Nitrogen and Phosphorus Dynamics Across an Elevational Gradient in a Swedish Subarctic Tundra

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Cover: The view from Mt Suorooaivi, 20 km south-east of Abisko, northern Sweden
(photo: T. Logan)

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Abstract

Rising temperatures associated with global climate change are likely to drive major shifts in plant and soil properties as well as plant-soil linkages that govern key ecosystem processes in subarctic tundra. However, the tundra landscape is not homogenous, but instead consists of a mosaic of vegetation types which differ greatly in vegetation characteristics and soil fertility. Two types of vegetation commonly co-occur across broad areas of the Fennoscandian subarctic tundra, i.e., heath vegetation dominated by slow-growing dwarf-shrubs and present on N-poor acidic soils, and meadow vegetation, dominated by herbaceous species and present in shallow depressions on more fertile soils. Temperature declines predictably with elevation, and therefore gradients of elevation are powerful natural experiments for studying the effects of long-term changes in temperature on ecosystem properties and processes. This thesis uses an elevational gradient to understand how temperature influences nitrogen (N) and phosphorus (P) dynamics, and how this is associated with shifts in plant and soil microbial properties, for both tundra heath and meadow vegetation. The overall results of this thesis showed that increasing elevation led to an increase in plant limitation of P relative to N, and a general decline in soil P availability but had highly variable effects of soil N availability. Such variation in soil N and P responses to elevation were often associated with the specific characteristics of the plant species that dominated at the different elevations. Importantly, the effect of elevation on aboveground and belowground characteristics differed greatly between tundra heath and meadow vegetation, leading to vastly different responses of litter decomposability, soil microbial properties, soil nutrient cycling, and ultimately N and P availability to elevation among these two vegetation types. In total these findings highlight how shifts in elevation and associated changes in abiotic factors such as temperature not only have contrasting effects on the availability of N and P, but also have fundamentally different influences on N and P cycling for two functionally contrasting vegetation types that co-occur in the same tundra landscape.

Keywords: plant functional leaf traits, litter quality, phenolic compounds, decomposition, mineralization, immobilization, fungal:bacterial ratio, microbial biomass, carbon

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Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Sundqvist, M.K., Giesler, R., Graae, B.J., Wallander, H., Fogelberg, E., & Wardle, D.A. (2011). Interactive effects of vegetation type and elevation on aboveground and belowground properties in a subarctic tundra. *Oikos* 120, 128-142.

II Sundqvist, M.K., Giesler, R. & Wardle, D.A. Within- and across-species responses of plant traits and litter decomposition to elevation across contrasting vegetation types in a subarctic tundra. *Submitted manuscript.*

III Sundqvist, M.K., Olofsson, E., Giesler, R., Gundale, M.J. & Wardle, D.A. Plant polyphenolics across an elevational gradient: does subarctic vegetation support plant polyphenolic allocation theory? *Manuscript.*

IV Sundqvist, M.K., Wardle, D.A., Vincent, A. & Giesler, R. Contrasting nitrogen and phosphorus dynamics across an elevational gradient for subarctic tundra heath and meadow vegetation. *Manuscript*.

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1 Introduction

1.1 Tundra

Tundra ecosystems are found on all continents. Although they differ in climate, seasonal length, and seasonal variation in temperature, factors they have in common are low mean air temperatures during the growing season, and the general absence of trees (Billings 1973, Wielgolaski 1997). The term "mountainous alpine tundra" generally applies to vegetation which occurs at high altitudes above the climatic treeline regardless of climatic zone (Nagy & Grabherr 2009), while Arctic and Antarctic tundra is found at high latitudes beyond the altitudinal or latitudinal treeline (Wielgolaski 1997). Thus, the term "subarctic tundra" generally refers to the high elevation tundra that occurs above the tree line at latitudes between 50° and 70° but lower than the latitudinal limit for tree growth. Mean annual temperatures are low in most tundra ecosystems (<0 °C) (Wiegolaski 1997). Therefore, above- and belowground process rates such as plant growth and decomposition are generally slow compared to other ecosystems, and this is especially true for high latitudinal tundra (Stark 2007). These factors in combination have often resulted in long-term accumulation of soil organic matter. A significant portion of the tundra ecosystem carbon (C) pool is therefore found belowground (Melillo et al. 1990), and so alpine and arctic soils contain a large proportion of the global soil C (Post et al. 1982). While direct human disturbances are relatively low in most tundra ecosystems compared to other biomes (Hannah et al. 1995), there is increasing evidence that tundras are highly responsive to global climate change (e.g. ACIA 2005, IPCC 2007a,b, Wookey et al. 2009). Therefore, a considerable amount of research in these ecosystems is focused on understanding how changes in climate change drivers such as temperature, precipitation and nitrogen deposition might influence key ecosystem properties and processes that control tundra ecosystem functioning.

1.1.1 Nitrogen and Phosphorus and the heterogeneity of tundra

Nitrogen (N) and phosphorous (P) are essential nutrients limiting primary production worldwide (Aerts & Chapin 2000). Nitrogen is commonly described as the main limiting nutrient for plant growth in tundra ecosystems (Tamm 1991, Vitousek & Howarth 1991, Aerts & Chapin 2000). However, co-limitation of N and P, or limitation of P, is increasingly recognized as of importance in some tundra areas (e.g. Seastedt & Vaccaro 2001, Soudzilovskaia et al. 2005, Giesler et al. 2011). The relative importance of P versus N in limiting plant productivity can vary across tundra ecosystems due to differences in a range of factors such as N deposition, parent material, soil age (time since glaciation), pH, and concentrations of soluble aluminium (Al), iron (Fe) and calcium (Ca) (Walker & Syers 1976, Brady & Weil 2008, Weintraub 2011). Furthermore, studies from both alpine and arctic tundra show that the limitation of N and/or P for plant productivity can also vary both among individual plant species and tundra vegetation types (e.g. Seastedt & Vaccaro 2001, Giesler et al. 2011, Weintraub 2011). Due to topographic differences that govern wind exposure, snow-depth and local scale hydrology, tundra landscapes commonly consist of a mosaic of different vegetation types which vary in soil moisture and fertility (Billings 1973, Björk et al. 2007). In alpine tundra, increased P limitation in the more fertile and moist areas can be associated with high N deposition and redistribution of N accumulated in snow via melt-water to depressions in the landscape (Weintraub 2011). In ecosystems with lower N deposition such as the Swedish boreal forest (Dentener et al. 2006), influxes of water carrying Fe, Al and Ca ions from surrounding higher areas to down-slope areas, can result not only in increased pH and N availability (Giesler et al. 1998), but also in increased P fixation and thus reduced availability of P for plants and microbes (Giesler et al. 2002, Giesler et al. 2005). Recent evidence suggests that a similar pattern is found at higher latitudes in subarctic tundra (Björk et al. 2007, Giesler et al. 2011, Figure 1). Further, the availability of N and P is regulated by microbial decomposition and mineralization of organic matter, which releases soluble organic N forms, and mineral N and P forms available to plants (Chapin et al. 1978, Stark 2007, Weintraub 2011). As the rates of these processes are controlled by temperature, moisture and the quality of the organic material, changes in climate are likely to greatly influence nutrient availability for tundra plants. Although an increasing amount of evidence suggest that N versus P limitation varies among tundra plant communities, relatively little is known about how the availability and the relative importance of these nutrients in limiting plant growth will be influenced by long-term changes in climate.

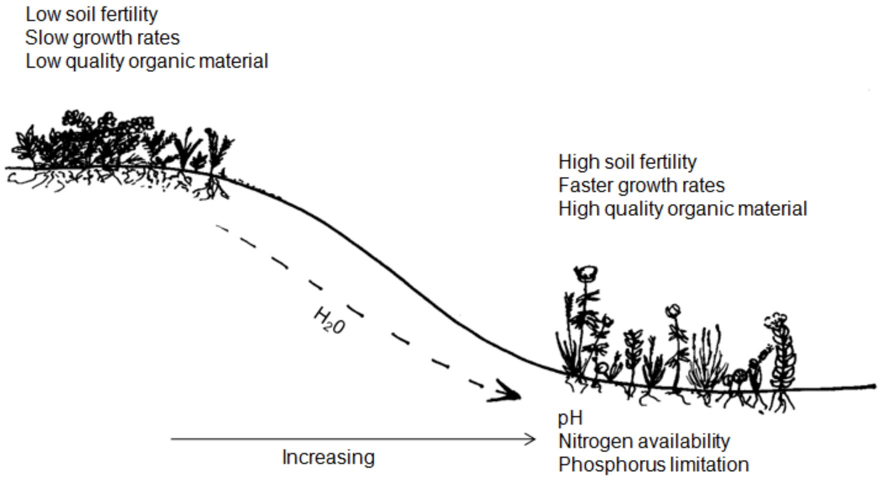

Figure 1. Simplified illustration of how local scale topography can shape the tundra landscape. Water movement from higher placed sites (left) to shallow depressions (right) is commonly associated with an increase in soil pH and nitrogen availability, and a shift from plant communities dominated by slow-growing plants towards those dominated by faster growing species. In high latitude ecosystems, the movement of water can also be associated with an influx of base cations, Al and Fe; the latter two can form stable complexes with P which leads to an increase in the limitation of P relative to N for plant productivity.

