A study of factors controlling pH in Arctic tundra soils

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// Abstract
In Arctic tundra soils pH serves as an important parameter related to several biotic parameters such as, plant and microbial community composition, biodiversity, nutrient dynamics and productivity. Both abiotic and biotic factors, for instance, base saturation (BS) and plant nutrient uptake may exert a control on soil pH, while it is still unclear to what extent different factors can explain soil pH across different tundra vegetation types. The aim of this study was to investigate to what extent different abiotic and biotic factors influence soil pH in the humus layer across different tundra vegetation types. To do so, eight different tundra vegetation types of which four were underlaid by permafrost (Arctic Alaska) and four with no permafrost (Arctic Sweden) were studied in detail with regard to different properties affecting soil pH. I found that BS was the main factor controlling soil pH across the different vegetation types regardless if the soil was underlain by permafrost or not. Factors, such as, ionic strength or soil water content could not explain any overall pH variation and did only significantly affect the heath soils. Further, the uptake of the most abundant base cations (Ca^{2+}, Mg^{2+} and K^{+}) from meadow and heath vegetation revealed a high difference between plant functional groups within the same vegetation types. The higher dominance of slow growing woody species in heath vegetation which had a lower uptake corresponded with a lower BC content (especially (Ca^{2+}), pH and BS in the humus soil relative the meadow meanwhile the content of K^{+} was more than three times higher in heath. Overall, this study suggests that the degree of neutralization (base saturation) regulates pH either via the influence of bedrock and hydrogeochemistry and/or via plant traits that affects the uptake and turnover of base cations.

Key words: pH, Arctic tundra soils, base saturation, base cations, cation exchange capacity

Terms and abbreviations

ANC: Acid neutralization capacity
BC: Base cations
BNC: Basic neutralization capacity
BS: Base saturation
$CaCl_2$: Calcium chloride
CEC: Cation exchange capacity
OH^-: Hydroxide ion
LOI: Loss on ignition
pKa: Acid strength
SOM: Soil organic matter

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1.Introduction

pH variation in the Arctic tundra (Fig. 1) can be explained by factors within two completely different scales. The macroscopic scale (1) focusing on the characteristics of the landscape, such as soil properties, topography and biogeochemistry whereas the microscopic scale (2) is more related to the characteristics of the surface chemistry of soil minerals and the properties of the soil solution (Valentine and Binkley, 1992). If we start from a broad macroscopic perspective the physical and chemical weathering of bedrock might be one of the most obvious factors controlling the soil pH. The input of chemicals, ions and secondary minerals from the weathering consumes hydrogen ions (H^+) in the soil and can thus buffer and rise the soil alkalinity which will counteract from soil acidification (SLU, 2019). However, the rate of chemical weathering differs markedly between different minerals, for instance granite which consist of quarts and muscovite is highly weathering resistant while limestone which consists of calcite is not (Karlsson, 2018).

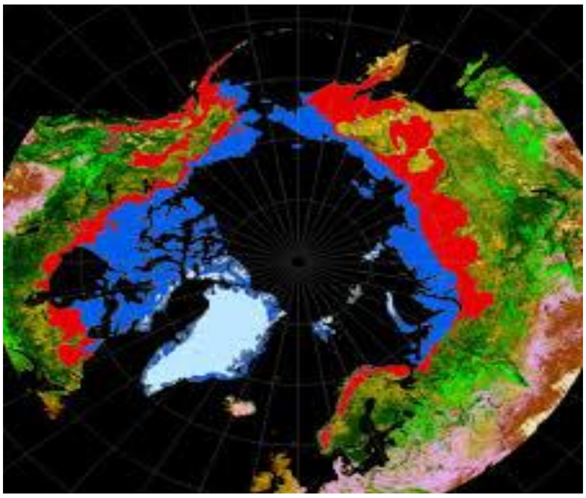

Fig 1. The distribution of tundra soils is represented by blue and red colour, (Olson *et al.*, 2001; Kaplan *et al.*, 2003) seen from a circumpolar map (Virtanen *et al.*, 2015).

Bedrock, hydrogeochemistry and topography are identified to be the main abiotic drivers causing local pH variation across different vegetation types in the landscape (Valentine and Binkley, 1992). In a previous Swedish study (Giesler *et al.*, 1998) the soil pH ranged nearly three units at a local productivity gradient in the boreal forest, from 3.5 in the groundwater recharge area to 6.4 in the ground discharge area. The vegetation differed markedly between these sites, from a pine forest with a field-layer dominated by dwarf shrubs in the groundwater recharge area to a spruce forest with a field layer dominated by tall herbs in the groundwater discharge area. Similar local pH variations have been found in the Arctic tundra of northern Scandinavia with pronounced pH differences between the two dominating vegetation types; heath and meadow (Björk *et al.*, 2007; Sundqvist *et al.*, 2011; Giesler *et al.*, 2012). Meadow type vegetation has overall a higher soil pH, N availability, biodiversity and is dominated by fast growing species such as herbaceous plants, graminoids and forbs whereas the heath has a lower soil pH, N availability and consists of more slow growing woody and evergreen species (Coleman *et al.,* 1983).

Seen from a micro scale perspective there are five important factors to consider which control the soil pH (Valentine and Binkley, 1992). Acid quantity (1); refers to the size and quantity of the undissociated acid complex or base neutralization capacity (BNC). The BNC differs markedly between different soils; clay has a relatively low charge which ranging from 50-1000 $mmol_c\ kg^{-1}$ whereas soil organic matter commonly varies between 1000-5000 $mmol_c\ kg^{-1}$ (Binkley and Fisher, 2019). A soil containing a larger acid complex has a greater potential to buffer against bases and can thus consume more alkalinity. The degree of neutralization (2) depends on what types of cations that are bound to the exchange complex of the negatively charged soil particles; mineral, soil colloid or soil organic matter (Valentine and Binkley, 1992). The most common acid cations are H^+, Fe^{2+}, Fe^{3+} and Al^{3+}, expressed as the exchangeable acidity (EA) whereas the most common base cations (BC) are; Ca^{2+}, K^+ Mg^{2+}, Mn^{2+} and Na^+ (Olofsson, 2016). A high proportion of acid cations relative BC results in an acidic soil with a low soil pH whereas the opposite proportions occur for an alkaline soil. The percentage ratio of BC binding to the soil exchange sites is an important parameter defined as the base saturation (BS) and is calculated as:

$$\text{Base saturation}=\frac{100^{*}\ \text{BC}\ (\text{Ca}^{2+},\ \text{Mg}^{2+},\ \text{Na}^{+}\text{and K}^{+})}{\text{Cation exchange capacity}}\ \text{(eq. 1)}$$

(Eriksson *et al.*, 2011) where the BS is expressed as the percentage BC in relation to the cation exchange capacity (CEC). Additionally, the BS has often a strong positively relation to the soil pH (Valentine and Binkley, 1992; Binkley and Fisher, 2019). The acid strength (3) associates to the acid dissociation constant (pK_a value) where strong acids which have a low pK_a will be nearly totally dissociated, therefore they have a high capacity to donate H^+ which results in a lower pH value relative to a weaker acid with a higher pK_a which won't dissociate to the same degree (Binkley and Fisher, 2019). The ionic strength (4) explains the concentration of ions in a solution. An altered ionic strength can, for instance results in two different scenarios: the soil pH could decrease when H^+ are displaced from the exchange site which could acidify the soil solution (Reuss and Johnson, 1986). But it could on the other hand decrease the activity of the electrolytes in the soil solution (Stumm and Morgan., 1981), which could rise the soil pH. A changing redox potential (5) due to either a reduction or an oxidation can also affect the soil pH, but this effect is often more cyclic, harder to predict and not as persistent compared to as the other factors (Valentine and Binkley, 1992).

However, biotic factors also play an important role and need to be considered when studying pH variation in soils. If the plant nutrient uptake mainly consists of BC or ammonium (NH_4^+) a depletion of the BS and a decline in the soil pH could be expected (Binkley *et al.*, 1989). Meanwhile an uptake of nitrate (NO_3^-) could result in the opposite situation, thus a rise in pH (Raven *et al.*, 1976; Marschner *et al.*, 1991). Previous studies (Binkley and Valentine, 1989) confirmed that different tree species could either lower or rise the soil pH as a result of the litter content, altered acid strength or nutrient uptake. Differences in soil pH will not only affect the vegetation but will also support different microbial communities (Fierer and Jackson, 2006). In a heath soil with a low pH, the nutrient cycling is slow and dominated by a fungi soil food web while in a more fertile meadow soil dominated by graminoids, herbaceous plants and forbs the vegetation will promote a bacterial based soil food web with a rapid cycling of nutrient and a high nutrient availability (Coleman *et al.*, 1983; Wardle, 2002). The high nutrient cycling in a fertile soil leads to a higher concentration of ammonium (NH_4^+) which is related to a higher soil pH (Sundqvist *et al.*, 2014).

