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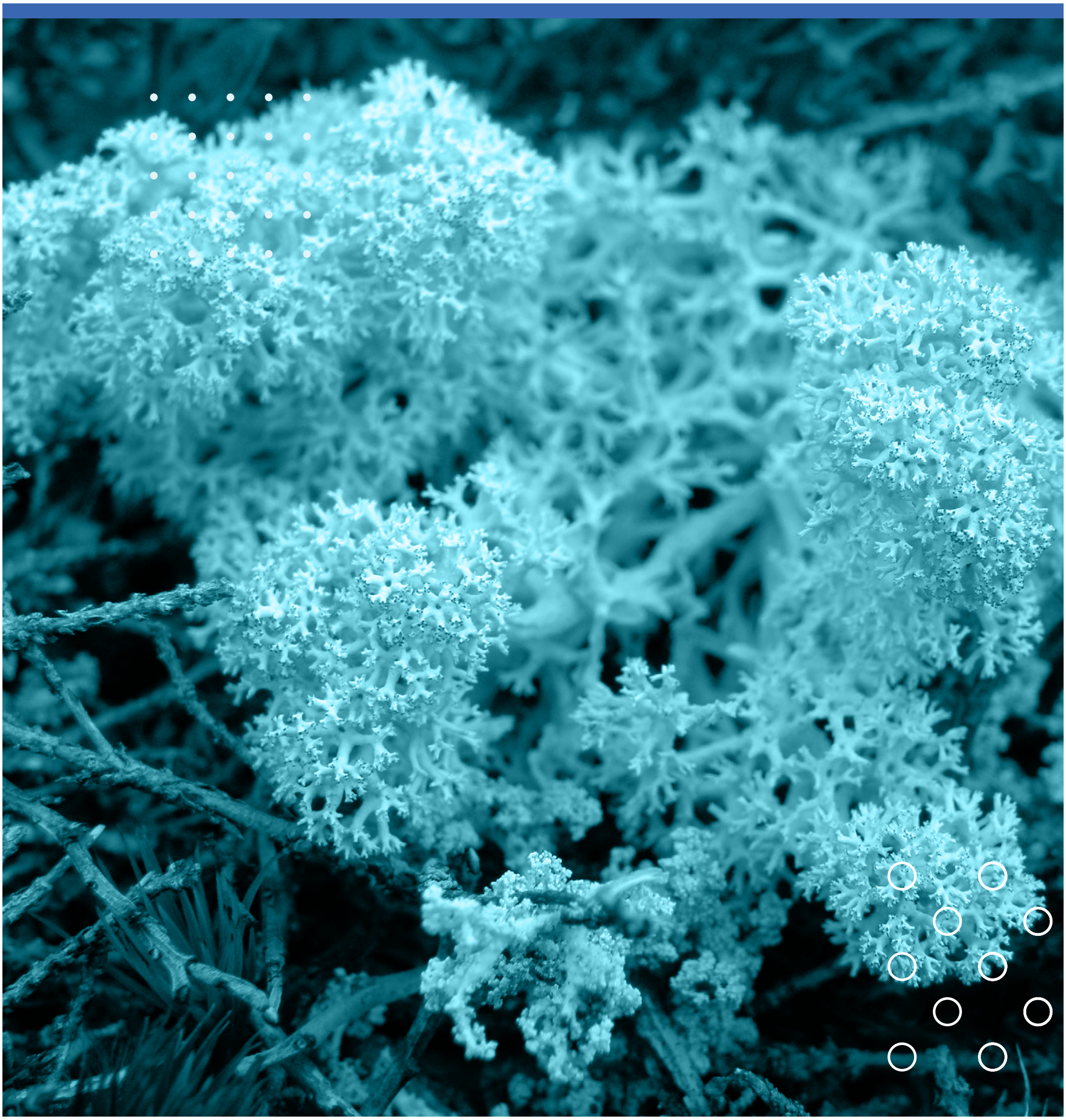
Shea Allison Sundstøl

Ecology of Alpine Lichen Heaths: Relationships Between Vegetation, Soil Temperature, and Edaphic Factors in Southern Norway



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“*Objective truths exist outside of your perception of reality, such as the value of pi; E=mc*^{2}*; Earth's rate of rotation; and that carbon dioxide and methane are greenhouse gases. These statements can be verified by anybody, at any time, and at any place. And they are true, whether or not you believe in them*.”