1.1.2 Aboveground and belowground linkages in the tundra landscape

It is well known that interactions between the above- and belowground components of terrestrial communities can greatly influence ecosystem properties and processes (Wardle 2002, Wardle et al. 2004). There are several pathways by which different tundra plant species and functional groups can influence nutrient cycling and soil nutrient availability, for example through differences in nutrient uptake, root exudation and the amount and quality of litter that they produce (e.g. Hobbie 1996, Steltzer & Bowman 1998, Meier et al. 2008). Further, an increasing body of literature shows that plants which dominate in more fertile sites often have a set of traits associated with faster growth, high nutrient acquisition, and high litter quality (e.g., high specific leaf area (SLA) and leaf tissue N-content, and low amounts of phenolic compounds), relative to plants which dominate in less fertile sites and produce more recalcitrant organic material (Wardle 2002, Díaz et al. 2004, Freschet et al. 2010). Evidence from both tundra and other ecosystems have shown that plants adapted to high soil fertility and which produce high quality litter are commonly associated with a more bacterial-based microbial community, compared to those which grow on less fertile soils where the relative dominance of fungi is often higher (Coleman et al. 1983, van der Heijden et al. 2008, Eskelinen et al. 2009). Fungal-based decomposer subsystems generally promote more conservative cycling of nutrients compared to bacterial-based decomposer subsystems (Wardle et al. 2004, Bardgett 2005, Högberg et al. 2006). Given that soil fertility can shift over short distances in tundra (Figure 1), plant communities which support a more bacterial-based versus those which support a more fungal-based microbial community commonly co-occur as a mosaic in the same tundra landscape (Björk et al. 2007, Eskelinen et al. 2009). Therefore, different tundra vegetation types are likely to differ in terms of several aboveground and belowground properties and in also in how the linkages and feedbacks between them influence soil nutrient cycling processes (Figure 2).

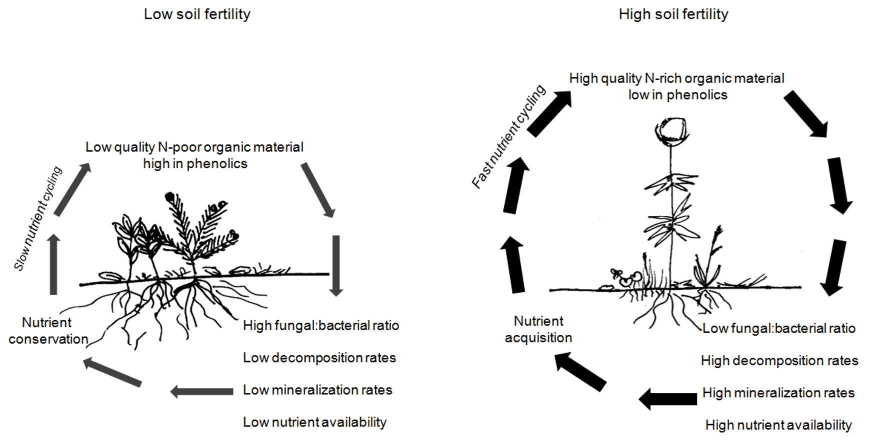

Figure 2. Slow-growing plants which dominate on poor soils generally produce low quality organic matter, which decomposes slowly, and supports a more fungal-based microbial community that promotes conservative nutrient cycling (left). Plants which dominate on more fertile soils often produce higher quality N-rich organic matter that decomposes rapidly, and supports a more bacterial-based microbial community which promotes faster nutrient cycling (right).

Increased plant growth and shifts in plant community composition have already been documented in several tundra regions as a result of climate change (e.g. Chapin et al. 1995, Hill & Henry 2011, Wookey et al. 2009). Such shifts are expected to have large consequences for tundra soil microbial community composition and nutrient cycling processes and therefore tundra ecosystem functioning (Hobbie 1996, Wookey et al. 2009). There is still little information about how long-term influences of abiotic factors affect linkages between plant- and microbial communities for contrasting tundra vegetation types, although such information is essential for predicting how future shifts in climate will influence the functioning of tundra ecosystems.

1.2 Elevational gradients

Natural gradients act as useful tools in the study of large scale, long-term ecosystem responses to alterations in abiotic factors (Diamond 1986) and are a valuable complement to shorter-term experimental studies (Dunne et al. 2004). Gradients of topography (Giblin et al. 1991) and snow depth (Seastedt & Vaccaro 2001, Liator et al. 2005) have provided much information on how variation in such abiotic factors can influence the composition of plant communities and nutrient cycling processes in tundra ecosystems. As temperature declines predictably with elevation, gradients of elevation are powerful natural experiments for enabling investigation of the long-term impacts of changes in temperature (Fukami & Wardle 2005, Körner 2007). As such, studies along elevational gradients have provided valuable information on how ecosystem properties and processes respond to temperature, and associated climatic factors that change with elevation, for a wide range of ecosystems (e.g. Körner 1989, Dunne et al. 2004, Loomis et al. 2006, Normand et al. 2009, van de Weg et al. 2009). While vegetation characteristics such as plant biomass and productivity are well known to decline with increasing elevation in association with shifts in plant community composition (Wiegolaski 1997, Körner 2007, Jansson et al. 2008, Nagy & Grabherr 2009), our understanding of how microbial communties respond to elevation is limited. Some recent studies have pointed to associated changes in soil microbial community structure with increasing elevation (Bryant et al. 2008, Groffman et al. 2009, Djukic et al. 2010), but others have not (Zhao et al. 2009). In addition, while some have found an increase in elevation (and thus a decline in temperature) to be associated with a decline in soil microbial activity, nutrient mineralization and nitrogen availability (Schinner 1982, Sveinbjörnsson et al. 1995, Hart & Perry 1999, Sjögersten & Wookey 2002), others have revealed contrasting results (Griffiths et al. 2009). Further, there is still a limited understanding of how an increase in elevation simultaneously influences above- and belowground communities and ecosystem processes in treeless tundra ecosystems, although such an approach can provide information on the long-term effect of temperature on tundra ecosystem functioning. Therefore, the main objective of this thesis is to gain further understanding of how elevation and associated shifts in temperature influence N and P dynamics, for two contrasting vegetation types which co-occur in a subarctic tundra, by integrating studies of above- and belowground components through which these nutrients cycle.

2 Study system

2.1 Fennoscandian tundra

The Fennoscandian tundra ranges from southern Norway to the northernmost parts of Finland and Norway and thus comprises both alpine tundra south of the polar circle and subarctic tundra in the north. The main parts of the Fennoscandian Mountains were covered by ice during periods of the Pleistocene, and the ice retreat started ~10000 years ago (Wielgolaski 1997). Local-scale topography plays an important role in shaping the Fennoscandian tundra landscape which consists of a mosaic of different vegetation types (Weih 1998, Björk et al. 2007). Vegetation dominated by slower-growing dwarf-shrub species generally occurs on soils with low pH, and low N availability, while vegetation dominated by faster-growing herbaceous species generally occurs in shallow depressions and/or on less acidic soils with higher N availability (Björk et al. 2007, Eskelinen et al. 2009, Figure 1). Recent findings also suggest that local scale topography and hydrology is an important mechanism driving patterns of N versus P limitation in Fennoscandian subarctic tundra (Figure 1), and that the relative importance of P limitation is higher in vegetation which dominates on the more fertile soils (Giesler et al. 2011). Nitrogen deposition over this region is low relative to for high elevation tundra at lower latitudes in Europe, North America and Asia (Dentener et al. 2006). Temperature is a highly limiting factor for primary production in the Fennoscandian tundra (Wiegolaski 1997), and annual air temperature is projected to increase by 3-5 °C within the coming century in these ecosystems (ACIA 2005, IPCC 2007a,b). The Fennoscandian mountains contains large gradients of elevation (and thus temperature), and plant biomass and production generally decline with increasing elevation (Wiegolaski 1997, Jansson et al. 2008); these gradients provide excellent opportunities for exploring how changes in temperature influence key ecosystem properties and processes in tundra.