Even though it is known that soil pH is controlled by several abiotic factors it is still relatively unknown to what extent biotic factors such as the nutrition of different plant functional groups and nutrients affect the soil pH, especially consider in the Arctic tundra (Valentine and Binkley, 1992). Understanding the factors controlling soil pH are crucial since it plays such an important role in the ecosystems and is related to plant and microbial community composition, plant species richness, nutrient dynamics and productivity (Giesler *et al.*, 1998; Gough *et al.*, 2000; Sundqvist *et al.*, 2011). It is thus of high importance to determine how the nutrition of different plant functional groups varies across different vegetation types in the Arctic tundra and its potential impact on the soil pH. Furthermore, it is vital to understand how different abiotic factors such as BS, ionic strength and buffer capacity individually affect the soil pH across different vegetation types.

To test to what extent BS can explain pH variation across tundra vegetation types from northern Alaska and Sweden I determined pH and BS across eight different tundra vegetation types encompassing both soils underlain by continuous permafrost and non-permafrost soils. I further reanalyzed published data on pH and BS from six different tundra vegetation types in northern Alaska (Valentine and Binkley, 1992) and compared their data with three different vegetation types from northern Sweden using their approach for pH and BS determinations. Additionally, since pH can be affected by short term variations in soil wetness and ionic strength, I conducted laboratory experiments to test how variations in the soil: solution ratio (e.g. proxy for water content) and ionic strength will affect soil pH in three tundra soils with different soil pH. I also conducted a storage experiment over a two-month period to test how soil heterotrophic activity can affect the soil pH. Finally, in order to test the potential effect of plant uptake and litter deposition on soil pH I determined the plant cation content in different functional plant types (stem/leaf's) in an adjacent heath and meadow site. Moreover, I compared the aboveground content in the plant biomass with the cation exchange capacity (CEC) in the soils from the two sites to evaluate to what extent uptake and litter deposition can affect soil pH on a short and long-term perspective.

Overall, I hypothesize that the BS of the soil CEC is the main explanatory variable for soil pH across surface soils in the tundra. I further hypothesize that water content and ionic strength cannot explain the spatial variability in pH that has been observed across different tundra vegetation types.

2. Methods

2.1 Study sites

2.1.1 Arctic Sweden

Fig 2. Map of the study sites in Arctic Sweden, the sampling locations are marked with a blue dot. Kärkevagge was the field location to the west, Miellajåkka in the center and Suorooaivi to the east.

The study was performed at three different locations (Fig. 2), all within 30 km distance from Abisko (68°35´N,18°83´E) in the subarctic tundra of northern Sweden: Kärkevagge (68°39´N, 18°31´E, 750-801 m above sea level, a.s.l.) Miellajåkka (68°30´N,18°91´E, 786-791 m a.s.l.) and Suorooaivi (68°29´N, 19°14´E, 796-805 m (a.s.l.). All sites were located above the treeline which is situated 500-600 m a.s.l. in the Abisko region (Sundqvist *et al.*, 2011). More specific site information is presented in table 1, Appendix 1. Permafrost in the area is sporadic (Brown *et al.*, 1998) and covers approximately 10-50% of the landscape but is more frequent above 880 m a.s.l. (Johansson *et al.*, 2006). Mean annual temperature and precipitation for Kärkevagge at 580 m a.s.l. is -1.8°C and 800-1100 mm (Klaminder *et al.*, 2009). Mean annual temperature and precipitation at Miellajåkka is -3.6°C and 350 mm (Lyon *et al.*, 2018), and -5.0°C and 230-290 mm (summer precipitation) at Suourojaure (Karlsson *et al.*, 2005; Sundqvist *et al.*, 2011).

In total four different vegetation types were studied; mesic meadow, mesic heath, dry heath and dryas heath (Fig. 3). Meadow type vegetation is dominated by vascular plants, graminoids, forbs and deciduous shrubs. The soil is characterized by a low C:N ratio, high pH and a low bacterial: fungi ratio (Björk *et al.*, 2007; Sundqvist *et al.*, 2011). The heath vegetation is characterized by woody evergreen species, such as, crowberry (*Empetrum hermaphroditium*), lingonberry (*Vaccinium vitis idaea*) and deciduous shrubs; Bog bilberry (*Vaccinium uliginosum*), bilberry (*Vaccininium myrtillus*) and dwarf birch (*Betula nana*). The other two vegetation types; dryas heath and dry heath were more uncommon and only sampled in Kärkevagge. Dryas heath is often found in soils influenced by calcareous bedrock (Eskelinen *et al.*, 2009) which create a vegetation dominated by forbs, graminoids and *Dryas octopetala* that dominates the vegetation type (Darmody *et al.*, 2004).

Dry heath vegetation is similar to mesic heath vegetation but with a slightly lower soil pH and situated on well-drained moraine ridges (Giesler *et al.,* 2012) or on top of boulders where the main source of water mainly comes from precipitation. The vegetation is dominated by evergreen shrubs, mosses and dwarf birch. The humus layers are relatively thin and rarely exceeds 10 cm in thickness (Sundqvist 2014). The geology shifted from a local influence of calcareous bedrocks in the eastern slope of Kärkevagge to schist in the valley of Kärkevagge. At Miellajåkka and Suorooaivi the bedrock included feldspathic, metasandstone and meta arkose bedrock to granitoid, svenitoid and metamorphic bedrock (SGU, 2019).

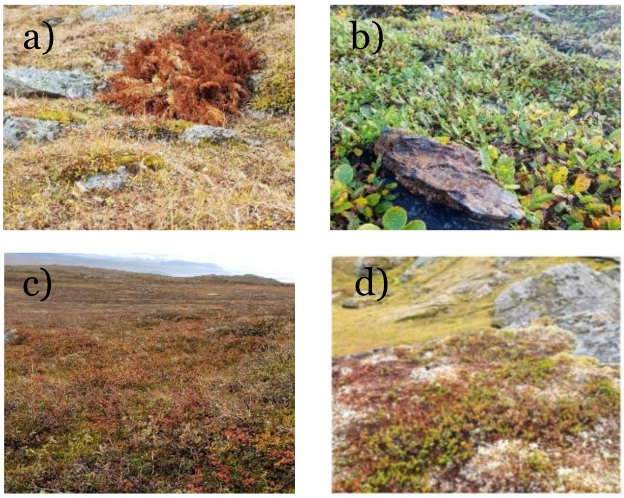

Fig 3. Characteristics of four different vegetation types (a, meadow vegetation, b, dryas heath, c, heath and d, dry heath) at the Swedish tundra in the Abisko region. Photo credit: Jacob Thomas.

2.1.2 Arctic Alaska

In Arctic Alaska, the study was performed (Fig. 4) at sites within 20 km from the Toolik research station (68°38´N, 149°36´W and 719 m a.s.l.) situated at the north slope of Brooks range in Alaska. In total four vegetation types were studied (Fig. 5); moist acidic tundra (MAT), non-acidic tundra (NAT), heath and wet sedge tundra (WST). Specific site coordinates are presented in table 2, Appendix 1. Mean annual temperature was -8°C and precipitation varies from 250-350 mm/year (Arctic long termed ecology research, 2019). The ground is underlaid by thick continuous permafrost (Hobbie and Gough, 2002).

The aboveground vegetation at MAT is dominated by dwarf shrubs (*Betula nana*), evergreen species, sphagnum mosses, forbs and sedges. In comparison to NAT which in the Toolik region was formed after the last deglaciation approximately 11.500-25.000 years ago at the Itkillik II surface (Hamilton, 2002) the MAT is much older and formed between 60.000-120.000 years ago (Hamilton, 2002) at the Itkillik I surface. MAT has a higher aboveground biomass but a lower soil pH. Even though MAT and NAT differ substantially in age, the soils in this region can be less than 2 km apart (Hobbie and Gough, 2002). The younger NAT has a lower abundance of *Betula nana* but has a higher dominance of sedges, mosses and forbs and has overall a higher species diversity (Hobbie and Gough, 2002). NAT is typically found both at terrains deglaciated relatively recently but also where there is a high input of loess and a high activity of cryoturbation (Hobbie and Gough, 2002). Heath vegetation in the Toolik region is similar to other Arctic areas, situated at well-drained ridges, and consists of evergreen woody species and deciduous shrubs (Britton, 1966). The WST in northern Alaska is dominated by vascular plants for instance cotton grass (*E. angustifolium*), carex species (*C. aquatilis*) and mosses which counts for approximately 20% of the plant biomass (Shaver and Chapin, 1991). The humus layer thickness was between 20-40 cm thick in all vegetation types except heath where the humus layer thickness was about 5 cm. The dominating bedrock types at the Toolik lake region are conglomerate and sandstone (Hamilton, 2002).

