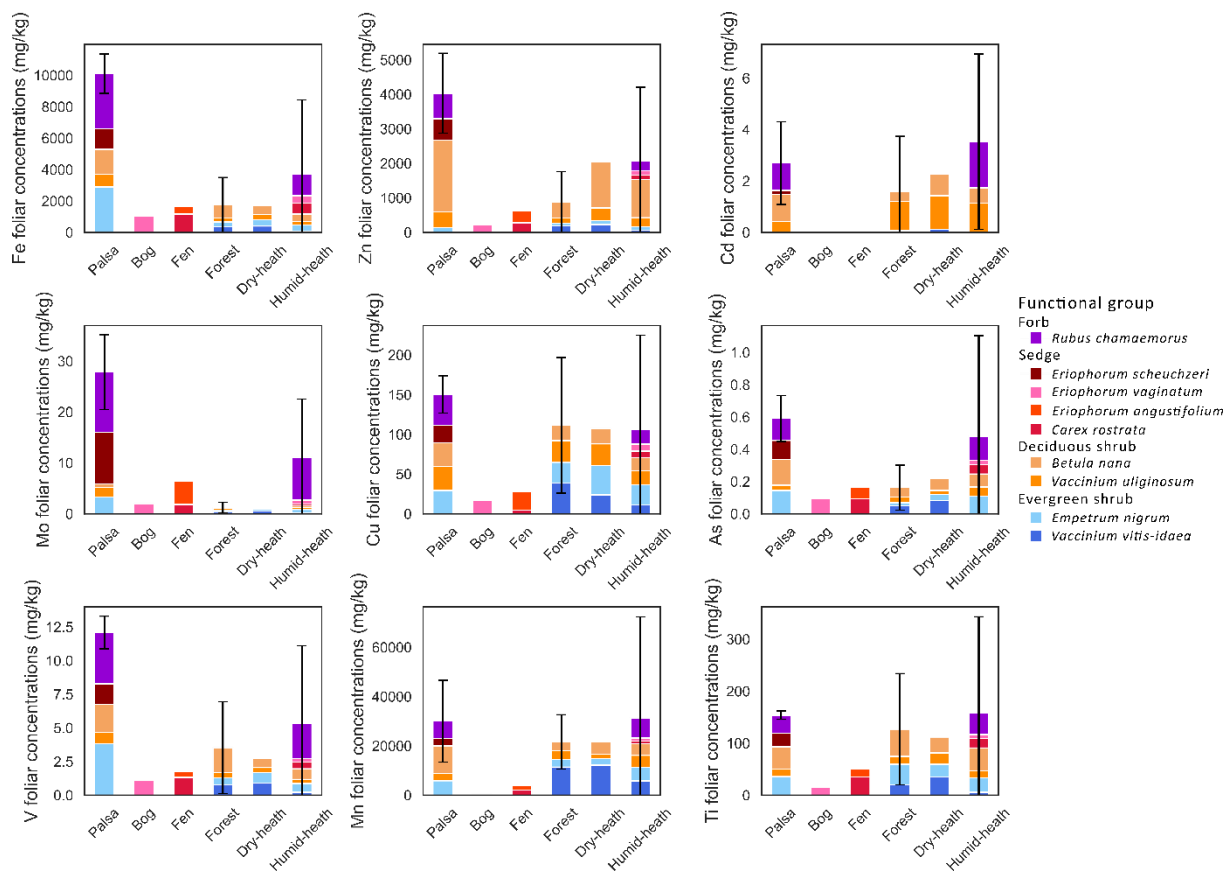


Figure 5-4: Average foliar concentrations of trace elements for each species in each habitat (mg kg^{-1}). Habitats are sorted by sites (i.e., mire and heathland) and each habitat is subdivided into species. Average foliar concentrations correspond to the average concentrations for sub-sites of the same habitat. Standard deviation values therefore represent the variability between sub-sites from the same habitat. Bog, Fen, and Dry-heath have no standard deviation value because there is only one sub-site in this habitat.

5.2.3. Influence of rooting depths

The previous subsection established that foliar element concentrations vary significantly between species. This subsection aims to determine whether these variations can be attributed to differences in rooting depth between species. To investigate this hypothesis, EFs between

plant and mineral horizon are calculated (Equation 4-2). By comparing EFs instead of concentrations, the influence of soil element concentrations on foliar element concentrations within a habitat can be eliminated, thanks to lithogenic normalization.

Before comparing EFs according to rooting depth, it is necessary to identify the thickest horizons and the deepest species' root systems. Data are provided in Appendix 1 and 4. Soil thicknesses are available for each habitat except for Fen due to a water table level higher than ground level (Figure 5-5A). Habitats in the heathland (i.e., Forest, Dry-heath, and Humid-heath) are less thick than those from the mire. As sampling was not carried out over the entire soil depth, mineral horizons may be thicker in the heathland before reaching the permafrost. The limit between the active layer and the permafrost, indicated by a blue band in the figure, is estimated between 60 and 80 cm across all habitats (Åkerman & Johansson, 2008). However, permafrost was observed after 110 cm in Bog (Potier et al., 2024).

Species rooting depths are global averages and are presented in ascending order, from *Vaccinium vitis-idaea* to *Rubus chamaemorus*, in Figure 5-5B (Appendix 4; Hewitt et al., 2019; Iversen et al., 2015; Saarinen, 1996). Sedges and forbs have deeper roots than shrubs with a maximum average value of 55 cm for *Rubus chamaemorus*. In most habitats, the rooting systems of species extend through both the organic and mineral horizons, except in Bog where all species remain in the organic horizon.

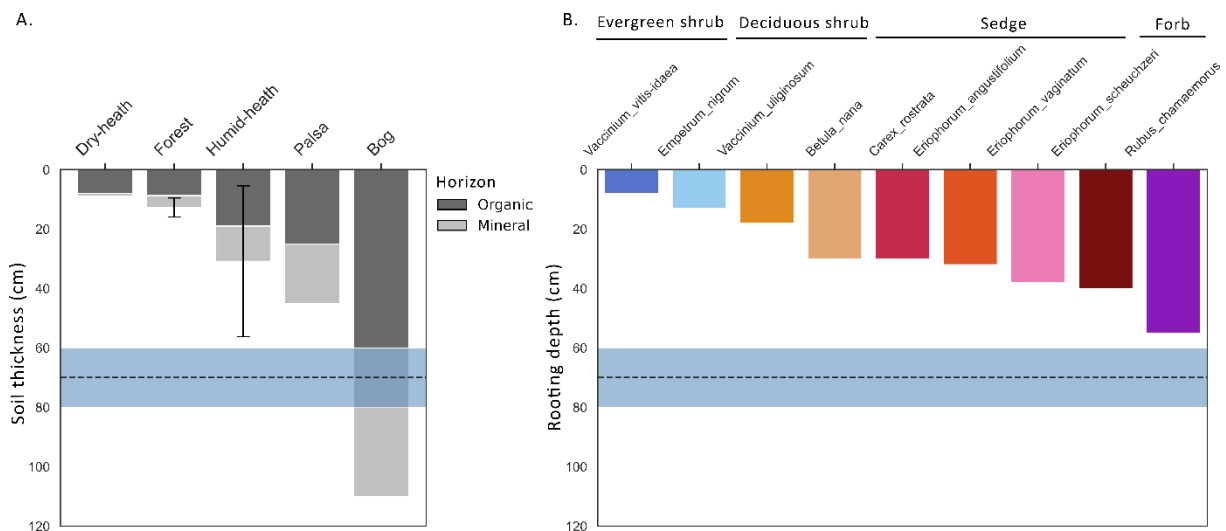


Figure 5-5: Horizon and rooting depths (cm). The limit between the active layer and permafrost is represented by a blue band between 60 and 80 cm (Åkerman & Johansson, 2008). A. Horizon thickness. Standard deviations represent variations between sub-sites of the same habitat. Sampling was carried out over the entire soil depth in the heathland (from 10 cm in Dry-heath to 55 cm deep in Humid-heath) but was limited to the active layer in the mire (from 45 cm in Palsa to 1 m deep in Bog). Fen soils were not sampled, as the water table was higher than the soil level. The values were from Hugo Potier's research (Potier et al., 2024).; B. Species rooting depth. Those rooting depths were taken from the literature and were not specific to the study site (Hewitt et al., 2019; Iversen et al., 2015; Saarinen, 1996).

To verify the hypothesis concerning the influence of rooting depth on foliar element content, average EFs for each species in each habitat are calculated and plotted as a function of the

species' rooting depth (Figure 5-6). EF values are available in Appendix 8. Different trends can be observed. Firstly, for Fe, Mo, and V, EF increases with rooting depth. Forbs, which possess the deepest rooting depth, exhibit higher EFs for Fe (~ 2 times), Mo (~ 8 times), and V (~ 2 times) compared to shrubs, which have shallower root systems. This result is consistent with other studies showing that evergreen species have lower foliar nutrient concentrations than deciduous shrubs, forbs, or sedges (Hobbie & Gough, 2002). Other studies have shown that deep-rooted plant species may have access to additional nitrogen released near the active layer base when permafrost thaws in response to higher temperatures (Keuper et al., 2012, 2017). Other elements may also be available in-depth for these species. This hypothesis could explain the EF values for Fe, Mo, and V increasing with rooting depth.

Secondly, EF values for Zn, Mn, and Cd are similar for all species in all habitats, except for one species enriched in this mineral element. The zinc EF shows high values for *Betula nana* which is known to accumulate Zn (Gosz et al., 1973). Regarding Mn, evergreen species, especially *Vaccinium vitis-idaea*, are also the most enriched (~ 3.5 times) compared to sedges. *Vaccinium vitis-idaea* is known for its ability to accumulate Mn due to its tolerance of high concentrations, which can otherwise be toxic (Kandziora-Ciupa et al., 2017; Miller, 1987). The highest EF values for Cd are found in *Vaccinium uliginosum*, a species that tolerates high levels of trace elements in the soil (Belanovic & Beloica, 2013). Even if a species is more enriched in Zn, Mn, or Cd, there are variations in EF values for this species between habitats.

Finally, Forest is the most enriched in Cu while Humid-heath is the most enriched in As. EF values for Cu and As are influenced by the habitat rather than the floristic composition. This finding aligns with the conclusion derived from foliar element concentrations in the previous sub-section, indicating that within a habitat, all species contribute similarly to the habitat's total concentration.

In conclusion, EF values observed in plants can be attributed on one hand to species' physiology, reflecting their different absorption and storage strategies (Hobbie & Gough, 2002; Iversen et al., 2015; Mauclet et al., 2022). On the other hand, within the same species, EF values differ from one habitat to another. This reaffirms the impact of habitat, and therefore soil element concentrations, on these variations (Hobbie & Gough, 2002).