2.2 Study site

This thesis is based on studies from an elevational gradient which ranges from 500 m to 1000 m along the north-east facing side of Mt Suorooaivi (1193 m), located 20 km south-east of Abisko, northern Sweden (68°21'N, 18°49'E) (Figure 3).

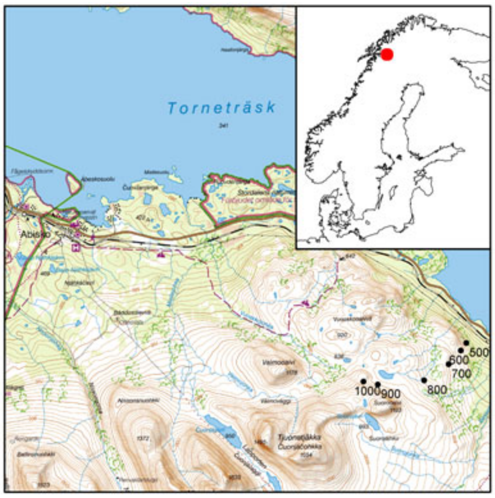

Figure 3. Location of the elevational gradient which is the study system for this thesis. The location of the six sites used in this thesis, ranging from 500 to 1000 m, is marked with filled black circles (lower right corner). The closest town is Abisko, which is located north-west from the study site, and situated in the northernmost part of Sweden (red filled circle). Figure made by I. Tjerngren. © Lantmäteriet, I2011/0032.

The bedrock consists of salic igneous rocks and quartic and phyllitic hard schists. The mean annual precipitation in the area, measured at the Abisko Scientific Research Station (1913-2000), is 310 mm with the highest mean monthly precipitation in July (51 mm) and the lowest in April (12 mm) (Kohler et al. 2006). The treeline at the study site, formed by mountain birch, *Betula pubescens* ssp. *czerepanovii*, is situated at 500 – 600 m (Figure 4). Two types of vegetation, heath and meadow, occur in a mosaic throughout the study area. The meadow vegetation, commonly found in shallow depressions, is characterized by graminoids such as *Anthoxanthum odoratum* and *Festuca ovina*, forbs such as *Saussurea alpina*, *Trollius europaeus* and *Viola biflora*, and sedges such as *Carex bigelowii*. The heath vegetation is characterized by *Betula nana* and ericaceous dwarf-shrubs such as *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Empetrum hermaphroditum* (Figure 4). In September 2007, four 2 x 2 m plots were placed in both heath and meadow vegetation at every 100 m along the gradient, which yielded a total of 48 plots. At 500 m the plots are situated in open mountain-birch forest while those at 600 m are located immediately above the forest line, and plots at 700-1000 m are devoid of trees. The soils on both vegetation types are Leptosols, but with only a thin organic layer on the meadow soils above the treeline.

Figure 4. Left; Photograph taken at 800 m in early June 2009 from the heath towards the meadow (marked with a yellow circle) with the top of Mt Suorooaivi (1193 m) in the background. Middle; Meadow vegetation with flowering *Trollius europaeus* (higher statured yellow flowers) and *Viola biflora*, (lower-statured yellow flowers), and the treeline formed by mountain birch (*Betula pubescens* ssp. *czerepanovii,* 550 m) in the background. Right; common heath species, *Empetrum hermaphroditum*, *Vaccinium uliginosum*, *Vaccinium vitis-idaea* (upper), and *Betula nana* and *Phyllodoce caerulea* (lower). Photographs by M. Sundqvist (left) and G. Blume-Werry.

The daily mean air temperature during most of the growing season 2008 and 2009 is given in Figure 5. The monthly mean air temperature in July 2008 at 400, 700 and 1000 m along the slope was 13.3 °C, 12.4 °C and 10.6 °C, respectively. The corresponding temperatures in August 2008 were 9.6 °C, 8.2 °C and 6.3 °C. In July 2009, the monthly mean air temperature at 500 m, 700 m and 1000 m were 13.2 °C, 12.3 °C and 10.1 °C, respectively, and the corresponding temperatures in August 2009 were 12.1 °C, 11.8 °C, and 9.9 °C.

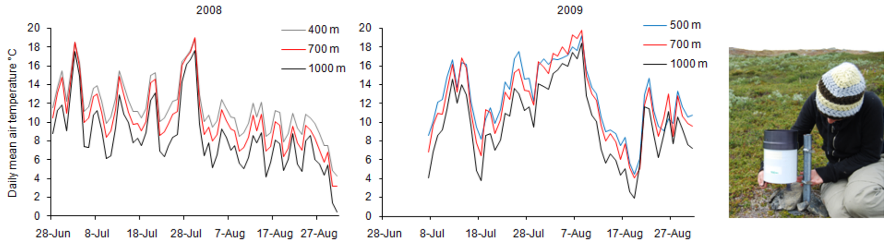

Figure 5. Daily mean air temperature from June 28 to August 31 2008 at 400, 700 and 1000 m and, from June 28 to August 31 2009 at 500, 700, and 1000 m in the vicinity of the studied plots. Photograph of installation of the temperature logger at 700 m in June 2009 (right). In photo: Gesche Blume-Werry. (Photograph by M. Sundqvist)

Elevational gradients of this type serve as powerful natural experiments to test for the effects of temperature and associated climatic variables that change with elevation on ecosystem processes, provided that other abiotic factors do not co-vary with elevation (Fukami and Wardle 2005, Körner 2007). Summer precipitation at Mt Suorooaivi ranges between 230 and 290 mm and has been found to vary little across elevations in the proximity of the studied area (Karlsson et al. 2005), in accordance with measurements of precipitation during the summer of 2008 at 700 m and 1000 m at the study site (Figure 6). While measurements of winter precipitation and snow depth have not been conducted across the study site, observations in late May and early June 2008-2010 point to a later snow melt in the meadow compared to in the heath vegetation, and at elevations just above the forest line compared to at higher elevations. The amount, distribution and duration of snow are well recognized as important drivers of vegetation patterns and ecosystem processes across topographic gradients in tundra, for example through influencing freeze-thaw events, plant and soil processes (Fisk et al. 1998, Buckeridge & Grogan 2010), nutrient availability (Bowman 1992, Weintraub 2011), plant-herbivore interactions (Torp et al. 2010) and pathogen outbreaks (Olofsson et al. 2011). Therefore, to minimize differences in snow depth and snow prolongation across the study site, plots which were still under snow in early June 2008 were excluded prior to sampling and replaced with new plots on snow free ground. Further, plots were selected with the same aspect (northeast facing), parent material and similar slopes (between 4° and 8°), so climate is the principal abiotic factor that varies with elevation across this study site.

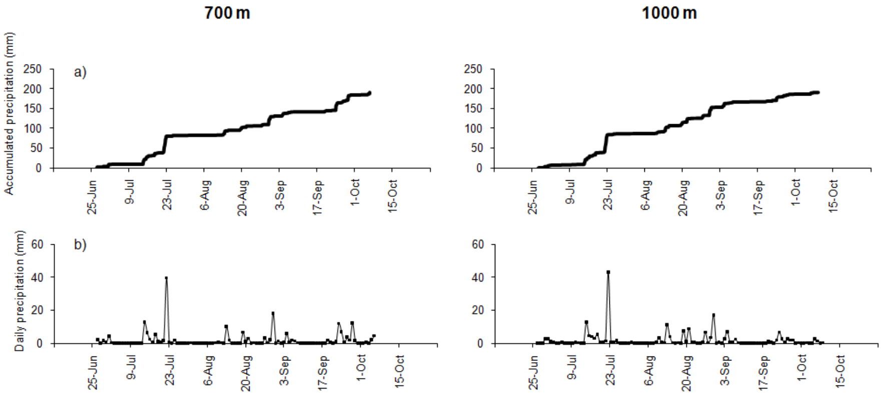

Figure 6. a) Accumulated precipitation (mm), and b) daily precipitation (mm), during the summer 2008, at 700 and 1000 m at the study site.

2.3 Objectives

The overarching goal of this thesis is to study the effect of elevation on N and P dynamics for two contrasting vegetation types which co-occur in the Swedish subarctic tundra. Paper I explores how aboveground factors such as plant community composition change with elevation and how this is associated with shifts in N and P availability and microbial community composition. Paper II focuses on the effect of elevation on leaf and litter traits and how this influences litter quality and litter decomposability. Paper III explores the effect of elevation on leaf litter phenolic properties. In both Papers II and III, shifts in leaf and litter traits with elevation are explored both within- and across-species, as well as at the community (whole-plot) level. Paper IV explores how soil nutrient dynamics and microbial biomass is influenced by elevation.

