

The Effect of Snow on Plants and Their Interactions with Herbivores

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Front cover:

Snow fence at the field site in Abisko, northern Sweden (photo: Mikaela Torp).

Back cover:

Autumnal moth larvae feeding on mountain birch leaves (photo: Mikaela Torp).

*The world is a beautiful book,
but of little use to those who cannot read it.*

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List of papers

This thesis is based on the following papers, which will be referred to in the text by the corresponding Roman numerals.

- I **Torp M**, Olofsson J, Witzell J, Baxter R (2010) Snow-induced changes in dwarf birch chemistry increase moth larval growth rate and level of herbivory.
Polar Biology, DOI: 10.1007/s00300-009-0744-9

- II **Torp M**, Witzell J, Baxter R, Olofsson J (2010) The effect of snow on plant chemistry and invertebrate herbivory: experimental manipulations along a natural snow gradient.
Submitted manuscript.

- III **Torp M**, Witzell J, Baxter R, Olofsson J (2010) Inter-annual variation in the effect of snow on plants and their interactions with herbivores.
Manuscript.

- IV **Torp M**, Baxter R, Olofsson J (2010) Effects of snow manipulation on nutrient concentrations in plants growing in habitats with contrasting snow cover.
Submitted manuscript.

- V Olofsson J, **Torp M**, Baxter R (2010) Increased snow cover causes a shift towards negative neighbor interactions in tundra plant communities.
Submitted manuscript.

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Preface

Plants are shaped by interactions with their surroundings. Environmental conditions control the length of the growing season, and plant growth and developmental stages are tightly linked to characteristics of the physical environment. Due to their lack of mobility, plants are restricted to utilizing resources available at their growth location and competition for resources such as water, light and nutrients is common between neighboring plants. Plants must also cope with natural enemies, pests and pathogens, and various degrees of environmental harshness. Therefore, plants have evolved an array of mechanical and chemical defense mechanisms that protect them from both biotic and abiotic stresses. Facilitative relationships between plants also appear to ameliorate environmental severity.

Arctic environments are characterized by high levels of abiotic stress. The growing season is short and cool. Plant-available nutrients in the soil are usually in short supply due to low mineralization and decomposition rates. Soil thickness and moisture content are highly variable and dependent on local topography. The annual distribution and duration of snow is of great importance for the structure and functioning of these ecosystems. The vegetation in arctic areas might appear simplistic since many habitats are dominated by only a few species. However, these ecosystems comprise complex mosaics of different plant growth forms including graminoids, evergreen and deciduous shrubs, lichens and bryophytes. Different life forms respond differently to changes in the environment. Shifts in plant species distributions and community composition, as a result of environmental change, might have further implications for the growth and survival of herbivores.

In arctic regions, the ongoing climate changes are predicted to increase both temperatures and precipitation. Although the length of the snow-covered season is generally expected to decrease in the future, snow depth may paradoxically increase in areas where a large amount of the elevated precipitation will fall as snow. The duration of snow-lie can thus increase or decrease depending on whether higher spring temperatures can or cannot compensate for the increased snow-fall in winter. Changes in snow cover might thus influence arctic ecosystems to the same extent as increased temperatures.

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1. INTRODUCTION

1.1. THE SIGNIFICANCE OF SNOW

At the global scale, snow plays an important role in the complex processes that determine the Earth's climate. Snow is both sensitive to temperatures and has a large effect upon them, and as a consequence of its high albedo snow has the ability to influence the heat regime and the radiation balance of the Earth (Chernov 1985; Bonan 2002). At smaller spatial and temporal scales, the annual distribution and duration of snow within a landscape shape the area in several ways, which in the end determine soil characteristics and community structure and composition (Gjærevoll 1956; Walker et al. 1993; Jones 1999; Darmody et al. 2004; Löffler 2005).

From an ecosystem perspective, one of the most important features of snow cover, besides the time of formation and melting, is the insulation capacity that determines the temperatures that soils and plants experience during winter (Sturm et al. 1997; Rixen et al. 2008). Snow is generally a good insulator (Bonan 2002) and the insulating capacity depends on the density of the snow, i.e. on the amount of air it contains (Chernov 1985). Thinner and denser snow-lies have lower insulation capacities (Sturm et al. 1997) causing higher variability in temperatures below the snow (Rixen et al. 2008). Throughout the winter, the snow cover protects soils and vegetation from low temperatures and harsh winds (Jones 1999; Walker et al. 1999; Sokratov and Barry 2002; Aerts et al. 2004; Darmody et al. 2004). Snow can act as a physical barrier restraining herbivores from reaching the vegetation (Kohler and Aanes 2004; Moen 2008), but, on the other hand, it also creates a protective environment which allows warm-blooded animals like lemmings and voles to be active below the snow (Chernov 1985). Moreover, the microbial activity in the soil is not ceased during the winter (Zimov et al. 1996; Oechel et al. 1997; Fahnestock et al. 1998), but it is highly temperature-dependent (Mikan et al. 2002) and thus sensitive to variations in snow depth. Deep snow-lies can thus maintain soil temperatures high enough to sustain microbial activities and mineralization processes during the winter (Schimel et al. 2004).

The depth of the snow cover is dependent on the quantity of snow that falls, but it is the interactive effects of winds, topography and vegetation structure that determine the

distribution of snow within a landscape. An important characteristic of the snow cover in arctic areas is its uneven spatial distribution (Gjærevoll 1956). Snow falling on wind-exposed sites is often redistributed in places where topography and vegetation provide shelter. Ridges, peaks and other sparsely vegetated areas are therefore more likely to accumulate small amounts of snow that, on the most exposed sites, may not even cover the low-growing vegetation. On the other hand, in hollows and valleys and areas occupied by shrubs or forests snow may form thick drifts (Chernov 1985).

In arctic areas, the timing of snow-melt determines when the growing season begins (Billings and Bliss 1959; Walker et al. 1995; Galen and Stanton 1999; Dunne et al. 2003; Aerts et al. 2006; Berg et al. 2008). The more snow that accumulates during the winter, the longer it will take to melt in the spring. Due to the patchy distribution of snow in arctic areas the length of the growing season can be highly variable even on a local scale (Gjærevoll 1956). In the same way as snow insulates soils and vegetation in winter, it also restrains the temperature equalization between vegetation and soils and the warmer air temperatures in spring. The ability of snow to delay warming of soils and vegetation is further amplified by its high albedo (Chernov 1985). The snow's albedo depends on its content of dust and particles (Steltzer et al. 2009). When snow-melt starts, organic debris accumulate and buried particles reemerge resulting in a rapid decrease in albedo (Chernov 1985; Steltzer et al. 2009). The environmental factors controlling the rate of snow removal from the landscape, such as air temperature, solar radiation and wind, are all influenced by the topography and vegetation in the area.

The ongoing climate changes are predicted to accelerate fast at northern high latitudes (ACIA 2005; IPCC 2007) with increases in both temperature and precipitation during the next century (IPCC 2007). The increased temperatures are expected to result in earlier melting of snow in the spring, and plant species that are dependent on a later snow-melt such as snowbed plants, are thus regarded to be threatened (Björk and Molau 2007). Although the duration of snow cover is generally expected to decrease in the future, snow depth may paradoxically increase in those areas where a large amount of the elevated precipitation will fall as snow (Pettorelli et al. 2005). The duration of snow cover in these arctic regions will thus increase or decrease depending on whether higher temperatures in spring can, or cannot, compensate for the increased snow-fall in winter. Long-term observations of the snow cover in Abisko, in

northern Sweden, have showed that the mean snow depth in this normally snow-poor area has increased by as much as 10% per decade over the last century (Kohler et al. 2006).

1.2. PLANTS IN A CHANGING ENVIRONMENT

1.2.1. Plant phenology

Plant phenology is an important aspect when studying possible effects of environmental change since the presence or absence of photosynthetically active canopies largely influences ecosystem processes and feedbacks with the atmosphere (Chapin et al. 2005). In arctic regions, plant activity in the spring is initiated by snow-melt and is therefore highly dependent on ambient temperatures (Aerts et al. 2006). On the other hand, leaf senescence in the autumn is determined by several factors including photoperiod and genetic controls (Fracheboud et al. 2009). The effect of increased temperatures on plant phenology should therefore be most pronounced in the spring. The general trend in arctic areas during the last decades has been a lengthening of the growing season, a phenomenon suggested to be linked to global warming. As expected, spring-time changes in plant phenology are most frequently reported (Arft et al. 1999; Aerts et al. 2006) and satellite data have confirmed an earlier greening in spring in high northern latitudes (Delbart and Picard 2007).

Many studies have investigated the effect of temperature on plant phenology in arctic areas and the results have shown that increased air and soil temperatures accelerate plant phenological development in a range of different species at several different locations (e.g. Wookey et al. 1993; Welker et al. 1997; Arft et al. 1999; Karlsson et al. 2003; Aerts et al. 2004). In addition to earlier budburst and flowering, plant vegetative growth and reproductive success have also been found to relate positively to experimental warming (Arft et al. 1999; Aerts et al. 2006).

In seasonally snow-covered areas, the duration of snow-lie influence plant phenology by determining when light, moisture, nutrient availability and temperatures suitable for growth become accessible in spring. In these ecosystems, where the length of the growing season is restricted by snow cover, phenological development is often rapid following snow-melt (Walker et al. 1999), probably due to more favorable conditions like warmer temperatures and better soil properties experienced by plants emerging from the snow later in the growing

season (Starr et al. 2000; Dunne et al. 2003; Aerts et al. 2006). As a consequence, phenological asynchrony of sites with different snow cover regimes is likely to decrease throughout the growing season as plants at the late snow-melt sites catch up.