-Dr. Neil deGrasse Tyson, “What Science Is, And How And Why It Works”, 2015

Summary

Alpine lichen heaths are found on nutrient-poor and deep soils in the mountain plateaus in southern Norway. These are generally characterized by terricolous or so-called “mat-forming” lichens dominated by those in the genera *Cladonia* and *Flavocetraria*. Lichens, technically speaking, are not plants; instead, they are a symbiosis between a fungus and a photosynthetic alga or cyanobacterium. They are an important component of the mountain vegetation community and are chiefly known for their importance as the winter forage for reindeer (*Rangifer tarandus*). Several studies have shown decreases in lichens throughout their range, and these declines are usually attributed to a combination of overgrazing, nitrogen deposition, and a mixture of direct and indirect effects of climate change. Lichens are also poor competitors and are quickly pushed aside by faster-growing, taller vascular species. As such they are usually found on sites with little to no competition from vascular plants.

This study was established to investigate the relationships between snow, soil temperatures, soil properties, and vegetation in areas with differing climates, with a particular emphasis on lichen-dominated communities. Three mountain areas were chosen along a climactic gradient from a semi-oceanic area in the southwest to a semi-continental area in the northeast. Transects of varying length were laid out across the landscape, following the local topography from windy, generally snow-free ridges down to early snowbed communities. Vegetation analyses were performed using 2X2 meter subplots randomly placed within subjectively chosen plots located in areas of heterogeneous vegetation along the transects. Soil temperatures were recorded at 5 and 30 cm below the surface in the plots. The soils in the subplots were also sampled to a depth of ca. 10 cm, and three soil profile pits were excavated at each study area to aid in characterizing the soils and growing conditions at these areas.

Daily average soil temperatures at 5 cm over a period of 33 months were used in the analyses and were compared to vegetation composition using both regression and ordination analysis. Several composite ecological variables based on soil temperatures were defined and compared to vegetation abundances. These included growing season start, end, and length; number of days with soil temperatures below 0° C; the amount of time it took for the soils to thaw completely, frost sum, and heat sum. The soil samples from profiles and from subplots were analyzed for pH, percent carbon (C), nitrogen (N), and organic matter (OM) along with concentrations of plant available phosphorus (P), potassium (K), magnesium (Mg), and calcium (Ca). These data were also compared to both soil temperature and vegetation data.

Lichen-dominated plots were generally characterized by seasonally frozen soils with low concentrations of N, P, K, and Mg. The analyses showed a strong correlation between lichen abundances and soil temperatures. Lichens were dominant on sites where the soils were coldest, and were scarcest where soil temperatures were above freezing throughout the year. Additionally, lichen-dominated sites had lower mean daily soil temperatures throughout the year. This is most likely due to a combination of their high albedo and the insulating effect of the lichen vegetation itself, which forms thick mats comprised of living tissues at the top and dead and decaying tissues at the bottom. There were also a number of correlations between vegetation abundances and the composite ecological variables. Differences were found at both the species and functional group level and shows the importance of soil temperatures for the vegetation distribution pattern.

Climate models for southern Norway predict increasing precipitation throughout the year, increased snow depths in mountain areas, and shortened snow seasons – a more oceanic climate. These changes could affect vegetation abundances primarily due to the effects of snow on soil temperature patterns. Lichen species and other vegetation types that rely on frozen soils could face increasing competition and a reduction of suitable habitat. This work has shown the importance of seasonally frozen soils to vegetation distribution patterns in alpine areas.

