Terrestrial Si dynamics in the Arctic: a study on biotic and abiotic controls

Alfredsson, Hanna

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Terrestrial Si dynamics in the Arctic:
A study on biotic and abiotic controls

Hanna Alfredsson

DOCTORAL DISSERTATION
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Faculty opponent
Sophie Opfergelt
Université catholique de Louvain
Abstract

Silicon is the next most abundant element in the Earth’s crust and its biogeochemical cycle is linked with that of carbon. Further, silicon is a beneficial nutrient for plants in terrestrial ecosystems and a key nutrient for diatoms in aquatic ecosystems. During the last decade the important role of terrestrial vegetation in controlling Si fluxes downstream aquatic environments, via incorporation of Si into biomass (as amorphous Si) and subsequent storage in soil, has been realized. Due to the high prevalence of high Si-accumulating plants, cold temperatures and perenially frozen soil conditions, Arctic terrestrial ecosystems is hypothesized to store a significant fraction of the global soil ASi stock. The Arctic environment is highly sensitive to climate change, with unknown effects for terrestrial Si cycling.

Hence, in this thesis we utilized archived soil samples collected from different geographical regions of the Arctic tundra and continuous permafrost region. By combining results obtained through soil chemical analysis with literature review this thesis provide a conceptual framework for how climate change may alter the biological component of terrestrial Si cycling in Arctic regions underlain by permafrost. Further, permafrost thaw can mobilize previously frozen soil material initiating biogeochemical processing of the newly thawed material, such as dissolution of plant derived amorphous silica stored in soil. Hence, an additional aspect of this thesis is to shed light on the potential biotic control (i.e. microbial influence) on plant derived Si dissolution rates during litter degradation. This question was explored by utilization of microcosm laboratory experiments.

Dependent on land cover type, we found total ASi storage to range between 1,290 - 94,300 kg SiO₂ ha⁻¹ in Arctic shrub/graminoid tundra and peatland ecosystems. Further, the first estimate of total ASi storage (0 - 1 m) in the northern circumpolar tundra regions is presented in this thesis. Our estimates, based on speculating by vegetation and soil classes provide an estimated storage of 219 to 510 T mol Si, which represents 2 - 6 % of the estimated global soil ASi storage. The results also show that the majority of the total ASi storage is allocated to the mineral subsoil, indicating that pedogenic rather than biogenically derived Si fractions dominate the ASi pool in the Arctic. Furthermore, the results suggest that at least 50 % of the total ASi pool is allocated to the permafrost layer, thus potentially representing an additional pool of Si that will become available for biogeochemical processing in a future warmer Arctic.

Regarding the influence of microbes (bacteria and fungi) on amorphous silica dissolution during plant litter decomposition, we find that microbes can reduce the apparent release of Si and that the reduction in Si release increases with greater microbial colonization and decomposition of litter. This result is contrary to predicted results and common belief (i.e. that microbes can enhance Si release rates during litter decomposition). While the work carried out herein do not allow for the exact mechanism behind this pattern to be resolved, the results indicate that microbes may influence the availability of released Si.

Overall, the work carried out in this thesis fills some of the existing knowledge gaps regarding the size and geographical/landscape distribution of the Arctic ASi pool, its significance in a global context as well as how microbes can influence Si release during plant litter decomposition, which previously were understudied.

Key words: Amorphous silica; Arctic; Litter decomposition; Microbes; Peatlands; Permafrost; Silica dissolution; Tundra.

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"How many years can a mountain exist, before it is washed to the sea?"
- Bob Dylan -
List of papers

This thesis is based on 3 papers which are listed below. The papers have been appended to the thesis. Paper I is published in the journal Biogeochemistry and reprinted with the permission of Springer. Paper II has been submitted to the indicated journal while Paper III is an unpublished manuscript.

Paper I

Paper II

Paper III
Acknowledgments

The time has come to think back of the 4+ past years during which I have worked with this thesis. The road has been paved by both less good times when wanting to quit but also by many good times which made be thankful for continuing. However, this work would not have been possible without the help and support from a number of people which made it all work out in the end.

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During my time as a PhD student I have had the opportunity to meet and work together with people from all over the world as well as taking part in many courses, sometimes very far away. I feel very greatful for having been given these opportunities with the trips to Svalbard and Alaska being highlights. These trips has made be develop a special interest for Arctic environments and I hope to go back in the future, as a researcher or a tourist.

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Introduction

Biogeochemical cycles describe how elements, such as carbon, nitrogen, and silicon, are transformed (i.e. cycled) and moved through the land-ocean continuum by biological, geological, chemical, and physical processes. These processes take place on various time scales, from millions of years to more comprehensible time scales (years).

Found in most minerals, silicon (Si) represents the second most abundant element by weight in the Earth's crust, but its occurrence in nature is not restricted to rocks. In the living biosphere, Si has an important role where it is found incorporated into the biomass of plants, algae and other specific organisms (Clarke 2003; Sommer et al. 2006). On biological time-scales, Si availability has an important role in the functioning of marine food webs (Kristiansen and Hoell 2002), while Si biogeochemistry has influenced the Earth’s climate on geological timescales (Street-Perrot and Barker 2008). Hence, improved understanding of the biological, geological, chemical and physical processes that governs the transformation and movement of Si in the natural environment becomes important.

The global Si biogeochemical cycle

Chemical weathering of Si-minerals (e.g. quartz) release Si into its dissolved monomeric form – H4SiO4. For Si-minerals containing calcium or magnesium (e.g. CaSiO3) the result is a net consumption of atmospheric CO2 via precipitation of carbonates at the deep ocean floor (Sommer et al. 2006; Street-Perrot and Barker 2008; Struyf et al. 2009; Song et al. 2012). This establishes an important link between the global biogeochemical cycles of Si and carbon (C) where chemical weathering of Si-minerals have influenced global climate at geological time scales (Kump et al. 2000). To balance the loss, CO2 is ultimately returned to the atmosphere via tectonic processes such as volcanism and metamorphism (Berner and Kothavala, 2002) (Fig. 1).

Dissolved Si (DSi) reaching the world’s oceans via groundwater flow and rivers is consumed by diatoms, a group of Si-requiring microscopic algae, that frequently dominates the phytoplankton community in temperate and high-latitude marine ecosystems (Lalli and Parsons 1997). DSi availability can control diatom primary productivity in the oceans (Allen et al. 2005) and thus, via the biological carbon-pump (Raven and Falkowski 1999), influence C sequestration in deep ocean sediments (Dugdale et al. 1999; Dugdale and Wilkerson 1998; Bidle et al., 2003; Ragueneau et al. 2006). A biological carbon pump influenced by ocean DSi availability establishes a second link between the global biogeochemical cycles of Si and C (Fig. 1).

Si biogeochemical cycling within the terrestrial biosphere

The occurrence of Si in soil

Soils are formed by the products of mineral weathering and the input of organic matter from primarily decay- ing plants (Ashman and Puri 2002). Besides, soils are described as “the main reactor” for biogeochemical processes in terrestrial ecosystems (Sommer et al. 2006). Si occurs in several forms in soil including crystalline, poorly crystalline and amorphous forms as well as Si adsorbed onto Al/Fe hydroxides and dissolved Si (H4SiO4) (Sauer et al. 2006; Cornelis et al. 2011).

Crystalline forms represent by far the largest Si pool in soil and are divided into primary (e.g. quartz, feldspar) and secondary (e.g. kaolinite) minerals (Sauer et al. 2006; Becker et al. 2006). While primary minerals are principally unaltered by chemical weathering, secondary (clay) minerals have been chemically altered (Ashman and Puri 2002). Poorly crystalline forms found in soil include allophane and imogolite and are formed via pedogenic processes (i.e. linked to soil formation) (Cornelis et al. 2011). Allophane and imogolite are commonly found in, but not restricted to, volcanic ash soils (Sommer et al. 2006).

Amorphous forms refer to solids that lack a clearly definable structure (as opposed to crystalline forms) (Ashman and Puri 2002). Depending on origin of formation, this fraction is further divided into either biogenic or a pedogenic amorphous Si (ASi) pool. The biogenic pool includes plant phytoliths (Clarke 2003), diatom frustules (Kokfelt et al. 2009; Van Kerckvoorde et al. 2000) and the tests of testate amoebae (Aoki et al. 2007; Sommer et al. 2013; Puppe et al. 2014). The pedogenic Si pool is linked to soil formation processes and includes among others Opal-A spheres (formed when DSi concentrations reach saturation) and volcanic glass shards (tephra) (Sauer et al. 2006; Cornelis et al. 2011; Clymans et al. 2015). Compared to crystalline Si, the highly un-
structured amorphous forms dissolve more easily (Frayse et al. 2009) and are the focus of attention in Papers I – III (Fig. 2).