1.2.2. Stoichiometric relationships in plants

Plants require essential elements in certain proportions to maintain cell functions and produce new biomass. Macronutrients (e.g. N, P, K, Ca, Mg, S) are needed in large quantities while micronutrients (e.g. Fe, Cu, Mn, Zn and Mo) are needed in smaller amounts. The specific functions of these elements in plants are well known (Pugnaire 2001) and the relationships between carbon (C), nitrogen (N) and phosphorus (P), the three main constituents in biological molecules (Sterner and Elser 2002), are by far the most investigated (Güsewell 2004). Terrestrial plant growth is usually considered nitrogen- or phosphorus-limited and the plant N:P ratio is often used as an indicator of nutrient limitation (Koerselman and Meuleman 1996; Güsewell 2004; Reich and Oleksyn 2004). However, large variation in the N:P ratio both within and between plant species indicates shifts in the limiting nutrient (Güsewell 2004, Ågren 2008). The use of stoichiometry alone for determining which nutrient limits plant growth is thus restricted, but shifts in the N:P ratio along natural gradients or in experimental manipulations might still indicate changes in plant nutrition.

On a global scale, the N:P ratio in plants decreases with increasing altitude and latitude (Körner 1989; Reich and Oleksyn 2004). This pattern supports the traditional view that plants in arctic ecosystems are nitrogen-limited since most nitrogen is bound in recalcitrant forms in soil organic matter and because low temperatures and water saturation limit decomposition and mineralization rates (Chapin and Shaver 1996; Aerts and Chapin 2000). However, the large variation in the N:P ratio of arctic plants suggests that phosphorus limitation or nitrogen and phosphorus co-limitation might be more common than previously assumed. Plant nutrient concentrations vary along topographic gradients in alpine ecosystems where nitrogen concentrations (Kudo et al. 1999, 2001; Choler 2005; Mårell et al. 2006) and N:P ratios (Esberg et al. unpublished) in plants are higher in snow-rich habitats. The snow-lie *per se* could be expected to contribute to these spatial differences in plant nutrient concentrations since nitrogen availability in the soil (Schimel et al. 2004) and plant nitrogen concentrations (Walsh et al. 1997; van der Wal et al. 2000; Welker et al. 2005; Aerts et al. 2009) have increased in studies where the snow cover has been experimentally enhanced. In addition, the

snow cover itself can function as a nitrogen source for plants (Bowman 1992; Forsum et al. 2008; Onipchenko et al. 2009).

1.2.3. Plant secondary compounds

Plant metabolites are often divided into two major groups: primary compounds and secondary compounds. The former are produced by and involved in primary metabolic processes such as photosynthesis and respiration. The specific roles of secondary compounds have been more unclear and in early literature they used to be considered waste products since they seemed to lack apparent functions in plants. However, it is currently known that many of these secondary substances are important in plant defense against herbivores and pathogens, they contribute to the scents, tastes and colors of plants and they are involved in protection against various environmental stresses (Bennett and Wallsgrove 1994).

One of the most widely distributed groups of secondary compounds in plants is the phenolics. Phenolic compounds, such as tannins, flavonoids and phenolic acids, are characterized by an aromatic ring (C_6) with one or several hydroxyl groups. The amino acid phenylalanine is the precursor of plant phenolics, which are formed through different routes of the phenylpropanoid pathway. Most phenolics occur as glycosides since free forms are potentially harmful to plant tissues (Harborne 1980).

The concentration and composition of phenolic compounds varies extensively both within and among species. Large differences in both ambient concentrations and the responsiveness of phenolics to environmental manipulations have been observed in plants of the same species but from different arctic areas (Graglia et al. 2001). Such data suggest that the effect of environmental changes on plant chemistry will be highly variable and species-specific. In addition, the concentration of phenolic substances in plants generally demonstrates high seasonal variability. In several studies, concentrations of many phenolic compounds have been high early in the growing season (e.g. Graglia et al. 2001; Turunen et al. 2009), although the within-seasonal fluctuation patterns of different phenolics often vary compound-specifically (e.g. Kause et al. 1999; Ruusila et al. 2005; Hansen et al. 2006).

The phenolic pool responds readily to environmental changes. In addition, the high individual (compound-specific) variation in responses of phenolic substances to altered environmental conditions (Witzell and Shevtsova 2004; Hansen et al. 2006) and phenolic profiles of different plant parts may therefore vary significantly across temporal and spatial gradients in

environmental conditions, such as light, temperature and nutrient availability (Haukioja et al. 1998; Graglia et al. 2001). Graglia et al. (2001) showed that shading and fertilization decreased the concentrations of condensed and hydrolysable tannins while warming increased condensed tannin concentration but decreased the concentration of hydrolysable tannins in *Betula nana* plants. Many phenolic compounds, especially flavonoids, appear to play a major role in protecting plants from damaging UV-light (Searles et al. 2001; Turunen et al. 2009). The concentrations of these substances have been found to decline in plants subjected to shading (Hansen et al. 2006; Nybakken et al. 2008) and increase when plants were subjected to high light conditions (Tegelberg et al. 2001; Turtola 2005; Turunen et al. 2009). Drought has also been shown to decrease the concentration of phenolic compounds in plants (Turtola 2005). The strong spatial variation in phenolic concentrations apparently reflects the effects of several environmental factors on plant metabolism (Graglia et al. 2001; Hansen et al. 2006) and the multiple functions these compounds have in plants (Close and McArthur 2002; Ruuhola et al. 2008).

1.2.4. Plant community composition in arctic areas

Although the structure of arctic vegetation might appear simple at first sight with many habitats generally dominated by only a few species, these ecosystems are complex mosaics of different plant growth forms such as graminoids, evergreen and deciduous shrubs, lichens and bryophytes. Different life forms will respond differently to environmental changes with some plant groups benefiting with the expense of others, and these changes can thus cause shifts in the composition and abundance of plant species (Wookey et al. 2009). Warming experiments have generally been found to increase the height and cover of deciduous shrubs and graminoids while the cover of mosses and lichens has decreased (Walker et al. 2006). Snow manipulation experiments that have recorded changes in plant community composition are less common, but an eight-year study in Alaska demonstrated increases in deciduous dwarf shrubs following enhanced snow-lie in a dry heathland while graminoids were the main beneficiaries of snow addition in the moist tundra (Wahren et al. 2005).

1.2.5. Shrub expansion and the positive feedback of snow

The increasing shrub abundance that has been observed throughout the circumpolar tundra (Sturm et al. 2001; Tape et al. 2006) is one of the most discussed climate-related changes in arctic areas. Although increased temperatures (Sturm et al. 2001) or a lengthening of the

growing season (Goetz et al. 2005; Euskirchen et al. 2006) probably are the main drivers behind the shrub expansion, a positive feedback may accelerate these vegetation changes (Weintraub and Schimel 2005). The canopies of shrubs trap and hold snow, resulting in deeper snow cover in areas with high shrub abundance. This promotes better insulated soils (Goetz et al. 2007) and higher winter soil temperatures, which increases the below-ground microbial activity (Sturm et al. 2005; Schimel et al. 2006). This, in turn, leads to higher rates of soil nitrogen mineralization in winter and early spring (Schimel et al. 2004, 2006) and more plant-available nitrogen that further favor shrub growth the following summer (Sturm et al. 2005). However, recent studies suggested that herbivores might be able to slow down or even inhibit this positive feedback (Olofsson et al. 2009). Especially reindeer have been found to reduce the abundance of shrubs in arctic heathlands (Manseau et al. 1996; Crete and Doucet 1998; den Herder et al. 2004; Post and Pedersen 2008), but also herbivory by voles (Dahlgren et al. 2009; Olofsson et al. 2009) might be important.

1.3. PLANT – HERBIVORE INTERACTIONS

1.3.1. Herbivores in arctic areas

The main vertebrate herbivores in arctic areas are ungulates (muskoxen, reindeer/caribou), rodents (lemmings, voles) and birds (geese) (Mulder 1999). Most of these herbivores are generalists since they consume plants from a wide range of taxonomic groups, but all of them also feed selectively by preferring certain species or plant parts during different times of the year (Jefferies et al. 1994). Moreover, many arctic herbivores demonstrate dramatic population density fluctuations over time. The most significant might be the lemming outbreaks; lemmings occurring in high densities at irregular intervals have huge effects on the vegetation (Oksanen et al. 2008). Voles are also showing strong density fluctuations with intervals of three to five years (Oksanen et al. 2008). Although the vole population peaks are less dramatic compared to the lemming ones, they still exhibit a marked effect on the vegetation during these years (Olofsson et al. 2004). During the low phase of their population density fluctuations, the effect of voles and lemmings on the vegetation is minor (Dahlgren et al. 2007).

Compared to vertebrates, invertebrate herbivores are considered less important for the plant community composition and ecosystem functioning in arctic areas (Aunapuu et al. 2008).

However, insect species demonstrating outbreaks, mainly geometrids like *Operophtera brumata* and *Epirrita autumnata*, defoliate vast parts of the vegetation and therefore have large effect on ecosystem functions during years of outbreak (Ims et al. 2008). In addition, recent ecosystem modeling has shown that non-outbreak invertebrate herbivores might possess a greater impact on these ecosystems than previously expected (Wolf et al. 2008).