Fig 4. The state of Alaska with the Toolik field station marked (Toolik field station, 2019).

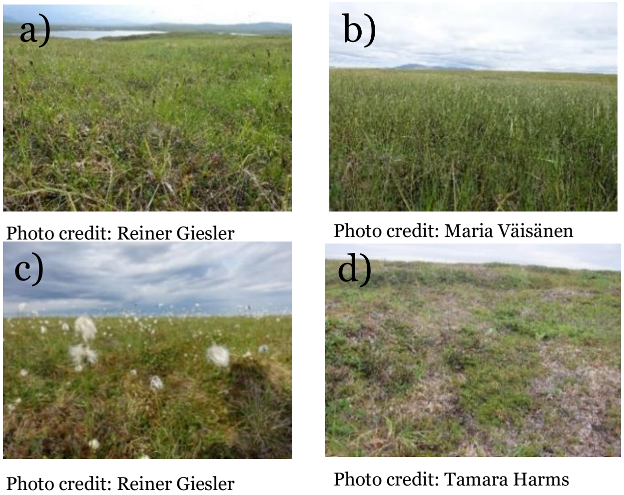

Fig 5. Characteristics of four Alaskan vegetations: a, non-acidic tundra, b, wet sedge tundra, c, moist acidic tundra and d, heath.

2.2 Soil sampling

Soil sampling in the Swedish tundra sites took place in the second half of September 2018, at the end of the growing season. The Alaska samples were collected at end of July 2018, at the peak of the growing season. At each site three humus layer samples were collected within a radius of about 10 m radius and bulked into one composite sample. The humus soil samples were collected with a soil corer (10 cm diameter) down to a maximum depth of 15 cm if possible and avoiding the mineral soil. All live plant material and coarse roots were removed in the field. The soil samples were stored at 4°C on arrival to the laboratory at the same day of sampling. The samples were homogenized by sieving (2 mm mesh size) within 4 days of sample collection. The homogenized samples were stored in freezers (-20°C) until further treatment.

2.3 Laboratory methods

2.3.1 Water content and loss on ignition

The frozen soil samples were thawed for approximately 60 hours in a refrigerator (6°C) before water content determinations. The water content was determined from oven-dried samples (24 hours, 105°C) and loss on ignition (LOI) on the dried samples in a muffle furnace (550°C, 5 hours).

2.3.2 Shaking time and reproducibility of pH measurements

To establish a shaking time for the pH measurements I conducted a shaking experiment (shaking table, 250 rpm) for two of the sites in Abisko (meadow Miellajåkka and meadow Suorooaivi) with 3 replicates per site. A series of 5-time intervals, 2, 4, 18, 24 and 48 hours was chosen, and pH analysed afterwards (pH/Ion meter S220, Mettler Toledo). Soil pH was measured after sedimentation for two hours in the upper part of the soil suspensions and this procedure was followed for all pH-measurements in this study. The experiment revealed a pH decline as a result of an increased shaking time. The effect was not linear, but most pronounced for the first 24 hours. Based on this experiment, 24 hours were set as an appropriate shaking time for this study. Additionally, to test the reproducibility I measured soil pH in five replicates for meadow Miellajåkka and meadow Suorooaivi. The test revealed that the variation within a sample was small with a maximum pH difference of 0.03 pH units for meadow Miellajåkka and 0.02 pH units for meadow Suorooaivi.

2.3.3 Determination of pH in water and 0.01 M $CaCl_2$

To determine soil pH in water and 0.01 M $CaCl_2$ in all tundra soils (n=24), I used fresh soil equivalent to 1 g of soil organic matter (SOM) and a soil solution ratio (s:s ratio) of 1:20 based on the SOM content. $CaCl_2$ is used since it is more resistance to the impact of soil electrolytes and overcomes the issues of seasonal pH variation in the soil relative to MQ-water and is thus a more accurate and consistent test (Minasny *et al.*, 2011).The s:s ratio of 1:20 was henceforth used for all the soil measurements in this study. Ultraclean milliQ water (MQ water) was added to a total volume of 20 ml which included already existing water in the fresh soil. After determination of pH in water 100µl of 2.04 M $CaCl_2$ was added to reach a final concentration of 0.01 M $CaCl_2$ in the soil extracts. The same procedure as above was thereafter followed before pH determination.

2.3.4 Extraction test

To determine the effective CEC, exchangeable acidity, BC and BS I used 1.0 M NH_4NO_3 as an extractant following the protocol in Giesler *et al.*, 1998. In total 27 samples were prepared (all 24 samples from the Swedish and Alaskan sites and 3 blanks). A total volume of 50 ml 1 M NH_4NO_3 solution was added to 1 g of SOM, shaken for 2 hours and thereafter filtered through a *00H* Munktell filter paper (Munktell Filter AB, Sweden). An aliquot of the filtrate was used for pH determination and the remaining filtrate was filtrated through a 0.45 µm syringe filter (Filtropur Sarstedt, Nümbrecht Germany) and acidified with concentrated HNO_3, (10 µl acid per 1 ml solution). The acidified filtrate was stored in a refrigerator (+4°C) until further analyses. The extracts were analysed on inductive coupled plasma – optical emissions spectrophotometer (ICP-OES; Varian Vista Ax.) for Al, Ca, Fe, K, Mg, Mn and Na. Further, the BC in the soil stock was calculated from the extraction data and first converted to mmolc/kg OM and then to mmolc SOM/m^2 by calculating the amount of OM in the humus layer per m^2.

2.3.5 Plant digestions

Plants functional types from meadow and heath vegetation were analysed for their cation content after microwave digestion. Biomass determinations were done for the following plant functional types: forbs, graminoids, evergreen shrubs (*E. hermaphroditum*), deciduous shrubs (*mainly V. myrtillus* and *B. nana)*. All the plants had been sampled in an earlier study (Krohn, 2017) at the same location as this study at Suorooaivi. Stems and leaves were treated separately for *E. hermaphroditum* and *B. nana*. The dried plants were ball milled (Retsch MM 301) before digestion. About 105 mg of the ball milled plant material was transferred to a 20 ml digestion vessel and 4 ml of concentrated HNO_3 (suprapur) and 1 ml H_2O_2 (suprapur) was added. The samples were digested at 185°C for 30 min and thereafter diluted to 10 mL with MQ water. The samples were thereafter analysed on an ICP-OES as above.

2.4 Experimental setup

2.4.1 Storage experiment

To test the effect of storage on soil pH I incubated soils from heath, meadow and dryas heath for two months in darkness at room temperature (approximately 21°C). A fresh weight equal to 3 g of SOM was transferred to 150 ml jars that were aerated on a weekly basis to check evaporation. If the evaporation exceeded more than 5% of the original sample weight MQ water was added to reach the same water contents relative the start of the incubation. After two months MQ water was added to a s:s ratio 1:20, thereafter shaken for 24 hours before pH was measured in the supernatant. The pH of the incubated samples was then compared with pH_{water}, to estimate the incubation effect. The overall idea with the incubation effect is to study the decomposition in SOM from different vegetation types and to analyse how pH varies after the incubation.

2.4.2 Ionic strength and buffer capacity

Ionic strength and buffer capacity were tested in soil samples from three vegetation types in Abisko (heath, meadow and dryas heath). I used a combination of three different s:s ratios and conductivities giving in total 9 treatments (Table 1). Sodium chloride (NaCl) was used as ionic medium for the 250 and 500 µS cm^{-1} solutions whereas MQ water was used for the solution with a conductivity of 0 µS cm^{-1}. The conductivity is an important property that reflecting the amount of salt in a soil solution which is crucial for the plant nutrient availability and the activity of microorganism (USDA, 2019). By increasing the conductivity in SOM from different vegetation types it is possible to estimate if the effect is pH dependent and to what extent the pH will differ.

Table 1. Design of ionic strength and buffer capacity experiment, 9 test per site, thus 81 samples in total.