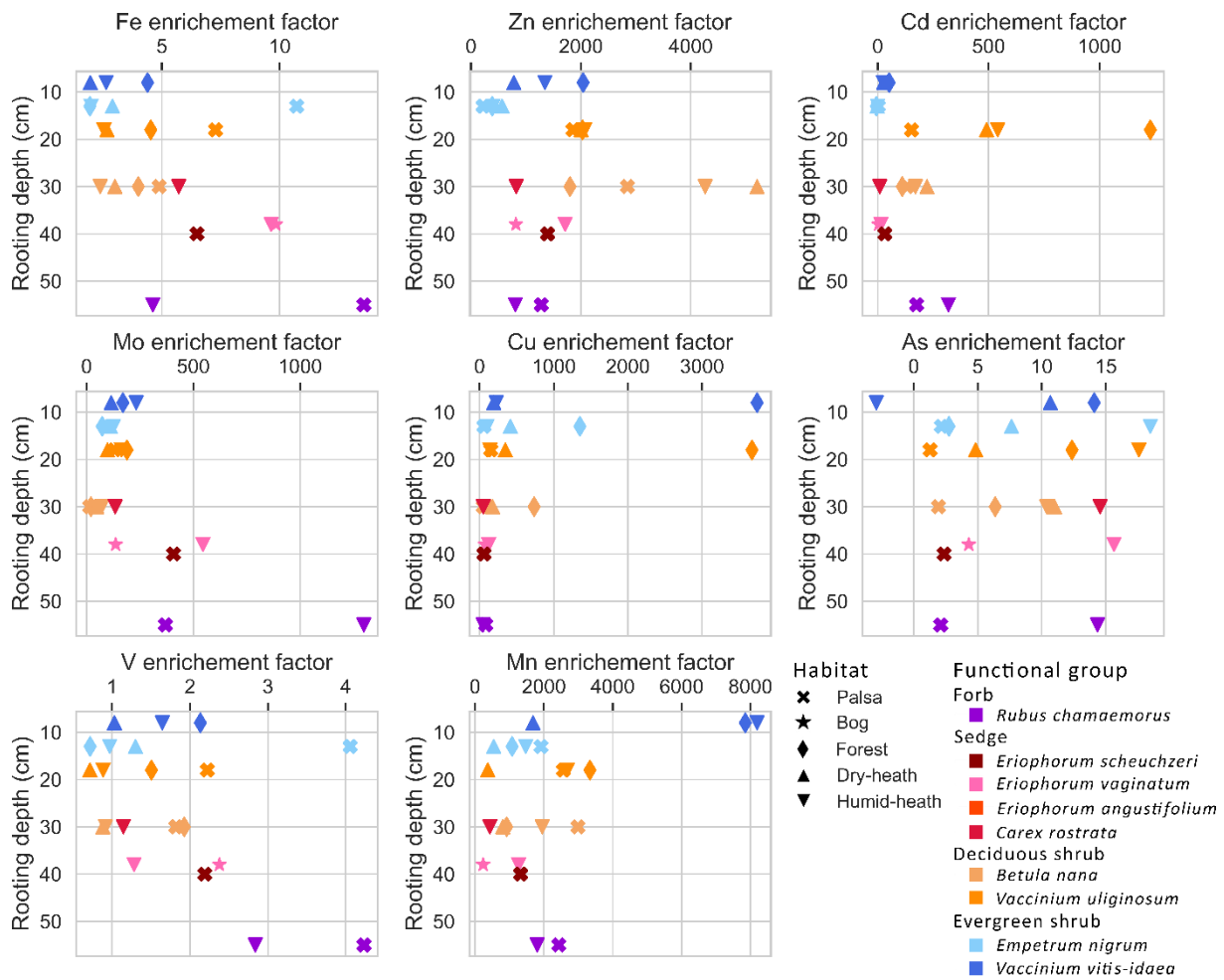


Figure 5-6: Enrichment factor in vegetation as a function of species' rooting depth. The enrichment factor is normalized to Ti and mineral soil horizons of the same study sites. Enrichment values are averages for each species of each habitat. Those rooting depths were taken from the literature and were not specific to the study site (Hewitt et al., 2019; Iversen et al., 2015; Saarinen, 1996). Markers correspond to the habitat and the color of the species.

In summary, the foliar element concentrations vary between different Arctic habitats driven by several factors. Soil element concentrations play a significant role, with pH and redox potential affecting element sorption and availability. Higher soil element concentrations generally correlate with higher foliar element concentrations for most micro-nutrients, except for Mn and V. Additionally, the floristic composition of habitats contributes to variations in foliar concentrations between habitats. The EF analysis between species indicates species-specific enrichments, with certain species exhibiting notable accumulation patterns. Rooting depth also partly influences foliar concentrations, with deep-rooted species showing greater enrichment for certain elements. Overall, soil properties, floristic composition of a habitat, and plant physiology influence the plant uptake of trace elements in Arctic ecosystems.

Now that the factors have been identified, we can understand how plant nutrient uptake will evolve in ecosystems impacted by Arctic warming. Arctic warming modifies the soil characteristics and floristic composition of habitats. The increase in temperature, nutrient availability, and the change in soil moisture lead to vegetation shifts in the Arctic region (Figure

2-10; Nadelhoffer et al., 1992; Walker et al., 2005). Permafrost thaw releases previously frozen pools of nutrients (Keuper et al., 2017), newly available for species with long root systems. Deep-rooted sedges take advantage of this opportunity, extending into the thaw front and accumulating high concentrations of nutrients in their tissues, thus enhancing their growth. Hence, sedges dominate during the early stages of permafrost degradation (Hewitt et al., 2019). In addition, the initial saturation of the soil with water, as a result of permafrost thawing, offers further advantages to sedges, which prosper in these moist conditions. However, this initial advantage of sedges is not maintained over time. As temperatures continue to rise and soil moisture changes, shrubs begin to benefit from increased nutrient availability and warmer climates, stimulating their growth. Although some habitats are ecologically favorable for sedges, the increase in shrub biomass favors competitive conditions, including shading effects, ultimately leading to the gradual decline of heliophile species such as sedges (Salmon et al., 2019). Consequently, permafrost degradation initially leads to an increase in sedge biomass, followed by a gradual increase in the biomass of shrubs and forbs to the detriment of sedges. Shrubs generally dominate well-drained or dry soils. Although sedges can tolerate extremely wet environments where shrubs struggle, sedges do not become dominant in these habitats as permafrost degradation progresses (Jorgenson & Osterkamp, 2005; E. A. G. Schuur et al., 2007; van der Kolk et al., 2016). In Abisko, sedges are initially expected to dominate in Bog, Fen, and Humid-heath, gradually giving way to shrubs as permafrost degradation progresses. In drier habitats such as Palsa and Dry-heath, shrubs are likely to predominate.

The proliferation of shrubs in Arctic and sub-Arctic regions can have a significant impact on climate change feedback loops (Heijmans et al., 2022). These shrubs can trap thicker layers of snow during winter, insulating the ground from extreme cold and thus exacerbating permafrost degradation (Myers-Smith et al., 2015). In addition, shrubs have a smaller albedo effect than sedges, further increasing soil temperatures (Marsh et al., 2010). Changes in soil temperature and moisture also have a major influence on microbial activity. Warmer and drier conditions favor microbial activity and organic matter decomposition (Schimel et al., 1999). The increase in shrub cover, leading to higher soil temperatures, intensifies microbial decomposition. However, it is important to note that evergreen shrubs, which have a slower decomposition rate than sedges, forbs, and deciduous shrubs, can impede organic matter decomposition processes (Hobbie, 1996). Overall, we anticipate an increase in the organic matter decomposition rate at Abisko due to the predominance of shrubs in the habitat and their impact on the surface energy balance.

5.3. Influence of vegetation biomass composition on foliar stocks and fluxes

The second objective of this master's thesis is to determine the influence of plant biomass composition on foliar element stocks and fluxes. It provides an understanding of the contribution of plant tissues to the soil litter reservoir throughout seasonal litterfall. This

highlights the consequences between habitats on plant nutrient cycling. Several habitats are tested to determine the influence of their floristic composition on foliar stocks (Appendix 10) and annual fluxes (Appendix 12).

Before representing the foliar stocks and fluxes in the different habitats, the total foliar biomass in the different habitats has to be weighted (Figure 5-7; Appendix 6). Total foliar biomass is divided into the biomass of each of the nine species sampled, with an additional “Others” category for species not sampled. Hereafter, the total sampled foliar biomass in a habitat will be used to describe the total foliar biomass of a habitat without the “Others” category. The total sampled foliar biomass varies from 534 gDW m⁻² for Fen to 129 gDW m⁻² for Forest (as Fen > Palsa > Dry-heath > Humid-heath > Bog > Forest). Wetter habitats (i.e., Bog and Fen) are mainly composed of sedges. For instance, in Fen, the biomass is composed of 25% *Carex rostrata* and 75% *Eriophorum angustifolium*. Forest is mainly populated by evergreen shrubs while in Dry-heath, deciduous shrubs are also found. Both Palsa and Humid-heath are characterized by species from each functional group but sedges account for 42% of Humid-heath biomass. The foliar biomass in each habitat underlines that the floristic composition of habitats depends on abiotic conditions (Section 5.1.). Finally, we can add that the high variability in habitat foliar biomass is due to the heterogeneity of floristic composition between sub-sites of the same habitat. Humid-heath, for example, is made up of three sub-sites, one with sedge species and the other two with shrubs and forbs (Table 4-3). This heterogeneity explains the high variability of this habitat. Bog, Fen, and Dry-heath have no standard deviation value because there is only one sub-site in this habitat.