Specifically, the questions for each paper are:

I. Does N and P availability decline with an increase in elevation, and how is this linked to shifts in the above- and belowground community for heath and meadow vegetation in subarctic tundra?
II. Is an increase in elevation associated with a shift in leaf and litter traits towards those traits which are associated with higher nutrient conservation, low litter quality and low litter decomposability, and is the effect of elevation similar for heath and meadow vegetation?
III. Do leaf litter phenolics increase with elevation and is the effect of elevation similar for heath and meadow vegetation?
IV. Does net N and P mineralization decline with elevation and is this associated with a shift in microbial biomass C, N and P? Further, are these patterns similar for heath and meadow vegetation across the growing season?

By addressing these questions in combination the aim of this thesis is to gain further understanding of how elevation and associated abiotic factors such as temperature influence key ecosystem processes in a subarctic tundra landscape.

3 Materials and Methods

Papers I-IV of this thesis are all based on studies from the elevational gradient described above.

3.1 Field sampling

Paper I is based on above- and belowground measurements in heath and meadow vegetation across the elevational gradient, during the field season of 2008. A vegetation survey was performed in a 1 x 1 m subplot within each of the 48 plots (2 x 2 m). For each plot, plant species richness was determined and the total cover of each species was measured by point quadrat analysis (Goodall 1952) through recording the total number of times the vegetation of each species was intercepted from a total of 100 downwards projecting points in each plot (Wardle et al. 2003a). This cover data was also used for determining Simpson's diversity index and total vegetation density.

Further, in Paper I, humus and mineral soil were sampled in the 2 x 2 m plots outside the 1 x 1 m subplots used for the vegetation survey. A minimum of five soil cores (45 mm diameter) were taken, and split into humus and the top 5 cm of mineral soil. Samples from each plot were then bulked to yield one bulk sample of humus and one of mineral soil. Both humus and mineral soil samples were analyzed for soil nutrients, pH and bulk density and, the microbial properties of humus samples were also analyzed for microbial phospholipid fatty acids (PLFA).

To study the effect of elevation on leaf and litter traits and litter decomposability, both within- and across species as well as at the whole-plot level (Paper II), fresh foliage was collected for 4 - 6 species in 10 x 10 m plots, centered around each of the 2 x 2 m plots, between 26 June - 27 July 2008 (Figure 7). This foliage was used to determine N and P concentration, leaf dry matter content (LDMC) and SLA. This yielded a total of 18 species; seven species from heath and 11 species from meadow. For the same species, senesced litter was collected during 7-17 September 2008 for analysis of N and P content and for measurement of litter decomposability.

To explore the effect of elevation on litter phenolic properties (Paper III), senesced leaf litter was also collected from three to four species in each 10 x 10 m plot during September 7-17 2008. For this study, a total of 13 species were collected; three species from the heath, eight species from the meadow, and two species were collected in both heath and meadow.

In Papers II and III, species were selected to ensure that the commonest species at different elevations and those species which occurred across a wide range or the entire gradient were sampled, to facilitate the exploration of both across- and within-species leaf and litter trait responses to elevation.

Figure 7. Soil sampling in the meadow at 1000 m (left) and leaf collection in the heath at 800 m (right). In photographs, Maja Sundqvist (left) and Kerstin Gonschorrek (right). Photographs by T Logan (left) and M Sundqvist (right).

Paper IV is based on measurements of N and P dynamics across the study site performed on each of three occasions (July, August and September) throughout the growing season of 2009. For this study, humus was sampled to full depth within each of the 2 x 2 m plots across the gradient. For each sample, net mineralization of N and P and net amino-N consumption was determined *in situ* using the buried-bag technique (Eno 1960, Adams et al. 1989). As such, a minimum of four cores (45 mm diameter, Figure 7) were taken in each plot and then mixed together to form one bulk sample for each plot. Each sample was then split, and put into two semi-permeable polyethylene bags. One bag was brought back to the lab immediately after sampling for measurements of pH, moisture and organic matter content, and concentrations of amino-N and mineral N and P. The other bag was buried in the humus layer in the same plot from which it was sampled and incubated in the field for 28-29 days before being analyzed for exactly the same soil properties as each pre-incubated soil sample. For the August and September sampling occasions, microbial biomass C, N and P was measured on the pre-incubated humus soil samples.

3.2 Methodological aspects

3.2.1 Soil nutrient measurements

In Papers I and IV, soil pH was measured on fresh soil samples after shaking over night in 50 ml de-ionized water, and organic matter content was determined by loss on ignition on subsamples of fresh soil after oven-drying (105°C, 12 h) and placement in muffle furnace (550°C, 4h). A subsample of fresh soil was extracted with 80 ml 1 M KCl and analyzed for concentrations of PO_4^{3-}, NO_3^{2-} and NH_4^+ by colorimetry on an AutoAnalyzer III (SEAL Analytical, Kontram, OmniProcess AB, Sweden). In Paper IV these extracts were also analyzed for concentrations of amino-N (leucine-equivalent) by colorimetry, using ninhydrin and lithium acetate as reagents and leucine as a standard (Moore 1968). In Paper I total soil C and N were measured on an elemental analyzer, and total P and Ca were analyzed using a spectrometer after acid digestion (HNO_3 in an autoclave at 120°C), on dried and ground humus and mineral soil.

3.2.2 Soil microbial measurements

In Paper I, the soil microbial community composition in humus soil was assessed with the phospholipid fatty-acid analysis (PLFA) technique (Bligh & Dyer 1959). The method used followed that of Frostegård et al. (1991), where extracted lipids were fractionated into neutral lipids, glycolipids and polar lipids on silic acid columns by successive eluation with chloroform, acetone and methanol. The methanol fraction, which contains phospholipids, was further subjected to mild alkaline methanolysis in order to transform the fatty acids into free methyl esters and analyzed on a gas chromatograph. From the total number of fatty acids identified, the PLFA’s used to indicate bacteria and fungi followed those of Frostegård & Bååth (1996), the markers used to indicate actinobacteria followed those of Lechevalier (1977) and Kroppenstedt (1985), and the marker used as an indicator of arbuscular mycorrhiza followed that of Olsson (1999).

In Paper IV, microbial C and N were determined by $CHCl_3$ fumigation-extraction (Brookes et al. 1985, Vance et al. 1987). Unfumigated and fumigated (24 h) soil samples were extracted with 0.5 M K_2SO_4 and filtered through Munktell 00H filter paper. After fifty-fold dilution, organic C and N in the extracts were measured by automated combustion (TOC-V cph analyzer; Shimadzu, Tokyo, Japan). Microbial P was determined on the same soil samples by a simultaneous liquid fumigation and extraction method with anion resins in bicarbonate form for 16 h (Kuono et el. 1995) but using hexanol instead of chloroform as a fumigant (McLaughlin et al. 1986). Resins were eluted with 0.1 M NaCl/HCl and phosphorus in the extracts was measured by molybdate colorimetry. As extractability factors used to convert microbial C, N and P into actual biomass values are known to be soil-specific and therefore vary considerably among different soils (Oberson et al. 1997, Turner et al. 2002), microbial C, N and P were presented as relative values, i.e. the difference between the fumigated and unfumigated fractions for each element (Paper IV).

3.2.3 Leaf and litter traits and weighted averages

In Paper II, LDMC was determined on green foliage by calculating the ratio of the mass after oven-drying to constant mass and the mass before drying, and SLA was determined as the ratio of leaf area to leaf dry mass. Foliage and litter N and P content were determined on dried and ground (Ball Mill, Retsch MM 310) material by Kjeldahl digestion followed by automated colometric methods (Technicon Instruments 1977).

In Paper III, total phenolic content, total tannin content and protein complexation capacity was measured on litter water extracts following Garnett et al. (2004) and Joanisse et al. (2008). A subsample of 0.3 g ground litter (Ball Mill, Retsch MM 310) and 100 mL deionized water were left to shake for 24 h, after which samples were filtered first through coarse filters, followed by filtering through 0.2 µg disposable filters under vacuum. The Prussian blue technique (Stern et al. 1996) was used to measure total extractable phenolics using catechin (+/-) as a standard. Total tannins were measured by the Acid-butanol method (Porter et al. 1986), using procyanidin B2 (Sigma-Aldrich) as a standard. The protein complexation capacity (PCC) of each litter extract was measured using the method described by Gundale et al. (2010) in which an external protein (Bovine Serum Albimun, BSA) was added to each litter extract after which the quantity of precipitated protein in that extract was measured.