DSi in soil solution, originating from dissolution of the above solid fractions, mainly occurs in its uncharged monomeric form (H₂SiO₃⁻) (Wonisch et al. 2009) but can also form polymers (Sommer et al. 2006). Further, DSi can be adsorbed onto solid surfaces of mainly Al and Fe hydroxides (Cornelis et al. 2011).

The role of Si in terrestrial biology

Plants take up Si from the soil solution in its uncharged monomeric form H₂SiO₃⁻ (Casey et al. 2003). During transport in the plants xylem, H₂SiO₃⁻ monomers start to polymerize to eventually form solid precipitates of amorphous Si (opal-A or SiO₂ × nH₂O) (Epstein 1994; Wonisch et al. 2008) but can also form polymers (Sommer et al. 2006).

Further, DSi can be adsorbed onto solid surfaces of mainly Al and Fe hydroxides (Cornelis et al. 2011). The size of the soil ASi pool is dependent on several interacting factors, including aboveground net primary productivity (Blecker et al. 2006; Melzer et al. 2010), type of vegetation (Cornelis et al. 2010, 2011b; Alexandre et al. 2011), climate (Blecker et al. 2006), lithology (Melzer et al. 2012), weathering degree of parent material (Henriet et al. 2008) and human perturbations (e.g. deforestation and agricultural practices; Conley et al. 2008; Clymans et al. 2011; Keller et al. 2012; Vandevenne et al. 2015).

Uptake of DSi from the soil solution is thought to occur either through passive flow via the transpiration stream or by an active uptake mechanism (Eppstein 1994; Pychich et al. 2004; Meena et al. 2008). A gene responsible for the active uptake of DSi has been identified in rice (Ma and Yamaji 2006). In addition to uptake by plants, Si is consumed by diatoms and testate amoebae that also occur in the terrestrial environment (Van Kerckvoorde et al. 2006; Kokfelt et al. 2009; Sommer et al. 2013; Puppe et al. 2014).

At present, Si is not regarded as being essential for plant growth. Instead, Si is observed to exert several positive effects including improved growth (Meena et al. 2014) and resistance to biotic (e.g. pathogens) (Fautrezx et al. 2005; Shetty et al. 2011; Gunzter et al. 2012) and abiotic stress (e.g. drought, metal toxicity) (Kidd et al. 2001; Gunzter et al. 2012) as well as providing structural support (Schoolnik et al. 2010) and defense against grazing herbivores (Massey et al. 2006, 2007; 2008).

The terrestrial Si filter

Uptake and fixation of Si by terrestrial plants on a global scale is estimated to range between 55 – 200 Tmol Si year (Conley 2002; Laruelle et al. 2009; Carey and Fulweiler 2012) which is similar to the estimate of Si fixed by diatoms in the global ocean (240 ± 40 Tmol Si year; Tréguer et al. 1995; Tréguer and De La Rocha 2013). Note that these estimates for terrestrial vegetation do not include Si fixed by diatoms and Si requiring organisms found in terrestrial habitats.

Through litterfall, phytoliths are returned to the top soil. This pool of biologically fixed ASi is commonly much larger (orders of magnitude) than that stored in aboveground biomass (Markewitz and Richter 1998; Blecker et al. 2006; Sommer et al. 2013) and forms a pool of higher reactivity than that of crystalline Si (Frayse et al. 2009) and, thus, increases its bioavailability to plants (Gocke et al. 2013). Diatoms and testate amoebae also contribute to this ASi pool (Van Kerckvoorde et al. 2000; Kokfelt et al. 2009; Sommer et al. 2013). Estimates of ASi storage in soil, based on either extracted phytolith content or alkaline extractable Si, range between 963 – 800,000 kg SiO₂ ha⁻¹ (Struyf and Conley 2012; Paper I). The size of the soil ASi pool is dependent on several interacting factors, including aboveground net primary productivity (Blecker et al. 2006; Melzer et al. 2010), type of vegetation (Cornelis et al. 2010, 2011b; Alexandre et al. 2011), climate (Blecker et al. 2006), lithology (Melzer et al. 2012), weathering degree of parent material (Henriet et al. 2008) and human perturbations (e.g. deforestation and agricultural practices; Conley et al. 2008; Clymans et al. 2011; Keller et al. 2012; Vandevenne et al. 2015).

By regulating Si fluxes through the land-ocean continuum, via a plant-soil Si cycle, terrestrial ecosystems including wetlands have been termed the “ecosystem Si filter” (Struyf and Conley 2012). Depending on dominant plant species (low vs. high Si-accumulators), the “eficiency” of this filter can vary between land-cover types. For example, Cornelis et al. (2010) found the output of DSi in deep mineral horizons to be negatively correlated with the annual DSi uptake by different tree species. In
Anthropogenic perturbations

A change in the river load of dissolved and amorphous Si ultimately reaching coastal zones will influence DSi availability for marine diatoms. This will have implications for marine primary productivity, phytoplankton community composition, the food-web and associated C-cycle dynamics (Kristiansen and Hoell 2000; Tréguer et al. 1995; Tréguer and De La Rocha 2013). Today we know that several anthropogenic activities including construction of river dams (Triplett et al. 2012), deforestation (Conley et al. 2008), land-use change (Struyf et al. 2010; Carey and Fulweiler 2012b) and agricultural practices (Clymans et al. 2011; Keller et al. 2012; Vandevenne et al. 2012, 2015) cause perturbations to the global Si cycle such as alterations in soil ASi storage and DISi river fluxes. Ongoing climate warming can be expected to alter global Si biogeochemistry in multiple and intricate ways, which has yet remained largely unexplored (Laruelle et al. 2009).

The Arctic perspective

In the Arctic, warming of surface air temperatures are occurring at a rate twice that of the global average (Anisimov et al. 2007) which makes the region particularly sensitive to climate change. Reduced permafrost extent and a thickening of the active layer depth will follow with warmer temperatures (Vaughan et al. 2013). Together with more abrupt permafrost degradation processes, such as permafrost thaw combined with alterations in vegetation cover (Johansson et al. 2006; Tape et al. 2006; Bidle et al. 2002, 2003; Roubeix et al. 2008; Holstein and Hensen 2010) due to ecoenzymatic decomposition of an outer organic coating (Bidle and Azam 1999, 2001). Based on their role as primary decomposers of organic matter, it is hypothesized that microbes will enhance dissolution of phyoliths embedded in an organic matrix (Sommer et al. 2006; Schoelyncx et al. 2010; Struyf and Conley 2012; Schaller and Struyf 2013). While the interactions between soil microbial colonization and release of nutrients during decomposition of plant litter are well studied for C, other plant material constituents, such as Si, have not received equal attention. Struyf and Conley (2012) proposed this to be one of the key aspects needing further attention to better understand the function of the terrestrial vegetation Si cycle.

Little studies designed to investigate Si release from plant litter in the presence of a live microbial decomposer community are available (Struyf et al. 2007; Frayse et al. 2010) and they were not designed to explicitly investigate the role of microbes. These studies indicate no or a slight enhancement of phyolith dissolution rates during microbial litter decomposition, but methodological limitations make interpretation less straightforward. For instance, both studies (Struyf et al. 2007; Frayse et al. 2010) evaluated the influence of an actively degrading microbial community indirectly, without confirming the presumed difference in colonization between controls and inhibited or sterilized treatments. Hence, the question whether microbes enhance phyolith dissolution during plant litter degradation remains unclear. Improved understanding of this matter would provide insight into how biotic factors control Si release into pore water and how DSi fluxes are influenced by the rate and type of microbial decomposition of submerged plant litter.

With the presented background in mind, the general scope of this thesis was to investigate size and partitioning of ASi storage in Arctic permafrost affected soils. An additional aim is to shed light over the potential influence of microbes on phyolith dissolution during plant litter decomposition. The recently improved understanding of the importance of biological processes in terrestrial Si cycling provides the rationale for this thesis.

The general working hypotheses were that 1) Arctic tundra and peatlands underlain by permafrost represent hotspots of soil ASi storage due to high prevalence of Si-accumulating plant species and cold climates favoring preservation and 2) microbes enhance phyolith dissolution during plant litter mineralization, thus playing a key role with regards to Si cycling within the plant-soil continuum.

In specific terms, the aims of this thesis were to:

- Quantify ASi storage (0 – 1 m) and investigate partitioning between land-cover types, soil type and type of microbial litter decomposition could alter rates of ASi recycling within the vegetation-soil continuum.
- Study sites

A map (Fig. 4) showing the location of all study sites, together with photos (Fig. 5) depicting the common landscape at most sites, is provided.