Oksanen et al. (1981) suggested that terrestrial primary production is influenced by predator-prey interactions at higher trophic levels. Their hypothesis (Exploitation Ecosystem Hypothesis) stated that, in productive habitats, vertebrate herbivores and their predators have the potential to regulate their respective resources. However, in unproductive habitats, vertebrate herbivores are predicted to be food-limited resulting in herbivore densities too low to support predators. In these habitats, the prevalent interactions are between herbivores and their food plants. Although this hypothesis has been heavily debated (Strong 1992, Borer et al. 2005), spatial patterns and experimental results support a stronger effect of herbivores on plant biomass in the unproductive arctic regions than in more productive forest ecosystems (Aunapuu et al. 2008).

1.3.2. The importance of phenology

Seasonal variation in plant chemical traits has the potential to influence herbivore growth and performance. Plant quality in terms of nutrient concentrations shows dramatic changes during leaf maturation and the changes are usually most noticeable early in the growing season. In the beginning of the growing season, leaf nutrient concentrations are generally high. Throughout the growing season, the nutrient concentrations in leaves tend to decline as a result of dilution by accumulated carbon, translocation to reproduction and recovery of nutrients during senescence (Körner 1999). Consequently, plant palatability generally differs between young and old leaves since many traits that are characteristic for young leaves, i.e. high nutrient concentrations and low toughness, are beneficial for the performance of herbivores (Haukioja 2003; Turunen et al. 2009).

In seasonal environments, plant phenology is crucial for the quality and quantity of food available for herbivores. For instance, large herbivores such as reindeer and caribou select new emerging plant growth of high nutritional value and migrate into new areas as the emergence of new leaves proceeds along environmental gradients (Jefferies et al. 1994; Mårell et al. 2006). High spatial variability in plant phenology should thus be favorable for

these ungulates, since they can forage on high quality food for a longer period of time (Post et al. 2008). The enhanced plant nutritional quality in spring and early summer coincides with the period of high nutrient requirements for reindeer due to birth of calves and lactation (Mårell et al. 2006; Turunen et al. 2009). Changes in plant phenology can thus, through a trophic mismatch, result in reduced fecundity of caribou if the ungulates are unable to compensate for these alterations with changed migration patterns (Post and Forchhammer 2008). However, in most cases, ungulates seem to be able to track the phenology of their forage plants (Jefferies et al. 1994) and domesticated reindeer in Scandinavia appear to benefit from the earlier plant phenology observed during the last ten years (Turunen et al. 2009).

Invertebrate herbivores are often less able to migrate in their search of phenologically suitable food plants. Therefore, an important aspect of plant-invertebrate herbivore interactions is the relative timing of plant and insect phenologies (van Asch et al. 2007). Herbivorous insects have to synchronize their development with that of their host plants. For many insects, the most critical stage in this association is the timing of budburst in spring (Watt and McFarlane 1991; Komatsu and Akimoto 1995). Optimal conditions for larval development are attained if hatching occurs in synchrony with budburst. Temperature changes can have a larger effect on egg hatching than on budburst; if eggs hatch prior to budburst, the larvae will experience difficulties in finding forage whereas late hatching results in a risk of reduced growth and survival due to rapid decrease in forage quality during leaf maturation (Ayres and MacLean 1987; Kaitaniemi et al. 1997; Riipi et al. 2002). Consequently, early or late egg hatching in relation to budburst can lead to differences in herbivore damage on plants (Harrington et al. 1999) and phenological asynchrony between larval emergence and budburst has been considered the major setback of an altered climate on insect abundance and plant-herbivore interactions (Dewar and Watt 1992; Harrington et al. 1999; Watt and Woiwod 1999; Dixon 2003).

1.3.3. The importance of plant stoichiometry for herbivores

Plant nutrient concentrations do not only reflect plant nutrition, they also largely determine the quality of plants as food for herbivores. Due to their high content of carbon-based structures, plants are imbalanced food for herbivores that contain more nitrogen- and phosphorus-rich tissues (Sterner and Elser 2002). Most herbivores thus demand more nitrogen

than their food plants contain (Mattson 1980). Elevated nitrogen concentrations and a reduction in the C:N ratio can therefore be expected to increase the nutritional quality of plants (Sterner and Elser 2002). The fact that herbivores prefer nitrogen-rich plants is well-known in the ecological literature (Mattson 1980; White 1993; Sterner and Elser 2002) and evidence points toward higher preference and higher performance of herbivores on phosphorus-rich plants as well (Ngai and Jefferies 2004; Cherif and Loreau 2009). It should be noted that although nitrogen and phosphorus are by far the most studied nutrients, there is also evidence that other macro- and micronutrients can limit wild herbivore populations (Belovsky 1979, 1981; McNaughton et al. 1997; Pastor and Moen 2004; Anderson et al. 2007). The high nitrogen and phosphorus concentrations in arctic plants (Körner 1999; Reich and Oleksyn 2004) have been suggested as one factor contributing to the high level of herbivory in arctic ecosystems, since the high quality food should allow the build-up of high herbivore densities that consume a large fraction of plant biomass (van der Wal and Hessen 2009).

1.3.4. The importance of phenolics

In woody plants, phenolic compounds have traditionally been assigned important functions in defense against herbivores (Fraenkel 1959; Feeny 1976; Haukioja 1980; Treutter 2006) and pathogen attacks (Witzell and Martin 2008). For example, salicylates, a group of phenolic glycosides commonly found in *Salix* spp., appear to be important in herbivore resistance (Ruuholta et al. 2001), possibly due to their deterrent or toxic effects. However, all phenolics are not directly toxic to herbivores in the concentrations that the herbivores are exposed to while feeding on plants. The defensive impact of such phenolics might instead be due to their ability to decrease the quality of the forage, resulting in reduced growth and performance of the herbivores (Haukioja 2003). For instance, condensed tannins reduce the uptake of proteins by binding to them and forming tannin-protein complexes (Kraus et al. 2003). It has also been suggested that the primary role of phenolics is as antioxidants protecting the plants from damaging UV-light, and that the variation in phenolic patterns would mainly be a result of the spatially and temporally varying risk of UV-light damage (Close and McArthur 2002).

The relationship between plant phenolics and herbivory has been thoroughly studied, but the results have been highly varying. For instance, studies have shown a large variation in the relationship between individual phenolic compounds and developmental characteristics of the

autumnal moth, *Epirrita autumnata*, a common insect herbivore in arctic regions. Haviola et al. (2007) demonstrated that gallotannin concentration in mountain birch (*Betula pubescens* spp. *czerepanovii*) leaves was positively correlated to pupal weight and larval developmental rate, but showed a negative correlation to the survival rate of the larvae. A negative relationship between gallotannin concentration in young mountain birch leaves and the performance of *E. autumnata* larvae has also been found in other studies (Kause et al. 1999; Ossipov et al. 2001). Moreover, flavonoid glycosides and catechins have been found to exhibit negative relationships to larval survival (Haviola et al. 2007), a negative relationship has been found between tannins and larval growth (Kause et al. 1999) and the concentration of kaempferol and myricetins derivatives (flavonoids) in mature mountain birch leaves were negatively related to larval performance (Kause et al. 1999). On the other hand, Lempa et al. (2004) found that flavonoid and chlorogenic acid concentrations in mountain birch leaves were positively related with leaf consumption by fifth instar *E. autumnata* larvae. These, in many cases very compound-specific, effects of phenolics on insect herbivores are noteworthy since individual phenolic substances, or groups of phenolic substances, display different seasonal dynamics (Haukioja 2003; Witzell and Shevtsova 2004).

1.4. PLANT – PLANT INTERACTIONS

1.4.1. Competition and facilitation

One of the major forces behind coexistence of species and the structure of ecosystems is competition between organisms (Grime 1979; Tilman 1988). All plants require the same fundamental resources, i.e. nutrients, water and light. Plants are thus competing for these shared resources wherever they can be depleted (Tilman 1988). However, evidence from empirical studies show that plants growing in stressful environments can also have positive effects on their neighboring plants by facilitating the environment (Callaway 2007). For example, plants can facilitate their neighbors by shading the soil and thus increase soil moisture in dry desert ecosystems (Franco and Nobel 1989), by ameliorating soil conditions in salt marshes (Bertness and Hacker 1994) or by increasing soil and air temperatures in cold habitats (Cavieres et al. 2006).

Based on these results, the stress gradient hypothesis was formulated stating that positive interactions between plants increase on the expense of negative ones along gradients of

increasing environmental stress (Bertness and Callaway 1994; Callaway 2007). In harsh environments, facilitation should thus be more important than competition and positive interactions between plants should prevail. Although the generality of this model has been questioned by recent meta-analyses (Maestre et al. 2005), there is substantial support for the significance of facilitation in plant communities in a wide range of stressful environments (Callaway 2007). Facilitation can thus be a way for plants to expand their realized niches (Bruno et al. 2003).

1.4.2. Interactions between plants in arctic ecosystems

Neighbor removal experiments in arctic plant communities have demonstrated negative (Shevtsova et al. 1997; Aksenova et al. 1998), positive (Sammul et al. 2000; Gerdol et al. 2002) and neutral (Bret-Harte et al. 2004; Totland et al. 2004) interactions between plants. This suggests that both competition and facilitation are important in arctic ecosystems and that the dominating interaction vary in space, time and between species (Wipf et al. 2006). However, the spatial pattern in plant interactions supports the stress gradient hypothesis since facilitation is generally more common in high-altitude sites while competition increases toward lower altitudes (Callaway et al. 2002). Moreover, the intensity and direction of interactions have also been reported to shift along local topographic gradients from positive in exposed sites to negative in more sheltered sites (Choler et al. 2001).