In order to explore the effect of vegetation type (heath and meadow) and elevation on leaf and litter traits at the whole plot level (Papers II and III), a weighted average approach was used. For each variable, a plot weighted average was calculated by weighting all species according to their relative abundance in each plot, which yields a single value for each plot (Garnier et al. 2007, Fortunel et al. 2009). The relative abundance data for each species was obtained by point quadrat analysis (Goodall 1952), as described above. As such, for each variable the weighted average value for each of the 48 plots was calculated according to the following equation, described by Garnier et al. (2007):

$$trait_{aggr} = \sum_{i=1}^{n} p_i \times trait_i$$

where trait_{aggr} is the aggregated value for that leaf or litter trait for all species collected in that plot, p_i is the abundance of species i as a portion of the total abundance of all species collected in that plot, and trait_i is the value of the leaf or litter trait for species i.

3.2.4 Litter decomposition assay

In Paper II the decomposability of each litter sample was determined by a standardized decomposition assay as described by Wardle et al. (2002). This method enables determination of the relative decomposability of different litters under standardized conditions and is therefore a powerful method in assessing relative differences of litter quality and decomposability among and within species (Wardle et al. 2009). Here, Petri-dishes (9 cm diameter) were two-thirds filled with a standardized humus substrate and a dish of nylon mesh (1 mm holes) was placed on the surface of the substrate. Dried litter (cut into 5 mm fragments when necessary) was placed on top of the mesh. The Petri-dishes were then sealed with tape to minimize water loss and incubated at 22°C for 119 days after which all remaining litter was removed, rinsed and dried and weighed for determination of litter mass loss. For each litter sample from each plot, three Petri-dishes were set up with 1 g litter in each Petri-dish (except when insufficient litter was available in which case one or two Petri dishes were used). For each species in each plot, the material left after decomposition was bulked and ground and further analyzed for N and P by Kjeldahl digestion followed by automated colometric methods, as described above. For each litter sample, nutrient release during decomposition was calculated as the total mass × nutrient content prior to incubation minus that after incubation (Wardle et al. 2002).

To assess the decomposability of each litter sample as well as N and P release during decomposition at the whole plot level, a weighted average approach was used exactly as described above.

3.3 Statistical analysis

In Papers I-III the effect of vegetation type and elevation on each response variable measured (i.e. species richness, Simpson's diversity, vegetation density, nutrient concentrations, microbial measures, leaf and litter traits, litter decomposability) was analyzed by two way Analysis of Variance (ANOVA). When ANOVA yielded significant treatment effects differences among means was further analyzed by using the Least Significant Difference (LSD) test at $P = 0.05$, with P-value adjustment to reduce Type I Error following the method of Benjamini and Hochberg (1995) (Paper I), or by Tukey's honestly significant difference (h.s.d.) at $P = 0.05$ (Papers II and III). In Papers II-III the effect of elevation on leaf and litter traits, and decomposability within individual species, was analyzed by one way ANOVA; when effects of elevation were significant, differences among elevations were further explored by Tukey's h.s.d. at $P = 0.05$.

In Paper IV, the effect of sampling month, vegetation type and elevation on nutrient concentrations, net mineralization of N and P, net amino-N consumption and microbial C, N and P were analyzed by Repeated Measures ANOVA, and differences among months were further explored with Bonferroni-correction at $P = 0.05$. When significant main effects of elevation were found, differences among elevations for each month within each vegetation type were further analyzed by Tukey's h.s.d. at $P = 0.05$.

In Paper II, correlation analysis was used to explore the relationship between leaf and litter traits and litter mass loss and nutrient release during decomposition. In this thesis, correlation analysis was also used to explore the relationship of net N and P mineralization and net amino-N consumption with soil moisture (data from Paper IV), and the relationship of phenolic properties (data from Paper III) with mean growing season net N and P mineralization (data from Paper IV). In Paper I, linear regression was used to explore the effect of temperature on each plant and microbial response variable by using measurements of mean growing season temperature across the gradient (Figure 5), to confirm unidirectional trends identified through ANOVA. To explore the effect of elevation on across-species leaf and litter traits and decomposability in Papers II-III, the average value for each trait or process for each species across all elevations was calculated, as well as the mean elevation for which that species occurred. This data was then analyzed by linear regression with each species serving as an independent data point, as described by Wardle et al. (2009).

In Paper I, multivariate statistics were used to explore the relationship between the plant and microbial communities as well as their association with soil abiotic properties. The plant species data set was first subjected to detrended correspondence analysis (DCA) which revealed a gradient length of > 4 SD for the first axis, indicative of a unimodal response (ter Braak and Šmilauer 2002). To determine the relationship between plant species composition and soil abiotic properties across the 48 plots, the plant species data set was therefore subjected to a constrained canonical correspondance analysis (CCA) (ter Braak 1986). To correct for any colinearity between pH and elevation, soil pH was used as a covariable, and all other abiotic soil properties were used as explanatory variables. Each explanatory variable that explained an additional amount of variation at $P > 0.05$ (as determined using Monte Carlo permutation tests with 999 unrestricted permutations) was retained by forward selection (ter Braak and Šmilauer 2002). The sample scores for the plots derived from the CCA were further analyzed for effects of vegetation type and elevation by two way ANOVA, with means compared using the LSD test with *P*-value correction according to Benjamini and Hochberg (1995).

To further explore the relationship between microbial community composition, humus abiotic factors, and dominant plant species in Paper I, the microbial data set was first analyzed by DCA, which revealed a gradient length of the first axis < 2 SD, indicative of a linear response (ter Braak & Šmilauer 2002). The microbial data set was therefore analyzed by constrained (partial) Redundancy Analysis (RDA) with species standardized by error variance, and with plant and soil abiotic factors as explanatory variables and pH as a covariable as described above. Each explanatory variable that explained an additional amount of variation at $P > 0.05$ (determined using Monte Carlo permutation tests as described above) was retained by forward selection. This method enables the determination of the variance in microbial community composition explained by abiotic soil properties and plant species. Thus, the amount of variance explained by each of the two groups of explanatory variables was determined by variance partitioning (Borcard et al. 1992). The sample scores derived from the RDA were further analyzed by two way ANOVA to test for the effect of vegetation type and elevation on microbial community composition. When a significant effect of elevation was detected, differences among means were further explored by the LSD test as described above.

In Paper I, all univariate tests were performed using R 2.7.2., and all multivariate analyses were performed using CANOCO 4.5. In Paper II, all analysis were performed using SPSS Statistics 17.0. In Papers III and IV, all analyses were performed using SPSS (PASW) statistics 18.0.

4 Results and Discussion

4.1 Characteristics of two contrasting tundra vegetation types

This thesis focuses on how an increase in elevation influences two vegetation types: heath and meadow. The heath vegetation is found in less fertile patches and is dominated by dwarf-shrubs, and the meadow vegetation is found on more fertile soils in shallow depressions and is dominated by herbaceous species. Papers I-IV showed that these two vegetation types differ in terms of several important above- and belowground properties and processes (Figure 8), which are now discussed.

First, the meadow soils supported a higher plant species richness, and had higher pH and NH_4^+ concentrations but lower C:N ratios compared to the heath (Papers I and IV). Meadow soils also had higher net N mineralization rates, fungal:bacterial ratios and microbial biomass C, N and P values compared to the heath (Papers I and IV). These results are generally consistent with previous findings from subarctic tundra showing that soil pH is an important determinant of soil fertility and hence of plant (Gough et al. 2000) and microbial properties (Eskelinen et al. 2009). Other studies have shown that high soil pH and fungal:bacterial ratios and low C:N ratios are often indicative of high nutrient turnover rates (Bardgett 2005, Högberg et el. 2006), and the results from Paper I and IV are therefore indicative of higher N turnover rates in the meadow than in the heath.

Second, plant species which dominated in the meadow produced leaves with higher SLA, tissue N-content, and lower LDMC, compared to plants which dominated in the heath (Paper II, Figure 8). These results are consistent with literature showing that plants which dominate in more fertile sites generally have a set of leaf traits which are associated with nutrient acquisition and high growth rates relative to those which are adapted to less fertile sites (Wardle et al. 2004, Díaz et al. 2004). Leaf litter from the meadow plants also had higher decomposability and released a higher amount of nutrients during decomposition relative to that from heath plants (Paper II). This is consistent with the findings of several studies that leaf traits act as strong determinants of leaf litter quality (Killingbeck 1996, Cortez et al. 2007) and ultimately litter decomposability (Cornelissen et al. 2004, Kazakou et al. 2006, Cornwell et al. 2008, Fortunel et al. 2009). As such, these findings further reinforce a growing literature that shows that plant species adapted to more fertile soils often produce N-rich litter of higher quality which decomposes faster and promote a more bacterial based-based soil food web, relative to those that are adapted to poorer soils (Coleman et al. 1983, Wardle 2002, van der Heijden et al. 2008, Figure 2).