Abbreviations

DCA: Detrended correspondence analysis

FD: Frost days

FS: Frost sum

GLMM: Generalized linear mixed models

GSL: Growing season length

GSS: Growing season start

HS: Heat sum

LM: Linear model

LOI: Loss on ignition

MAT: Mean annual (soil) temperature

NMDS: Non-metric dimensional scaling

OM: Organic matter

PCA: Principal components analysis

RDA: Redundancy analysis

SGS: Start of growing season

TD: Thaw date

WASI: Weighted average snow index

WT: Warming time

Main Aims

We assume that soil temperatures differ on two scales: locally, along topographical gradients, and between distant areas with differing climate patterns and mineralogy. We also assume that the differences in soil temperature patterns will be related to observable changes in vegetation community along snow-depth gradients. Based on these assumptions, this study had the following main aims:

1. To describe and quantify the vegetation composition along snow-depth gradients at three alpine sites with differing climactic conditions and geology.
2. To identify the relationships between snow, soil temperatures and vegetation distribution patterns at both the species and functional group levels.
3. To identify the relationships between snow, soil temperatures and edaphic factors such as soil texture and fertility in nutrient-poor alpine areas.
4. To describe and compare soil profiles in different alpine areas.

List of Articles

Article 1

Sundstøl, S. and A. Odland. 2017. Responses of alpine vascular plants and lichens to soil temperatures. Annales Botanici Fennici 54: 17-28.

Article 2

Sundstøl, Shea Allison and Arvid Odland. 2018. Importance of soil temperatures and snow for the distribution of different alpine plant functional types. Submitted.

Article 3

Sundstøl, S. A. Odland, and L. Semb Vestgarden. 2018. Soil differences along topographical gradients and relationships between soil temperatures and N, P, and K. Manuscript.

Article 4

Odland, A., S. Sundstøl, and D. K. Bjerketvedt. 2018. Alpine lichen-dominated heaths: ecology and effects of reindeer grazing and climate change. A review. Oecologia Montana 27(2)(*Author's proof provided*).

Summary of Articles

Article 1: Sundstøl, Shea A. and Arvid Odland. 2017. Responses of alpine vascular plants and lichens to soil temperatures. Annales Botanici Fennici 54:17-28.

In this article we describe the relationships between soil temperatures (expressed as several soil temperature variables) and several commonly-occurring species of vascular plants and lichens in alpine areas. Soil temperatures are important and are often overlooked in studies of plant ecology; vegetation abundances and growing conditions are often described in terms of air temperatures. In the case of vascular plants, however, this does not take into account the plant biomass that lives below the surface and which is only indirectly affected by air temperatures. The variables were created to summarize both warm- and cold-season conditions. The most important result we found was the highly significant relationship between lichen species and frost sum. The coldest plots were dominated by lichen species such as *Flavocetraria nivalis* and *Bryocaulon divergens*, while those with milder soil temperatures were dominated by vascular plants such as *Vaccinium uliginosum* and *Nardus stricta*. Winter soil temperature variables were much more important than spring or summer temperature variables. The next most important variable was thaw time, which is the amount of time for the soil to transition from a frozen state to temperatures that are associated with plant growth. There were both positive and negative responses in several species to increases in the amount of time between soil thaw and start of the growing season. Some of the most common alpine plant species, such as *Betula nana*, could not be correlated to soil temperature patterns. Changes in soil frost patterns can affect the distribution of species, dependent upon their relationship with cold soils.

Article 2. Sundstøl, Shea Allison and Arvid Odland. 2018. Importance of soil temperatures and snow for the distribution of different alpine plant functional groups. Submitted.

In this article the relationships between vegetation functional groups and the soil temperature variables created in Article 1 were investigated. In this article we also included the snow index, which is based on plants' tolerances to snow cover. Groups of morphologically similar plants have long been used to describe and classify sites, as it can be assumed that plants within the groups will have similar responses. We grouped the vegetation species identified on the sites into five functional types; we were in this way able to include species that were excluded from the previous article because they only occurred at one of the study areas. We confirmed that lichens are most common on sites with more than 150 days of frozen soils and little snow cover, and that shrubs generally respond positively to increasing soil temperatures, although there were exceptions among individual species in each group. Ordination analysis revealed four different, nearly orthogonal response patterns to soil frost and thawing time; these responses were closely related to the functional type. The snow index was also related to the soil temperature variables, which was interpreted as a confirmation of the soil temperature/vegetation community relationship. Increases in snow depth in alpine areas can therefore contribute to the reported increases in shrub abundance in alpine areas and lead to decreasing lichen abundances.