S:S ratio - ^{1}g SOM	Conductivity 0 µS cm^{-1}	Conductivity 250 µS cm^{-1}	Conductivity 500 µS cm^{-1}
1:10	x	x	x
1:25	x	x	x
1:40	x	x	x

2.4.3 Titration of soil samples

A titration study was conducted on heath, meadow and dryas heath soils from the Abisko region to determine the buffer capacity and BS. I used heath and meadow soils from Suorooaivi and meadow and dryas heath soils from Kärkevagge; in total four soils covering an almost three pH unit difference. The titrations followed a somewhat modified protocol as described in (Valentine and Binkley, 1992). Here I used fresh soil equivalent to 1 g of SOM for the titrations. A series of 8-11 individual additions of either acid (11.95 M HCl) or base (10 M NaOH) was used to reach the two endpoints, pH 3.0 and 8.2. A s:s ratio of 1:20 and a shaking time of 2 hours was used before pH was determined. Ionic strength was kept constant during the whole experiment (34 mM NaCl), similar as in Binkley and Valentine, 1992). The pH values were plotted against the added amounts of acid or base (expressed as mmol g^{-1} dw) and the titration curves were used to determine the acid and base neutralizing capacity, (ANC and BNC, respectively). The ANC is calculated by the amount of H^+ that has been added in the solutions to reach pH 3.0, while BNC is instead the amount of OH^- to reach pH 8.2. When ANC and BNC are determined BS can be calculated as follows:

$$BS = ANC/(ANC + BNC) \quad \text{(eq. 2)}$$

The results of the titration study were then compared with the six different Alaskan tundra vegetation types described in Valentina and Binkley (1992); tussock tundra, dry heath, shrub lupine tundra, e*quisetum*, wet sedge tundra (WST), and willow. For comparison, I recalculated the ANC and BNC values in Valentine and Binkley (1992) to mmol g^{-1} dw since they are given in on an area basis (mmol m^{-2} dw). To do so I used their published data on bulk density and the thickness of the soil layers that they sampled (Valentine and Binkley; 1992).

2.4.4 Theory and calculations

To describe the relationship between pH and the BS, I used the extended Henderson-Hasselbalch equation (Katchalsky and Spitnik, 1947). The relationship is described as:

$$pH = pK_a^{app} + n \log([A]/[HA]) \quad \text{(eq. 3)}$$

where the pK_a^{app} is the apparent acidity constant, A^- is the dissociated organic acids and (HA) is the protonated acids. The term n is an empirically estimated constant (cf. Stevenson, 1982).

For soils, A^- corresponds to the part of the CEC that is balanced by BC whereas the protonated organic acids (HA) correspond to exchange sites binding to acid cations, EA (Giesler *et al.*, 1998). Thus, the quotient A^-/HA can be rewritten as BS/(1-BS) and the linear relationship between pH and BS described as;

$$pH=pK_a^{app} + n \log (BS/(1-BS)) \text{ (eq. 4)}$$

2.5 Statistics

For statistical comparison between the eight different vegetation types and the plant content of BC in different functionals groups, one-way analysis of variance (ANOVA) was used. Multiple comparisons in variance analyses were performed with Tukey's HSD test, while Students pair t-test was used to study the incubation effect. All statistical analyses were performed in R Studio Version 3.5.2 (www.rstudio.com/products/rstudio). Statistical significance refers to the 0.05 level unless otherwise stated.

3. Results

3.1 pH, CEC, EA and BC across tundra vegetation types

The mean pH (pH_{water}) of the humus soil for the eight different tundra vegetation types differed significantly (One-way ANOVA, $p<0.001$); the average pH ranging from 4.3-7.2 across the different vegetation types (Fig. 6). The lowest soil pH was found in the Abisko heath whereas the highest was in the dryas heath in Abisko. The four Alaskan vegetation types had overall a smaller pH variation and ranged from 4.7-6.5 as compared to the Abisko vegetation types. The lowest pH for the Alaskan sites was found in the MAT whereas the highest was in the NAT. The pH_{water} and pH_{CaCl_2} were positively linearly related ($R^2=0.93$, $p<0.001$) where pH_{CaCl_2} gave a similar distribution across the different vegetation types (Table 3, Appendix 1).

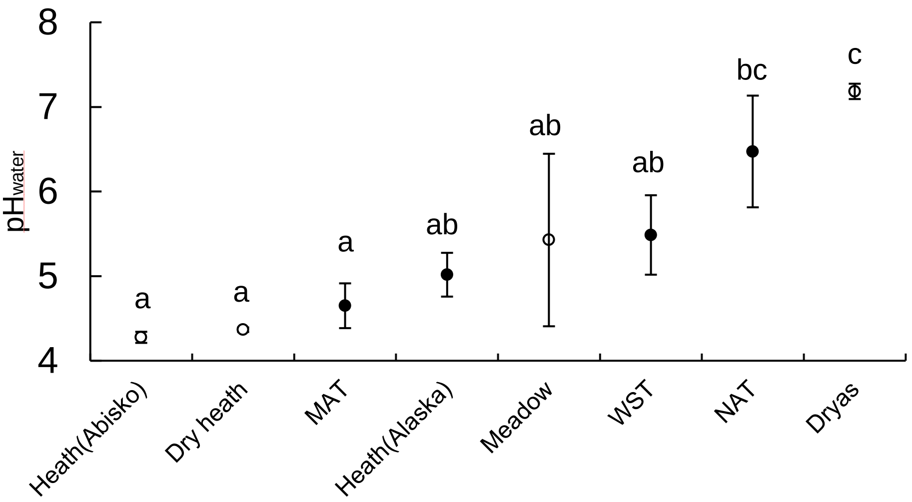

Fig 6. Mean pH_{water} across eight tundra vegetation types in Sweden (non-filled circle) and Alaska (filled circle). The error bars denote the 95% confidence interval. The difference between the marked letters denotes significant difference at $p<0.05$, (Tukey's HSD test).

The CEC ranged from 484-1674 mmolc kg^{-1} SOM (Table 2) and was highest in dryas heath and lowest in WST. Most of the cations that bind to the negatively charged exchange sites in dryas heath are BC (1673 mmolc kg^{-1} SOM) whereas less than 1 mmolc kg^{-1} SOM consist of H^+ and Al^{3+}. Dry heath which had the lowest BC, 120 mmolc kg^{-1} SOM had instead the highest EA, 606 mmolc kg^{-1} SOM. The mean proportions of the different BC for all vegetation types ranged from 73.8% Ca^{2+}, 15.2% Mg^{2+}, 7.7% K^+, 2.1% Mn^{2+} and 1.2% Na^+, but the proportions differed markedly between different vegetation types (Fig. 7).

Table 2. BC, H^+ and Al^{3+} (EA), CEC and BS for the eight Arctic vegetation types. Values are mean ± 95 % confidence interval.

Vegetation types	BC	EA (mmolc kg^{-1} SOM)	CEC	BS (%)
Dryas heath	1673 ± 105	1 ± 0.2	1674 ± 105	100 ± 0.01
Dry heath	120 ± 31	606 ± 36	726 ± 64	16 ± 0.3
Heath (Abisko)	231 ± 20	583 ± 227	814 ± 243	31 ± 0.71
Heath (Alaska)	509 ± 97	163 ± 70	673 ± 65	75 ± 0.11
MAT	419 ± 34	285 ± 108	703 ± 82	61 ± 0.11
Meadow	580 ± 517	359 ± 282	939 ± 271	53 ± 0.35
NAT	1041 ± 323	15 ± 21	1056 ± 302	98 ± 0.03
WST	405 ± 123	79 ± 65	484 ± 58	82 ± 0.17

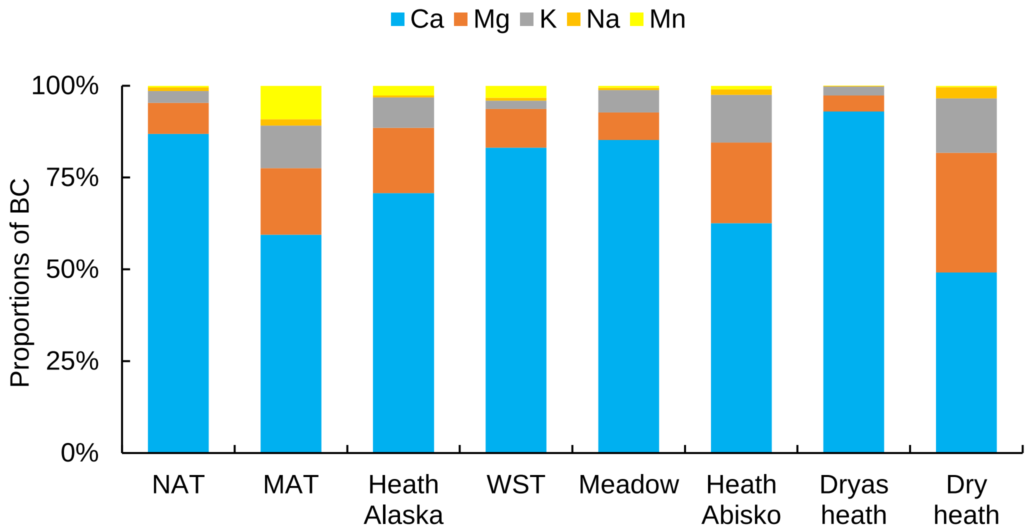

Fig 7. The mean proportions (%) for the five BC (Ca^{2+}, Mg^{2+}, K^+, Na^+ and Mn^{2+}) in the eight different tundra vegetation types.