Third, the results from Paper III revealed that the heath vegetation produced litter that was higher in total tannins than that from the meadow (Figure 8). This is partly in line with theories that plants which dominate in less fertile sites invest more C into secondary metabolites compared to those dominating in more fertile sites (Bryant et al. 1983, Coley et al. 1985). However, and inconsistent with this theory, the total phenol content did not differ between the vegetation types. Surprisingly, the results from Paper III also revealed that meadow plants produced litter with a higher amount of phenolic compounds that have a high capacity to complex proteins relative to the heath plants (Hagerman 1987, Hättenschwiler & Vitousek 2000, Joanisse et al. 2007), and therefore potentially have a greater capacity to influence soil nutrient cycling processes (Northup et al. 1995, Kraus et al. 2003). Therefore, these results add to recent findings that herbaceous plants dominating in more fertile soils in Fennoscandian mountains can produce high amounts of total phenolics (Saetnan & Batzli 2009). They also provide further support for suggestions that predictions of plant C allocation to secondary metabolites cannot solely be based on variation in abiotic factors such as soil fertility (Hamilton et al. 2001).

Finally, the findings in Papers I and IV showed that available soil PO_4^{3-} concentrations were generally higher in the heath than in the meadow vegetation (Figure 8). The results from Paper II also showed that N:P ratios of leaves and litter, which are powerful indicators of the relative importance of N versus P limitation (e.g. Koerselman & Meuleman 1996, Aerts & Chapin 2000, Güsewell et el. 2003) were lower in the heath compared to the meadow. In addition, resorption proficiency, (i.e., nutrient concentration in senesced litter), commonly used as a measure of the ability for a plant to withdraw nutrients prior to senescence (Killingbeck 1996, Richardson et al. 2005), was similar for both vegetation types for P but higher in the meadow for N (Paper II). This overall pattern could be due to an influx of Ca in the meadow (Paper I) that is driven by local-scale topography and hydrochemistry, and which promotes the formation of Ca-phosphates that reduce the availability of P (Tunesi et al. 1999, Giesler et al. 2011). In any case, these results highlight how the relative importance of N and P limitation can vary across vegetation types which co-occur in the same tundra landscape (Weintraub 2011) and further support that P availability is higher in heath than meadow vegetation in Swedish subarctic tundra (Giesler et al. 2011).

In summary, Papers I-IV show that two vegetation types which co-occur in the Swedish subarctic tundra, and across the elevational gradient forming the basis of this thesis, differ fundamentally in several aboveground and belowground properties and processes (Figure 8).

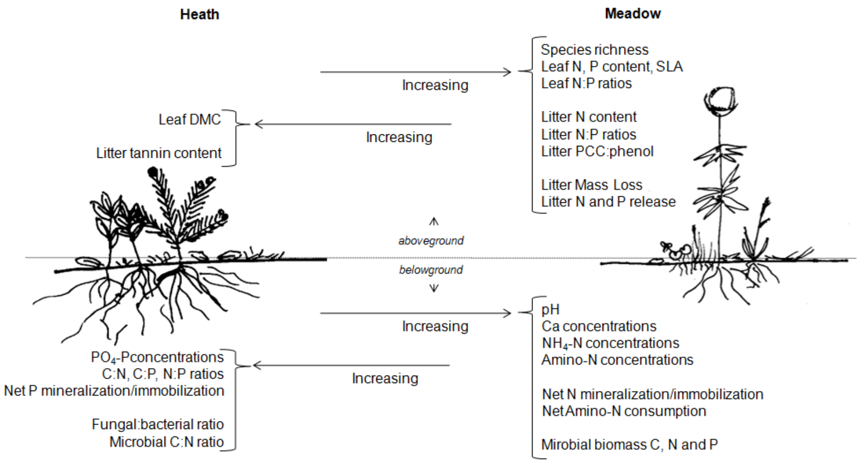

Figure 8. A summary of significant differences between the heath vegetation (dominated by dwarf-shrubs) and the meadow vegetation (dominated by herbaceous species) in above- and belowground properties and processes across the study site (Papers I-IV).

4.2 The effect of elevation on aboveground and belowground properties and processes

4.2.1 Linking N and P availability and plant and microbial communities

Paper I explored the effect of elevation on soil N and P availability and associated shifts in plant and microbial community composition in both tundra heath and meadow vegetation. For the heath vegetation, an increase in elevation was associated with a decrease in soil NH_4^+ and PO_4^{3-} concentrations, and the soil fungal:bacterial ratio was lowest at the lower elevations. As such, these findings are broadly consistent with previous studies showing how increasing elevation can be associated with declining nutrient availability (Sveinbjörnsson et al. 1995, Hart & Perry 1999), and studies revealing that low nutrient availability is often associated with a more fungal-based microbial community (Coleman et al. 1983, Wardle 2002, van der Heijden et al. 2008). However, belowground properties for the meadow vegetation showed quite a different response, in that increasing elevation was never associated with a decline in available soil nutrients for the meadow. Instead, NH_4^+ and PO_4^{3-} concentrations often varied significantly but idiosyncratically with elevation, and were greatest at the highest elevations for the mineral soil. This is inconsistent with previous findings of low nutrient availability at high elevations (Sveinbjörnsson et al. 1995, Hart & Perry 1999). In addition, the fungal:bacterial ratio was highest at mid-elevations for the meadow, and increasing elevation was associated with a much greater shift in microbial community composition for the meadow relative to the heath. As such, these results highlight that heath and meadow differ greatly not only in several belowground properties (Figure 8), but also in the responses of these properties to elevation.

Further, Paper I also revealed that the heath and meadow vegetation differed in terms of aboveground responses to elevation. For example, vegetation density was unresponsive to elevation for the heath but was highest at the two lowest elevations for the meadow. In addition, while it is well known that plant characteristics and community composition can shift with elevation (Nagy & Grabherr 2009, Körner 2007, Wiegolaski 1997, Jansson et al. 2008), Paper I found that increasing elevation led to a much greater turnover of plant species and plant functional groups in the meadow than in the heath. Further, species which dominated at different elevations were often associated with nutrient and microbial properties at specific elevations. As such, the differences in plant community responses to elevation for the two vegetation types could account for the contrasting effects of elevation on belowground properties between them. Tundra species and functional groups can differ in terms of nutrient uptake, the amount and quality of the litter they produce, and in their and root exudates, all which can influence microbial properties and soil nutrient availability (e.g. Hobbie 1996, Steltzer & Bowman 1998, Nordin et al. 2004, Miller et al. 2007, Meier et al. 2008). In this light, changes in climate have been found to exert a strong indirect influence on soil processes by driving shifts in plant species and functional groups (Kardol et al. 2010). The findings of strong but idiosyncratic effect of elevation on nutrient availability for the meadow might therefore be associated with a high turnover of species in response to elevation. As such, the results from Paper I suggest that while shifts in elevation (and thus temperature) can have direct effects on nutrient availability through controlling microbial activity (Schinner 1982) and soil process rates (Hart & Perry 1999, Sjögersten & Wookey 2002), plant species and functional groups that dominate different portions of the elevational gradient can also strongly influence soil processes and nutrient availability. These findings support the view that shifts in tundra plant community composition as a result of a changing climate can influence linkages and feedback mechanisms between the above- and belowground components (Wookey et al. 2009). They also highlight how direct and indirect effects of changes in temperature may vary considerably among tundra heath and meadow vegetation.

4.2.2 Plant leaf traits, litter quality and decomposability

In Paper II the effect of elevation on plant functional leaf and litter traits, and litter decomposability, was explored both for those species which dominated at different portions along the elevational gradient and for individual species that spanned a larger portion of the gradient. In addition, in Paper II, a community-weighted average approach was used to further explore how leaf and litter traits, and litter decomposability, responded to elevation for the heath and meadow vegetation at the whole plot level.