Article 3. Sundstøl, Shea Allison, Arvid Odland, and Live Semb Vestgarden. 2018. Soil differences along topographical gradients and relationships between edaphic factors, vegetation, and soil temperatures. Submitted.

In this article the relationships between soil physical and chemical properties and soil temperatures were investigated, and the characteristics of soils beneath lichen-dominated vegetation were described. We have also described soil profiles at each of the three study areas and compared our findings to previous studies of alpine soils. We sampled soils from each of the vegetation plots (n = 38), and have also excavated three soil profile pits at each study area, chosen along the topographic snow-depth gradient to represent the three most common vegetation community zones. The soils at all three study areas have coarse textures and can be classified ranging from sand to loamy sand. They had well-developed profiles with distinct organic horizons at the surface. Many of the profiles had characteristics typical of podzols, which are associated with acidic, oligotrophic, coarse-textured soils, including a distinct white eluviated horizon just below the organic horizons. There were differences in plant-available nutrient ions in the vegetation plots between the study areas, which were related to the relative coldness or warmness of the soils in the area. Warmer soils had generally higher levels of N, P, K, and organic matter.

Article 4: Odland, Arvid, Shea Allison Sundstøl, and Dag Kjartan Bjerketvedt. 2018. Alpine lichen-dominated heaths: ecology and effects of reindeer grazing and climate change. A review. Accepted by Oecologia Montana.

In this article the ecological basis for alpine fruticose lichen vegetation distribution is reviewed in detail. Previous research has often led to the a number of explanations for the distribution and extent of lichen heaths. The most common conclusion is that they appear on sites that are uninhabitable for other species due to shallow soils or a lack of moisture. With this article we challenge this assumption after describing in detail the ecological conditions most favorable to lichen heaths and discuss some of the biggest challenges facing these habitats. We propose that it is soil temperature, and more specifically soil frost, that is the most important determinant of the extent of lichen heaths. The most common challenges to lichen heaths come from reindeer grazing and trampling, and from climate changes. Most climate models for southern Norway predict an increase in snow accumulation in alpine areas, which would lead to increases in winter soil temperatures. Our research, combined with other studies, has shown that the strongest predictor of lichen heath extent is a period of extended soil frost followed by a long thaw period. These conditions occur only in the absence of snow.

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1. Introduction

Mat-forming lichens are one of the most ubiquitous and characteristic vegetation types in Fenno-Scandinavian mountain areas. They occupy and often dominate sites that are otherwise inhospitable for most other vegetation. In the past there have been many explanations as to why lichens are found where they are: on wind-swept ridges with little snow cover. With this study the relationships between lichens and their habitat is explored in detail. Vegetation distribution and abundance along snow-depth gradients is compared to soil temperatures and edaphic factors in three different mountain areas, which were chosen to represent differing climate patterns and geology.

1.1. Biology of Terricolous Fruticose Lichens

Lichens are one of the most common life forms on the planet, and can be found in nearly every type of habitat. Lichens exist as a symbiosis between a fungus (called the *mycobiont*) and either an alga or cyanobacteria (called the *photobiont*) (Holien & Tønsberg, 2008). The mycobiont provides a growth structure and protection to the photobiont, which in turn contributes energy to the lichen symbiosis via photosynthesis. Lichens can be grouped into roughly 16 different biogeographic patterns (Galloway, 2008) and are found at altitudes and in environments that exclude vascular plants (Körner, 2003). They can grow and metabolize in near-freezing temperatures as long as light is available (Klein & Shulski, 2011). The poikilohydric nature of lichens means that they can survive being completely desiccated (Nash, 2008) and quickly re-hydrate and photosynthesize when exposed to moisture from rain, fog, or dew (Green et al., 2008). The disadvantage of poikilohydry is that during warm, sunny, and dry conditions the lichen dries out and becomes dormant (Klein & Shulski, 2011) while rooted plants are limited by soil water availability rather than atmospheric humidity (Dahl et al., 1998). However, the thallus (body) of some species of mat-forming lichens has a very large surface area and a low ratio of surface area to volume which can help to inhibit water loss (Longton, 1988). Terricolous lichens are only loosely situated upon their substrate; they have no roots nor any other permanent attachment to their substrates such as other groups of lichens (e.g. epiphytic or saxicolous) have. Fragments of desiccated lichens are often distributed by wind or animals, which can lead to colonization of new areas where conditions are favorable (Büdel & Scheidegger, 2008).