Tulemalu Lake, central Canadian Arctic

The Tulemalu Lake study site (Paper I) is located in the central Canadian Arctic close to the shore of Tulemalu Lake (Fig. 4; 62°55‘N, 99°10‘W). The climate is continental with mean annual air temperature (MAT) ranging between -9.4 to -14.3 °C and total annual precipitation (MAP) being < 300 mm of which 40 % falls during the winter period (mean temperature < 0°C) (Hugelius et al. 2011). The area is located within the continuous permafrost zone, meaning that > 91 % of the land area is underlain by permafrost (Tarnocai et al. 2009). Elevation in the study area range between 281 and 303 meter above sea level (a.s.l.). The bedrock is dominated by granite and is overlain by quaternary deposits from previous glaciations in the area. Quaternary deposits are glacial till (sand) loam to loamy sand) and glaciofluvial materials (sandy). In depressions, thick peat deposits have accumulated over time. Soils developed on glacial till are classified (World Reference Base of Soil Terminology; WRB) as Turbic (or Histic) Cryosols while soils developed on glaciofluvial materials are classified as Cambic or Haplic Cryosolls (Hugelius et al. 2011). Where thick peat deposits have developed, soils are classified as Cryic Hemic Histosols ( bog peatland) or Histic Cryosols/Cryic Histosol (fen peatland) (Hugelius et al. 2011).

Vegetation cover in the study area consists of bog and fen peatlands intermixed with shrub tundra having different drainage conditions depending on slope position. Bog peatlands (typically occurring in high-centered ice wedge polygons) are dominated by mosses, lichens and prostrate shrubs (Vaccinium uliginosum, Empetrum palustre, Rubus chamaemorus) whereas fen peatlands are dominated by graminoids (Eriophorum spp.) and mosses (Drepanocladus spp., Sphagnum spp.). Shrub tundra sites are dominated by Salix spp. and Betula nana shrubs while lichen tundra is dominated by lichens (Cladonia spp.) together with Empetrum spp. and Vaccinium spp. shrubs (Hugelius et al. 2011). According to the Circumpolar Arctic Vegetation Map (CAVM Team 2003; see Walker et al. 2005) the vegetation in the region is dominated by erect dwarf-shrub tundra (S1), low-shrub tundra (S2) and sedge, moss, low-shrub wetland (W3).

Adventdalen, Svalbard

The Adventdalen study site (Paper III) is a U-shaped valley located in a mountainous landscape nearby the
community of Longyearbyen in central Svalbard (Fig. 4; 78°12’N, 16°20’E). The climate is high-Arctic with a MAT of -6 °C and a MAP of 190 mm of which most falls as snow (Christiansen 2005). Adventdalen is situated within the continuous permafrost zone and the area consists of sedimentary rocks of Early Permian to Eocene age (Dallman et al. 2001). The area has been glaciated and the valley is covered by glacial till, fluvioglacial and eolian material.

According to CAVM, the vegetation cover in Adventdalen is dominated by rush/grass, forb, cryptogam tundra (G1) and sedge, grass, moss wetland (W1). Presence of low-centered ice wedge polygons are common which leads to a distinct vegetation zonation with high-tundra grasses, sparsely vegetated rims and an extensive moss cover in the low-polygonal centers (Christiansen et al. 2005).

Zackenberg, NE Greenland

The Zackenberg study site (Paper III) is located in the surrounding area of the Zackenberg Research Station situated by the coastline of NE Greenland (Fig. 4; 74°28’N, 20°34’W). The area is mountainous and the study site is located in a broad, flat central valley (altitudinal range; 0 – 1372 m a.s.l). The climate is high-Arctic with MAT of -9.2 °C and MAP of 200 mm with approximately 10 % falling as rain during summer (June – September) (Hansen et al. 2008). A large fault system dividing Caledonian granite/gneiss bedrock (west) and Cretaceous/Tertiary sedimentary rocks (east) have created the Zackenberg valley (Escher and Watt 1976), which has been glaciated. The valley is covered by quaternary glaciofluvial, deltaic, eolian and glacial till deposits while solifluction material is dominant on slopes. The dominant soil type in the Zackenberg central valley has been classified as Tyric Pseudoturbels (Elberling et al. 2008). On hill slopes, the dominant soil type is Gelorthents whereas fen peatlands are classified as Histels or Histoturbels (Palmtag et al. 2015). The valley is covered by glaciofluvial, deltaic, eolian and glacial till deposits while solifluction material is dominant on slopes. The dominant soil type in the Zackenberg central valley has been classified as Tyric Pseudoturbels (Elberling et al. 2008). On hill slopes, the dominant soil type is Gelorthents whereas fen peatlands are classified as Histels or Histoturbels (Palmtag et al. 2015).

The vegetation in Zackenberg forms a zonal pattern ranging from fell fields at the hilltops to fen peatlands in the lowland areas of the central valley. In the lowland valley, Cassiope tetragona heaths, Salix arctica snow beds, grasslands and fen peatlands are intermixed with each other whereas Eriophorum spp. heaths are common at higher elevations (Elberling et al. 2008). Fen peatlands, located in depressions and dominated by grasses (e.g. Eriophorum scheuchzeri), are typically surrounded by grasslands, which are common on slightly sloping terrain. The grasslands are dominated by Eriophorum triae, Arct-

Shalaurovo, NE Siberia

The Shalaurovo study site (Paper III) is located in the Kolyma Lowlands of NE Siberia (Fig. 4; 69°27’N, 161°48’E). The region has a continental climate with a MAT of -11.3 °C and MAP of 290 mm of which 50 % falls during the summer months. Compared to the three previous field sites, the area stayed largely unglaciated during the Last Glacial Maximum (LGM) (Brubaker et al. 2005). The parent material comprises late Pleistocene Yedoma Ice Complex (IC) deposits. Yedoma IC deposits consist of fine grained silty material with a high content of ground ice (up to 80 % by volume) that can rise 30 m above the neighboring terrain (Schirrmeister et al. 2015). Histoturbels represent the dominant mineral soil type at tundra sites while Haploturbels are dominating on floodplains. Bog peatlands and fen peatlands in the area are classified as Folistsels and Histels, respectively (Palmtag et al. 2015).

At Shalaurovo, upland areas are dominated by shrubby tussock tundra while areas with gentle slopes are dominated by shrubby grasslands. Depressions of low lying areas are characterized by sedge fen and willow communities while steep slopes are primarily dominated by Equisetum spp. (Lashchinskiy et al. 2013). According to CAVM, the vegetation in the region is dominated by tussock-sedge, dwarf-shrub, moss tundra (G4), low-shrub tundra (S2) and sedge, moss, shrub wetlands (W2 and W3).

Kytalyk, NE Siberia

The Kytalyk study site (Paper III) is located in the Indigirka Lowlands of NE Siberia (Fig. 4; 70°49’N, 147°28’E) and is situated in the continuous permafrost zone. The region has a continental climate with a MAT of -10.5 °C and MAP of 212 mm of which approximately 50 % falls during the summer months (Van der Molen et al. 2007). Similar to Shalaurovo, the region stayed mostly unglaciated during the LGM and the parent material comprises late Pleistocene Yedoma IC deposits.

According to CAVM, the vegetation in Kytalyk is dominated by tussock-sedge, dwarf-shrub, moss tundra (G4), low-shrub tundra (S2) and sedge, moss, shrub wetlands (W2 and W3). Blok et al. (2010) described moister tussock tundra in Kytalyk to be dominated by Eriophorum vaginatum and shrubs of Betula nana, Salix pulchra and Ledum palustre whereas wet areas are dominated by E. angustifolium, Carex aquatilis and Sphagnum mosses.
Alaska, USA

Soil samples were collected in Alaska during a field study course ("Alaska Soil Geography Field Study", Université of Alaska Fairbanks, Fairbanks, Alaska) in July/August 2012. The field course followed the route of Dalton Highway starting in Fairbanks of interior Alaska, going north through the Brooks Range toward the Arctic coastal plains and ending in Prudhoe Bay (Fig 4) located at the coastline of the Beaufort Sea. Stops were made along the route where soil pits were dug. The climate changes from continental in interior Alaska (Fairbanks) to high-Arctic in the coastal plains.

While travelling from interior Alaska toward the Arctic coastal plain, the landscape changes from spruce dominated forests (Picea glauca, Picea mariana inter-mixed with e.g. Alnus spp., Betula spp. and Salix spp.) to shrub and graminoid tundra. The permafrost zonation changes from discontinuous permafrost in interior Alaska to continuous permafrost in the high-Arctic regions.