3.2 The relationship between pH and base saturation

The relationship between pH and log (BS/(1-BS)) across the eight tundra vegetation types resulted in a strong positive linear relationship where log (BS/(1-BS) explained 96% of the pH variation (Fig. 8). The BS ranged from 16-99% and was lowest in the dry heath and highest for dryas heath. The four Alaskan samples had a smaller variation, ranging from 61-98%, lowest in MAT and highest in NAT. The Alaskan heath had overall a higher pH and BS as compared to the heath in Abisko, 5.02 and 75% (heath, Alaska) and 4.28 and 31% (heath, Abisko). In meadow in Abisko there was a large variation in pH and BS between the three sites where the meadow Kärkevagge had a substantially higher pH value as compared to the two other sites. Except for the meadow soils in Abisko the other vegetation types had smaller site variation and thus relatively similar pH and BS values.

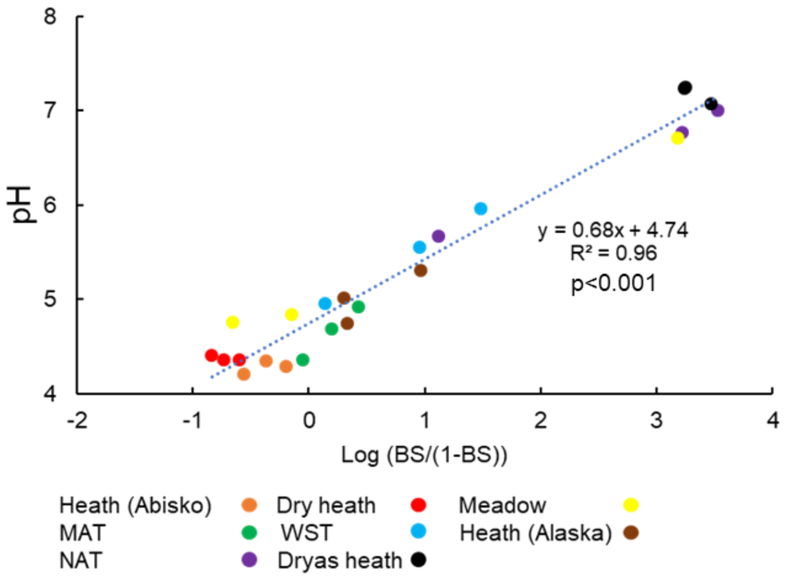

Fig 8. Relation between pH and Log (BS)/(1-BS)) across tundra vegetation types. Notice, two of the dryas heath sites had the same pH and BS and therefore overlap.

3.3 Acid/base neutralizing capacity across different tundra vegetations

pH and BS from the titration study (Fig. 9) revealed a highly positive linear relation where BS explains 93% of the pH variation, the same positive linear relation also occurs when using the extended Henderson-Hasselbalch equation and transforming BS to log (BS/(1-BS)) (Fig. 1, Appendix 1). The samples with the lowest BS did also have the lowest pH while the opposite condition occurred for the samples with highest BS. BS ranged from 12-95% (Table 3), lowest in heath from Suorooaivi and highest in dryas heath. ANC (pH 3) varied from 0.09-0.55 mmolc g^{-1}dw (Fig. 2, Appendix 1) lowest in meadow Miellajåkka and highest at meadow Kärkevagge whereas BNC (pH 8.2) ranged from 0.03 mmolc g^{-1}dw in dryas heath 1 to 1.04 mmolc g^{-1}dw in heath Suorooaivi. The BS for the Alaska samples varied from 42-95% lowest at heath and highest at willow which had the same rate as dryas heath 1. ANC varied from 0.16-1.38 mmolc g^{-1}dw, again lowest for heath but highest for *equisetum* while BNC ranged from 0.04-0.32 mmolc g^{-1}dw, lowest at willow and highest in tussock tundra.

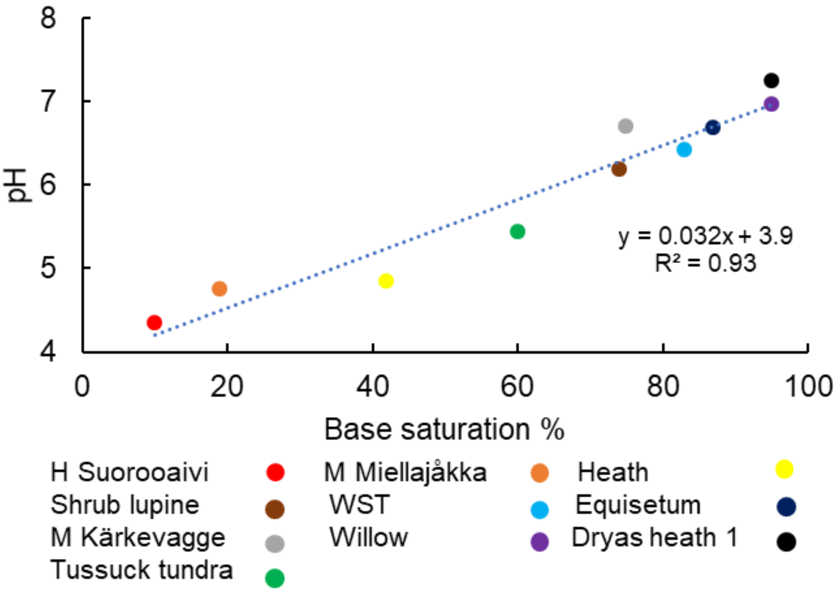

Fig 9. The relation of pH and BS for 10 different samples, four from the Swedish tundra and six from the Alaskan tundra.

Table 3. ANC, BNC and BS across 10 different tundra vegetation types. Values are mean ± 95 % confidence interval.

Vegetation types	ANC (pH 3)	BNC (pH 8.2)
	(mmolc g^{-1} dw)	
Dryas heath 1	0.52	0.03
Equisetum	1.38	0.21
Heath (Alaska)	0.16	0.21
H Suorooaivi	0.14	1.04
M Kärkevagge	0.55	0.19
M Miellajåkka	0.09	0.39
Shrub lupine	0.57	0.20
Tussock tundra	0.49	0.32
Willow	0.71	0.04
WST	1.12	0.23

3.4 Effects of ionic strength, buffer capacity and storage

The effect of ionic strength (0.01M$CaCl_2$) was highly pH-related (Fig. 10) and strongest for the vegetation types with lowest pH (heath Abisko and dry heath) while the effect declined with increasing soil pH and had practically no effect for dryas heath and NAT. When instead combining both ionic strength and buffer capacity (Fig. 11) the samples with MQ water solutions (0 µS cm^{-1}) had the highest pH regardless of vegetation types, whereas the pH decreased with increasing conductivity (250 µS cm^{-1} and 500 µS cm^{-1}. A changing buffer capacity (s:s 1:10-1:40) increased the pH, but again the effect differed between the vegetation types. The effect of ionic strength and buffer capacity was strongest for the heath vegetation and statistically significant ($p=0.025$ for ionic strength and $p=0.01$ for the buffer capacity, Tukey's HSD). In meadow and dryas heath neither ionic strength nor buffer capacity were statistically significant; the p values >0.09 in all cases. The storage effect after two months of incubation was only statistically significant for dryas heath which resulted in a lower pH (-0.22, $p=0.046$, student t-test) whereas there was no tendency of a pH change in either heath or meadow (Table 4, Appendix 1).

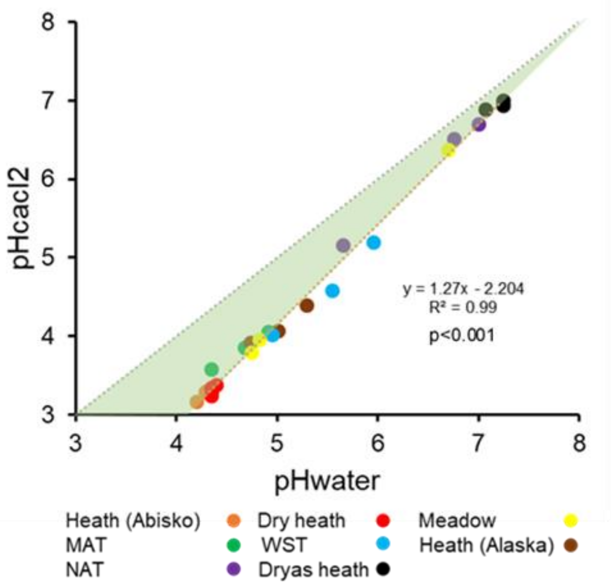

Fig 10. Relation between pH_{CaCl_2} and pH_{water} for the 24 tundra samples from the eight different vegetation types, the transparent field illustrates the ionic strength effect of 0.01M $CaCl_2$.