1.2. Lichen Ecology in Scandinavia

Lichens often dominate the surface of boreal and tundra ecosystems (During & Tooren, 1990) and as a consequence are commonly associated with permafrost and/or carbon-rich soils (Zimov et al., 2005; Schuur et al., 2008; Tarnocai, 2009). A well-developed lichen mat strongly affects the moisture and thermal regimes of forest soils by maintaining soil moisture at or near field capacity throughout the growing season which reduces drought stress (Kershaw, 1985; Bonan, 1989; Bonan & Shugart, 1989). The lichen mat's high reflectivity and low thermal conductivity block the flux of heat into the soil, reducing soil temperature during summer and dampening daily temperature fluctuations (Kershaw, 1985).

Lichen-dominated communities can be found both in alpine areas and in forests. Lichens are common throughout the Norwegian lowlands and are often associated with both pine (*Pinus*) and spruce (*Picea*) forests. In both forest types lichens are often the dominant ground cover in areas with sandy, drought-prone, and nutrient-poor soils (Fremstad, 1997; Bjerkely, 2008). The presence of lichens, primarily from the *Cladonia* genus, gives the forest floor a characteristic yellow-white color (Fremstad, 1997). According to Ahti & Oksanen (1990), lichen-rich boreal forests are dependent upon three factors: edaphic requirements, zonal variation, and successional stage. The edaphic requirements refer to oligotrophic sites, while the zonal variations describes the regional and topographic characteristics where lichen-rich forests occur. Successional stage refers to the degree and frequency of disturbance and type of management activity of these forests. Lichen communities in these forests also have their own successional patterns and relationships to other vegetation (Ahti & Oksanen, 1990).

Lichen-dominated alpine heaths are primarily found in the eastern and central parts of Norway where a drier, more continental climate is the norm (Löffler, 2005; Holten & Aune, 2011). The distribution of individual lichen species is very dependent upon climatic variables such as temperature and precipitation (Ahti, 1999). Terricolous species including those from the genera *Cladonia*, *Cetraria*, *Flavocetraria*, and others dominate in these heaths in Scandinavia (Ahti, 1999). Many of these including *Cladonia arbuscula* and *C. rangiferina* are best known as the main winter forage for reindeer across their range (Stenroos et al., 2013). Lichens are a reflection of the conditions of their environments (Flock, 1978) and can be used as indicators of winter conditions such as snow depth. They are often classified (as are other alpine vegetation types) on a scale ranging from strictly chinophobous (snow-hating) to strictly chinophilous (snow-loving) (Gjærevoll, 1956; Dahl, 1957). Chinophobous species are generally found on windswept, snow-free ridges and can tolerate stresses such as wind erosion and drought. Species commonly found on these sites in calcium-poor areas include *Alectoria ochroleuca*, *A. nigricans*, *Flavocetraria cucullata*, *F. nivalis*, and *Bryocaulon divergens*. Vascular plant species common to these sites include *Empetrum nigrum* and *Loiseluria procumbens*. *C. arbuscula* and *C. rangiferina* are in general slightly less chinophobous and tolerate minimal snow cover. At the lowest points on the landscape where the snow takes the longest to melt, chinophilous lichen species such as *C. bellidiflora* and *C. ecmocyna* and the grasses *Nardus stricta*, *Anthoxanthum odorata*, and *Deschampsia flexuosa* are commonly found (Gjærevoll, 1992; Fryday, 2001; Löffler, 2003; 2005; Odland & Munkejord, 2008a). Lichen biomass varies across a snow-depth gradient and is highest in areas that are snow-free in mid-April; biomass is also affected by precipitation and is lowest in areas with where mean exceeds 900 mm yr $^{-1}$ (Odland et al., 2014). Myrvold (2013) found that the lichen biomass was generally highest in plots with an average snow index (SI) value between 1.5 and 2.0.