Other sites

In addition to the above described field sites, data retrieved from two soil pedons collected in Hudson Bay Lowlands, central Canada (Kuhry 1998, 2008) and two soil pedons collected from the European Russian Arctic (Oksanen et al. 2001, 2005) were included in Paper III. All four soil pedons were retrieved from raised bog peatlands (palsas and peat plateaus) consisting of meter thick Sphagna spp. and Carex spp. peat.

Materials and Methods

Soil material

Field campaigns to the described study areas (except Alaska) in late summer were originally conducted to study storage and landscape distribution of soil organic carbon (SOC) in Arctic permafrost terrain (Hugelius et al. 2010, 2011; Palmtag et al. 2015; Siewert et al. in review). These samples were archived at the Department of Physical Geography, Stockholm University, Sweden. Subsamples were retrieved from these sites for the purpose of investigating ASi storage and landscape distribution in permafrost terrain (Paper I and Paper III).

A transect based sampling method has been used at all study sites for the collection of soil pedons. When using this approach, initial scuffing of the field is performed to establish transects that are representative for the investigated study area. After this, the sampling of soils is made at equidistant intervals (Hugelius et al. 2010; Palmtag et al. 2015; Siewert et al. in review). Such a sampling approach leads to a combination of subjective selection of sites (thought to be characteristic for the investigated landscape) and a degree of randomness (represented by small-scale vegetation and micro-topography patterns) (Hugelius et al. 2011).

At each site, soil cores were retrieved by hammering steel tubes into the frozen ground (Fig. 6) in - 0.05 – 0.10 m vertical depth increments after cutting out blocks of the top organic layer. At tundra sites (but not for peatlands) three randomly selected replicates of the top organic layer were cut out. This was done since spatial fine-scale variability of the top organic layer thickness can vary greatly. In some cases, soil samples were collected using fixed volume cylinders inserted horizontally at unfrozen exposed surfaces (e.g. at exposed erosion sites or dug soil pits) while a Russian peat corer was sometimes used to collect unfrozen peatland deposits. Depth of the top organic layer and active layer together with a description of the vegetation cover and other parameters (e.g. slope, aspect) was recorded while sampling.

For some of the study sites (e.g. Tulemalu Lake in Paper I and Advenrdalen in Paper III) field work was carried out in late June and July. At this time of the season, the maximum seasonal thaw depth of the active layer is not yet reached. Therefore, the estimates made for ASi stored in permafrost do not entirely correspond to the maximum seasonal thaw depth.

Soil sampled during the field study course along the Dalton Highway, Alaska, was collected by digging soil pits (using sand hammers when reaching permafrost) and a sample was collected from each described soil horizon.

Quantification of ASi in soil and vegetation

To quantify the content of ASi in soil (Paper I and Paper III) and vegetation (Paper II) samples, a wet alkaline digestion method was used. The digestion method applied here was originally described by DeMaster (1981) to quantify ASi in marine sediments but have been evaluated for and widely applied to soil samples (Sauer et al. 2006; Saccone et al. 2007; Melzer et al. 2010, 2012; Struyf et al. 2010; Clymans et al. 2011; Cornelis et al. 2011b; Opdekamp et al. 2012).

In this procedure, a 30 mg dried and homogenized soil sample is digested in 1 % Na2 CO3 (pH=11.2) at 85 °C while shaken (100 rpm) for 5 h. During digestion, a 1 mL subsample is collected and neutralized with 0.01 M HCl after 3, 4 and 5 h, respectively. DSi extracts are colorimetrically analyzed using the molybdenum blue reagent (Amornthammarong and Zhang 2009). In Paper II, DSi extracts (obs. not from soil) had to be analyzed by Inductively Coupled Plasma - Atomic Emission Spectroscopy (ICP-AES) due to interference from very high phosphate concentrations.

The method to determine ASi described by DeMaster (1981) relies on two basic assumptions: 1) ASi of biogenic origin is non-linearly and completely dissolved within the first 2 h of extraction and 2) increasing DSi concentrations after 3 h is solely due to a continued dissolution of clay minerals and primary silicates which follows a linear pattern over time. These two assumptions allow for a mineral correction to be made (Fig. 7), where the fraction of DSi released from amorphous components (as opposed to mineral Si) is determined by linear extrapolation of the slope to time zero for the three time-course measurements at 3, 4 and 5 h (DeMaster 1981). For digestion of pure plant material (Paper II) no mineral correction is necessary, instead an average value of DSi for the three time-course measurements is used. This method allows for a relatively large number of samples (ca. 150 – 200 samples) to be analyzed during a relatively short time-span (1 week) compared to other methods (e.g. Georgiadis et al. 2013, 2014; Barão et al. 2014, 2015).

Methodological considerations

The presence of different Si fractions in soil, forming a continuum from highly ordered crystalline (less dissolvable) to amorphous forms (more dissolvable) (Sauer et al. 2006), complicates the quantification of biologically formed ASi in soil. Several methods have been used to quantitate ASi in soil including digestion in 1 % Na2 CO3 (DeMaster 1981), NaOH (Saccone et al. 2007) or Tiron (Meunier et al. 2014), a sequential separation procedure suggested by Georgiadis et al. (2013, 2014) and continuous extraction of Si and Al in NaOH (Koning et al. 2002; Barão et al. 2014, 2015). Extraction in Na2CO3, NaOH and Tiron is not phase specific. While a mineral correction is made for the simultaneous Si release from clay minerals and crystalline Si (DeMaster, 1981), no separation can be made between Si released from biogenic and pedogenic amorphous Si and other poorly crystallized Si fractions.

Digestion in Na2CO3, Tiron and NaOH produces comparable results when applied on fresh phytolith material and organic top soils (Saccone et al. 2007; Meunier et al. 2014; Barão et al. 2015), whereas incomplete digestion of ASi (in Na2CO3) can occur in samples containing aged phytoliths having a lower reactivity (Meunier et al. 2014). The incomplete digestion of biogenic ASi within 2 h violates the first assumption which the method by DeMaster (1981) relies on. The use of a stronger solvent, such as NaOH, may thus be a better choice to avoid underestimations of biogenic ASi. However, compared to Na2CO3, the use of NaOH can result in higher Si release, especially when applied on deep mineral samples (Saccone et al. 2007; Barão et al. 2015). This may result from enhanced dissolution of other non-biogenic Si fractions present in mineral soils. Moreover, dissolution of pedogenic amorphous Si, other poorly crystalline forms and clay minerals can release Si in a non-linear pattern during digestion in both Na2CO3 and NaOH (Barão et al. 2015; Clymans et al. 2015). This violates the second assumption made by DeMaster (1981) leading to potential overestimation of the biogenic ASi fraction.

Figure 6. Field work in Adventdalen, Svalbard. The collection of soils is carried out by hammering a fixed volume steel tube into the frozen ground.
In a method tested by Baró et al. (2014, 2015), the extraction of Si and Al from soil is continuously monitored during digestion in NaOH. By fitting the measured concentrations to mathematical models, a distinction can be made between Si released from clay minerals and ASi originating from organic material based on their Si/Al ratios. In Paper I and Paper III, we suggest that ASi of biogenic origin contribute to a larger relative fraction of the ASi pool in top organic layers as compared to mineral soils. This since the large contribution of biogenic ASi in organic top soils and a larger contribution of pedogenic ASi in deeper mineral soils were found for other mixed soils analyzed with the phase specific method described in Baró et al. (2014, 2015). Other studies support this pattern with depth between biogenic and pedogenic Si fractions (Blecket et al. 2006; Saccone et al. 2007; Sommer et al. 2013; White et al. 2012; Georgiadis et al. 2014).

Moreover, Si extracted from various soil types using three different methods (digestion in 1 % Na2CO3, digestion in 0.5M NaOH, and digestion in 0.5 M NaOH with 0.01 M Na2CO3) showed good agreement between methods (Baró et al. 2014). Extracted Si concentrations, as well as the vertical distribution pattern of extracted Si concentrations, agreed well between soils and methods (Baró et al. 2014). In summary, the 1 % Na2CO3 method used in Paper I and Paper III works well when applied to top soil and organic samples containing fresh phyoliths. In deep mineral soils, a dominant contribution of Si release from pedogenic and other non-amorphous fractions is expected. We therefore performed spot checks to confirm whether or not a microscope to better evaluate the contribution of biogenic versus pedogenic ASi in the different soil layers.