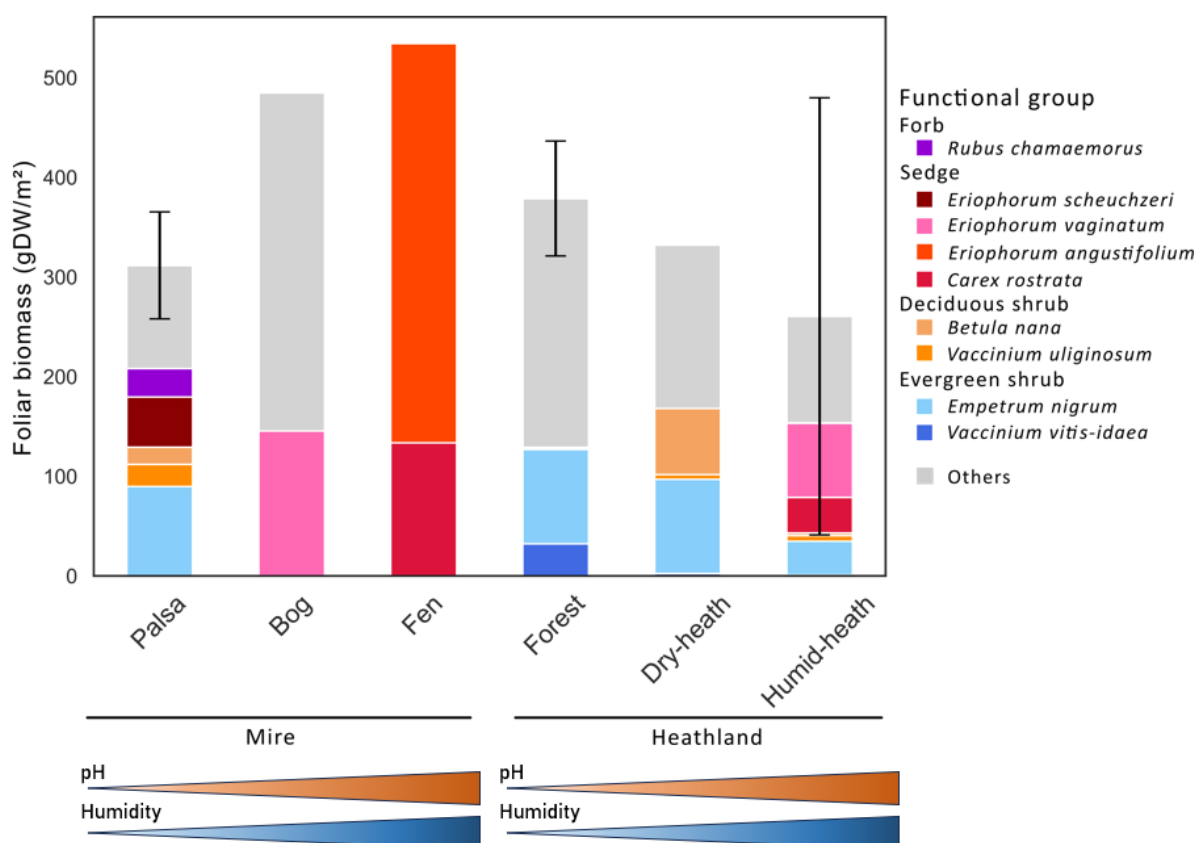


Figure 5-7: Foliar biomass for each species of each habitat (gDW m⁻²). Each bar represents the entire foliar biomass of the habitat and it is subdivided into species. Foliar biomass was calculated using the average foliar biomass of sub-sites in the same habitat. Standard deviation values therefore represent the variability between sub-sites from the same habitat. Bog, Fen, and Dry-heath have no standard deviation value because there is only one sub-site in this habitat. The pH and humidity indications come from the electronic flora, eFlore, of Tela Botanica (www.tela-botanica.org). Within a study site (i.e., mire and heathland), the habitats are sorted by following a gradient in abiotic conditions.

5.3.1. Influence of vegetation biomass composition on foliar stocks

In Abisko, across all habitats, the average foliar stocks vary from 622 mg m⁻² for Mn to 0.02 mg m⁻² for As (as Mn > Fe > Zn > Ti > Cu > Mo > V > Cd > As; Figure 5-8; Appendix 10). For all elements except Cd, Fen has the highest stocks. This habitat includes *Eriophorum angustifolium*, which accounts for 75% of total sampled foliar biomass, and *Carex rostrata*, representing the remaining 25% (Figure 5-7). Due to its high foliar biomass, *Eriophorum angustifolium* contributes over 50% of foliar stocks for all elements, with a maximum contribution of 94% for Cu. While *Eriophorum angustifolium* generally contributes less than 50% to foliar concentrations, its high biomass compensates for its lower foliar concentrations, following equation 4-4 for stock determination. For Cu, its contribution to foliar concentrations is 84%, which explains its considerable impact on stocks. Fen's high total sampled biomass explains why this habitat has the highest trace element stocks.

Palsa is the habitat with the second-highest stock values due to the highest foliar concentrations and the second-highest sampled foliar biomass. In Palsa, forb and sedge species have the highest stock values, but not because of their contribution to total sampled biomass, which is 38%, compared to *Empetrum nigrum*'s 43%. However, the combined contribution of forb and sedge species to concentrations in Palsa varies from 40 to 45%, while *Empetrum nigrum* contributes only 20 to 25%. We note that *Betula nana* stands out for Mn, Zn, and Cd, contributing around 35% to the total stock in Palsa, whereas this species represents only 8% of the total sampled biomass. This is due to *Betula nana*'s significantly higher concentrations of Mn, Zn, and Cd, which account for 37, 52, and 39% of total concentrations in Palsa, respectively.

For Bog, Forest, Dry-heath, and Humid-heath, it is noteworthy that stocks vary although their sampled foliar biomasses are similar, ranging from 129 g m⁻² to 168 g m⁻². The variations are therefore explained by foliar concentrations in habitats. Among these habitats, Humid-heath generally has the highest foliar concentrations, except for Cu. However, despite their high foliar concentrations, Humid-heath does not systematically show the highest stocks. It indicates that variations in foliar stocks are mainly influenced by the floristic composition of the habitat. As an example, Dry-heath has the highest Zn stock, mainly attributed to *Betula nana*, a species known for its Zn accumulation capacities. In Humid-heath, the lower Zn stock can be attributed to the comparatively lower biomass of *Betula nana*. In fact, in Dry-heath, *Betula nana* accounts for 39% of sampled biomass, whereas it represents less than 2% in the other four habitats. Another example is the high Cu stock values in Forest and Dry-heath, mainly due to the presence of *Empetrum nigrum*. This species represents a higher proportion of total sampled biomass and a higher proportion of total Cu concentration in these habitats than in Humid-heath or Bog.

In Abisko, in all habitats, foliar stocks are mainly determined by biomass, as in Fen, the habitat with the highest sampled foliar biomass. In addition, they are also determined by concentration, as in Palsa, where *Betula nana* contributes strongly to Mn, Zn, and Cd stocks. As previously mentioned, Arctic warming modifies temperature and humidity conditions, and permafrost degradation releases newly thawed nutrients. Vegetation distribution and productivity are altered, which in turn modifies foliar element concentrations. As foliar element concentrations are indirectly affected by Arctic warming, foliar stocks will be similarly affected. For example, if drier habitats undergo shrubification, the contribution of shrubs to foliar nutrient stocks will subsequently increase. Conversely, a sedge expansion in wetter habitats will lead to a greater contribution of sedges to foliar nutrient stocks.

There are a few additional points to mention concerning these data. Firstly, the large variability in foliar element stocks (Figure 5-8; Appendix 10) reflects the heterogeneity in species biomass and foliar concentration between sub-sites within similar habitats. Secondly, estimates of foliar element stocks at Abisko only take into account the contributions of the most abundant vascular plant species at the site. In most habitats, the studied species account for more than

50% of total foliar biomass, except for Bog (30%) and Forest (34%) habitats. Consequently, the results (Figure 5-8; Appendix 10) provide lower estimates of actual total foliar stocks in the various habitats.

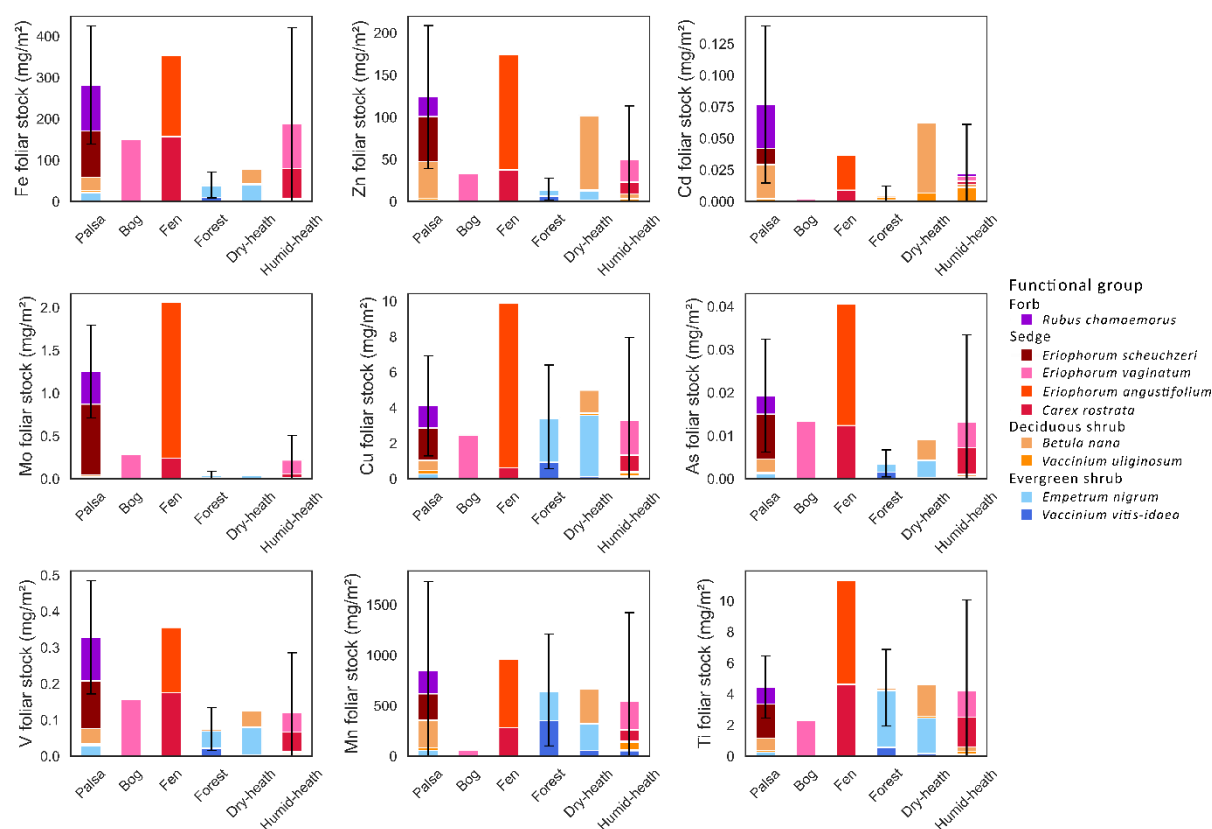


Figure 5-8: Average foliar stocks of trace elements for each sampled species in each habitat (mg m^{-2}). Habitats are sorted by sites (i.e., mire and heathland) and each habitat is subdivided into species. Average foliar stocks correspond to the average of stocks for sub-sites of the same habitat. Standard deviation values therefore represent the variability between sub-sites from the same habitat. Bog, Fen, and Dry-heath have no standard deviation value because there is only one sub-site in this habitat.