In arctic ecosystems, low temperatures and short growing seasons create harsh environments for plants (Brooker and Callaghan 1998). Increased temperatures should thus reduce environmental severity and cause a shift toward more negative interactions between neighboring plants (Klanderud 2005; Brooker 2006). However, both a warming experiment in northern Finland (Shevtsova et al. 1997) and a snow manipulation experiment in Alaska, where snow-melt was advanced (Wipf et al. 2006), resulted in more positive plant-plant interactions instead. These apparently contradicting results might be explained by increased, rather than decreased, environmental stress following earlier snow-melt since the risk for frost events can increase (Inouye 2000; Gorsuch and Oberbauer 2002).

1.5. GRADIENTS AND EXPERIMENTS IN ECOLOGICAL STUDIES

The complex interactions between ecosystem structure and function and environmental changes are usually addressed in two different ways. The first approach for obtaining understanding of ecosystem responses to environmental changes is to identify relationships between ecological variables and climatic conditions across different sites within a landscape or a region (Koch et al. 1995). In this kind of studies, natural gradients are used to suggest probable effects of environmental changes on different ecosystem traits. The second approach is to use experimental manipulations that, compared to gradient analyses, provide a more controlled, mechanistic way of studying ecosystem responses to environmental change and identifying the factors behind these responses (Dunne et al. 2004).

Both approaches are frequently used and can provide valuable and relevant scientific information. It is, however, important to keep in mind that the outcome of both natural gradient analyses and experimental manipulations must be carefully interpreted since they often seem to fail in supporting each other and thus may reflect only a particular part of the potential dynamics of an ecosystem's response to environmental change. The combination of gradient surveys and experiments is therefore particularly useful; experimental manipulations provide mechanistic effects of short-term perturbations while natural gradients offer possibilities to study ecosystem adjustments to longer-term environmental variability (Dunne et al. 2004).

Many studies have addressed of how changes in snow-lie affect plants and their interactions with herbivores. However, most studies of effects of snow cover on plant traits are either descriptive surveys along natural gradients of varying snow conditions (Kudo et al. 1999; Mårell et al. 2006) or short-term, small-scale, experiments manipulating the timing of snow-melt by various heating systems (Bokhorst et al. 2008, but see Dunne et al. 2004) or by snow fences (Walsh et al. 1997; van der Wal et al. 2000). The disadvantage with conducting surveys along natural snow cover gradients is that these snow-lie gradients generally coincide with topographic gradients in a landscape. The effect of snow-lie *per se* can thus be difficult to dissect and the observed results might as well be caused by other differences along the gradients. Snow manipulation experiments can, on the other hand, reveal information about short-term effects of snow cover, but any long-term responses, which might be opposing to the observed short-term ones, cannot be detected.

1.6. OBJECTIVES OF THE THESIS

The effect of snow on plants and their interactions with herbivores was investigated by increasing the snow cover in three different habitats along an environmental gradient. The aim of this thesis was to use this combined approach of natural gradient analysis and experimental manipulations to:

- 1) investigate the effect of snow on plant quality as food for herbivores and herbivore performance.
- 2) examine if differences in snow-lie explain spatial, seasonal and inter-annual variation in plant chemical traits and patterns of herbivory.
- 3) test if differences in snow cover explain variation in plant-plant interactions between habitats.

2. MATERIALS AND METHODS

2.1. STUDY SYSTEM

2.1.1. Field site description

The effects of an increased snow cover on plants and the interactions with their herbivores were studied in the southern part of the Abisko valley in northern Swedish Lapland (N68°25' E18°19'), about 200 km north of the arctic circle and approximately 730 m above sea level, on the southern shore of Lake Torneträsk. The mean annual temperature was 0.7 °C and the mean annual precipitation was 310 mm for the period 1913-2000 measured at the nearest climatic station, Abisko Naturvetenskapliga Station (Kohler et al. 2006), which is situated ca. 5 km from the field site and at 325 m lower altitude. During the last decade, temperatures in this area have been 1-2 °C higher than the long-term average (Olofsson et al. 2009). However, observations of the snow cover have revealed that the mean snow depth in this generally snow-poor area has increased by ca. 10% per decade over the last century (Kohler et al. 2006).

The field site is located above the tree line, between the upper limits of the mountain birch (*Betula pubescens* ssp. *turtuosa*) forest and the sparsely vegetated upper slopes of the mountain (Fig. 1A), and is characterized by four different habitats which form a mosaic pattern: exposed ridges, ericoid heathlands, graminoid-dominated fens, and stripes of willow thickets that run across the site (Fig. 1C-F). Exposed ridges are found on windswept and barren areas, and they are characterized by sparse and patchy vegetation; besides lichens and bryophytes, the most abundant species are low-growing *Betula nana*, *Empetrum nigrum* ssp. *hermaphroditum* and *Vaccinium uliginosum*. The heathlands are dominated by a continuous layer of *B. nana* and *E. nigrum* ssp. *hermaphroditum* with occasional findings of *Salix* spp. The vegetation in the fens is dominated by graminoids such as *Trichophorum cespitosum*, *Carex vaginata* and *Eriophorum vaginatum* with *B. nana*, *Salix* spp., *Vaccinium vitis-idaea* and *E. nigrum* ssp. *hermaphroditum* growing on drier locations. The willow thickets are found in hollows in the landscape and are characterized by shrubs like *Salix glauca*, *S. lanata*, *B. nana*, *Vaccinium myrtillus*, together with a variety of herbs.

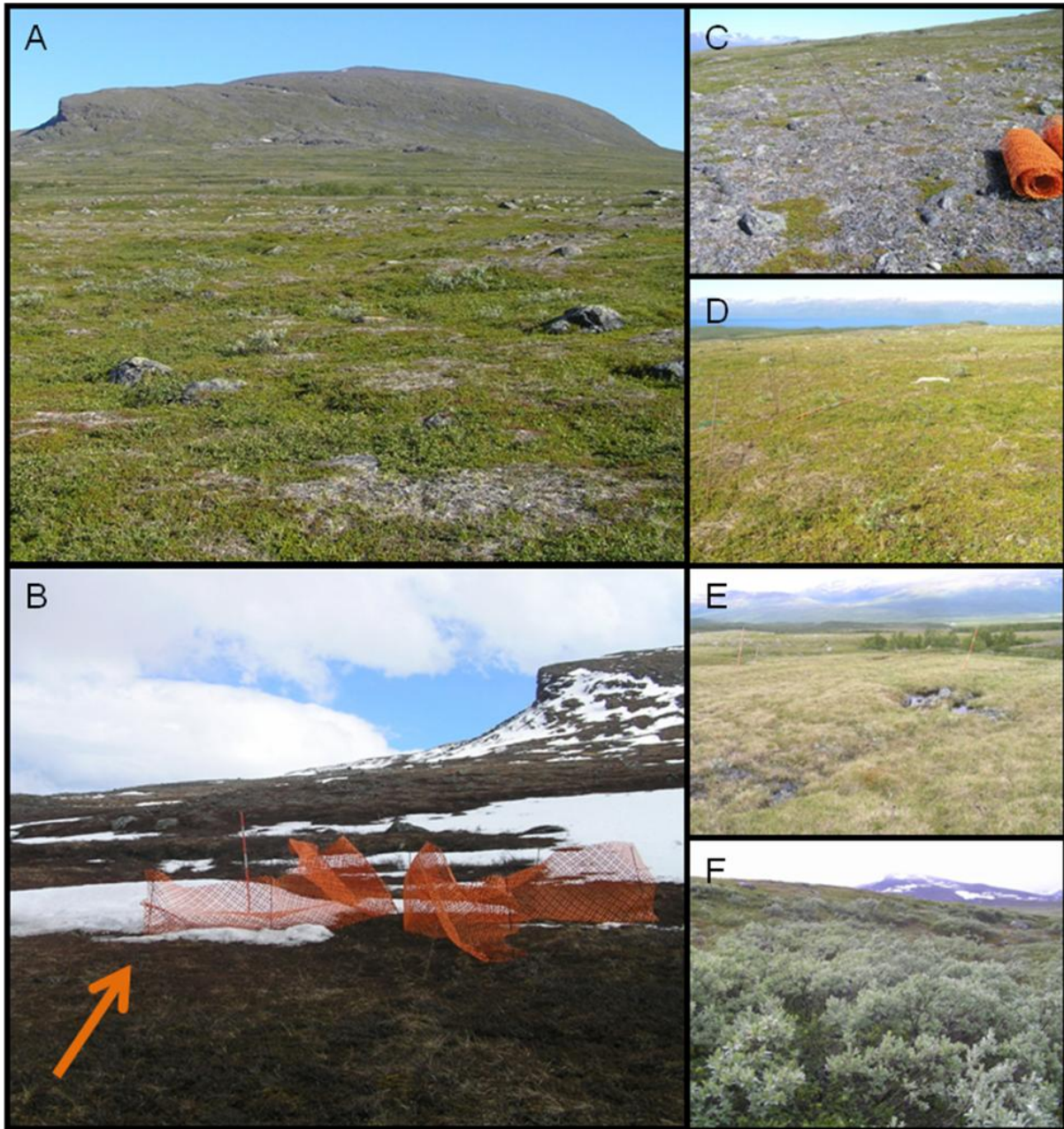


Fig. 1. A. Overview of the field site, which is located above the tree line. The snow fence and control plots are placed within ca. 50-1000 m of each other below the upper slopes of Mt. Nissuntjåkka, at approximately 730 m above sea level. B. One of the snow fences in the end of May. The increase in snow cover can be observed as the leftmost snow-lie situated in the northeastern sector of the snow fence (see the arrow) whereas the other sectors of the fence are virtually snow-free. C. The barren exposed ridge habitats with sparse and patchy vegetation. D. The ericoid heathlands characterized by a continuous layer of dwarf shrubs. E. The frequently wet graminoid-dominated fens. F. The willow thickets are found in hollows in the landscape and here shrubs can reach heights of about one meter. Photo: Mikaela Torp.