**Evaluating the contribution of biogenic Si**

Since no distinction between biogenic or pedogenic ASi can be made with the applied alkaline digestion method (DeMaster 1981) selected soil samples were investigated under a microscope to evaluate the composition of Si. Soil samples from both the top organic layer, intermediate depth and the deeper mineral horizons of soil profiles were evaluated under microscope. No quantitative enumeration of the biogenic fraction was made.

In Paper I, soil samples were investigated with both light microscopy (LM, SEM). Prior to analysis, organic matter was removed by treating the samples with H2O2 at ~ 80 °C (light microscopy) or by ignition at 550 °C (SEM). In Paper III, organic material was removed with H2O2 (~ 80 °C) and followed by heavy liquid separation using polytungstate (PTE, relative density 2.3 g cm-3) (Morley et al. 2004) in order to obtain the concentrated biogenic ASi fraction. This approach was selected since the large contribution of silt to the mineral soils of the Yedoma IC could potentially mask the presence of any biogenic Si remains. Samples were viewed under a light microscope (40 x magnifications) (Fig. 2).

**Storage calculations and upscaling**

The storage of ASi in each soil sample is calculated by using the DBD (kg ASi m-3), the concentration of Si (g SiO2 kg-1 dry weight) and the depth (d; m) of the sampled horizon (z):

\[ \text{Storage, } \text{DBD, } [\text{Si}] \cdot z \cdot d \cdot (1 - \text{CF}) \cdot 10 \]

A correction factor of (1 - CF) was applied to take the percent stone content (CF, course fraction > 2 mm) of each horizon into account. The factor 10 is to convert g m-2 to kg ha-1. In Paper I, no correction for the CF was made in the storage calculations since particle-size separations (sieving) were not conducted on the archived soil samples. This would result in potential overestimation of the calculated pools. However, descriptions of % CF were made for a limited number of soil pedons in the field and showed a negligible contribution of stones in the top organic layer of peatlands and shrub tundra. In the shrub tundra mineral soils, stone content varied between 2 to 100 % with an average of 12 ± 17 %, resulting in an average uncertainty range of 1,100 to 9,000 kg SiO2 ha-1. In Paper III, no CF needed to be included in the storage calculations for the Shalaunovo and Krytalyst study sites since no large stones were encountered in these soils.

Data needed for storage calculations (DBD, % CF) were retrieved from Hugelius et al. (2010), Palmtag et al. (2015) and Siewert et al. (in review). Where values of DBD and/or [Si] were missing, extrapolation was made by taking a mean from the sample directly above and below in the soil horizon. Total storage was calculated by summing the values of all soil horizons corresponding to the depth interval of interest. Extrapolation to 1 m depth was made from the last sample in the mineral horizon. Such extrapolation can lead to overestimations of the pool at depth. The triplicate top organic layers collected at tundra sites (not peatlands) were used to calculate a mean storage for the organic layer at each site. Regarding the Alaskan soil samples, sampling in the field were carried out without taking the volume of the sampled soil into account. Hence, no estimates of the DBD could be made for these samples. However, DBD and percent CF of soil profiles collected from the same soil type and area were available from previous investigations (Michaelson et al. 2005). A factor used in Paper III to estimate ASi storage at these sites.

In Paper III, we apply thematic upscaling to provide an estimate of ASi storage (Tmol Si) in the circum-Arctic tundra region. In thematic upscaling, the mean ASi storage for a specific thematic class is multiplied with the total areal coverage of that class. This approach relies on the assumption that the assigned thematic classes provide a correct representation of the diverse natural environment in the landscape of interest (Hugelius et al. 2009). To estimate ASi storage using the DBD method, we applied two upscaling scenarios based on available spatial data for the circum-Arctic region. The first scenario is based on vegetation classification using the Circumpolar Arctic Vegetation Map (CAVM) available at 1:1,000,000 scale. The CAVM map includes 15 different vegetation types occurring between the Arctic Ocean to the north and the northern limit of forests (treeline) to the south. The entire area is underlain by continuous permafrost. The second scenario is based on soil classification using the "Northern Circumpolar Soil Database (NCSCDv2)" (Tarnocai et al. 2009; Hugelius et al. 2014). The upscaling using soil classification (henceforth referred to as "CASM") was restricted to the same area covered by the CAVM map. Based on available site descriptions, all soil pedons were assigned a vegetation class (following CAVM) or soil type (following CASM).

**Investigating the role of microbes - study approach**

Commonly either laboratory batch (Struyf et al. 2007; Frayse et al. 2010; Schaller and Struyf 2013) or flow-through experiments (Frayse et al. 2006, 2009, 2010) are performed to study phyolith and diatom dissolution kinetics. We used laboratory batch experiments to assess whether microbes (bacteria and fungi) influence the rate of phyolith dissolution during plant litter mineralization (Paper II). In such experiments, a siliceous material (here phyoliths) is suspended in a liquid that is originally free from Si and the subsequent release of DSI is then observed over time. Of course, such experiments do not fully depict the complex natural environment but it enables the variable of interest (here phyolith dissolution) to be studied under controlled conditions. Compared to flow-through experiments, batch experiments are simpler to perform which allows for more replication of treatments. However, a potential drawback of using batch cultures (as opposed to flow-through experiments) is that the composition of the solution continuously changes over time (Loucaides et al. 2011).

To distinguish between biotic (i.e. microbial) and abiotic factors, phyolith dissolution in the presence of a microbial decomposer community need to be compared with such upscaling conditions being equal (Fig. 8). This necessitates the use of sterilization techniques; hence, autoclaving of plant litter was performed in Paper II to obtain sterile litter for use in the experiments. After inoculation with either a live microbial community (live soil) or a sterilized soil, batch cultures were incubated at room temperature for 1 month with microbial growth and DSi concentrations being monitored over time. The applied sterilization approach proved to be efficient for our purpose. However, sterilization of soil samples does not fundamentally alter the physical properties and chemical composition of the sterilized material (Berner et al. 2008). An initial pilot experiment testing a range of sterilization methods was therefore conducted, with litter being either heated at 80 °C or 110 °C. Both methods used to sterilize litter resulted in similar patterns of Si release from litter and the bacterial use of plant litter was identical between the two methods of sterilization. Together, this suggests that the sterilization of litter did not fundamentally alter the microbial community and its capability to microbial degradation. Additionally, pure phyoliths heated to 450 °C showed similar or slightly higher Si release rates when compared to unheated phyoliths over a range of different pH conditions (Frayse et al. 2006).

**Soil microbial parameters**

To verify the presence of growing microbes in live batch experiments, and their absence in sterile controls, measurements of bacterial growth and fungal abundance were performed over time (Paper II). Bacterial growth was estimated by Leucine incorporation which estimates the rate of protein synthesis as a proxy for bacterial growth. As described in the experimental section, the Leucine incorporation is measured in the presence of soil (after incubation) in the continuous use of the laboratory incubator for measuring bacterial growth and fungal abundance (after incubation) in the continuous use of the laboratory incubator for measuring bacterial growth and fungal abundance. The CAVM map includes 15 different vegetation types occurring between the Arctic Ocean to the north and the northern limit of forests (treeline) to the south. The entire area is underlain by continuous permafrost. The second scenario is based on soil classification using the Northern Circumpolar Soil Database (NCSCDv2) (Tarnocai et al. 2009; Hugelius et al. 2014). The upscaling using soil classification (henceforth referred to as "CASM") was restricted to the same area covered by the CAVM map. Based on available site descriptions, all soil pedons were assigned a vegetation class (following CAVM) or soil type (following CASM).
bacterial suspension followed by a 1 h incubation at room temperature without light. The incubation is terminated by addition of 100 % trichloroacetic acid (TCA). Samples are washed from non-incorporated [³H]Leu by a set of centrifugation steps (Bååth et al. 2001). Radioactivity is then measured using a liquid scintillation analyzer to determine the incorporated radioactivity and estimate the leucine incorporation rate. Methodological considerations include potential uptake of [³H]Leu by fungi. Though, fungi are mainly expected to be associated with the litter rendering their presence in the bacterial suspension likely insignificant (Rousk and Bååth 2011).

Fungal abundance was estimated by extracting ergosterol from freeze dried and homogenized plant litter (Rousk and Bååth 2007; Rousk et al. 2009). Ergosterol is a membrane lipid specific to fungi and is widely used for studies in soil systems (Rousk and Bååth 2011). Ergosterol was extracted, separated and analyzed as previously described (Bååth et al. 2001; Rousk et al. 2009). The extracts are analyzed by high performance liquid chromatography (HPLC) using methanol as the mobile phase and a UV detector (282 nm). Since ergosterol is extracted from collected plant litter, it was only estimated for the experiments final day and not followed over time as for bacteria.