5.3.2. Influence of vegetation biomass composition on annual foliar fluxes

Annual foliar element fluxes are quantified from deciduous species, such as sedges, deciduous shrubs, and forbs, which lose their leaves each season. Evergreen species are not included, due to the complex lifespan and senescence dynamics of their leaves and tissues (Park et al., 2020). The foliar net primary productivity values (fNPP) used in this study are from evaluations conducted in 2017 at the CiPEHR site in Eight Mile Lake, Alaska. Since the climate at the CiPEHR site is colder in winter than in Abisko (www.meteoblue.com), these fNPP values may be underestimated for the vegetation in Abisko. As a result, annual foliar element fluxes may be underestimated as well. It should be noted that the standard deviations for annual foliar flux estimates may be underestimated because the standard deviation of fNPP is not included in the calculations.

Across all habitats, the average foliar fluxes vary from 295 mg m⁻² a⁻¹ for Mn to 0.01 mg m⁻² a⁻¹ for As (as Mn > Fe > Zn > Ti > Cu > Mo > V > Cd > As; Figure 5-9; Appendix 12). Palsa has the highest flux values except for Cu and Cd. Thanks to its high fNPP value (87 g m⁻² a⁻¹), *Eriophorum scheuchzeri* contributes to more than 60% of Palsa flux values except for Cd, where its contribution is 38%. Despite contributing 29% to foliar concentrations in Palsa, *Rubus chamaemorus* only contributes 20% to fluxes, as its fNPP is 7-times lower than the one of *Eriophorum scheuchzeri*. The high flux values observed in the Palsa habitat are then attributed to its elevated foliar concentrations, which are the highest among all habitats, and the presence of a highly productive species.

Bog and Fen exhibit high flux values despite their low foliar concentrations. These results can be attributed to the presence of highly productive species such as *Eriophorum* sp. In some cases, Bog even demonstrates higher flux values compared to Fen, despite *Eriophorum vaginatum* having a lower fNPP value (139 g m⁻² a⁻¹) than *Eriophorum angustifolium* (157 g m⁻² a⁻¹). This outcome is explained by the lower concentrations of Fe, V, and As in *Eriophorum angustifolium* in Fen. In Humid-heath, despite the presence of *Eriophorum vaginatum*, flux values remain low due to the low concentrations in this species, accounting for approximately 6% of the total foliar concentrations.

Forest and Dry-heath show low flux values due to their low foliar concentrations and specific floristic composition, primarily comprising evergreen and deciduous shrubs. In particular, as foliar fluxes are calculated at an annual time scale, evergreen species are not considered in the calculations. In addition, deciduous shrubs such as *Betula nana* (with a fNPP of 2.2 g m⁻² a⁻¹) and *Vaccinium uliginosum* (with a fNPP of 14 g m⁻² a⁻¹) do not have fNPP values high enough to generate high flux values.

In summary, the floristic composition of the habitats, through foliar element concentrations, mainly influences the foliar fluxes. As *Eriophorum* species have the highest fNPP, habitats with those species show high flux values such as Palsa, Bog, or Fen. Therefore, there is an important seasonal transfer of elements in habitats composed of sedges, especially *Eriophorum* sp. Changes in the biomass composition of Arctic species in response to Arctic warming would thus strongly impact the annual foliar element fluxes during litterfall (Mauclet et al., 2022).

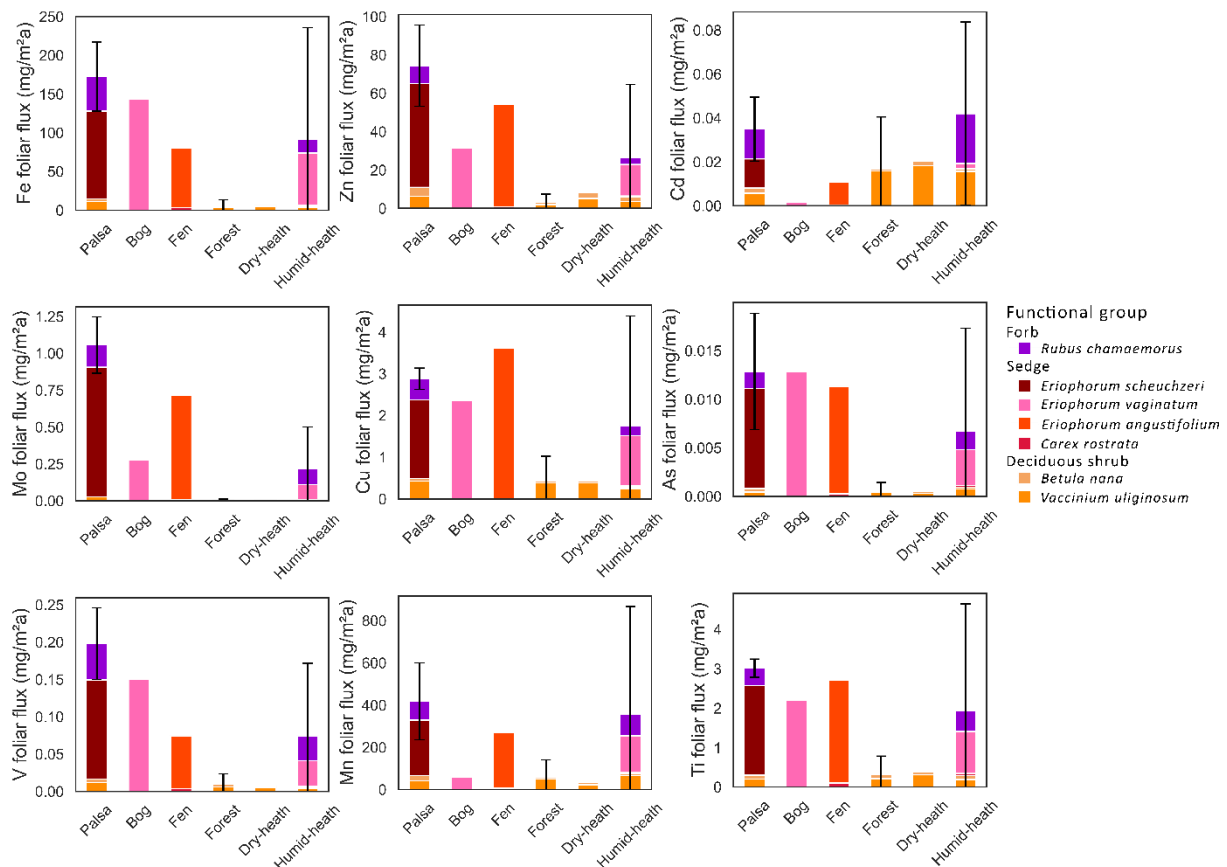


Figure 5-9: Average foliar fluxes of trace elements for each sampled species in each habitat (mg m⁻² a⁻¹). Habitats are sorted by sites (i.e., mire and heathland) and each habitat is subdivided into species. Average foliar fluxes correspond to the average fluxes for sub-sites of the same habitat. Standard deviation values therefore represent the variability between sub-sites from the same habitat. Bog, Fen, and Dry-heath have no standard deviation value because there is only one sub-site in this habitat.

In summary, foliar stocks and annual foliar fluxes are both influenced by the foliar element concentrations in different species. As seen in section 5.2., foliar element concentrations are determined by the soil concentrations, the floristic composition of the habitats, and the plant physiology. Over the past two decades, Arctic surface air temperatures have risen more than twice as fast as the global average (IPCC, 2021; Meredith et al., 2019). Warming Arctic has several impacts: an increase in temperature, changes in nutrient availability, and soil moisture. Those changes lead to vegetation shifts in the Arctic region (Nadelhoffer et al., 1992; Walker et al., 2005). If the floristic composition of ecosystems is modified, foliar element concentrations will be modified consequently, modifying foliar stocks and fluxes. In drier habitats, shrubs are expected to dominate, leading to an increased contribution of shrubs to foliar nutrient stocks and fluxes (Mauclet et al., 2022). Conversely, in wetter habitats, sedges are likely to expand, resulting in a greater contribution of sedges to foliar nutrient stocks and fluxes.

6. Conclusion and perspectives

This master's thesis aimed to understand how plants cycle trace elements across different Arctic habitats. To investigate this question, trace element concentrations in plants and soil were examined for 2021 at two study sites in Abisko, Sweden: a peatland mire and a heathland, each characterized by distinct environmental conditions. Within each site, three habitats were studied along gradients of abiotic conditions such as pH and soil moisture. In the mire, pH and moisture levels increased from Palsa to Bog to Fen. In the heathland, these levels increased from Forest to Dry-heath to Humid-heath. Each habitat hosted different species depending on the local environmental conditions. Sedges were predominantly found in wetter environments such as Bog, Fen, and Humid-heath, whereas shrubs and forbs primarily inhabited drier areas.

The first objective of the research was to identify the factors influencing plant nutrient uptake in various Arctic habitats. For this study, nine cosmopolitan Arctic plant species with different rooting depths were analyzed, most of which were present at both study sites. The research focused on trace elements including As, Cd, Cu, Fe, Mn, Mo, V, Ti, and Zn, which showed different concentrations among the plant species. In terms of foliar element concentrations within a habitat, the order from most to least concentrated was: $Mn > Fe > Zn > Ti > Cu > Mo > V > Cd > As$. This order generally corresponds to nutrient requirements, except that Mn concentrations were higher than Fe ones. The findings demonstrated that foliar element concentrations varied across Arctic habitats due to several factors. Soil element concentrations were crucial, with pH and redox potential influencing element sorption and availability. Higher soil element concentrations typically correlated with higher foliar element concentrations for most micro-nutrients, except Mn and V. Additionally, the floristic composition of the habitats contributed to variations in foliar concentrations between habitats. An EF analysis revealed species-specific accumulation patterns, with certain species, such as *Betula nana*, showing significant enrichment in Zn. Rooting depth also influenced foliar concentrations, with deeper-rooted species like *Rubus chamaemorus* exhibiting higher enrichment for Fe, Mo, and V. In summary, soil properties, habitat floristic composition, and plant physiology collectively affect trace element uptake by plants in Arctic ecosystems.