The habitats differ in depth and duration of natural snow-lie (Paper II). On the ridges, winter snow cover seldom reaches more than 15 cm and these areas become snow-free early in the spring. In heathlands and fens maximum snow depth is 20-30 cm. Although the differences might seem small, the vegetation in the fens and heathlands is protected by snow during most of the winter while plants living on the ridges are frequently exposed to the harsh winter conditions above the snow. The willow thickets are characterized by high snow accumulation with winter snow depths of up to 200 cm and a subsequent longer duration of snow cover in the spring. The time of snow-melt varies naturally more than a month between the extremes of the snow cover gradient that these habitats represent (Paper II). The habitats also constitute a gradient in soil conditions with very thin and dry soils on the ridges, at least temporarily wet soils in association to snow-melt and rain in the heathlands and almost continuously wet soils in the fens (Cook 2005). In the willow thickets, soil moisture content is high throughout the growing season.

2.1.2. Study species

Dwarf birch, *Betula nana* L. (Betulaceae), is a common shrub in arctic ecosystems. Its growth form is indeterminate with two kinds of shoots: short shoots and long shoots. Short shoot leaves (usually three leaves/shoot) burst simultaneously in spring and are therefore even-aged from a phenological perspective. This is in contrast to long shoot leaves, which are produced continuously at growing branch tips until late summer, and which thus differ in age even within the same shoot (Ossipov et al. 2001). To control for leaf age only short shoot leaves were used in our analyses.

Another commonly found shrub in arctic areas is greyleaf willow, *Salix glauca* L. (Salicaceae). It thrives in moist places and can reach substantial heights during favorable growth conditions. It is a dioecious species (Dudley 2006). The leaves are lanceolate and covered with silver-gray hairs. As branches grow, new leaves are continuously formed throughout the growing season. In accordance with other *Salix* spp., greyleaf willows frequently hybridize with other co-occurring willow species (Dudley 2006).

The larvae of the autumnal moth, *Epirrita autumnata* (Lepidoptera: Geometridae), were used in a herbivore performance study (Paper I). *Epirrita autumnata* is a common insect herbivore in arctic ecosystems and occurs throughout western Europe and most of northern Eurasia (Tenow 1972). It overwinters as eggs that hatch in spring in synchrony with budburst

(Kaitaniemi et al. 1997; Ruohomäki et al. 2000) and feed on the foliage of various deciduous trees and understorey plants (Seppänen 1970). In arctic regions, *Betula* spp. is their most important food source (Aunapuu 2004; Ruusila et al. 2005) and the larvae commonly feed on short shoot leaves in the beginning of their larval period since there simply are no long shoot leaves available (Ossipov et al. 2001). The larval stage consists of five instars. After 4-6 weeks, the larvae pupate within a cocoon buried in the leaf litter on the ground (Ruohomäki et al. 2000). The pupation stage lasts about a month and the adult moths hatch in the autumn. *Epirrita autumnata* population densities fluctuate and show regional peaks at ten-year intervals when they can defoliate vast areas of birch forests (Tenow 1972; Ruohomäki et al. 2000).

2.2. EXPERIMENTAL DESIGN AND FIELD MEASUREMENTS

2.2.1. Design of the snow fence experiment

In the ridge, heathland and fen habitats described above, the snow cover has been increased experimentally since 2002 by a snow fence treatment (Fig. 1B). In each habitat, five snow fences and paired control plots were placed in separate, replicated, patches within ca. 50-1000 m of each other (Fig. 2). The snow fences consist of 1.2 m high and 6 m long plastic fences (mesh size ca. 3 cm) placed in a cross shape, with snow accumulating in the northeastern sector as the area is dominated by winds from the southwest. The accumulation of snow follows the laws of physics as the wind speed on the downwind side is less than on the windward side, causing snow to settle behind the fence. The treatment results in an increased snow depth of approximately 0.6-0.8 m, and delays snow-melt with ca. one month (Paper II). The fences are removed in spring, directly after snow-melt, and put in place again in the autumn before the snow arrives. The snow fences should thus have minimal effects on plants during the growing season.

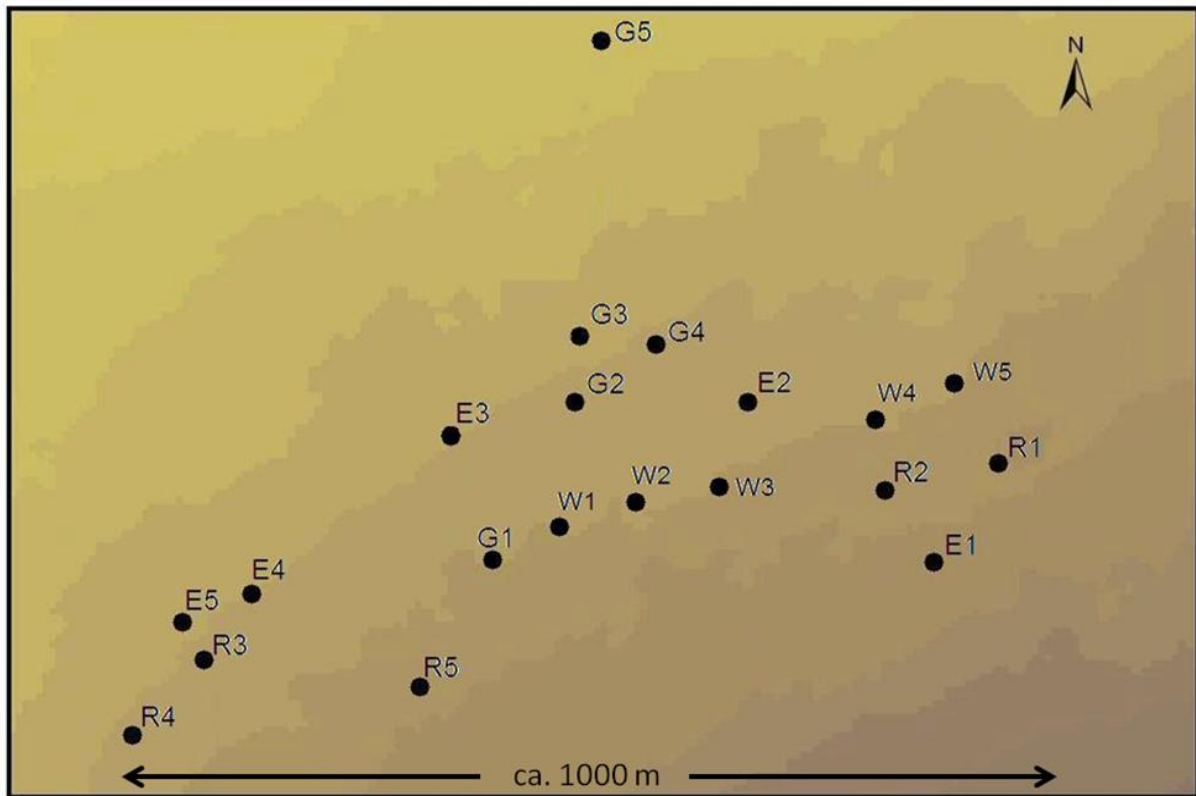


Fig. 2. Schematic map of the field site. Habitats are: R – exposed ridge (R1-R5), E – ericoid heathland (E1-E5), G – graminoid-dominated fen (G1-G5) and W – willow thicket (W1-W5). Each mark corresponding to the ridge, heathland and fen habitats represents the location of paired snow fence and control plots (five pairs/habitat). The snow fence treatment was not performed in the willow thickets. The gray scale corresponds to approximations of different altitudes; light grey represent lower altitudes and dark grey represents higher altitudes.

In paper I, merely the five snow fence plots and the five control plots in the heathland habitat were used since this was the only habitat where *B. nana* was present in sufficient amounts for the study. In paper II, all plots in all four habitats (35 plots; the snow fence treatment was not performed in the willow thickets) were used. In paper III, IV and V, we used snow fence and control plots in the ridge, fen and heathland habitats. *Betula nana* was used in papers I-IV whereas *S. glauca* was used in papers III and IV only. In paper V, we used *Empetrum nigrum* ssp. *hermaphroditum* and *Vaccinium vitis-idaea* as study species. Table 1 summarizes in which papers the different habitats and plant species were used. *Betula nana*, *E. nigrum* ssp.

hermaphroditum and *V. vitis-idaea* were present in all habitats while *S. glauca* was missing on the ridges.

Table 1. Summary of habitats, treatments and plant species used in the different papers (I-V).

Habitat	Treatment	<i>B. nana</i>	<i>S. glauca</i>	<i>E. nigrum</i> ssp. <i>hermaphroditum</i> and <i>V. vitis-idaea</i>
Ridge	Snow fence	II, III, IV	Missing	V
	Control	II, III, IV	Missing	V
Heathland	Snow fence	I, II, III, IV	III, IV	V
	Control	I, II, III, IV	III, IV	V
Fen	Snow fence	II, III, IV	III, IV	V
	Control	II, III, IV	III, IV	V
Willow thicket	Control	II	-	-

2.2.2. Species abundance

Abundance of *B. nana* and *S. glauca* was recorded in the heathland, fen and ridge habitats in 2004 and 2008. A point intercept method (Jonasson 1988), at 441 regular points, was used in 2m × 2m sub-plots situated within the larger snow manipulation and control plots. A thin metal stick was lowered vertically through the vegetation at each point and all hits of living plant parts were recorded. Abundance of *B. nana* and *S. glauca* was calculated as the fraction of the points where these two species were present and presented as percentage (%) cover of the species in each habitat.