Summary of Papers

Author contributions to the following papers are given in Table 1.

Paper I


In Paper I, we present the first estimate of vertical distribution, storage and landscape partitioning of amorphous Si (ASi) in Arctic permafrost terrain. Archived soil samples were retrieved from the Tulemala Lake study area, central Canadian Arctic, where a detailed study of soil organic carbon (SOC) storage had been previously performed (Hugelius et al. 2010).

We found two basic patterns describing the vertical distribution of ASi in the investigated study area. First, declining ASi concentrations with depth were found in shrub tundra and fen peatlands indicating addition of ASi rich material to the top soil and dissolution in deeper soil horizons. Contrarily, bog peatlands showed variable ASi concentrations with depth.

Total ASi storage (0 – 1 m) ranged between 9,600 – 83,500 kg SiO₂ ha⁻¹ dependent on landscape type (Fig. 8). These values fall within the mid-range of previous estimates from different temperate and tropical regions. Similar to SOC (Fig. 9a), ASi storage appears to decline along the shrub tundra moisture gradient (from wet to dry). Biologically derived ASi (phytoliths and diatoms) contributes to the ASi pool in peatlands and organic top soils of shrub tundra while we suggest that pedogenic ASi fractions contribute significantly to the ASi pool in mineral soils.

In summary, we conclude that bog peatlands underlain by permafrost can act as sinks for ASi, where ASi of biological origin (primarily diatoms) is preserved over millennia rather than being cycled through the plant-soil continuum or being leached out from the soil.

Additionally, by combining our results with a literature review we furthermore discuss the potential effects of climate change on terrestrial Si cycling in Arctic permafrost terrain. Our sole attempt is to provide a conceptual framework for future studies to build on. Focus is directed toward the biological part of the terrestrial Si cycle and the changes that may follow as a result of permafrost thaw, altered hydrology and changes in vegetation cover. In the framework, we suggest that climate change can cause mobilization of previously frozen ASi, altered soil storage of biologically fixed ASi and an increased Si-flux to the Arctic Ocean.

Paper II


Paper II explores the potential influence of microbes on phytoeholith dissolution during microbial decomposition of submerged plant litter (Equisetum arvense). Release of DSi together with parameters indicative of microbial growth were monitored for one month, with live microbial treatments compared to sterile controls. By combining the litter with nitrogen (N) and phosphorous (P) supplements at different levels the rates and level of microbial production was varied. This allowed us to study the effect of varying degree of litter decomposition on Si release.

Bacterial production responded positively to increasing levels of N and P supply while fungal abundance, however, remained unresponsive. The achieved differences in microbial utilization of litter between treatments allowed us to study its effect on Si release. Contrary to hypothesized results, a general reduction in total Si release from plant litter was observed in the presence of a live microbial community when compared to sterile control treatments. Higher levels of microbial growth corresponded with a larger reduction in total Si release, though, after 1 month only 10 – 15 % less of the total plant Si pool was dissolved in the presence of a live microbial community when compared to sterile treatments. The exact mechanism(s) causing this apparent reduction in total Si release is uncertain and cannot be evaluated by our experiments (which was beyond the goal of this study). However, we conclude our results to suggest that the microbial role in litter associated Si turnover is much smaller than what is commonly anticipated. Rather than resulting in a net release of Si from litter, it results in reductions through microbial immobilization (Fig. 10).

Paper III


Continuing on the topic of Paper I, we investigated vertical distribution, landscape partitioning and spatial var...
Global context of the northern circumpolar ASi reservoir

Paper I and Paper II represent the first reports of ASi storage (0 – 1 m) in Arctic permafrost soils. In Paper I, estimated total ASi storage range between 9,600 – 83,500 kg SiO$_2$ ha$^{-1}$ in a shrub tundra and peatland dominated landscape, while in Paper II total ASi storage range between 18,400 – 73,900 kg SiO$_2$ ha$^{-1}$ in graminoid tundra and fen peatlands across diverging landscape types. Further, the additional upsampling sites in Paper III provide estimated total ASi storage in the range of 1,030 – 94,300 kg SiO$_2$ ha$^{-1}$.

In the literature, a range of methods are applied to quantify soil ASi storage, such as alkaline digestion (Clymans et al. 2011; Melzer et al. 2012; Paper I; Paper III) and physical separation (Blecker et al. 2006). While the former will release Si from both biogenic and pedogenic Si fractions, estimates based on the latter method usually only considers the biogenic fraction. Together with differences in reported depth intervals, this makes direct comparisons between our estimates (Paper I and III) and the full range of reported literature values not always straightforward. Focusing on reports of total soil ASi storage based on comparable methodological approach (e.g. alkaline digestion methods) and calculated using similar depth intervals (0.85 – 1 m), our estimates from Arctic permafrost soils are placed within the same range as those reported from other regions, including temperate forests (66,900 – 104,000 kg SiO$_2$ ha$^{-1}$; Clymans et al. 2011; Sommer et al. 2013), North American grasslands (221,000 kg SiO$_2$ ha$^{-1}$; White et al. 2012) and agricultural land (21,950 – 72,000 kg SiO$_2$ ha$^{-1}$; Clymans et al. 2011, 2014), with the exception of South American savannahs having a considerably larger storage (300,000 – 800,000 kg SiO$_2$ ha$^{-1}$; Melzer et al. 2012).

Estimates based on phytolith extracted content, interpolated over the 0 – 1 m depth interval, range between 14,300 – 45,000 kg SiO$_2$ ha$^{-1}$ for North American grasslands (White et al. 2012), African savannah’s (Alexandre et al. 2011) and tropical rainforest (Alexandre et al. 1997), respectively. Using a continuous extraction method, the contribution of biogenically derived ASi in temperate forest soils is found to range between 8,600 – 54,600 kg SiO$_2$ ha$^{-1}$ (Barão et al. 2014; Vanvenem et al. 2015). If comparing these latter literature values with our estimates of topographic soils (assumed to largely consist of biogenic components), ASi storage is comparable with regards to peatlands and wet shrub tundra (3,400 – 45,400 kg SiO$_2$ ha$^{-1}$; Paper I and III) while storage of biogenic components in graminoid tundra and drier shrub tundra classes is considerably lower in Arctic regions than other temperate and equatorial regions (510 – 1760 kg SiO$_2$ ha$^{-1}$; Paper I and III).

Taken together, ASi storage in Arctic permafrost terrain do not stand out in comparison to other non-permafrost regions. Furthermore, in Paper III the first estimate of total ASi storage (0 – 1 m) in circumpolar tundra terrain is provided, which amounts to 219 ± 28 kg SiO$_2$ ha$^{-1}$ while covering an area of 4 – 6 % of the global land surface. In comparison, North American grasslands are estimated to contain 130 Tmol Si while covering an area of 1 % (Blecker et al. 2006) of the global land surface (Jobbágy and Jackson 2000). Hence, ASi storage in the northern circumpolar tundra region is of similar magnitude to that estimated to be stored in North American grasslands alone. Besides, the estimate by Blecker et al. (2006) is based on phytolith content while only considering the 0 – 0.5 m depth interval and is therefore likely underestimated. Moreover, estimated amounts of Si fixed by the major biome types temperate (13 Tmol Si yr$^{-1}$) and savannah (22 Tmol Si yr$^{-1}$) is nearly as high as that fixed by cultivated crops (29 Tmol Si yr$^{-1}$) (Carey and Fulweiler 2012). This provides a large input of biogenically fixed ASi to the top soil. Despite high Si-accumulating graminoids (Hodson et al. 2005) being a dominant feature of the tundra biome, only 3 Tmol Si yr$^{-1}$ is estimated to be fixed by vegetation on a yearly basis in part due to low terrestrial net primary productivity (Carey and Fulweiler 2012). Therefore, temperate grasslands together with savannahs, which stand out by having a notably large ASi soil reservoir (Melzer et al. 2010, 2012), may instead contribute significantly to the global stock of soil ASi. In contrast, although being responsible for 35 % of the Si fixed by vegetation per year (Carey and Fulweiler 2012), ASi storage in crop lands is usually lower (Haynes 2014) since agricultural practices tend to deplete soils of biogenically derived ASi (Clymans et al. 2011; Gunter et al. 2012b; Vanvenem et al. 2012; 2015).