1.3. Variations in Lichen Abundances

The local abundance of lichens in alpine heaths can be highly variable due to effects of different environmental factors. These include competition from vascular plants and grazing pressures. Lichens are poor competitors, and are most abundant in areas where the mean canopy height of all vegetation is about 5 cm (Crabtree & Ellis, 2010). Numerous studies have shown that increasing the temperature of vegetation plots leads to an increase in the growth of vascular plants, to the detriment of lichens (Cornelissen et al., 2001; Epstein et al., 2004; Turunen et al., 2009). At sites in the western Canadian Arctic lichens have decreased by an average of 24% and are being replaced by woody shrubs and other vascular plants (Fraser et al., 2014). An increase in tall shrub cover can also lead to an increase in forbs, to the detriment of lichens and other shade-intolerant species (Pajunen et al., 2011). Shrub vegetation is increasing not only in abundance but also in size (Crabtree & Ellis, 2010). In a study by Klanderud (2008), which simulated environmental changes, the five most common lichen species decreased in abundance, and in some cases disappeared completely as a result of a combination of increased temperature and nitrogen inputs. Lang et al. (2012) reported a decrease in lichen abundance with increasing temperature at study sites in Alaska and Sweden. Lichens are most competitive in areas where vascular plants cannot grow because of extended periods of drought in the growing season and of frost in the winter.

Lichens are also very susceptible to grazing and trampling pressures (Heggenes et al., 2017), and have declined or disappeared in sites with heavy reindeer traffic (Virtanen et al., 2003). Whereas vascular plants retain their root system which allows for quick regeneration post-grazing, the lichen is often completely devoured (Heggberget et al., 2002) leaving nothing behind to repopulate the site. Klein & Shulski (2009; 2011) found that climate changes including changes in temperature, precipitation, and fog patterns, coupled with a fertilization effect from reindeer droppings had hindered lichens from re-establishing on overgrazed, previously reindeer-free, lichen-rich Arctic islands. Fruticose lichens have also been significantly reduced in mountain birch forests in

Finnmark, where grazing pressures and milder, icier winters have depleted once-common species (Tannheiser et al., 2005); they predicted that, if current conditions continued unchanged, only half of the previous lichen cover could return. Grazing by reindeer has also been shown to have a positive effect on tree growth in forests with thick lichen ground cover (Fauria et al., 2008) by increasing the spring soil temperatures and effectively lengthening the growing season under the lichen-free soils. Tømmervik et al. (2004) found similar increases in birch forests due to the removal of the "lichen barrier" which had previously inhibited seedling establishment and growth. Trampling by reindeer has also been linked to losses in lichen abundance, but Heggenes et al. (2017) have found that both humidity and lichen species play an important role, with some species being more resilient than others.

1.4. Plant Functional Types

Vascular plants, lichens, and mosses employ a number of strategies to successfully co-inhabit their environments (Snapp, 2017). This leads to assemblies of plants that share similar traits, which are generally called functional types. Plants can be sorted into functional types based on any number of traits, including growth form, reproductive strategy, photosynthetic pathways (C3 vs. C4), and stress tolerance (Snapp, 2017), while a trait can be defined as a characteristic that is independent of the environment and which can be measured or evaluated in individuals (Violle et al., 2007). These types, and their occurrences and abundances on the landscape, can then be used to make generalizations about ecosystems, their functioning, and their characteristics (Diaz et al., 2004). Using functional groups when describing communities or environments has a number of advantages, including a reduction of "high-dimensional species space" (Laughlin, 2014); analyzing groups instead of individual species allows for a more general description of an area, since many individual species can perform the same role. Another advantage is that the traits used to assign species to types are easily and quickly measured, enabling a wider range of sites to be included in analyses, and that different traits can be used according to the aims of each study (Cadotte, 2017).