2.2.3. Leaf phenology

In 2005, leaf phenology was monitored in the beginning of the growing season in permanent sub-plots (1 m²) located within the larger snow manipulation and control plots. In the willow thickets, leaf phenology was examined randomly at five sites. The status of leaf buds was checked every third or fourth day. The first day of leaf bud-burst was defined as day zero

(June 9). Leaf development in each habitat and treatment was then described in relation to day zero as a measure of phenological variation due to different snow conditions.

2.2.4. Shoot length

Shoot length of *B. nana* was investigated in mid-August 2005 and 2008 in the fen, heathland and ridge habitats. The length of current year's long shoots was measured to the closest mm in the field using a plastic ruler. In 2005, 20 shoots were randomly selected in each control and treatment plot (30 plots), while in 2008, five shoots were measured. Mean shoot length for each plot was used for further statistical analyses.

2.2.5. Estimation of invertebrate herbivory in the field

Estimations of leaf damage by invertebrate herbivores in the field were performed annually during 2004-2008. In 2004 and 2006-2008, estimates were done once in the beginning of July. In 2005, estimations were repeated five times throughout the growing season (June 16, June 30, July 12, August 3 and August 22). Leaf area removed by invertebrate herbivores was estimated in control and treatment plots in all habitats where *B. nana* and *S. glauca* were present (35 plots for *B. nana* and 25 plots for *S. glauca*). The estimates were randomly done on leaves from several shoots. Leaf damage was estimated visually as percent of total leaf area. All estimates were made by the same three persons and the estimates were calibrated among the individuals in the field and carried out at random across the plots. In 2005, due to the repeated estimations, shoots and leaves were marked to ensure that the same leaves were used in all the estimates done throughout the growing season. On the first time of estimation, shoots of *S. glauca* and short shoots of *B. nana* were selected randomly and at least 100 leaves were permanently marked. The leaves were distributed on at least five different shoots per species in each plot. The estimations were used as a measure of the level of invertebrate herbivory on *B. nana* and *S. glauca* leaves during field conditions.

2.2.6. Soil analyses

Nitrogen mineralization rates in the soil were measured using the buried bag in situ incubation technique (Eno 1960; Binkley and Hart 1989). Paired soil cores (10-20 cm depth) were collected randomly from each of the five replicate control and snow fence plots in the heathland habitat. One sample was used to determine initial concentrations of extractable NH_4^+ and NO_3^- while the other was placed in a polyethylene bag and buried in situ. In 2004,

samples were collected at June 15 and September 21 while sampling occurred on May 25 and September 10 in 2005. Periods of incubation were ‘winter’ (September – late May/early June) and ‘summer’ (late May/early June – September). Winter incubation measured the release of inorganic nitrogen from the soil during winter; this nitrogen is available for plant uptake in the spring. Summer incubation measured the release of inorganic nitrogen from the organic matter in the soil during the summer. A nitrogen flush can be expected in the spring if mineralization rates are high during winter. After completed incubation, samples were removed from the ground and transported immediately to the laboratory, where they were stored at 4 °C overnight and extracted the next morning. The soil core samples were sieved (4 mm) and ca. 10 g were then extracted with 100 cm³ of 2 M KCl for 60 min. Soil extracts were filtered (Whatman no. 1 filter paper) and filter blank corrections applied. NH₄⁺ and NO₃⁻ concentrations were determined colorimetrically by the indophenols blue and cadmium reduction methods, respectively. Analysis was automated (SAN⁺ segmented flow analyzer, Skalar Ltd., Breda, The Netherlands). Net nitrogen mineralization was calculated as the difference between NH₄⁺ and NO₃⁻ concentrations in the incubated samples and their respective concentrations in the initial soil core samples.

2.2.7. Neighbor removal experiment

In 2007, all neighboring species in a 10 cm radius around shoots of two dwarf shrub species, *E. nigrum* ssp. *hermaphroditum* and *V. vitis-idaea*, were removed. *E. nigrum* ssp. *hermaphroditum* and *V. vitis-idaea* were chosen as target species in this study since they were used in a similar study in the Alaskan tundra (Wipf et al. 2006). Three pairs of shoots of each species were located in each treatment plot, and one shoot in each pair was randomly assigned to neighbor removal or control treatment, respectively. In order to minimize the impact of clonally integrated neighbors (Wipf et al. 2006), care was taken to select shoots that were not directly surrounded by other shoots of the same species. *Empetrum nigrum* ssp. *hermaphroditum* shoots were found in all plots while *V. vitis-idaea* shoots were present in all heathland plots but only in one plot in the fen habitat and in three plots on the ridges. The length of each shoot was recorded at the start of the experiment. The length of the current year’s shoot, the length of the longest leaves, the number of berries and the survival were documented at the end of the experiment in mid-August 2008. The neighbor removal plots were repeatedly weeded at several occasions during 2007 and 2008 and were thus kept virtually free from neighboring plants.

The effect of neighbors on current year's shoot growth and leaf length was calculated as reversed RNE: $(\text{neighbor removal shoot} - \text{control shoot}) / \max(\text{neighbor removal shoot}, \text{control shoot})$. Positive values indicated facilitation and negative values pointed toward competition. Because of the large number of zeros recorded, no indices were calculated for the number of berries or shoot mortality; they were presented as raw values. Neighboring plant biomass was estimated by collecting the neighboring plants removed at the start of the experiment. The collected plant biomass was dried to a constant weight and weighed immediately after drying.

2.3. ANALYSIS OF LARVAL GROWTH AND PERFORMANCE

The effect of snow addition on the quality of plants as food for herbivores was investigated by offering *B. nana* leaves from snow fence or control plots to *E. autumnata* larvae and studying their growth, pupation and hatching. At June 18, 2005, 100 naturally-hatched, first instar larvae were collected in the birch forests surrounding Lake Torneträsk and placed in separate plastic pots (height=7.0 cm, diameter=7.0 cm) with a nylon net covering under a tarpaulin shelter in the common garden of the Abisko Scientific Research Station, 5 km from the field site. The larvae were thus protected from direct sunlight and rainfall but did otherwise experience fairly similar climatic conditions as in the field site. Every third or fourth day until pupation, each larva was fed with 10 short-shoot *B. nana* leaves collected from one of the experimental plots in the heathland habitat. A replicate of 10 larvae were provided with leaves from each control or snow fence plot. The growth of the larvae was studied by weighing them once a week until they pupated. Larval weights were obtained at three occasions before pupation started (June 18, June 26 and July 2). Dates of pupation and hatching were recorded in order to observe larval development. Not all larvae survived and only live ones were included in the observations. Larval consumption was measured by weighing the fresh leaves before they were offered to the larvae and by weighing the remains of old leaves when they were replaced by new ones. To compensate for the potential weight loss of leaves by drying during the three to four days the larvae were able to feed, the old leaf remains were dried (60 °C, >48 h) before weighing. The dry weight of the fresh leaves offered to the larvae was estimated by determining both fresh and dry weight of ten additional leaves from each treatment plot.

2.4. CHEMICAL ANALYSES

2.4.1. Sampling of plant material

Sampling of leaves for chemical analyses was done once in the beginning of July in 2004, 2006, 2007 and 2008. In 2005, leaves were collected at five occasions throughout the growing season (June 16, June 30, July 12, August 3 and August 22). Leaves from *S. glauca* (10 leaves/plot) and short shoots of *B. nana* (60 leaves/plot) were collected for chemical analyses from control and treatment plots in all habitats where the species were present (25 plots for *S. glauca* and 35 plots for *B. nana*). The leaves were stratified to come from at least five different shoots of *B. nana* and three different plants of *S. glauca* to get a representative sample of the whole plot. The leaves were air-dried in ambient temperature in the laboratory and milled to fine powder using a ball mill (Retsch-Muhle, Haan, Germany).

2.4.2. Nitrogen and carbon analyses

Leaf nitrogen and carbon concentrations were analyzed using an Elemental Analyzer (Perkin-Elmer 2400 Series II CHNS/O-analyzer). Leaf material and reference samples were accurately weighed and encapsulated in tin vials, which were automatically inserted from the autosampler into the Elemental Analyzer system. The samples are combusted completely and reduced to the elemental gases CO₂, H₂O, N₂ and SO₂. The percentage of nitrogen and carbon in the samples could then be determined.

2.4.3. Analyses of phenolic compounds

The most abundant low-molecular-weight phenolics, including several phenolic acids and flavonoids, were analyzed from methanol extracts using RP-HPLC with a DAD detector (Witzell et al. 2003; Srivastava et al. 2007). About 10 mg of plant material was weighed in eppendorf vials and three tungsten carbide beads (Qiagen GmbH, Hilden, Germany), 3 mm in diameter, were added to each vial together with 1000 µL MeOH. The MeOH was cooled to +4 °C before addition and the vials were kept on ice. The samples were shaken in a mixer mill for 2 min, centrifuged for 5 min and the supernatant was transferred to a new glass vial. The remaining residue was extracted as before in 1000 µL MeOH and the supernatants were combined. The solvent was evaporated to dryness in a vacuum concentrator. The dried samples were dissolved in 300 µL dH₂O:MeOH (1:1) and filtered through a disposable syringe filter (pore size: 0.2 µm) before injection into the HPLC system (Merck Hitachi

LaChrom HPLC system: L-7100 pump, L-7200 autosampler, L-7360 column oven and L-7455 diode array detector, Darmstadt, Germany). The oven temperature was set to 30 °C. The compounds were separated on a reversed-phase column and the mobile phase consisted of a gradient of solvent A (H₂O, pH adjusted to 3.0 with H₂PO₄) balanced with MeOH. UV-spectra were recorded between 200 and 400 nm and individual phenolics were identified by comparing their retention times and UV-spectra to those of known standards.