The effect of elevation across- and within-species

At the across-species level (with each species represented as a single data point) those species which dominated at higher elevations had lower SLA, and leaf and litter P concentrations compared to those species which dominated at lower elevations. The results also showed that while LDMC and tissue N concentrations were unresponsive to elevation across species, leaf and litter N:P ratios increased with elevation, indicative of an increase in the limitation of P relative to N (Koerselman & Meuleman 1996, Aerts & Chapin 2000, Güsewell et el. 2003). These results are in line with suggestions that species which are adapted to different portions of an environmental gradient often differ in trait characteristics (Körner 1989, Kazakou et al. 2006, Wardle et al. 2009). Though, they are inconsistent with global patterns of a positive relationship between temperature and leaf N:P ratios (Reich & Oleksyn 2004). However, the results from Paper II also show that plants adapted to higher elevations have a set of traits which are associated with lower growth rates and higher conservation of nutrients (Freschet et al. 2010). One potential explanation for the increase in N:P ratios with elevation might thus be that slow growing heterotrophic, and sometimes also autotrophic organisms often have lower tissue P relative to N concentrations (Sterner and Elser 2002). Further, there was high within-species variability in trait characteristics for each of five species that spanned a large portion of the elevational gradient. However, species often differed in which traits were responsive to elevation, and leaf and litter traits only sometimes shifted in a manner indicative of higher conservation of nutrients at higher elevations. Therefore, the results from Paper II provides further support for the growing number of studies finding that traits of individual species can be highly responsive to environmental gradients (Crews et al. 1995, Oleksyn et al. 2003, Albert et al. 2010) such as elevation (Kang et al. 2011), but highlights that the strength and direction of these responses can vary greatly among species. Consistent with the results of leaf trait responses to elevation at the across-species level, tissue N:P ratios consistently increased with elevation within all five species that spanned a large portion of the elevational gradient. These results provide further evidence that the limitation of P relative to N increases with elevation across this study site.

The results from Paper II revealed that litter decomposability and nutrient release during decomposition did not decline with elevation at the across-species level (Paper II). Shifts in functional leaf traits across species have been shown to drive shifts in litter decomposability along environmental gradients in other ecosystems (Wardle et al. 2009), and litter decomposability of tundra species has previously been shown to be responsive to elevation (Schinner 1982) and temperature (Hobbie 1996). However, the results from Paper II show that those leaf and litter traits that are responsive to elevation across species in this study system are not necessarily the same as those that drive litter decomposability. Further, litter decomposability never consistently declined with elevation at the within species level. However, litter decomposability within individual species often varied greatly among different elevations. In addition, the release of P from litter during decomposition declined with elevation for two evergreen dwarf-shrubs: *E. hermaphroditum* and *V. vitis-idaea*. These results add to the findings in Paper I, by suggesting that within-species shifts in litter quality may also greatly influence soil processes linked to nutrient availability across this gradient. Therefore, these results are consistent with increasing evidence that within-species variability can be important in driving decomposition along environmental gradients (Wardle et al. 2009, Classen et al. 2007). In addition, as different traits were often important for driving litter mass loss for different species, they provide further evidence that trait-decomposition relationships can vary greatly among species (Hobbie 1996).

The effect of elevation on heath and meadow communities

Community-level traits measures, derived using plot-weighted averages, were often responsive to elevation for both vegetation types. However, the results from Paper II revealed that there were important differences between the heath and the meadow in how trait characteristics and trait-decomposition relationships responded to elevation. Leaf and litter traits, such as N:P ratios, SLA and LDMC were more responsive to elevation for the meadow than for the heath vegetation. In addition, trait values more consistently shifted with increasing elevations towards those associated with higher nutrient conservation for the meadow. Hence, while these results highlight that functional traits at the whole community level can be highly responsive to underlying environmental gradients (Cortez et al. 2007, Fortunel et al. 2009), they also highlight that the direction of such shifts (and the consequences for belowground properties and properties) are likely to differ across functionally contrasting vegetation types. The results from Paper II indicate that for plant communities dominated by herbaceous species which are adapted to more fertile soils, functional traits are more responsive to shifts in elevation and therefore temperature, relative to communities on poorer soils. In this light, it has recently been shown that plant functional traits and trait-decomposition relationships are more responsive across environmental gradients for which there is a high turnover of species (Wardle et al. 2009). Further, and in line with such suggestions, Paper II also revealed that litter decomposability and nutrient release during decomposition was lowest at higher elevations for the meadow, but displayed no simple relationship with elevation for the heath. This was because for the meadow, litter decomposability was more often related to those traits that were unidirectionally related to elevation, compared to for the heath vegetation. In combination, these results reveal how differences in community functional trait responses to elevation (and thus temperature) among vegetation types, can lead to highly contrasting effects on litter decomposability, litter nutrient release and thus nutrient cycling within the same tundra landscape.

4.2.3 Phenolic properties of plant litter

Plant secondary metabolites such as phenolics are C rich compounds well known to act as herbivory defenses (Coley et al. 1985, Joanisse et al. 2007). However, they can also act as important determinants of litter quality and litter decomposability, and thus nutrient cycling. Through their litter "afterlife effects", phenolic compounds can greatly influence litter decomposition, microbial nutrient immobilization and soil nutrient availability (Kraus et al. 2003, Cornelissen et al. 2004). Therefore, understanding how shifts in elevation influences tundra plant C allocation into secondary metabolites such as phenolics can provide useful information about how changes in temperature may indirectly influence ecosystem processes which govern soil nutrient availability in these systems.

It has previously been predicted that increased environmental stress and nutrient limitation should result in higher plant C allocation into secondary metabolites such as phenolics (Bryant et al. 1983, Coley et al. 1985). As temperature declines with elevation, and several leaf and litter traits shift in a manner indicative of higher nutrient limitation at higher elevations (Paper II), it was hypothesized in Paper III that increasing elevation would also lead to an increase in phenolics. However, in contrast to this prediction, the results from Paper III showed that at the across-species level, total phenolic content declined with elevation while all other phenolic properties were unresponsive. In addition, while total phenolic content increased with elevation within one of the heath-species present along the entire gradient (*V.vitis-idaea*), all phenolic properties measured instead declined with elevation within another (*E. hermaphroditum*). For the other three species which occupied a large elevational range, phenolic properties were mostly unresponsive to elevation. Further, at the level of the whole-plant community (determined using plot-weighted averages), only the total tannin content in the meadow vegetation was highest at the highest elevation, and all other phenolic properties were either unresponsive to elevation or highest at lower elevations. Notably, those phenolic compounds which have a capacity to complex proteins (Hagerman 1987, Hättenschwiler and Vitousek 2000, Joanisse et al. 2007), and thereby greatly reduce N mineralization (Northrup et al. 1995) and plant N availability (Kraus et al. 2003) peaked at the lowest elevations. As such, the results from Paper III mostly contrast with predictions of increasing plant polyphenolic production with increased environmental stress or nutrient limitation (Bryant et al. 1983, Coley et al. 1985). They further contrast with suggestions of increased plant phenolic content in response to lower temperatures, as a protection against oxidative stress and photodamage under reduced photosynthesis (Close & McArthur 2002). Instead, they are consistent with previous findings of positive relationships between temperature and phenolic content in tundra plants (Jonasson et al. 1986, Graglia et al. 2001, Hansen et al. 2006) as well as with studies which have found that plants which occur on more fertile soils can produce higher amounts of phenolics (Wardle et al. 2003b, Gundale et al. 2010). In addition, the results from Paper III further complement those in Paper I, by highlighting that plants which occur at different elevations across the gradient differ in terms of their litter afterlife effects on soil processes such as mineralization and nutrient availability.

The results in Paper III further add to the findings in Paper II, and showed that responsiveness of phenolic properties to elevation can vary greatly among contrasting tundra vegetation types. Specifically, all measured phenolic properties were more responsive to elevation for the meadow vegetation than the heath. Hence, the findings from Paper III provides additional support for suggestions that litter trait responses to underlying environmental gradients may be greater when they are associated with a higher turnover of species (Wardle et al. 2009, Paper II) which is the case here for the meadow compared to the heath (Paper I). Finally, these results suggest that the effects of elevation (and therefore temperature) on soil processes known to be influenced by phenolics such as litter decomposition (Cornelissen et al. 2004), N mineralization (Northrup et al. 1995, Table 2) and nutrient availability (Kraus et al. 2003), are likely to be greater for tundra vegetation dominated by herbaceous species than for that dominated by dwarf-shrubs.