The second objective was to determine how plant biomass composition affected foliar element stocks and fluxes. The results indicated that both foliar stocks and annual foliar fluxes were influenced by the foliar element concentrations in different species. In all habitats, foliar stocks were a function of foliar concentrations, as seen in Palsa, where *Betula nana* contributed significantly to Mn, Zn, and Cd stocks. They were also determined by foliar biomass, as in Fen, the habitat with the highest sampled foliar biomass. On the other hand, foliar fluxes were mainly influenced by the floristic composition of the habitats, through foliar element concentrations. Since *Eriophorum* species had the highest foliar net primary productivity (fNPP), habitats with these species, such as Palsa, Bog, and Fen, showed high flux values.

Consequently, there was a significant seasonal transfer of elements in habitats composed of sedges, particularly *Eriophorum* sp. Variations in soil concentrations or the floristic composition of the habitats altered the foliar concentrations, thereby impacting the foliar stocks and fluxes. It was noteworthy that estimates of foliar element stocks at Abisko only took into account the contributions of the most abundant vascular plant species at the site. Therefore, the results provided lower estimates of actual total foliar stocks in the various habitats. Moreover, since the fNPP was estimated in cooler ecosystems, it might have been underestimated, leading to an underestimation of the foliar fluxes.

Once the factors have been identified, it becomes possible to understand how plant nutrient uptake will evolve in ecosystems affected by Arctic warming. Arctic warming modifies soil characteristics and the floristic composition of habitats. The increase in temperature and nutrient availability, along with changes in soil moisture, lead to vegetation shifts in the Arctic region. Consequently, permafrost degradation initially increases sedge biomass, followed by a gradual increase in the biomass of shrubs and forbs at the detriment of sedges. Shrubs generally dominate well-drained or dry soils. If the floristic composition of ecosystems is modified, foliar element concentrations will be altered accordingly, modifying foliar stocks and fluxes. In drier habitats (i.e., Palsa, Forest, and Dry-heath), shrubs are expected to dominate, leading to an increased contribution of shrubs to foliar nutrient stocks and fluxes. Conversely, in wetter habitats (i.e., Bog, Fen, and Humid-heath), sedges are likely to expand, resulting in a greater contribution of sedges to foliar nutrient stocks and fluxes. The proliferation of shrubs in Arctic and sub-Arctic regions can have a significant impact on climate change feedback loops. Their ability to trap snow and their smaller albedo effect compared to sedges modify soil temperatures and moisture. The increase in shrub cover, leading to higher soil temperatures, intensifies microbial decomposition. Overall, an increase in the organic matter decomposition rate at Abisko is anticipated due to the predominance of shrubs in the habitat and their impact on the surface energy balance.

This master's thesis raises several questions concerning changes in plant nutrient cycling caused by Arctic warming. Extending the analysis to all habitats at all sites will provide a more solid basis for reflection. Additionally, studying other mineral elements beyond those analyzed in this study, such as Ca and Si, which are more prevalent in shrubs and sedges respectively, will support conclusions on species-specific elements. Exploring factors other than those examined in this study, such as the influence of active layer thickness, will help understand how these factors influence plant nutrient uptake. It will also be beneficial to study other plant species to gain a better understanding of their impact on a habitat's foliar stocks and to comprehend the influence of Arctic warming on other functional groups, such as mosses.

Studying foliar concentrations over the long term will be useful to confirm the impact of vegetation changes on foliar concentration shifts. To obtain flux values that are closer to reality, assessing the foliar net primary productivity of species at the Abisko site will be necessary, as

this parameter depends on local climatic conditions. Extending the studies conducted at the Abisko site in Sweden to other locations will allow testing whether the observations are valid at other Cryosol sites and could reveal different trends across various Arctic permafrost regions with distinct parent materials.

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Appendix

Appendix 1. Soil horizon description of the different sub-sites. For each horizon (i.e., organic or mineral), different values have been measured: humidity and thickness (Potier et al., 2024).

Site	Sub-site code	Horizon	Humidity (g g _{dry mass} ⁻¹)	Thickness (cm)
Mire	FLA1	Organic	3.84	20
	FLA1	Mineral	2.01	25
	FLA2	Organic	5.08	20
	FLA2	Mineral	3.28	25
	FLA7	Organic	17.05	60
	FLA7	Mineral	2.07	50
Heathland	PAD-A2	Organic	9.83	15
	PAD-A2	Mineral	7.28	45
	PAD-B2	Organic	5.00	10
	PAD-B2	Mineral	0.26	4
	PAD-C1	Organic	4.73	10.5
	PAD-C1	Mineral	2.52	8
	PAD-D4	Organic	2.04	8
	PAD-D4	Mineral	0.18	1
	PAD-F1	Organic	1.80	3
	PAD-F1	Mineral	0.13	7.5
	PAD-F8	Organic	1.22	5
	PAD-F8	Mineral	0.23	10

Appendix 2. Soil element concentrations in (means (μ), standard deviations (σ) for six habitats, at Abisko, Sweden, in 2021.

Site	Habitat	Subsite	Horizon	Soil element concentrations (mg kg ⁻¹)																	
				Mn		Fe		Zn		Cu		Mo		V		Cd		As		Ti	
				Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)
Mire	Palsa	1	Organic	66.42	33.47	3063	2021	22.75	5.39	7.66	4.06	0.32	0.18	8.42	8.25	0.14	0.08	0.94	0.05	193	258
			Mineral	99.41	112.22	8767	5303	19.51	10.44	16.13	13.49	1.10	0.63	30.56	27.56	0.21	0.11	2.18	0.68	1159	871
		2	Organic	66.42	33.47	3063	2021	22.75	5.39	7.66	4.06	0.32	0.18	8.42	8.25	0.14	0.08	0.94	0.05	193	258
			Mineral	99.41	112.22	8767	5303	19.51	10.44	16.13	13.49	1.10	0.63	30.56	27.56	0.21	0.11	2.18	0.68	1159	871
	Bog	7	Organic	21.12	8.25	2399	1144	18.4	7.75	8.19	3.64	0.90	0.44	7.8	5.59	0.12	0.05	0.91	0.05	125	120
			Mineral	244	90.09	14370	6175	38.16	8.79	31.7	6.42	1.99	0.55	62.41	23.58	0.36	0.09	2.94	1.19	2176	1109
	Fen	11	Organic	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/
			Mineral	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/
Heathland	Forest	F1	Organic	350.64	165.53	8035	5187	53.74	14.57	7.62	1.25	0.48	0.35	32.2	20.11	0.26	0.05	0.63	0.35	1707	1141
			Mineral	716.56	251.58	38880	18461	47.7	22.97	4.89	5.94	1.18	0.27	177.4	77.25	0.61	0.28	1.75	1.76	9820	2374
		F8	Organic	350.64	165.53	8035	5187	53.74	14.57	7.62	1.25	0.48	0.35	32.2	20.11	0.26	0.05	0.63	0.35	1707	1141
			Mineral	716.56	251.58	38880	18461	47.7	22.97	4.89	5.94	1.18	0.27	177.4	77.25	0.61	0.28	1.75	1.76	9820	2374
	Dry-heath	D4	Organic	1024.27	2039.68	13229	13784	57.13	37.35	22.26	19.3	0.59	0.48	48.76	52.19	0.63	0.50	0.92	1.00	1793	2022
			Mineral	1645.59	1861.38	46184	8751	65.99	25.43	28.7	37.48	1.16	0.34	195.83	40.49	0.97	0.40	1.72	2.14	7943	2213
	Humid-heath	A2	Organic	738.85	668.24	11424	8795	40.11	13.56	56.36	39.02	0.61	0.50	29	25.47	0.55	0.32	2.43	1.83	760	848
			Mineral	647.77	299.84	32809	17036	44.79	15.87	46.11	25.08	0.87	0.22	123.01	63.91	0.74	0.24	1.11	1.07	4985	2925
		B2	Organic	738.85	668.24	11424	8795	40.11	13.56	56.36	39.02	0.61	0.50	29	25.47	0.55	0.32	2.43	1.83	760	848
			Mineral	647.77	299.84	32809	17036	44.79	15.87	46.11	25.08	0.87	0.22	123.01	63.91	0.74	0.24	1.11	1.07	4985	2925
		C1	Organic	738.85	668.24	11424	8795	40.11	13.56	56.36	39.02	0.61	0.50	29	25.47	0.55	0.32	2.43	1.83	760	848
			Mineral	647.77	299.84	32809	17036	44.79	15.87	46.11	25.08	0.87	0.22	123.01	63.91	0.74	0.24	1.11	1.07	4985	2925

Appendix 3. Ecological characteristics of nine Arctic cosmopolitan species. Data are provided by eFlora Tela Botanica (www.tela-botanica.org). No information is available for *Rubus chamaemorus* in the database of Tela Botanica.

Species	pH		Humidity		Texture		Nutrients		Salinity		Organic matter	
	Index	pH range	Index	Legend	Index	Legend	Index	Legend	Index	Legend	Index	Legend
<i>Vaccinium vitis-idaea</i>	2	4-4.5	4	Mesoxerophilic	4	Fine sand	3	Oligotrophic	1	Hyperoligohaline	6	Mor
<i>Empetrum nigrum</i>	2	4-4.5	5	Mesohydric	4	Fine sand	2	Peroligotrophic	1	Hyperoligohaline	6	Mor
<i>Vaccinium uliginosum</i>	2	4-4.5	5	Mesohydric	2	Intermediate	3	Oligotrophic	1	Hyperoligohaline	6	Mor
<i>Betula nana</i>	2	4-4.5	6	Mesohygrophilic	1	Clay	2	Peroligotrophic	1	Hyperoligohaline	9	Peat
<i>Carex rostrata</i>	5	5.5-6.5	8	Hydrophilic	1	Clay	3	Oligotrophic	1	Hyperoligohaline	9	Peat
<i>Eriophorum angustifolium</i>	4	5-5.5	7	Hygrophilic	1	Clay	2	Peroligotrophic	1	Hyperoligohaline	9	Peat
<i>Eriophorum vaginatum</i>	2	4-4.5	7	Hygrophilic	1	Clay	1	Hyperoligotrophic	1	Hyperoligohaline	9	Peat
<i>Eriophorum scheuchzeri</i>	2	4-4.5	7	Hygrophilic	6	Gravel	2	Peroligotrophic	1	Hyperoligohaline	9	Peat
<i>Rubus chamaemorus</i>												

Appendix 4. Rooting depths of nine Arctic cosmopolitan species.