2.4.4. Analyses of mineral nutrients

Leaf concentrations of phosphorus (P), calcium (Ca), iron (Fe), magnesium (Mg), potassium (K) and sodium (Na) were analyzed with Inductively Coupled Plasma (ICP). Approximately 1.5 g dry weight of plant material was transferred to a 50 ml Kjeltec tube, 10 ml concentrated HNO₃ (nitric acid) was added and the samples were left overnight to start the breakdown of organic matter. The following day the samples were boiled in stepwise increasing temperature: 1 h at 60 °C, 1 h at 100 °C and 4 h at 125 °C. After 2 h at 125 °C, an additional 5 ml concentrated HNO₃ was added to each sample. After cooling, the samples were diluted to 50 ml with dH₂O and introduced into an ICP system. Recognition of different elements is based on their emission of characteristic wavelength specific light that can be measured.

2.5. STATISTICAL ANALYSES

Multivariate data on nutrient concentrations in leaves were visualized and explored by Principal Component Analysis (PCA) (Paper IV). The relationship between larval growth and different plant traits was investigated with stepwise backward multiple regression (Paper I). When the response variable was normally distributed and had homogenous variances, directly or following transformation, effects of treatments and habitats were tested with Analyses of Variances (ANOVAs). Repeated measure ANOVAs were used when repetitive measurements over time were carried out (Papers I, II, III). One- and two-way ANOVAs were used when appropriate (Papers II, IV). The relationships between continuous variables were analyzed with Pearson's product-moment correlation test (Paper IV), linear regressions (Paper III) and ANCOVAs (Paper III). In order to visualize the relationship between plant phenology and herbivory and leaf chemical traits, herbivory and plant chemical traits were plotted against leaf age. The best curve was fitted to the data with second order polynomial regression and model comparison with F tests was used to test if models with separate habitats had a better fit

to the data than common habitats (Paper II). If the response variable was not normally distributed, generalized linear models (GLMs) were used: the proportion of larvae that succeeded to pupate and hatch was analyzed with GLMs with gamma distributed errors (Paper I); dates of pupation and hatching (Paper I) and shoot survival (Paper V) were analyzed with GLM's with binomial distributed errors; and numbers of berries per shoot were investigated with GLM's with Poisson distributed errors (Paper V). All statistical analyses were carried out within the statistical package of R (R Development Core Team 2009).

3. RESULTS AND DISCUSSION

3.1. THE EFFECT OF SNOW ON PLANT QUALITY AND LARVAL PERFORMANCE

Increased snow cover can be expected to increase plant nitrogen concentration (Walsh et al. 1997; Welker et al. 2005; Aerts et al. 2009) and thus plant susceptibility to herbivory (Walsh et al. 1997; Virtanen 1998; Hambäck et al. 1998, 2002). In order to find out whether this was valid in our study system, we investigated, during the growing season of 2005, how plant chemistry responded to an increased snow cover and if changes in snow-lie and plant chemical traits affected the level of invertebrate herbivory and the performance of invertebrate herbivores in this arctic ecosystem (Paper I).

We found that increased and prolonged snow-lie increased the level of invertebrate herbivory on dwarf birch leaves under field conditions. In a common garden experiment, autumnal moth larvae feeding on leaves from snow addition plots grew faster and pupated earlier than larvae fed with leaves from control plots. These findings indicated that plants subjected to enhanced snow cover produced higher-quality food for herbivores. The increased larval growth rate was strongly correlated with higher leaf nitrogen concentration in plants that had experienced an enhanced snow-lie. Higher leaf nitrogen concentration was the most important factor explaining the enhanced plant quality in snow addition plots. Compared to nitrogen, phenolic compounds demonstrated weaker relationships with insect performance; these relationships were significant only when leaf nitrogen concentration was excluded from the model. Luteolin and chlorogenic acid concentrations were positively related to larval growth during the early instars while apigenins were negatively related to the larvae during the same period.

Leaf nitrogen concentration was highest in the beginning of the growing season and the concentrations of phenolic compounds fluctuated considerably during the growing season. The observed seasonal variation in leaf chemical traits emphasized the importance of synchrony between the development of herbivorous insects and their host plants. The results of our study (Paper I) showed that the level of herbivory in the field and the performance of larvae in the common garden experiment changed in parallel when the snow cover was manipulated, suggesting that our results were relevant also in field conditions. Snow-induced

changes in leaf chemistry that make plants more palatable to herbivores might thus have a negative feedback on the increasing shrub abundance that has been observed in arctic areas (Sturm et al. 2001; Tape et al. 2006).

3.2. THE EFFECT OF SNOW ON SPATIAL AND SEASONAL VARIATION IN PLANT CHEMISTRY AND LEVEL OF HERBIVORY

Plant nutrient concentrations vary both along altitudinal and latitudinal gradients (Körner 1989; Reich and Oleksyn 2004) and along local topographic gradients within arctic and alpine ecosystems (Kudo et al. 1999, 2001; Choler 2005; Mårell et al. 2006). The snow-lie *per se* could be expected to contribute to these patterns. Therefore, we investigated if the spatial and seasonal variation in plant chemistry and herbivore damage found within an arctic landscape could be explained by differences in snow-lie or if other environmental factors were more important (Paper II). In order to separate the effect of snow *per se*, we manipulated the snow cover in three habitats located along a natural snow gradient (Dunne et al. 2004).

Our results confirmed that snow-melt date controlled plant phenology (Galen and Stanton 1999; Dunne et al. 2003; Aerts et al. 2006) and that leaf nitrogen concentration decreased throughout the growing season (Graglia et al. 2001; Hansen et al. 2006). Leaf nitrogen concentration was higher in snow addition plots and in snow-rich habitats. The observed relationship between leaf nitrogen concentration and plant phenology in dwarf birch was consistent along the natural snow gradient and in plots where snow-melt was delayed experimentally. A delay in plant phenology thus appears as the most likely explanation for the higher leaf nitrogen concentrations found in our snow addition plots (see also Walsh et al. 1997; van der Wal et al. 2000). Although snow addition could be expected to elevate nitrogen mineralization rates in the soil (Schimel et al. 2004), that was not the case in our study system (Paper I). We therefore concluded that snow *per se*, via plant phenology, was controlling leaf nitrogen concentration in *B. nana* leaves.

The level of herbivory on dwarf birch increased throughout the growing season. Herbivore damage was lowest in snow-rich habitats in spring, toward the end of summer these habitats had the highest damage levels. Moreover, snow addition increased the level of herbivory in all habitats, an expected finding since an increased snow-lie increased the palatability of dwarf birch leaves by increasing their nitrogen concentration (Paper I). These results indicated that

the relationship between leaf age and level of invertebrate herbivory was positive in the beginning of the growing season and negative in the end of the growing season. Therefore, while the exposure time seemed to be the most important factor explaining the level of herbivory early in the growing season, plant palatability became more important as the growing season proceeded.

Differences in snow-lie *per se* did not explain the detected variation in leaf phenolic concentrations. The concentrations of phenolic compounds varied between habitats, treatments and sampling occasions indicating that dwarf birches were able to maintain a mosaic of secondary chemical quality across various snow conditions. We discovered a strong habitat-dependent variation in phenolic concentrations that apparently reflected the effects of several environmental factors on plant metabolism (Graglia et al. 2001; Hansen et al. 2006) and the multiple functions these compounds have in plants (Close and McArthur 2002; Ruuhola et al. 2008). The large variation in biologically active secondary chemicals across different spatial and temporal scales may act as a defensive mechanism, because it renders the vegetation to an unpredictable resource for insect herbivores that lack the ability to optimally track plant internal cues (Sipura 2000).

Most studies on plant nutrition in arctic ecosystems have focused on the significance of nitrogen alone, but there are several other macro- and micronutrients that are of vital importance for both plants (Pugnaire 2001) and their herbivores (Belovsky 1979, 1981; McNaughton et al. 1997; Pastor and Moen 2004; Anderson et al. 2007). In 2007, we thus investigated the effect of experimental snow addition on the concentrations of a number of nutrients in two dwarf shrub species growing in habitats with naturally contrasting snow cover regimes (Paper IV).

We found a pronounced topographic effect on the concentrations of several nutrients; *B. nana* and *S. glauca* plants from snow-poor habitats demonstrated higher nutrient concentrations compared to those from habitats with deeper snow-lie. Based on N:P ratio thresholds (Güsewell 2004), the nutrient limiting plant growth appeared to shift from nitrogen to phosphorus along the topographic gradient from snow-poor to more snow-rich habitats. However, snow addition had no significant effect on nutrient concentrations except nitrogen, and no significant effect on the N:P ratio in leaves. These results indicated that it was not spatial variation in snow cover that explained the observed differences in plant nutrient

concentrations and the N:P ratio among habitats in this arctic landscape. However, the large topographic variability in plant nutrient concentrations found in this study confirms that herbivores can optimize their nutrient uptake by foraging in different habitats (Mårell et al. 2006).