4.2.4 N and P dynamics

Future global warming is projected to influence nutrient cycling in high latitude tundra ecosystems, both directly by influencing microbial process rates, and indirectly by driving shifts in plant community composition and hence plant-soil linkages (Hobbie 1996, Robinson 2002, Stark 2007, Wookey et al. 2007). Therefore, in Paper IV, the effect of elevation on soil N and P availability, net N and P mineralization, net amino-N consumption, and microbial biomass C, N and P, was explored for heath and meadow vegetation across a growing season. The results from Paper IV revealed that amino-N concentrations sometimes increased with elevation for the heath, but showed variable responses to elevation for the meadow. In contrast, while NH_4^+ concentrations were mostly unresponsive to elevation for the heath, they were much more responsive for the meadow where they were highest at higher elevations. Further, while the net amino-N consumption rate had variable responses to elevation for both vegetation types, the net N mineralization rates were mostly unaffected by elevation for the heath, but were again highly responsive to elevation for the meadow where they were always highest at the highest elevation. Hence, these results highlight how increasing elevation may have vastly contrasting effects on N cycling processes when different vegetation types are considered. They are also generally inconsistent with some previous studies that have found increasing elevation to be associated with a decline in N mineralization and N availability (Sveinbjörnsson et al. 1995, Hart & Perry 1999, Paper I). In addition, while net N mineralization was sometimes positively related to soil moisture for the meadow, variation in soil moisture could not explain the overall pattern of mineralization rates in this study (Table 1).

Table 1. *Pearson's correlation coefficient between soil moisture content (% g^{-1} OM) and net N and P mineralization and net amino-N consumption (mg g^{-1} OM) in July, August and September 2009 for heath and meadow vegetation across an elevational gradient.*

		Heath			Meadow		
		N_{min}	amino-N_{co}	P_{min}	N_{min}	amino-N_{co}	P_{min}
July	Soil moisture	0.359	0.650**	0.391	0.328	0.236	-0.056
August	Soil moisture	-0.176	-0.220	0.596**	0.464*	0.308	-0.061
September	Soil moisture	0.118	-0.340	0.205	0.691**	0.065	0.044

min = mineralization; co = consumption. For all correlations n = 24, except between moisture content and net N mineralization for the meadow where n = 23. *,**Correlation coefficient is significantly different to 0 at $P = 0.05$ and 0.01, respectively.

Another factor known to be a strong regulator of microbial uptake and release of nutrients in tundra is variation in availability of C for the microflora (Schmidt et al. 1997). In this light, the mean growing season net N mineralization and amino-N consumption rates were positively correlated with leaf litter tannin content (Paper III) for the meadow, but there was no such relationship for the heath (Table 2). In addition, experimental warming studies have sometimes found higher net N mineralization rates at lower temperatures in subarctic tundra soils (Jonasson et al. 1993, Rinnan et al. 2007). The high net N mineralization at the highest elevation for the meadow may thus also reflect a lower microbial N demand, and thus lower N immobilization, at lower temperatures (Rinnan et al. 2007). In contrast, the generally low response of net N mineralization to elevation for the heath may point to an absence of any clear effect of temperature on N mineralization in this highly N limited vegetation type, which is consistent with findings from warming experiments of subarctic heath soils (Jonasson et al. 1993).

In contrast to soil N responses to elevation, the results from Paper IV showed that PO_4^{3-} concentrations often declined with increasing elevation for both heath and meadow. Further, PO_4^{3-} concentrations were more responsive to elevation for the heath compared to the meadow. These results reinforce findings in Paper I that soil P availability is more unidirectionally responsive to elevation for the heath compared to the meadow, and those in Paper II that the relative importance of P versus N limitation increases with elevation across the gradient. Further, the results from Paper IV also revealed that net P immobilization was often highest at the lowest elevation. While these results in combination could be interpreted as an increased plant demand for P at higher elevations, this contrasts not only with commonly reported findings of declining net primary production with increasing elevation (Wiegolaski 1997, Jansson et al. 2008, Nagy & Grabherr 2009) but also with evidence of a decline in leaf and litter P concentrations with increasing elevation across this gradient

(Paper II). Alternatively, the decline in PO_4^{3-} concentrations with increasing elevation might instead be associated with a decrease both in the overall production of P, and a decline in microbial P immobilization, in line with findings of increasing microbial P immobilization with increasing temperatures (Nadelhoffer et al. 1991). In addition, the mean growing season net P mineralization was negatively correlated with leaf litter concentrations of those phenolics that are highly capable of complexing proteins (Table 2), and these relationships were stronger for the heath. Again, this demonstrates how plant species which occur at different elevations vary in the degree of their influence on nutrient cycling processes across the elevational gradient. Further, these findings further highlight the need for an increased understanding of the ecological functions of specific polyphenolic compounds, including their role in influencing soil nutrient cycling (Salminen & Karonen 2011, Hättenschwiler et al. 2011).

Table 2. *Pearson's correlation coefficient between mean growing season net N mineralization, net P mineralization and net amino-N consumption (July, August and September, 2009) and litter phenolic properties (whole-plot level data, 2008). Nutrient data is derived from Paper IV and the data for litter phenolic properties is derived from Paper III.*

	Heath			Meadow		
	net N_{min}	net $aminoN_{co}$	net P_{min}	net N_{min}	net $aminoN_{co}$	net P_{min}
Tot phenols (mg g^{-1}dw)	0.104	0.348	0.408*	-0.270	0.143	-0.368
Tot tannins (mg g^{-1} dw)	-0.076	0.311	-0.251	0.678**	0.735**	0.041
PCC (mg g^{-1} dw)	-0.252	-0.032	-0.719**	-0.210	-0.198	-0.465*
PCC:phenols	-0.225	-0.055	-0.809**	0.093	-0.122	-0.493*

min = mineralization; co = consumption; PCC = Protein complexation capacity. *,**Correlation coefficient is significantly different to 0 at $P = 0.05$ and 0.01, respectively.

Microbial biomass was only weakly responsive to elevation for the heath and varied more, but mostly idiosyncratically, with elevation for the meadow (Paper IV). Meanwhile, the results for the meadow also revealed that microbial P can sometimes decline predictably with elevation even though microbial C and N do not (Paper IV). These results are consistent with previous findings that sometimes there may be little or no relationship between elevation and microbial properties (Zhao et al. 2009). The results do, however, clearly demonstrate how the responsiveness of microbial biomass C, N and P can vary substantially among functionally contrasting vegetation types, and is consistent with suggestions that responses of microbial properties to increasing elevation may be closely linked to how vegetation responds to elevation (Djukic et al. 2010). In summary, the findings from Paper IV further highlight that tundra heath and meadow vegetation fundamentally differ in terms of the relative importance of abiotic versus biotic controls on microbial properties and cycling of both N and P.

4.3 Conclusions

The results from this thesis show that increased elevation in a Swedish subarctic tundra leads to a consistent decline in soil P availability, but highly variable effects on soil N availability. These shifts in the availability of soil nutrients are associated with an increase in plant leaf and litter N:P ratios, indicative of an increase in the limitation of P versus N with increasing elevation. In addition, this thesis highlight that species which dominate at different elevations often produce leaf litter which differs in quality, and this may contribute to variation in soil processes and soil nutrient availability among different elevations. Importantly, this thesis shows that the effect of elevation on aboveground and belowground properties and soil processes differs greatly for two common and widespread vegetation types that co-occur in the Swedish subarctic tundra, i.e., heath and meadow vegetation (Figure 8, Björk et al. 2007, Eskelinen et al. 2009). For the heath vegetation, shifts in elevation have relatively weak effects on some aboveground properties such as plant species turnover, several plant functional leaf traits, and litter quality. Some belowground properties for the heath, such as litter decomposability, soil microbial biomass, and N availability are also only weakly responsive to elevation, while others such as P availability are highly and predictably responsive. For the meadow, elevation promotes a high turnover of plant species and plant functional groups, and a greater shift in functional leaf traits and litter quality than for the heath. Further, several soil microbial properties and nutrient cycling processes are more responsive to elevation for the meadow. Increasing elevation for the meadow is in turn associated with declining P availability, but highly variable and sometimes even increasing availability of soil N. As such, the results from this thesis provide detailed information about some of the key underlying mechanisms regulating how changes in plant community composition along environmental gradients can drive shifts in soil nutrient cycling processes. They suggest that increasing temperature can lead to a decrease in the relative importance of P versus N limitation for subarctic tundra plants. They further highlight that shifts in soil processes along underlying environmental gradients are likely to be greater when there is a significant turnover of species across them (Wardle et al. 2009). Finally, they suggest that a future increase in temperature will greatly influence plant-soil linkages that govern tundra nutrient cycling, but in fundamentally different ways for contrasting vegetation types which co-occur in the same tundra landscape.

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