1.5. Present and Future Climate in Southern Norway

Several factors influence the Norwegian climate. Among these the most important are the Gulf Stream and proximity to the Atlantic Ocean, which keeps Norway significantly warmer than other areas at the same latitude, such as Siberia and the Alaskan interior (Tikkanen, 2005). In Norway, mean annual temperatures have increased by between 0.5 and 1.5 degrees C in the last 130 years (Hanssen-Bauer, 2005) with the most dramatic increases occurring in the past 4 decades; the increases were greatest in the spring and fall seasons (Klimaservicesenter, 2015). Minimum temperatures are increasing more rapidly than average daily temperatures (Klimaservicesenter, 2015). Some climate models predict an increase in mean October temperatures at high altitudes, which could lead to delayed autumn snows (Benestad, 2004). Increases in autumn precipitation have contributed to the general trend of increasing annual precipitation in southern Norway (Moberg et al., 2005).

High-elevation sites are also expected to see an increase in winter precipitation leading to increased snow cover in southern Norway, while lowland sites will have a reduction in snow cover (Hanssen-Bauer et al., 2003; Klimaservicesenter, 2015). Dyrrdal et al. (2013) report that despite decreases in snow cover in lower-altitude areas, snow depths were increasing in mountains in southern Norway due to increases in winter precipitation and air temperatures. Snow depth increases of about 2 cm per decade since the early 1900s have also been recorded at Abisko in northern Sweden, despite there being no changes in snow season duration (Kohler et al., 2006). In alpine environments, this has led to a shift towards an oceanic climate and an increase in species that prefer moist habitat (Odland et al., 2010). While snow cover is generally highly variable in Scandinavia, there have been increases in the duration of winter snow cover in the Norwegian mountains resulting from increases in precipitation and winds from the west (Moberg et al., 2005).

1.5.1. Growing Season Length

Growing season length has been defined and estimated in numerous ways (Odland, 2011), and therefore comparisons between different studies are difficult. It has usually been defined in terms of air temperatures or length of the snow cover season. Moen (1999) has defined it as the number of days with average air temperatures above 5° C. Kollas et al. (2013) defined the growing season as the period after five consecutive days of air temperature above 5°C until there are five consecutive days with temperatures below this threshold in the autumn. However estimating the length of the growing season on air temperatures poses many challenges. One of these is that air temperatures are often measured at 2 meters above the surface, which is well above the canopy of most non-woody plants. Air temperatures at the soil surface can reach as high as 40° C in the summer (Oechel & Van Cleve, 1986) and generally fluctuate more than temperatures higher up. Air temperatures do not take variations in micro-climate into account (Graae et al., 2012) and therefore do not necessarily provide a good estimate of the local growing conditions.

The increasing availability and decreasing cost of remote temperature recorders has led to an increased understanding of the relationships between soil temperatures and plant growth. This has also made it possible to define the growing season based on soil rather than air temperatures which more closely reflect the ecological conditions experienced by plants. Accordingly, there is an increasing body of work that has based the growing season on soil temperature measurements. Reinhardt & Odland (2012) set the growing season as the period from when the soil temperature exceeds 6° in the spring until the temperatures fell below 5° the following autumn. Körner & Paulsen (2004) set a temperature threshold of 3.2° at 10 cm depth below the soil surface. A soil temperature of 5° is widely considered to be a “biological zero” (Rabenhorst, 2005) below which nutrient availability and biological activity are impaired (Holtmeier, 2009). Blume-Werry et al. (2016) found that plants could continue to grow new roots long after above-ground growth had stopped and attributed this in part to the stability and relative warmth of the soil versus the fluctuating air temperatures.

Regardless of how one defines the growing season, there is a consensus (based largely on phenological records) that it is increasing. In Norway, the total area of land with a growing season of more than 6 months has increased from 37,000 to 45,000 km^2 between the reference periods of 1971-2000 and 1985-2014, and is predicted to increase to between 105,000 and 165,000 km^2 by the year 2100 (Klimaservicesenter, 2015). Keyser et al. (2000) reported an average increase in GSL of 2.66 days per decade in forested areas of Alaska and Northern Canada. Walther & Linderholm (2006) used climate data archives from several countries and found that GSL has increased by an average of 19 days across the greater Baltic region.