Species	Rooting depth (cm)	References
<i>Rubus chamaemorus</i>	40-65	(Hewitt et al., 2019; Iversen et al., 2015)
<i>Betula nana</i>	30	(Hewitt et al., 2019)
<i>Vaccinium uliginosum</i>	10-25	(Iversen et al., 2015)
<i>Empetrum nigrum</i>	10-15	(Iversen et al., 2015)
<i>Vaccinium vitis-idaea</i>	5-10	(Iversen et al., 2015)
<i>Carex rostrata</i>	25-30	(Saarinen, 1996)
<i>Eriophorum angustifolium</i>	25-40	(Iversen et al., 2015)
<i>Eriophorum scheuchzeri</i>	30-70	(eFlora of North America, 2003; Juanita A. R. Ladyman, 2006)
<i>Eriophorum vaginatum</i>	35-40	(Iversen et al., 2015)

Appendix 5. Aboveground biomass (g m⁻²) and ratio between foliar biomass and aboveground biomass (-). Aboveground biomass was collected at Abisko, Sweden, in 2021. Ratios were calculated by H. Potier (Potier et al., 2024).

Site	Sub-site	Species	Aboveground biomass (g m ⁻²)	Ratio between foliar biomass and aboveground biomass (-)
Mire	FLA-1	<i>Empetrum nigrum</i>	108.5189	0.675
	FLA-1	<i>Vaccinium uliginosum</i>	21.8943	0.401
	FLA-1	<i>Rubus chamaemorus</i>	27.3731	1
	FLA-1	<i>Betula nana</i>	33.8647	0.281
	FLA-1	<i>Eriophorum scheuchzeri</i>	95.3532	1
	FLA-2	<i>Empetrum nigrum</i>	70.9782	0.675
	FLA-2	<i>Betula nana</i>	0.6646	0.281
	FLA-2	<i>Vaccinium uliginosum</i>	22.4625	0.401
	FLA-2	<i>Rubus chamaemorus</i>	29.6307	1
	FLA-2	<i>Eriophorum scheuchzeri</i>	5.3984	1
	FLA-7	<i>Eriophorum vaginatum</i>	145.4280	1
	FLA-11	<i>Eriophorum angustifolium</i>	400.6800	1
	FLA-11	<i>Carex rostrata</i>	133.5600	1
Heathland	PAD-A2	<i>Carex rostrata</i>	70.1440	1
	PAD-A2	<i>Eriophorum vaginatum</i>	161.3312	1
	PAD-B2	<i>Rubus chamaemorus</i>	0.4637	1
	PAD-B2	<i>Empetrum nigrum</i>	26.9904	0.675
	PAD-B2	<i>Betula nana</i>	1.4139	0.281
	PAD-B2	<i>Vaccinium uliginosum</i>	4.7021	0.401
	PAD-C1	<i>Vaccinium uliginosum</i>	12.6555	0.401
	PAD-C1	<i>Rubus chamaemorus</i>	1.0452	1
	PAD-C1	<i>Betula nana</i>	6.9748	0.281
	PAD-C1	<i>Empetrum nigrum</i>	74.9938	0.675
	PAD-C1	<i>Vaccinium vitis-idaea</i>	2.3864	0.730
	PAD-D4	<i>Vaccinium uliginosum</i>	6.6440	0.401
	PAD-D4	<i>Betula nana</i>	47.2815	0.281
	PAD-D4	<i>Vaccinium vitis-idaea</i>	4.0443	0.730
	PAD-D4	<i>Empetrum nigrum</i>	127.0940	0.675
	PAD-F1	<i>Betula nana</i>	2.8129	0.281
	PAD-F1	<i>Vaccinium vitis-idaea</i>	60.1503	0.730
	PAD-F1	<i>Empetrum nigrum</i>	63.0085	0.675
	PAD-F8	<i>Empetrum nigrum</i>	250.1376	0.675
	PAD-F8	<i>Vaccinium uliginosum</i>	8.9666	0.401
	PAD-F8	<i>Vaccinium vitis-idaea</i>	13.6452	0.730

Appendix 6. Foliar biomass (means (μ), standard deviations (σ) for six habitats, at Abisko, Sweden, in 2021.

Site	Habitat	Species	Foliar biomass (g m ⁻²)	
			Mean (μ)	SD (σ)
Mire	Palsa	<i>Betula nana</i>	17.265	17.099
		<i>Empetrum nigrum</i>	89.749	10.133
		<i>Eriophorum scheuchzeri</i>	50.376	17.236
		<i>Rubus chamaemorus</i>	28.502	2.994
		<i>Vaccinium uliginosum</i>	22.178	6.231
		Others	103.576	30.929
	Bog	<i>Eriophorum vaginatum</i>	145.428	/
		Others	339.332	/
	Fen	<i>Carex rostrata</i>	133.560	/
		<i>Eriophorum angustifolium</i>	400.680	/
		Others	0	/
Heathland	Forest	<i>Betula nana</i>	1.395	1.973
		<i>Empetrum nigrum</i>	94.590	15.568
		<i>Vaccinium uliginosum</i>	0.921	1.302
		<i>Vaccinium vitis-idaea</i>	32.216	38.811
		Others	106.909	90.905
	Dry-heath	<i>Betula nana</i>	66.306	/
		<i>Empetrum nigrum</i>	94.590	/
		<i>Vaccinium uliginosum</i>	4.702	/
		<i>Vaccinium vitis-idaea</i>	2.386	/
		Others	163.995	/
	Humid-heath	<i>Betula nana</i>	2.796	3.937
		<i>Carex rostrata</i>	35.616	61.689
		<i>Empetrum nigrum</i>	33.995	1.587
		<i>Eriophorum vaginatum</i>	74.330	128.743
		<i>Rubus chamaemorus</i>	0.503	0.733
		<i>Vaccinium uliginosum</i>	5.576	17.309
		<i>Vaccinium vitis-idaea</i>	0.795	5.334
		Others	249.648	280.268

Appendix 7. Foliar element concentrations for each species in each sub-site, at Abisko, Sweden, in 2021. Data from ICP-MS.

Site	Habitat	Subsite	Species	Foliar element concentrations (mg kg ⁻¹)								
				Mn	Fe	Zn	Cu	Mo	V	Cd	As	Ti
Mire	Palsa	1	<i>Betula nana</i>	16992	1849	2528.0	32.41	0.9958	2.4222	1.6784	0.1778	43.91
			<i>Empetrum nigrum</i>	7568	2802	167.7	37.43	2.7779	3.8134	0.0186	0.1586	35.76
			<i>Vaccinium uliginosum</i>	3950	687	350.4	27.01	0.8922	0.7410	0.2691	0.0434	12.65
			<i>Rubus chamaemorus</i>	9435	3395	641.1	38.20	14.1433	3.7730	1.4035	0.1236	32.36
			<i>Eriophorum scheuchzeri</i>	3839	1622	749.7	23.00	9.0293	1.8878	0.1828	0.1630	27.52
		2	<i>Eriophorum scheuchzeri</i>	2185	979	490.7	20.38	11.1378	1.1685	0.1227	0.0742	24.94
			<i>Empetrum nigrum</i>	4163	2984	97.7	21.33	3.8430	3.8219	0.0194	0.1311	35.60
			<i>Betula nana</i>	5339	1354	1633.0	26.97	0.3345	1.7399	0.4171	0.1384	42.56
			<i>Rubus chamaemorus</i>	4531	3627	839.3	40.36	9.5830	3.8535	0.7278	0.1489	36.12
			<i>Vaccinium uliginosum</i>	2083	910	567.4	33.77	2.9036	0.9547	0.5543	0.0225	16.30
	Bog	7	<i>Eriophorum vaginatum</i>	418	1027	226.5	16.91	1.9730	1.0779	0.0113	0.0920	15.82
Heathland	Fen	11	<i>Eriophorum angustifolium</i>	1685	493	340.5	23.04	4.5296	0.4496	0.0682	0.0705	16.63
			<i>Carex rostrata</i>	2122	1174	281.2	4.75	1.8181	1.3166	0.0671	0.0926	34.65
		F1	<i>Betula nana</i>	3774	1456	353.3	26.11	2.1856	0.7260	0.0487	0.0799	22.96
			<i>Vaccinium vitis-idaea</i>	3019	2033	398.8	25.07	1.2652	1.5248	0.0728	0.1751	54.00
			<i>Empetrum nigrum</i>	7059	440	555.1	34.82	0.6683	0.5012	2.2868	0.1417	21.64
		F8	<i>Vaccinium vitis-idaea</i>	2597	898	1891.5	26.51	0.3954	1.6189	0.6177	0.1666	107.88
			<i>Vaccinium uliginosum</i>	4850	3086	406.4	32.78	9.3784	2.9279	2.2266	0.3829	76.09
			<i>Empetrum nigrum</i>	3876	586	159.8	37.93	0.8229	1.0745	0.0069	0.2178	37.99
		D4	<i>Vaccinium vitis-idaea</i>	17531	286	198.9	34.25	0.6698	0.6683	0.0604	-0.0107	16.46
			<i>Empetrum nigrum</i>	19439	970	438.6	21.54	15.8060	4.8655	3.1302	0.0652	47.88
			<i>Betula nana</i>	11649	558	1424.5	21.79	0.5097	0.7286	1.0800	0.0744	24.13
			<i>Vaccinium uliginosum</i>	7267	259	225.6	18.77	0.5167	0.4032	1.0813	0.0252	19.68
		A2	<i>Eriophorum vaginatum</i>	12765	495	135.8	37.57	1.0102	0.8904	-0.0115	0.1137	45.55
			<i>Carex rostrata</i>	12190	399	226.2	24.01	0.5898	0.8863	0.1132	0.0807	34.92
		B2	<i>Vaccinium uliginosum</i>	2732	411	114.4	36.54	0.3988	0.7807	-0.0070	0.0403	24.36
			<i>Betula nana</i>	5143	538	1329.0	19.43	0.2136	0.6680	0.8328	0.0731	30.72
			<i>Rubus chamaemorus</i>	1677	341	364.9	27.43	0.3143	0.3863	1.3130	0.0230	21.91
			<i>Empetrum nigrum</i>	7062	1669	921.1	38.53	0.2642	3.6633	0.7237	0.1195	105.28
		C1	<i>Vaccinium vitis-idaea</i>	10883	272	197.6	27.31	0.2804	0.6551	0.0367	0.0480	17.29
			<i>Rubus chamaemorus</i>	3169	340	90.1	28.97	0.2076	0.5556	-0.0209	0.0229	44.45
			<i>Betula nana</i>	11937	442	194.1	49.64	0.5724	0.9054	0.0991	0.0520	23.11
			<i>Vaccinium uliginosum</i>	7286	537	294.9	54.73	0.6819	0.8135	2.2847	0.0659	29.92
			<i>Empetrum nigrum</i>	2927	266	58.6	23.67	0.4424	0.4573	-0.0094	0.0159	34.06

Appendix 8. Enrichment factors for each species in each sub-site, at Abisko, Sweden, in 2021.