The estimates of 219 ± 28 to 510 ± 59 Tmol Si being stored in circumpolar tundra (Paper III) represents 2 – 6 % of the current global estimate (8,250 Tmol Si; Laruelle et al. 2009). In Paper III, we suggest the current global estimate to be an underrepresentation and that a reassessed estimate should take into account spatial variability of ASi storage between different biomes (Carey and

Discussion

This PhD project was initially set out to explore the size and landscape distribution of ASi in Arctic permafrost soils. In a later stage, the project was extended to also explore the role of microbes (bacteria and fungi) in turnover of biologically fixed ASi. The outcome of this thesis has filled some of the existing knowledge gaps regarding terrestrial Si cycling in permafrost terrain, which can provide the basis for future research concerning what the effects of climate change will be. Further, this work provides new insights into how Si release from degrading plant litter is affected by the presence of a live microbial community that stand in contrast to common beliefs.

Table 1. Author contributions for Papers I to III. Names within brackets are non-author contributions.

<table>
<thead>
<tr>
<th>Paper</th>
<th>Concept and study design</th>
<th>Field sampling of soils</th>
<th>Laboratory work</th>
<th>ArcGIS work/ soil classifications</th>
<th>Data interpretation</th>
<th>Writing of manuscripts</th>
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<tr>
<td>I</td>
<td>H. Alfredsson</td>
<td>P. Kuhry</td>
<td>H. Alfredsson</td>
<td>W. Clymans</td>
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<td>II</td>
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Figure 11. Spatial distribution of ASi storage (0 – 1 m) in soils of the northern circumpolar tundra region produced using soil classifications following Tiemanski et al. (2009) and Hugelius et al. (2014).
Soil storage as an indicator of biological Si cycling

In a global context, our knowledge concerning soil storage and distribution of ASi in soil has improved during the last decade since the early work by Bartoli (1983) showed the importance of considering biological Si cycling in terrestrial ecosystems. Studying soil ASi pools and the relative contribution of biogenically derived Si fractions can be indicative of the extent to which biological influence on Si cycling. Though, to fully comprehend the dynamics of Si cycling and the influence of biology in terrestrial ecosystems, additional information is needed. When formulating the basic ideas that provided the rationale for this project, the concept of “hotspots” was used to describe Arctic tundra as an important region of high ASi accumulation in soil. If defining the concept of a biological soil pool as the potential of biological cycling of Si within the plant-soil environment and its effects on Si fluxes through the landscape, the solitary study of soil pools will not necessarily indicate the complete picture. Instead, pool sizes may reflect a difference in preservation regimes (i.e. turnover rates) between different landscapes, which Paper III as well as the work of others clearly indicates. For instance, Bleeker et al. (2006) studied phytolith storage in both soil and aboveground vegetation across a bioclimatic sequence along the coastal plains of North America. In their study, an increased degree of Si plant fixation (i.e. exerting a biological control on Si cycling) was coherent with a decreasing degree of biological Si cycling and the influence of biology on Si cycling. Therefore, the actual time needed to alter long-term soil ASi storage and terrestrial Si cycling in the circumpolar region is

Biotic components of phytolith turnover – controlling factors

To understand how terrestrial Si cycling is altered by environmental change, such as global warming, it becomes important to study its controlling factors. How biological factors can influence turnover rates of ASi stored in soil is especially interesting in the permafrost thaw that will initiate the biogeochemical processing of previously thawed material. Turnover rates for phytoliths stored in temperate soils are estimated to range between 19–1300 years (Bleeker et al. 2006; Sommer et al. 2013) and providing that a microbial influence on phytolith turnover during soil organic matter decomposition exists, the response of the microbial community to permafrost thaw (Jansson and Tas 2014) could have an important influence. For instance, recent results suggest that the relative contribution of microbial communities to Si release in permafrost thaw may be low, resulting in a time lag between thaw and decomposition of the newly available material (Ernakovich and Wallenstein 2015). Microbes are known to play different roles in Si biogeochemistry and includes (1) aiding smectite dissolution through reduction of iron (Kim et al. 2004; Vorhies and Gaines 2009), 2) production of exogenous metabolites enhancing dissolution rates of non-biogenic Si materials (Bennett and Siegel 1987, Bennett et al. 1988, 2001; Welch and Ullman 1996), and 3) producing bacteria ("silica solubilizing bacteria") as bio-fertilizers to improve crop yields (Mienaa et al. 2014). Taken together, the results of Paper II may seem unexpected, where a higher degree of microbial litter decomposition resulted in greater reductions in total Si release from plant litter. A set of different mechanisms for this observation is proposed. One of these is that a microbial influence on Si cycling was coherent with a decreasing degree of biological Si cycling and the influence of biology on Si cycling. Therefore, the actual time needed to alter long-term soil ASi storage and terrestrial Si cycling in the circumpolar region is

Soil storage as an indicator of biological Si cycling

The effects of organic metabolites are commonly studied with respect to Si dissolution (Bennett et al. 1988; Ullman et al. 1996; Pokrovsky et al. 2009) as well as assessing the available data of soil ASi concentrations quantified by means of different methods. Although we have not pro-
The results presented in Paper I and III also indicate that the majority of ASi stored (0 – 1 m) in circum-polar tundra is allocated to the mineral layer, especially concerning the granular and shrub tundra that are a dominant feature of the tundra landscape (CAVM Team 2003). This also implies that pedogenic ASi fractions, rather than biogenic ones, contribute significantly to the total ASi pool (Paper I and III). A consequence of the increased active layer thickness is increased deep subsurface flow on the expense of surface flow (Law- rence and Slater 2005; Keller et al. 2010). This means a reduced contact time between soil water and organic top soils (dominated by biogenic Si sources), while an increased interaction will occur with mineral soils (domi- nated by lithogenic/pedogenic Si sources) (Harms and Jones 2012). This implies that dissolution of Si from litho- genic and pedogenic Si fractions can become more im- portant in the future (Pokrovksy et al. 2013), especially in soils having thin organic layers. Investigating the reactivity of non-biogenic versus biogenic Si sources and determine their respective role in short-term Si cycling thus becomes important (Barão et al. 2015; Vandevenne et al. 2015). Whether the DSi released from weathering of lithogenic Si sources in deep mineral soil will be fed into a biological plant-soil cycle may depend on rooting depth of the vegetation cover, which may be relatively shallow if considering e.g. moss dominated wetlands. Contrary, elevated weathering of pedogenic Si sources may as well contribute to the new formation “tertiary” Si fractions as the “weathering front” is progressively moving downward (Cornelis et al. 2014), thus influencing the flux of Si through the land-ocean continuum.

An aspect not discussed in the conceptual framework presented in Paper I only depict a simplified view of how climate change can come to alter terrestrial Si cycling. Nonetheless, the hope is that the results presented in this thesis will ultimately stimulate further research related to Si biogeochemistry in permafrost terrain and the impact of climate change. Indeed, the Arctic Ocean exemplifies an area of high productivity during the Arctic summer with populations of migrating birds, mammals and fish schools returning every year to take advantage of the short peak in high productivity (Lalli and Panons 1997), where Si availability plays a key role at the base of the food web.

Conclusions and future research prospects

The outcome of this thesis has enhanced our understanding of two yet relatively unexplored research fields; storage of ASi in permafrost terrain and the influence of a

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Figure 12. Conceptual scheme of factors determining permafrost thaw type and soil-water interactions (left panel), mobilization and transport of material released from thawing permafrost in aquatic ecosystems (center panel) and the resulting effects on aquatic ecosystems (right panel). The response of downstream aquatic ecosystems (e.g. foodwebs) to permafrost thaw depicted in the right panel can, in part, depend on how Si fluxes through the terrestrial landscape is influenced. Figure from Vonk et al. 2015.

Figure 13. Permafrost thaw feature at the northern foothills of Alaska. The stratified mound is formed due to aggravation of ground ice that pushes the top soil upwards.
microbial community on phytolith dissolution during plant litter degradation. Based on the discussion and three appended papers the main conclusions of this thesis, together with future research prospects, are summarized below:

- Vertical distribution of soil ASi concentrations in permafrost terrain was found to largely follow two patterns, the first being declining concentration with depth while the second represents increasing or maximal concentrations with depth (Paper I and III).

  The first case is commonly described by others (e.g. Bleeker et al. 2006) and shows that biological and pedogenic processes together govern vertical distribution of elements in soil. In the latter case, our results indicate that processes involved in vertical redistribution of ASi in permafrost terrain, including slope processes/solifluction in mountainous regions, cryoturbation and the potential precipitation of pedogenic ASi near the permafrost table as a result of repeated freeze-thaw cycles.

- Rather than being cycled through the soil-plant continuum or contributing to the leaching of DSi into the hydrosphere, ASi of biological origin can be preserved on a centennial to millennial time scales both in the permanently frozen ground as well as in the seasonally thawed active layer. In Paper I, this was particularly observed in bog peatlands of high centered ice-wedge polygons. Paper III showed that this can also occur in other land cover types than bog peatlands, such as fen peatlands and graminoid tundra.