3.3. THE EFFECT OF SNOW ON INTER-ANNUAL VARIABILITY IN PLANT TRAITS AND PATTERNS OF HERBIVORY

Plant traits and patterns of herbivory are influenced by environmental conditions and annual variability in climatic parameters is therefore of great importance for plant-herbivore interactions in arctic ecosystems (Post and Stenseth 1999; Tyler et al. 2008; Gilg et al. 2009). Although many environmental manipulations are conducted as long-term experiments (e.g. Graglia et al. 2001; Welker et al. 2005; Hansen et al. 2006; Aerts et al. 2009), the direct effect on plants and herbivores is often described for one year only (e.g. Walsh et al. 1997; van der Wal et al. 2000; Graglia et al. 2001; Roy et al. 2004; Welker et al. 2005; Hansen et al. 2006; Aerts et al. 2009). Snow manipulation experiments have often demonstrated a positive relationship between snow cover and plant nitrogen concentration (Walsh et al. 1997; van der Wal et al. 2000; Welker et al. 2005; Aerts et al. 2009). However, when we investigated the effect of increased snow-lie on plant nitrogen concentration in two separate years, we found opposing results (Papers I, II vs. IV) indicating that the relationship between snow cover and plant nitrogen concentration differed between years. We therefore performed a long-term, five-year, study to further explore the relationship between snow and plant nitrogen concentration (Paper III).

We found opposing effects of increased snow-lie on plant chemical traits between years and in contrast to most previous findings, the effect of snow on plant nitrogen concentration was predominantly negative. Although a lack of long-term recordings, studies that combine snow addition and warming indicate that the effect of increased snow cover on plant nitrogen concentration should differ between years and that temperatures in summer could be important for this inconsistency (Welker et al. 2005; Aerts et al. 2009). However, we did not find any relationship between summer temperatures and the inter-annual variation in plant chemical response to snow addition.

The nitrogen concentration in plants is generally regarded as an indicator of the nutritional quality of plants as food for herbivores (Mattson 1980; White 1993; Sterner and Elser 2002). In 2005, we found that the higher plant nitrogen concentration in snow-rich sites was positively related to larval growth (Paper I) and thus might explain the increased level of herbivory observed in snow addition plots (Paper II). However, in the long-term study, the effect of snow addition on the level of herbivory was predominantly positive and no longer related to plant nitrogen concentration. Other plant chemical characteristics, such as secondary metabolites, that were not measured in this study could thus be the cause of this observed pattern.

Our long-term study did not reveal any conclusive evidence for any single factor causing the inter-annual opposing effect of snow-lie manipulation on plant traits and patterns of herbivory. However, we did discover some relationships that might indicate some important processes. The effect of snow on plant nitrogen concentration appeared to be related to winter temperatures and might probably be explained by the temperature-dependent nitrogen mineralization by soil microbes (Mikan et al. 2002; Schimel et al. 2004). On the other hand, the effect of snow on plant carbon concentration and level of herbivory seemed to be linked to temperatures in summer. In this area, the growth of dwarf birch is highly correlated to temperatures (Olofsson et al. 2009) and we also found an increase in the cover of both dwarf birch and grey-leaf willow following snow addition (Paper III). The more protected environment in snow addition plots might collaborate with summer temperatures to increase the growth rate of these shrubs. In addition, activity of invertebrate herbivores in summer is dependent on ambient temperatures (Bale et al. 2002).

3.4. THE EFFECT OF SNOW ON PLANT – PLANT INTERACTIONS

Interactions between plants shift from negative to positive along gradients of increasing environmental harshness (Hunter and Aarssen 1988; Bertness and Callaway 1994; Callaway 2007). In arctic ecosystems, this applies to both altitudinal (Carlsson and Callaghan 1991; Brooker and Callaghan 1998; Callaway et al. 2002) and local topographic (Choler et al. 2001) gradients, and studies indicate that differences in snow-lie might be responsible for the observed shift in plant-plant interactions. We addressed this issue by conducting a snow

addition and neighbor removal experiment in habitats with naturally contrasting snow cover regimes (Paper V).

We found that neighboring plants have strong effects on plant growth, but that the effects change from positive in snow-poor, exposed, habitats to negative in more snow-rich, protected, ones. Snow addition caused a shift toward more negative interactions in all habitats. However, since snow addition resulted in a similar response in all habitats, we suggested that snow *per se* was not the factor causing the differences in plant-plant interactions between the habitats. Other factors must therefore be causing the differences in interactions between plants in these habitats and depth of the organic layer in the soil (Wilson and Keddy 1986), soil moisture (Cavieres et al. 2006) and wind exposure (Olofsson 2004) are the most likely candidates. Our results indicated, together with the findings of Wipf et al. (2006), that snow might be able to ameliorate environmental conditions in snow-poor arctic ecosystems, thus causing a shift in interactions between plants from positive to negative.

This study has improved our understanding of how abiotic conditions shape plant interactions. In arctic ecosystems, increased temperatures associated with a changing climate might create more favorable conditions for plant growth (Walker et al. 2006) and is thus expected to cause a shift toward more negative plant-plant interactions (Brooker 2006). However, we showed that the effect might be the opposite in areas where snow cover will decrease as a consequence of global warming.

4. CONCLUSIONS

In this thesis, I have showed that snow cover affects plant chemistry and that this has implications for the growth and performance of herbivorous larvae. Enhanced and prolonged snow-lie increased the level of herbivory in the field and increased larval growth rate in a common garden experiment, indicating that plants that experience deeper snow-lie produce higher-quality food for herbivores. Within years, I found a consistent, positive relationship between plant nitrogen concentration and plant phenology, indicating that snow *per se*, via a delayed phenology, was responsible for the higher plant quality in snow-rich sites. However, this relationship did not explain inter-annual variation in the effect of snow addition. Therefore, the effect of snow appears to vary in time and space and depending on the identity

of the chemical compounds considered. The importance of long-term studies for identifying the mechanisms behind this variation is therefore crucial and even longer time series will be needed in order to fully understand the factors behind the observed variability in plant traits and patterns of herbivory. Fig. 3 provides a summary of the most important interactions present between snow and various components of an arctic ecosystem.

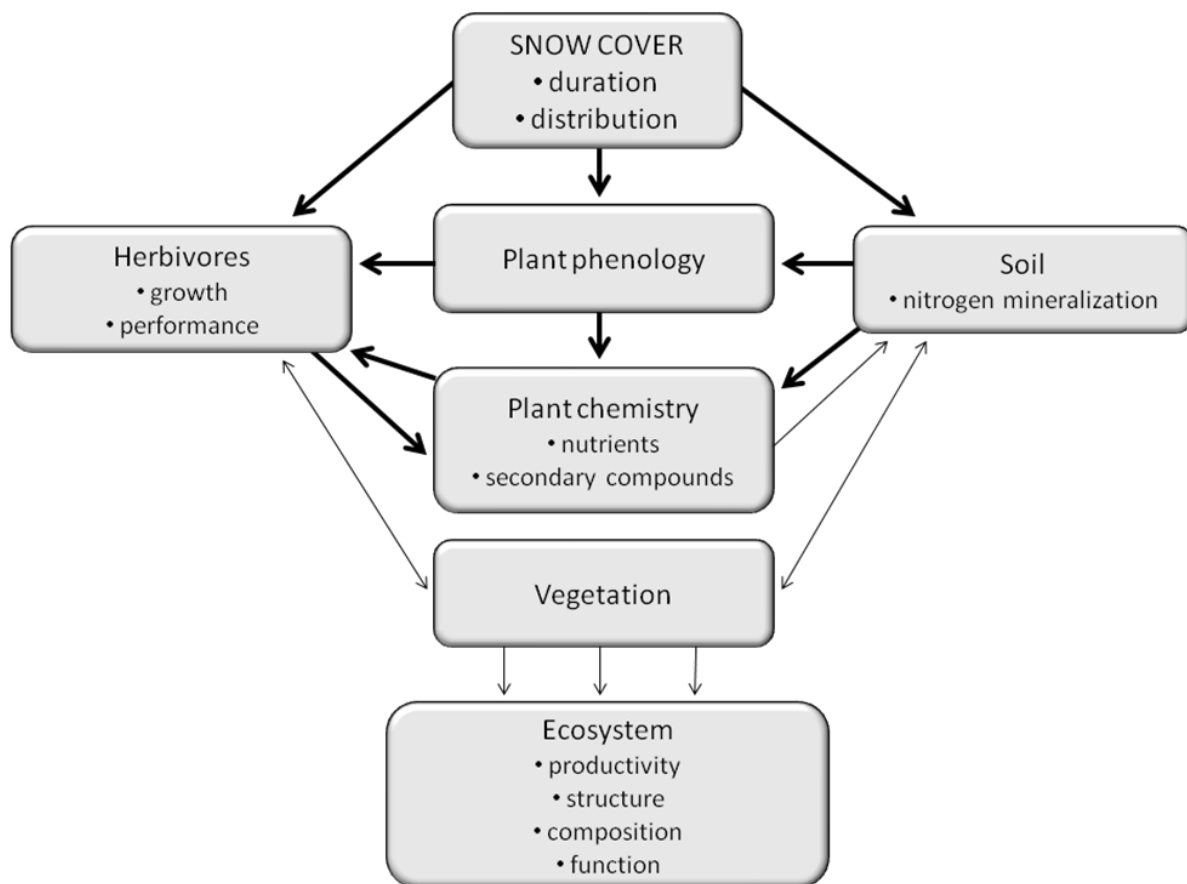


Fig. 3. A schematic overview of the main interactions present between snow cover and different aspects of arctic ecosystems. The interactions presented as thick arrows correspond to interactions considered in this thesis while the thinner arrows represent interactions that have not been investigated.

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