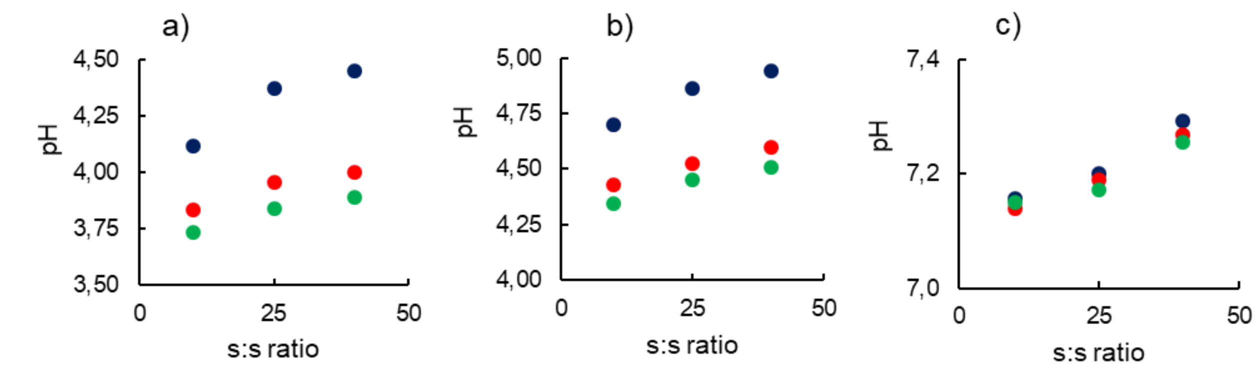

Fig 11. The effect of different conductivities; 0 µS cm^{-1}(blue dots), 250 µS cm^{-1} (red dots) and 500 µS cm^{-1} (green dots) and s:s ratio (1:10, 1:25 and 1:40 for heath (a), meadow (b) and dryas heath vegetation(c). The x-axis represents s:s ratio (1:10-1:50) and y-axis the soil pH.

3.5 Plant and soil stocks of base cations

In the heath, the amount of Ca^{2+} and Mg^{2+} (Fig. 12) were highest in deciduous stem (34.4 and 12.7 mmolc m^2, respectively) while evergreen stem instead had the highest amount of K^+ (22.9 mmolc m^2) but lowest Ca^{2+} and Mg^{2+} (0.4 and 0.2 mmolc m^2). In the meadow, graminoids had the highest Ca^{2+}, Mg^{2+} and K^+ content (33.2, 18.6 and 48.8 mmolc m^2 whereas deciduous shrub had the lowest (8.1, 1.6 and 4.4 mmolc m^2, respectively). The graminoids, which were found at both vegetation sites had a significantly higher content of BC in meadow relative to the heath site ($p=0.0289$, One-way ANOVA), the biomass of the different plant functional types in heath and meadow are illustrated in Fig. 3, Appendix 1.

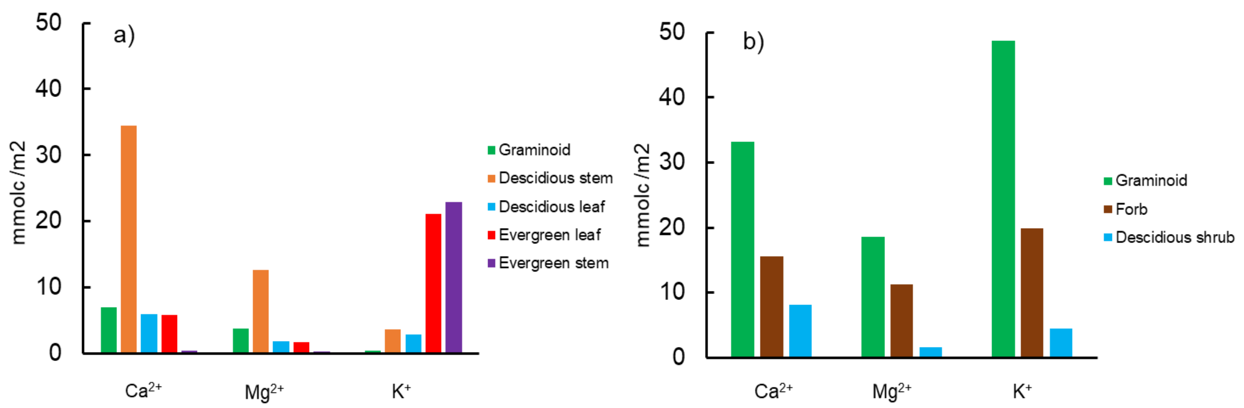

Fig 12. Plant contents of BC (Ca^{2+}, Mg^{2+} and K^+) for five different plant groups in heath Suorooaivi (a) and three plant groups in meadow Suorooaivi (b).

When comparing the total soil stock by summing all the BC (Ca^{2+}, K^+ Mg^{2+}, Mn^{2+} and Na^+) in the humus layer (Table 4) the total concentration was higher in meadow (1068 mmolc SOM/m^2) than in heath (722 mmolc SOM/m^2). The majority of the BC in meadow consists of Ca^{2+} with a soil stock more than twice as high than in heath (906 mmolc SOM/m^2 relative to 439 mmolc SOM/m^2). Except for Ca^{2+}, all the other BC were higher in heath (Mn^{2+} below the detection limit in meadow). When instead analysing the total plant content by summing all functional groups the BC concentration is higher in heath (153 mmolc m^2) and correspond to 21% of the soil stock relative 119 mmolc m^2 and 11% in meadow. The plant content of Ca^{2+}, Mg^{2+} and Mn^{2+} were higher in heath compared to the meadow while K^+ and Na^+ were higher in meadow as compared to the heath. In the meadow the plant content of K^+ and Na^+ exceeded the soil stock whereas the plant content of Mn^{2+} in heath exceeded the soil stock there.

Table 4. Contents of BC (mmolc SOM/m^2) in the soil stock and in the plant for 1 m^2 for heath and meadow in Suorooaivi. The values in the bracket denotes the percentage ratio between plant content/soil stock. Notice, since there was no data for soil stock Mn^{2+} in meadow this ratio couldn't be calculated.

BC	Heath Soil stock content	Meadow Soil stock content	Heath Plant content	Meadow Plant content
	mmolc SOM/m^2		mmolc m^2	
Ca^{2+}	439	906	60 (14)	28 (3)
K^+	125	38	57 (46)	73 (191)
Mg^{2+}	139	124	20 (15)	16 (13)
Mn^{2+}	11	0	15 (136)	1 (-)
Na^+	10	0.2	0.4 (4)	0.8 (400)
Total	722	1068	153 (21)	119 (11)

4.Discussion

4.1 The relationship between pH and base saturation

The first hypothesis was to test to what extent BS can explain pH variation across different tundra vegetation types and the results revealed that BS represent the main factor controlling the soil pH. The strong positive linear relation between BS and pH was not only observed in the extraction data for the eight different vegetation types from Arctic Sweden and Alaska (Fig. 8) but is also confirmed by the titration study between the Abisko samples and the comparison with Valentines and Binkleys Alaskan data from 1992 (Fig. 9). Regardless of method (extraction or titration) or if the variable was present as BS or log(BS/(1-BS)) (extended H and H equation) the results clearly demonstrate that BS is the main factor controlling soil pH in the Arctic tundra which not only confirms my first hypothesis but the results are also in line with findings from previous studies (Beerly and Wilding, 1971; Binkley *et al.,* 1989). Noticeable is that the highly significant positive relationship between pH and BS remains regardless if the soil was underlain by permafrost or not. Even though melting of permafrost can alter the hydrology and change the vegetation and soil surface pH (Camill,1999) the findings from this study suggest that the same positive relation between pH and BS most likely will persist in the soil even if the permafrost is melting. An earlier study from the boreal forest of northern Sweden (Giesler *et al.*, 1998) also showed a high positive linear relation between pH and BS which implies that even if the treeline would advance in some parts of the tundra region as a consequence of climate change (Van Bogaert *et al.*, 2011) the same positive relation between pH and BS could persist in the future. Even though the high relation between pH and BS in the Arctic seems to exist in a future climate there might be some situations where the soil pH will change. An altering hydrology, for instance an increase in the groundwater flow could result in a higher input of base cations and thus rise the soil pH and BS (Herndon *et al.*, 2019), whereas a lower soil pH could be caused by an accumulation of acid cations (Al and Fe).