- Combining the results of Paper I and III, we find ASi storage in Arctic permafrost soils to range widely between 1,030 – 94,300 kg SiO2 ha-1 depending on land cover type. This range corresponds to those generally found in the literature, with the exception of savannah’s having a considerably higher soil ASi reservoir (Melzer et al. 2010). Furthermore, Paper III illustrate that common patterns in 1998 ASi storage exist between similar land cover types dispersed across different geographical locations supporting the use of thematic classes for upscaling (e.g. vegetation).

- Through application of thematic upscaling, following vegetation and soil classification, a first estimate of total ASi storage (0 – 1 m) in circumpolar tundra is provided (Paper III). Depending on classification method, we provide an estimate of 219 ± 28 to 510 ± 59 Tmol Si, which correspond to 2 – 6 % of the current estimate of global ASi soil storage (Laruelle et al. 2009) while covering an area of 4 – 6 % of the global land surface. Hence, we cannot currently conclude that this soil ASi reservoir represents a hotspot in a global context, as shown for SOC storage.

- Furthermore, the upscaling results presented in Paper III show that most ASi is allocated to storage in the marine horizon, rather than to top organic soils. This is especially true for soils having thin organic surface horizons, such as for drier graminoid and shrub tundra. Among the investigated land cover types, peatlands generally have the largest relative storage of ASi allocated to top organic soils.

- As supported by microscopy and analysis of mineral dissolution slopes (MDS; Paper III), biogenically fixed ASi contribute majorly to the total ASi pool in top organic soils, while pedogenic Si fractions dominate in mineral soils (although biogenically derived ASi fractions are still present). Being that the majoritvity of total ASi storage is allocated, we have applied in studies of temperate soils (Barão et al. 2014, 2015; Vandevenne et al. 2015). This would be especially important if considering extending the estimate of total ASi storage beyond the 0 – 1 m depth range, since lithogenic/pedogenic Si fractions will dominate in mineral soils. Also, the estimate of ASi storage should be extended to also include the entire area of the northern circumpolar permafrost region (i.e. below the treeline), which represents 15 % of the global land area(!).

- Most ASi harbored within the circumpolar tundra soil reservoir (0 – 1 m) is allocated to the seasonally thawed active layer, rather than being perennially frozen. We estimate that at least 30 % is allocated to permafrost (Paper III), which upon thaw will become available for biogeochemical cycling.

- Hence, a conceptual framework for how climate change may alter Si biogeochemical cycling in Arctic permafrost terrain is provided. For instance, we hypothesize that climate change will lead to altered soil ASi storage and Si fluxes through the land-ocean continuum via alterations in hydrology and dominant vegetation caused by permafrost thaw. The sole purpose of the framework is to spur future research within this currently understudied field.

- In addition, the outcome of Paper II shows how Si release from phytoliths appears to be reduced in the presence of a live microbial community during plant litter decomposition. This result stands in sharp contrast to common anticipations and previous results reported in the literature showing no or slight enhancement of Si release during microbial litter decomposition. The contribution to improved understanding of terrestrial Si cycling provided by this thesis inevitably also raises a set of new questions to be answered. First, an obvious continuation is to further improve the estimate of total ASi reservoir in the northern circumpolar tundra region. An overarching goal is to collect more soil pedon data that are representative of the full range of land cover and soil types represented in the Arctic, while simultaneously having a broad geographical coverage.

- For this type of research just initiated, while compared to investigations of soil organic carbon storage (0 – 1 m) the latest circumpolar estimate is based on 1778 individual soil pedons (Haugaas et al. 2014). Moreover, to improve our understanding regarding the contribution of biogenically derived Si sources a different technique than the alkaline digestion method by DeMaster (1981) should be utilized where a distinction between biogenic and pedogenic Si fractions can be made. The continuous extraction of Si and Al in NaOH represents valuable approach, which have been applied in studies of temperate soils (Barão et al. 2014, 2015; Vandevenne et al. 2015). This would be especially important if considering extending the estimate of total ASi storage beyond the 0 – 1 m depth range, since lithogenic/ pedogenic Si fractions will dominate in mineral soils. Also, the estimate of ASi storage should be extended to also include the entire area of the northern circumpolar permafrost region (i.e. below the treeline), which represents 15 % of the global land area(!).

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Svensk sammanfattning

Inom forskningsområdet biogeokemi studerar man hur naturens olika grundämnen, såsom kol, kväve, fosfor och kisel ändrar form och transporterats genom landskapet för att via bäckar och vattendrag till slut nå havet. Tillsammans beskriver dessa olika processer, som sker på olika tidsskalor, från sekunder till flera miljoner år, ett grundämnes kretslopp (eller biogeokemiska cykler).

Grundämnet kisel (Si) är det näst vanligaste i jordens avsedda för att via bäckar och vattendrag genom landskapet. På vägen mot kust och hav tas en del av detta löst kisel upp av vegetation och av små mikroskopiska organismer, t.ex. kiselalger, som lever i jorden, för att bilda så kallat amorft kisel. När växter och kiselalger dör, ackumuleras detta amorfa kisel till olika grad i jorden där det kan bevaras i tusentals år. Sammanfattningsskriven innebär detta att biologiska processer på land kan reglera flödet av löst kisel till akvatiska ekosystem nedströms. Hur mycket löst kisel som när akvatiska ekosystem har stor betydelse för produktionen av kiselalger som utgör en av de vanligaste grupperna av växtplanktonet i sjöar och hav. Förändringar i flödet av löst kisel till akvatiska ekosystem kan därmed ha inverkan på näringsväsen i sjöar och hav. Många av människan orsakade processer, som t.ex. byggande av dammar för vattenkraft, kan minska flödet av löst kisel som när havet. Förändringar i landskapet, såsom vegetationsskifte och förändringar i hur vattnet rinner till följd av klimatförändringar, kan också påverka flödet av löst kisel till akvatiska miljöer.

I stort syntetiserar denna avhandling till att öka vår förståelse kring hur mycket amorft kisel som lagras i jord och hur det skiljer sig mellan olika landskapstyper, med speciellt fokus på Arktis permanent frusna jordar, det vill säga områden med permafrost. Inom detta område har det hittills saknats kunskap och det är ett viktigt förståelsekring om, speciellt då uppvärmingen av klimatet sker mycket snabbare i Arktis jämfört med i övriga världen. Dessutom belyser denna avhandling hur bakterier och svamp kan påverka upplösningen av det amorfa kisel som idag är lagrat i permafrost i rörelse, vilket kan leda till förändrade flöden av kisel till nedströms akvatiska miljöer.

I den andra delstudien undersökte jag hur mikrober, i form av bakterier och svampar, påverkar upplösningen av amorft kisel under nedbrytningen av organiskt material. Till detta experiment inkluderade vi växtmaterial med hög halt av amorft kisel, i frånvaro av eller tilltillt med levande mikrober. I motsats till vår hypotes, så kunde vi inte påvisa att upplösningshastigheternas av amorft kisel ökar i närvaro av levande bakterier. Istället såg vi det motsatta, det ville säga att levande bakterier minskar mängden kisel som kan frigöras. Vårt experiment tillåter dock inte några slutsatser gällande möjliga mekanismer som kan förklara detta, och det var heller inte huvudsakligt med studien. Detta kan betyda att levande bakterier kan påverka tillgängligheten av löst kisel, men detta måste testas vidare för att några större slutsatser ska kunna dras.

Den tredje och sista delstudien bygger vidare på de resultat vi erhöll i delstudie ett, detta genom att inkludera jordprover från fler områden i Arktis (Svalbard, Grönland och Sibirien) för analys av amorft kisel. Dessa resultat användes sedan för att uppskatta mängden amorft kisel som totalt finns lagrat (0 - 1 m) i marken i Arktis tundraregion. Vi uppskattar att det finns mellan 219 och 474 Tmol (T=terra, 10¹²) kisel vilket motsvarar 70 - 160 gånger mer kisel än det som uppskattas bindas utav växter årligen. Denna pol av amorft kisel kan komma att bli tillgänglig för det biogeokemiska kretsloppet när permafrosten tinar, vilket kan få konsekvenser (bra eller dåliga?) för akvatiska ekosystem nedströms.


Vidare påvisar vi att levande mikrober kan minska mängden kisel som frigörs under nedbrytning av kiselrits växtmaterial. Med tanke på att klimatet blir varmare med smältande permafrost till följd, utgör detta en huvudsaklig fråga för framtida undersökningar som även utöverbör förstå de processer som påverkar kretsloppet av kisel.