Site	Habitat	Subsite	Species	Enrichment factor EF							
				Mn	Fe	Zn	Cu	Mo	V	Cd	As
Mire	Palsa	1	<i>Betula nana</i>	4510	5.565	3419	53.02	23.88	2.091	210.87	2.152
			<i>Empetrum nigrum</i>	2467	10.356	279	75.18	81.82	4.043	2.87	2.357
			<i>Vaccinium uliginosum</i>	3641	7.175	1646	153.41	74.31	2.221	117.42	1.824
			<i>Rubus chamaemorus</i>	3398	13.867	1177	84.79	460.38	4.421	239.31	2.030
			<i>Eriophorum scheuchzeri</i>	1626	7.789	1618	60.03	345.62	2.601	36.66	3.148
		2	<i>Eriophorum scheuchzeri</i>	1021	5.187	1169	58.72	470.45	1.777	27.14	1.581
			<i>Empetrum nigrum</i>	1363	11.077	163	43.04	113.71	4.070	3.01	1.957
			<i>Betula nana</i>	1462	4.205	2279	45.52	8.28	1.550	54.07	1.728
			<i>Rubus chamaemorus</i>	1462	13.268	1380	80.26	279.43	4.044	111.17	2.191
			<i>Vaccinium uliginosum</i>	1489	7.376	2066	148.76	187.57	2.220	187.54	0.733
	Bog	7	<i>Eriophorum vaginatum</i>	236	9.836	817	73.39	136.43	2.377	4.33	4.305
	Fen	11	<i>Eriophorum angustifolium</i>	/	/	/	/	/	/	/	/
			<i>Carex rostrata</i>	/	/	/	/	/	/	/	/
Heathland	Forest	F1	<i>Betula nana</i>	919	4.004	1801	735.00	20.88	1.926	110.66	6.369
			<i>Vaccinium vitis-idaea</i>	8624	3.965	2352	3171.43	134.95	2.097	34.15	15.560
			<i>Empetrum nigrum</i>	977	1.931	417	1308.58	38.87	0.692	-7.58	2.887
		F8	<i>Vaccinium vitis-idaea</i>	7078	4.826	1729	4313.63	206.13	2.169	69.03	12.634
			<i>Vaccinium uliginosum</i>	3337	4.532	2029	3673.24	189.67	1.505	1229.27	12.359
			<i>Empetrum nigrum</i>	1178	1.973	354	1395.90	108.11	0.743	-4.43	2.623
	Dry-heath	D4	<i>Vaccinium vitis-idaea</i>	1685	1.965	780	190.29	115.66	1.030	26.56	10.674
			<i>Empetrum nigrum</i>	541	2.905	565	415.21	112.12	1.300	-2.36	7.637
			<i>Betula nana</i>	808	3.012	5208	175.07	47.61	0.882	222.02	10.996
			<i>Vaccinium uliginosum</i>	370	2.678	2005	346.53	98.23	0.715	490.74	4.839
	Humid-heath	A2	<i>Eriophorum vaginatum</i>	1265	9.638	1713	122.98	545.52	1.282	14.28	15.638
			<i>Carex rostrata</i>	430	5.720	822	50.19	134.26	1.144	9.08	14.562
			<i>Vaccinium uliginosum</i>	2511	3.094	2856	174.00	176.98	0.939	712.04	29.424
		B2	<i>Betula nana</i>	185	1.265	1952	26.57	21.00	0.608	38.58	6.937
			<i>Rubus chamaemorus</i>	491	6.163	594	46.57	706.28	1.559	197.14	22.603
			<i>Empetrum nigrum</i>	785	2.346	468	107.95	124.11	1.146	1.22	25.742
			C1	<i>Vaccinium vitis-idaea</i>	8195	2.641	1345	224.91	233.12	1.645	24.72
		<i>Rubus chamaemorus</i>		3125	3.077	1020	48.63	1891.69	4.118	440.45	6.114
		<i>Betula nana</i>		3716	3.516	6572	97.63	121.06	1.224	301.57	13.841
		<i>Vaccinium uliginosum</i>		2842	2.003	1276	103.16	150.46	0.831	370.23	5.741
		<i>Empetrum nigrum</i>		2157	1.651	332	89.19	127.10	0.792	-1.71	11.212

Appendix 9. Foliar element concentrations in (means (μ), standard deviations (σ) for six habitats, at Abisko, Sweden, in 2021.

Site	Habitat	Species	Foliar concentrations (mg kg ⁻¹)																	
			Mn		Fe		Zn		Cu		Mo		V		Cd		As		Ti	
			Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)
Mire	Palsa	<i>Betula nana</i>	11165	8240	1602	350	2080	633	29.69	3.85	0.665	0.468	2.081	0.482	1.048	0.892	0.158	0.028	43.234	0.958
		<i>Empetrum nigrum</i>	5866	2407	2893	128	133	50	29.38	11.38	3.310	0.753	3.818	0.006	0.019	0.001	0.145	0.019	35.677	0.114
		<i>Eriophorum scheuchzeri</i>	3012	1170	1300	455	620	183	21.69	1.85	10.084	1.491	1.528	0.509	0.153	0.043	0.119	0.063	26.225	1.824
		<i>Rubus chamaemorus</i>	6983	3467	3511	164	740	140	39.28	1.53	11.863	3.225	3.813	0.057	1.066	0.478	0.136	0.018	34.238	2.662
		<i>Vaccinium uliginosum</i>	3016	1320	798	158	459	153	30.39	4.78	1.898	1.422	0.848	0.151	0.412	0.202	0.033	0.015	14.475	2.588
	Bog	<i>Eriophorum vaginatum</i>	418	/	1027	/	227	/	16.91	/	1.973	/	1.078	/	0.011	/	0.092	/	15.817	/
	Fen	<i>Carex rostrata</i>	2122	/	1174	/	281	/	4.75	/	1.818	/	1.317	/	0.067	/	0.093	/	34.646	/
		<i>Eriophorum angustifolium</i>	1685	/	493	/	340	/	23.04	/	4.530	/	0.450	/	0.068	/	0.071	/	16.629	/
Heathland	Forest	<i>Betula nana</i>	3531	4993	834	1180	461	651	19.27	27.25	0.132	0.187	1.832	2.590	0.362	0.512	0.060	0.084	52.641	74.445
		<i>Empetrum nigrum</i>	3048	171	303	52	74	22	26.32	3.74	0.325	0.166	0.506	0.070	-0.015	0.008	0.019	0.005	39.255	7.353
		<i>Vaccinium uliginosum</i>	3643	5152	268	380	147	209	27.36	38.70	0.341	0.482	0.407	0.575	1.142	1.616	0.033	0.047	14.960	21.157
		<i>Vaccinium vitis-idaea</i>	11410	745	357	120	196	2	38.48	15.79	0.426	0.206	0.780	0.177	0.068	0.044	0.050	0.003	20.203	4.114
	Dry-heath	<i>Betula nana</i>	5143	/	538	/	1329	/	19.43	/	0.214	/	0.668	/	0.833	/	0.073	/	30.718	/
		<i>Empetrum nigrum</i>	2732	/	411	/	114	/	36.54	/	0.399	/	0.781	/	-0.007	/	0.040	/	24.357	/
		<i>Vaccinium uliginosum</i>	1677	/	341	/	365	/	27.43	/	0.314	/	0.386	/	1.313	/	0.023	/	21.909	/
		<i>Vaccinium vitis-idaea</i>	12190	/	399	/	226	/	24.01	/	0.590	/	0.886	/	0.113	/	0.081	/	34.917	/
	Humid-heath	<i>Betula nana</i>	4749	6115	485	453	1105	985	16.10	14.14	0.302	0.267	0.782	0.811	0.566	0.542	0.080	0.083	44.001	56.618
		<i>Carex rostrata</i>	1006	1743	678	1174	133	230	8.36	14.47	0.422	0.730	0.508	0.880	0.024	0.042	0.058	0.101	18.000	31.177
		<i>Empetrum nigrum</i>	5547	6544	360	316	99	86	25.17	21.80	0.611	0.537	0.655	0.575	-0.002	0.009	0.110	0.109	27.846	24.409
		<i>Eriophorum vaginatum</i>	1258	2179	485	841	118	204	8.70	15.08	0.729	1.262	0.242	0.419	0.016	0.028	0.027	0.046	7.653	13.255
		<i>Rubus chamaemorus</i>	8096	10118	1352	1578	282	244	18.10	16.66	8.395	7.949	2.598	2.449	1.786	1.611	0.149	0.205	41.323	38.466
		<i>Vaccinium uliginosum</i>	4775	4137	233	221	260	279	17.86	17.43	0.395	0.350	0.301	0.266	1.123	1.144	0.056	0.076	13.771	11.966
		<i>Vaccinium vitis-idaea</i>	5844	10121	95	165	66	115	11.42	19.77	0.223	0.387	0.223	0.386	0.020	0.035	-0.004	0.006	5.488	9.505

Appendix 10. Foliar element stocks (means (μ), standard deviations (σ) for six habitats, at Abisko, Sweden, in 2021.