Further, the CEC differed markedly between different vegetation types. Dryas heath and NAT had both the highest pH, BS, CEC and a high proportion of Ca^{2+} meanwhile the sites with lowest BS (dry heath and heath Abisko) instead had highest EA and proportion of K^+, but lowest BC and pH. This implies that the proportion of K^+ increases with decreasing BS which could be a result of a lower K^+ nutrition (Jobbágy and Jackson, 2001) from the vegetation in heath and dry heath. The high Ca^{2+} level in the dryas heath are most likely a result of weathering from calcareous dolomite bedrock located at the slopes of Kärkevagge (Eskelinen *et al.,* 2009). Whereas NAT is a relatively young soil situated at recently deglaciated areas which are affected by inputs of loess (Hobbie and Gough., 2002) and have a fine-grained soil which is associated with a high Ca^{2+} concentration (Walker *et al.*, 2001). The high proportion of Ca^{2+} in dryas heath and NAT further implies that Ca^{2+} is the main cation contributing to a high BS, CEC and a high pH which presumably is an effect of weathering of calcareous bedrock (Thorn *et al.*, 2001).

4.2 Ionic strength/buffer capacity and storage effect

While BS controls most of the variation in soil pH, neither ionic strength nor the buffer capacity can explain the landscape pH variation. The ionic strength and buffer capacity were only pronounced in the heath vegetation whereas there was barely any effect for the other vegetation types, which confirm my second hypothesis. The results reveal that with an increasing conductivity the soil pH decreases which is a relation also seen in previous studies (Critchfield and Johnson, 1958). When increasing the conductivity by adding salt to a solution it causes cations exchange and displace H^+ from the exchange site of the soil colloids. When H^+ ions are exchanged it induces to a pH decrease in the soil solution (Bolan and Kandaswamy, 2005). But the effect was highly pH dependent and most pronounced in soil solutions with a low pH and buffer capacity whereas the effect was barely noticeable for soil solutions with a neutral pH as the buffer capacity was substantially higher. In the nature the salt effect is an example of a situation when the conductivity increases as a result of deposition from salt (for instance NaCl) and occurs frequently in coastal areas due to the sea salt or in areas where there is an accumulation of nitrate or acid deposition. These effects commonly result in a pH decrease of 0.1-0.4 units. (Binkley and Fisher, 2019). But the salt effect is greater in soils with a low conductivity whereas it has a smaller impact in soils with a high conductivity (Richter *et al.,* 1988). When instead lowering the buffer capacity by increasing the s:s ratio the pH tends to increase which was seen for all vegetation types even though the effect was only statistically significant for heath vegetation, which had the lowest pH. The response can be expected since an increased s:s ratio by adding MQ water which has a neutral pH will cause dilution for an acid solution and thus rise the pH (Reeves and Liebig, 2016).

The declining soil pH which only was statistically significant in dryas heath after two months of incubation reveals that microbial activity most likely affects the soil pH since all the phototrophs are excluded. Organic matter which is degraded by microbes can result in nitrification, which is a process where first ammonium oxidizes to nitrite ($2NH_4^+ + 3O_2$ $2NO_2^-$ + $4H^+ + 2H_2O$), which is an acidified process lowering the soil pH (De Boer and Kowalchuk, 2001). The second step of the nitrification; ($2NO_2^- + O_2 \rightarrow 2NO_3^-$) is a neutral process where nitrite oxidize to nitrate. The declining pH after the incubation is likely a result of the first step of the nitrification process. The pH decline was however, only significant for dryas heath whereas there was no such tendency for the other vegetation types. This implies that the nitrification rate in soils is pH dependent and causes a greater pH effect in soils with a neutral pH relative acidic soils which complies with findings from previous studies (Dancer *et al.*, 1973; Sörensen and Jörgensen, 1993). Another process caused by the long incubation is microbial decarboxylation (Rengel, 2003) where the carboxylic acids (COOH) are converted to CO_2 and H_2O. This process consumes protons (H^+) and will thus increase the soil pH. However, since the incubation overall caused a pH decrease in the majority of the samples it can be assumed that the nitrification effect was more pronounced than the decarboxylation process.

4.3 Plant contents and soil stock contents

The total soil stock of BC was substantially higher than in the plant content in both heath (five times greater) and meadow (ten times greater). In the heath there is a situation where a relatively high proportion of the plant BC are bound to the biomass of evergreen and deciduous stems which results in both a small uptake and a small and prolonged litter degradation, therefore a slow return of the BC back to the soil stock (Coleman *et al.,* 1983). This could induce to a scenario where the heath soil gets more acidified over time if not the BC are supplied from the weathering, which is a slow process. In the meadow on the other hand the situation is the opposite with fast degrading plants containing a high concentration of BC. The annual litterfall will thus be greater and contribute to a higher pH and BC content in the humus layer, but it is difficult to estimate to what degree it controls the soil pH. What seems to be of higher importance is the hydrology. Considering that meadow soils are highly distributed in depressions and valleys (Darmody *et al.*, 2004) surrounded by heath it can be assumed that the bedrock is the same, what differs is the supply of alkalinity transported by the groundwater, which is much greater in meadow soil relative the heath (Herndon *et al*, 2019). This could imply that abiotic factors (topography and hydrogeochemistry) are the main drivers causing a high BC and pH in the humus layer in the meadow, the result are thus in line with findings from previous studies (Valentine and Binkley, 1992).

Further, the total plant content/soil stock ratio of BC shows that the total plant content makes up a nearly twice as high percentage proportion of BC in the soil stock in heath compared to meadow (Table 4). This could indicate that the nutrition from vegetation might cause a higher impact to the BS and soil pH in heath relative to meadow, but again it is difficult to estimate to what extent, therefore more studies would be needed to confirm this. Additionally, one needs to take into consideration the nutrition of other elements for instance nitrogen (N) which has been considered as one of the most limited nutrients in subarctic ecosystems (Aerts and Chapin, 1999) where an uptake of NH_4^+ tends to lower the soil pH meanwhile NO_3^- could result in the opposite situation and thus rise the soil pH (Raven *et al.*, 1976; Marschner *et al.*, 1991). The lower plant content/soil content ratio in meadow implies that there is a higher abundance of BC there, especially Ca^{2+} which results in a higher pH, CEC, and BS (Björk *et al.*, 2007; Eskelinen *et al.*, 2009). Focusing on the individual contribution from each plant functional group in heath and meadow the majority of them had a higher content of BC (Ca^{2+}, K^+ and Mg^{2+}) in meadow relative heath, especially graminoids which were present in both vegetation types which most likely is a results of the higher abundance of BC in meadow.

Overall, more studies are needed to clarify to what extent plants from different vegetation types affect the soil pH. A suggestion of a future study could be conducted by studying the annual uptake of base cations in different plant functional groups and determine the litterfall. Studying the content of N (NO_3^- and NH_4^+) would also be crucial in order to estimate the N uptake from different plant functional groups and compare it with the N soil stock in the humus layer. Additionally, one could also include more vegetation types and use samples from different elevations across an altitude gradient.

4.4 Conclusion

This study aimed to investigate which are the main drivers affecting soil pH in the Arctic region of northern Sweden and Alaska. BS which had a high positively significant relation to pH was determined as the primary factor affecting the soil pH. Moreover, the relationship was confirmed regardless of method (extraction or titration) or if the soil was underlain by permafrost or not. A high BS also corresponded with a high CEC and a high proportion of Ca^{2+}. Other factors as ionic strength, buffer capacity and storage effect tended to affect the soil pH, but the effect was pH dependent and mostly not statistically significant. Further, when studying the plant content of BC in heath and meadow and comparing it with the total BC in the soil stock, the total plant content/soil stock ratio was nearly twice as high in heath vegetation compared to meadow, which reveals that the nutrition from heath vegetation might have a greater impact on pH and BS compared to meadow. However, a long-term study including the annual uptake and litterfall, more elements (for instance nitrogen) and more replicates across an altitude gradient would be needed to confirm this. Finally, seen from a broader perspective this report suggests that the highly positively linear relation between BS and pH could persist even if climate change occurs as the relation seems to be universal and has been confirmed in other landscapes. Therefore, although it is known that an altering hydrology can change the soil pH the results from this study indicates that there are scenarios where climate change might not have such a large effect on the soil pH.

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Appendix 1

Table 1. Geographical site information (coordinates and altitude) for the 12 Swedish samples from the Abisko region.

Vegetation types	Coordinates WGS84 N	E	Altitude (m a.s.l.)
Dryas 1	68.395973	18.333972	751
Dryas 2	68.395711	18.334632	766
Dryas 3	68.395129	18.335670	773
Dry heath 1	68.395019	18.322427	755
Dry heath 2	68.396222	18.318151	774
Dry heath 3	68.396622	18.315517	801
Heath K	68.398319	18.329375	750
Heath M	68.302730	18.916851	791
Heath S	68.292594	19.149090	796
Meadow K	68.397397	18.327308	750
Meadow M	68.302368	18.915409	786
Meadow S	68.292035	19.148021	805

Table 2. Geographical site information for the 12 Alaskan samples, notice that one reference point (WT1 REF) also was taken.

Vegetation types	Coordinates WGS84 N	W
Heath 1	68.644974	149.416849
Heath 2	68.618603	149.327004
Heath 3	68.616803	149.327000
MAT WT 1	68.651998	149.436542
MAT WT 4	68.643045	149.392269
MAT WT 5	68.622207	149.345603
NAT 1	68.516926	149.475809
NAT 2	68.643254	149.599439
NAT 3	68.690371	149.058869
WST A	68.653348	149.309330
WST B	68.647810	149.318619
WST C	68.644127	149.399397
WT1 REF	68.653970	149.439894

Table 3. pH_{water} and pH_{CaCl_2} for all the Alaskan and Abisko sites, respectively.

Vegetation types	pH_{water}	pH_{CaCl_2}
Dryas heath 1	7.24	7
Dryas heath 2	7.24	6.94
Dryas heath 3	7.07	6.89
Dry heath 1	4.35	3.24
Dry heath 2	4.35	3.33
Dry heath 3	4.4	3.38
Heath 1 (Alaska)	4.74	3.91
Heath 2 (Alaska)	5.01	4.06
Heath 3 (Alaska)	5.3	4.39
Heath Kärkevagge	4.2	3.16
Heath Miellajåkka	4.29	3.29
Heath Suorooaivi	4.34	3.27
MAT 1	4.92	4.05
MAT 2	4.68	3.85
MAT 3	4.35	3.58
Meadow Kärkevagge	6.7	6.37
Meadow Miellajåkka	4.75	3.79
Meadow Suorooaivi	4.83	3.95
NAT 1	5.66	5.15
NAT 2	7	6.7
NAT 3	6.76	6.51
WST 1	5.55	4.58
WST 2	5.96	5.19
WST 3	4.95	4.01

Table 4. pH difference after two months of incubation for the sites in Abisko except dry heath.

Vegetation	pH before incubation	pH after incubation	pH difference
Dryas heath 1	7.24	7.01	-0.23
Dryas heath 2	7.24	6.92	-0.32
Dryas heath 3	7.07	6.97	-0.1
H Kärkevagge	4.2	3.96	-0.24
H Miellajåkka	4.29	4.16	-0.13
H Suorooaivi	4.34	4.26	-0.08
M Kärkevagge	6.7	6.46	-0.24
M Miellajåkka	4.75	4.74	-0.01
M Sourooaivi	4.83	5.01	0.18

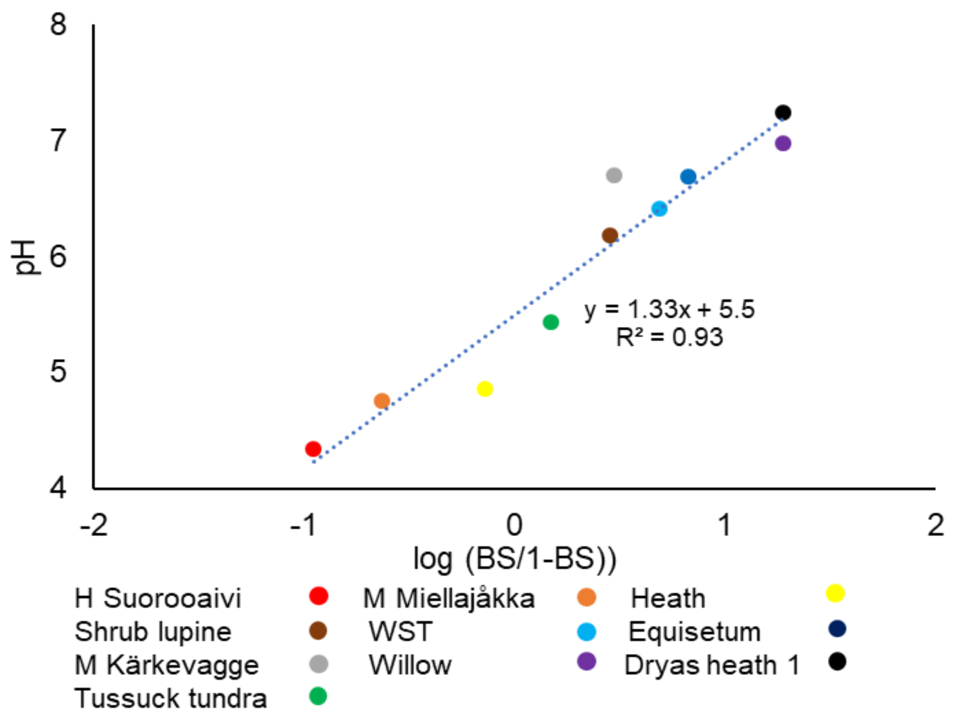

Fig 1. The relationship between pH and log (BS/(1-BS) for 10 different tundra samples, six from Alaska and four from Sweden.

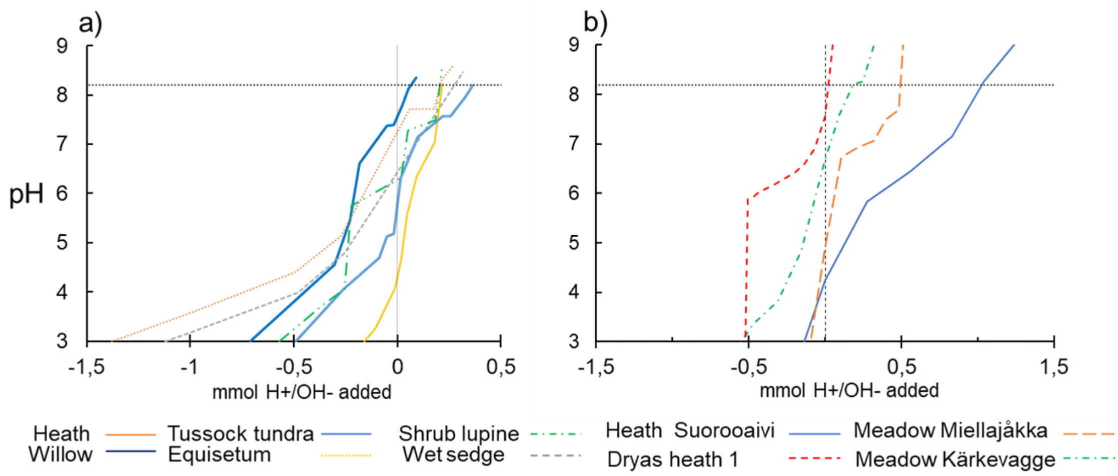

Fig 2. Comparison of acid/base neutralisation capacity between six different vegetation types from the Alaskan tundra (a) and three from the Abisko region (b), notice that two samples are from the meadow type vegetation but from different sites. Negative values on the x-axis define an addition of (H^+) and positive values (OH^-).

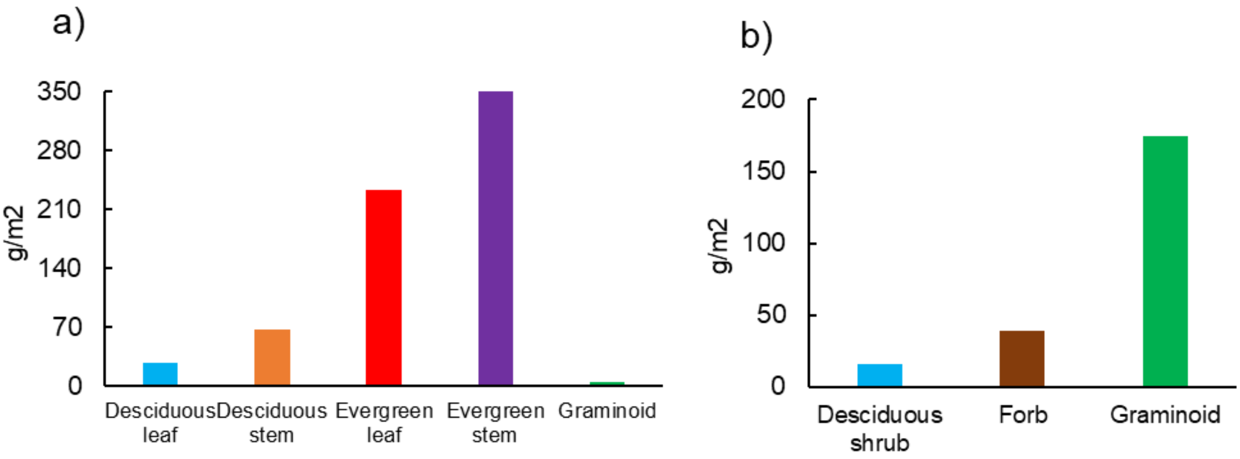

Fig 3. The biomass (g/m²) of different plant functional types in heath (a) and meadow (b).

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