Site	Habitat	Species	Foliar stocks (mg m ⁻²)																	
			Mn		Fe		Zn		Cu		Mo		V		Cd		As		Ti	
			Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)
Mire	Palsa	<i>Betula nana</i>	275.92	333.17	32.47	33.43	43.70	46.50	0.5793	0.5741	0.0162	0.0194	0.0424	0.0439	0.0269	0.0333	0.0031	0.0032	0.8038	0.7558
		<i>Empetrum nigrum</i>	56.86	275.50	21.38	40.83	1.26	5.79	0.2814	1.3194	0.0214	0.1011	0.0290	0.0392	0.0001	0.0002	0.0012	0.0032	0.2722	0.3718
		<i>Eriophorum scheuchzeri</i>	260.58	110.86	112.07	45.32	53.16	19.92	1.8198	0.4670	0.8258	0.2489	0.1315	0.0520	0.0131	0.0048	0.0104	0.0052	2.1968	0.5439
		<i>Rubus chamaemorus</i>	226.88	119.73	111.22	15.18	23.29	6.21	1.2447	0.1612	0.3815	0.1274	0.1210	0.0130	0.0345	0.0168	0.0043	0.0009	1.0830	0.1784
		<i>Vaccinium uliginosum</i>	23.93	48.08	4.75	8.48	2.54	6.26	0.1848	0.2954	0.0080	0.0434	0.0051	0.0086	0.0021	0.0070	0.0003	0.0005	0.0870	0.1476
	Bog	<i>Eriophorum vaginatum</i>	60.73	/	149.38	/	32.94	/	2.4586	/	0.2869	/	0.1568	/	0.0016	/	0.0134	/	2.3002	/
	Fen	<i>Carex rostrata</i>	283.45	/	156.78	/	37.56	/	0.6342	/	0.2428	/	0.1758	/	0.0090	/	0.0124	/	4.6273	/
		<i>Eriophorum angustifolium</i>	675.28	/	197.38	/	136.42	/	9.2308	/	1.8149	/	0.1802	/	0.0273	/	0.0283	/	6.6631	/
Heathland	Forest	<i>Betula nana</i>	9.85	13.93	2.33	3.29	1.28	1.82	0.0537	0.0760	0.0004	0.0005	0.0051	0.0072	0.0010	0.0014	0.0002	0.0002	0.1469	0.2077
		<i>Empetrum nigrum</i>	286.99	63.67	28.25	9.65	6.86	3.26	2.4604	0.7639	0.0320	0.0208	0.0474	0.0145	-0.0014	0.0005	0.0018	0.0008	3.6559	1.3066
		<i>Vaccinium uliginosum</i>	6.71	9.49	0.49	0.70	0.27	0.38	0.0504	0.0713	0.0006	0.0009	0.0007	0.0011	0.0021	0.0030	0.0001	0.0001	0.0276	0.0390
		<i>Vaccinium vitis-idaea</i>	353.13	466.83	9.15	17.71	6.36	7.68	0.9332	2.0021	0.0097	0.0232	0.0217	0.0360	0.0013	0.0041	0.0016	0.0020	0.5710	0.9166
	Dry-heath	<i>Betula nana</i>	341.01	/	35.67	/	88.12	/	1.2884	/	0.0142	/	0.0443	/	0.0552	/	0.0048	/	2.0368	/
		<i>Empetrum nigrum</i>	258.42	/	38.91	/	10.82	/	3.4565	/	0.0377	/	0.0738	/	-0.0007	/	0.0038	/	2.3040	/
		<i>Vaccinium uliginosum</i>	7.89	/	1.60	/	1.72	/	0.1290	/	0.0015	/	0.0018	/	0.0062	/	0.0001	/	0.1030	/
		<i>Vaccinium vitis-idaea</i>	57.32	/	1.88	/	1.06	/	0.1129	/	0.0028	/	0.0042	/	0.0005	/	0.0004	/	0.1642	/
	Humid-heath	<i>Betula nana</i>	14.18	35.80	2.64	3.18	5.71	7.11	0.0813	0.1029	0.0013	0.0019	0.0046	0.0053	0.0023	0.0037	0.0005	0.0005	0.2885	0.3315
		<i>Carex rostrata</i>	107.53	124.17	72.40	83.60	14.20	16.40	0.8929	1.0310	0.0451	0.0520	0.0543	0.0627	0.0026	0.0030	0.0062	0.0072	1.9233	2.2208
		<i>Empetrum nigrum</i>	10.95	231.27	0.89	11.30	0.24	3.09	0.0603	0.7809	0.0014	0.0192	0.0016	0.0206	0.0000	0.0003	0.0003	0.0039	0.0646	0.8740
		<i>Eriophorum vaginatum</i>	280.49	323.88	108.24	124.99	26.26	30.33	1.9410	2.2412	0.1625	0.1876	0.0540	0.0623	0.0036	0.0042	0.0059	0.0069	1.7065	1.9704
		<i>Rubus chamaemorus</i>	9.06	11.03	1.79	1.79	0.34	0.33	0.0230	0.0217	0.0099	0.0102	0.0031	0.0031	0.0021	0.0021	0.0002	0.0002	0.0525	0.0497
		<i>Vaccinium uliginosum</i>	73.28	105.72	2.63	5.27	2.30	6.06	0.1904	0.4064	0.0052	0.0088	0.0041	0.0067	0.0110	0.0258	0.0003	0.0014	0.1986	0.3051
		<i>Vaccinium vitis-idaea</i>	53.99	39.22	0.88	0.64	0.61	0.45	0.1055	0.0766	0.0021	0.0015	0.0021	0.0015	0.0002	0.0001	0.0000	0.0000	0.0507	0.0368

Appendix 11. Foliar net primary productivity of the different species ($\text{g m}^{-2} \text{a}^{-1}$).

Species	fNPP ($\text{g m}^{-2} \text{a}^{-1}$)	Site	References
<i>Vaccinium uliginosum</i>	13.97	CiPEHR, 2017	(E. A. G. Schuur et al., 2007)
<i>Betula nana</i>	2.20	CiPEHR, 2017	(E. A. G. Schuur et al., 2007)
<i>Carex rostrata</i>	2.87	CiPEHR, 2017	(E. A. G. Schuur et al., 2007) Value for <i>Carex bigelowii</i>
<i>Eriophorum vaginatum</i>	139.26	CiPEHR, 2017	(E. A. G. Schuur et al., 2007)
<i>Rubus chamaemorus</i>	12.75	CiPEHR, 2017	(E. A. G. Schuur et al., 2007)

Appendix 12. Foliar element fluxes (means (μ), standard deviations (σ) for six habitats, at Abisko, Sweden, in 2021.

Site	Habitat	Species	Foliar fluxes ($\text{mg m}^{-2} \text{a}^{-1}$)																	
			Mn		Fe		Zn		Cu		Mo		V		Cd		As		Ti	
			Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)	Mean (μ)	SD (σ)
Mire	Palsa	<i>Betula nana</i>	24.56	18.13	3.524	0.770	4.577	1.392	0.0653	0.0085	0.0015	0.0010	0.0046	0.0011	0.0023	0.0020	0.0003	0.0001	0.0951	0.0021
		<i>Eriophorum scheuchzeri</i>	262.17	101.84	113.184	39.578	53.982	15.944	1.8880	0.1609	0.8777	0.1298	0.1330	0.0443	0.0133	0.0037	0.0103	0.0055	2.2826	0.1588
		<i>Rubus chamaemorus</i>	89.03	44.21	44.767	2.087	9.438	1.787	0.5008	0.0195	0.1513	0.0411	0.0486	0.0007	0.0136	0.0061	0.0017	0.0002	0.4365	0.0339
		<i>Vaccinium uliginosum</i>	42.14	18.45	11.153	2.208	6.411	2.143	0.4245	0.0668	0.0265	0.0199	0.0118	0.0021	0.0058	0.0028	0.0005	0.0002	0.2022	0.0361
	Bog	<i>Eriophorum vaginatum</i>	58.15	/	143.046	/	31.543	/	2.3544	/	0.2748	/	0.1501	/	0.0016	/	0.0128	/	2.2027	/
	Fen	<i>Carex rostrata</i>	6.09	/	3.369	/	0.807	/	0.0136	/	0.0052	/	0.0038	/	0.0002	/	0.0003	/	0.0994	/
		<i>Eriophorum angustifolium</i>	264.04	/	77.176	/	53.343	/	3.6093	/	0.7097	/	0.0704	/	0.0107	/	0.0111	/	2.6053	/
Heathland	Forest	<i>Betula nana</i>	7.77	10.99	1.836	2.596	1.013	1.433	0.0424	0.0599	0.0003	0.0004	0.0040	0.0057	0.0008	0.0011	0.0001	0.0002	0.1158	0.1638
		<i>Vaccinium uliginosum</i>	50.89	71.98	3.750	5.304	2.060	2.913	0.3823	0.5406	0.0048	0.0067	0.0057	0.0080	0.0160	0.0226	0.0005	0.0007	0.2090	0.2956
	Dry-heath	<i>Betula nana</i>	11.31	/	1.184	/	2.924	/	0.0427	/	0.0005	/	0.0015	/	0.0018	/	0.0002	/	0.0676	/
		<i>Vaccinium uliginosum</i>	23.43	/	4.766	/	5.097	/	0.3832	/	0.0044	/	0.0054	/	0.0183	/	0.0003	/	0.3061	/
	Humid-heath	<i>Betula nana</i>	10.45	13.45	1.068	0.998	2.432	2.168	0.0354	0.0311	0.0007	0.0006	0.0017	0.0018	0.0012	0.0012	0.0002	0.0002	0.0968	0.1246
		<i>Carex rostrata</i>	2.89	5.00	1.945	3.368	0.382	0.661	0.0240	0.0415	0.0012	0.0021	0.0015	0.0025	0.0001	0.0001	0.0002	0.0003	0.0517	0.0895
		<i>Eriophorum vaginatum</i>	175.17	303.40	67.598	117.082	16.402	28.409	1.2122	2.0995	0.1015	0.1757	0.0337	0.0584	0.0023	0.0039	0.0037	0.0064	1.0657	1.8458
		<i>Rubus chamaemorus</i>	103.23	129.01	17.237	20.123	3.591	3.117	0.2308	0.2124	0.1070	0.1013	0.0331	0.0312	0.0228	0.0205	0.0019	0.0026	0.5269	0.4904
		<i>Vaccinium uliginosum</i>	66.71	57.79	3.259	3.093	3.636	3.900	0.2496	0.2435	0.0055	0.0049	0.0042	0.0037	0.0157	0.0160	0.0008	0.0011	0.1924	0.1672

Factors influencing trace element cycling by Arctic vegetation in different habitats

A case study in Abisko, Sweden

Claire Lathuy

Arctic warming and permafrost degradation are reshaping northern ecosystems by altering microtopography, soil water dynamics, nutrient availability, and vegetation succession. These shifts in vegetation composition and changes in soil physical and chemical conditions may influence mineral element cycling by vegetation. This master's thesis aims to understand how plants cycle trace elements across different Arctic habitats. To investigate this, trace element concentrations in plants and soil are examined for 2021 at two study sites in Abisko, Sweden: a peatland mire and a heathland. Within each site, three habitats are studied along gradients of abiotic conditions such as pH and soil moisture. Nine widely distributed Arctic plant species with varying rooting depths are analyzed. Within a habitat, the order of foliar element concentrations from most to least concentrated is $Mn > Fe > Zn > Ti > Cu > Mo > V > Cd > As$. The results demonstrate that foliar element concentrations varied across Arctic habitats due to several factors: soil properties, habitat floristic composition, and plant physiology. They also indicate that variations in soil concentrations or the floristic composition of the habitats alter the foliar concentrations, thereby impacting foliar stocks and fluxes. As Arctic warming modifies soil characteristics and the floristic composition of habitats, foliar element concentrations will be altered accordingly, modifying foliar stocks and fluxes.