1.5.2. Relationships Between Snow and Alpine Vegetation

Effects of snow on plants in alpine areas in Scandinavia are well known, primarily due to the studies of Gjærevoll (1956) and Dahl (1957). Snow season duration and snow quantity are among the factors that determine the length of the growing season for a site (Walker et al., 2001). Changes in snow cover can have effects throughout the year. Bjerke et al. (2015) found strong correlations between the number of snow-free frost days and primary productivity in grassland soils. In their models growing season temperatures played little to no role; however, the long thaw time of uninsulated frozen soils delayed the start of growing seasons. Increasing shrub cover can affect snow depth by reducing surface-level wind speeds and creating physical hindrances which stop snow from blowing across the landscape (McFadden et al., 2001), which increases the insulating effect of snow (Myers-Smith & Hik, 2013) leading to alterations in the winter soil temperature patterns at the local scale. Additionally, Jonas et al. (2008) found that the timing of weather changes at the beginning and end of the snow season were important factors in determining vegetation growth patterns. For example they found a two-week lag between snowmelt and the start of vegetative growth; changes in the timing of snowmelt could then lead to phenological changes in alpine species (Jonas et al., 2008).

1.5.3. Snow Effects on Soil Temperature

Winter soil temperature in alpine areas is a function of snow cover, and changes in snow cover directly affect the temperatures of the underlying soils. As with air temperatures, soil temperatures decrease with increasing altitude; however the decrease in soil temperature is slower than for air temperature (Holtmeier, 2009). Several factors, including bulk density, moisture content, texture (Holtmeier, 2009) and others including presence or absence of snow (Löffler, 2005) work together to influence the soil surface temperature. Snow acts as an insulator that influences not only temperature but also the extent to which the soil is exposed to freeze-thaw events (Edwards et al., 2007). The presence or absence of snow explains the large differences in winter soil temperatures between exposed ridge and snowbed sites (Walker et al., 2001) and has long been recognized as a factor influencing vegetation distributions and abundances (Dahl, 1957; 1960). Kullman (2007) reported an increase in maximum and minimum soil temperatures in the Swedish Scandes from 1985-2005; the increase was greater in winter which could be a result of increased snow cover. Qian et al. (2011) also report increases in soil temperatures across most of Canada; the exception was in the easternmost part of the country where decreases in snow cover were leading to colder soils in the winter and spring months. Kaste et al. (2008) recorded significantly lower soil temperatures in sites where snow was removed comparted to sites with intact snow cover or extra insulation against freezing. Local topography can also influence snow distribution and soil temperature patterns. Reinhardt & Odland (2012) identified topographic differences in soil temperature patterns, which correlated with snow distribution and plant community composition.

1.5.4. Lichen and Bryophyte Effects on Soil Temperature

Vegetation and snow cover contribute to the overall energy balance in climate systems, primarily through their effect on albedo which is a measure of the overall reflectivity of a surface. Dark surfaces such as mosses, shrubs, and bare soil have much lower albedo than lighter surfaces such as snow, ice, or lichens. The albedo of lichen-dominated tundra sites is only surpassed by that of ice and snow due in part to the light color of the vegetation (Davies, 1963). Beringer et al. (2005) measured the albedo in tundra sites (with an average of just 18% lichen cover) as 0.19, while Eugster et al. (2000) reported values of 0.16 for dry upland heaths in sub-arctic Alaska. Sites with greater lichen cover should have even higher albedos. Studies have shown that there are differences in albedo on the two sides of a fence along the border between Finland and Norway, with the ungrazed Norwegian ground having higher albedo in the snow-free season due to the higher abundance of lichens (Stoy et al., 2012; Cohen et al., 2013)

Lichens have an insulating effect on the ground (Klein & Shulski, 2011) and there is very little belowground heat transfer under lichen cover compared to other, bryophyte-dominated canopies or in shrub-dominated stands. Soil temperatures are several degrees lower under bryophyte cover (Gornall et al., 2007; Gornall et al., 2011; Myers-Smith & Hik, 2013) and are even lower under lichens due to the combination of insulation and albedo (Klein & Shulski, 2011; Stoy et al., 2012). Soil moisture is also generally higher and evaporation lower in undisturbed lichen stands than in nearby areas where the lichens have been reduced or removed (Peth & Horn, 2006) and lichens can provide a “mulching” effect which can contribute to increased soil moisture during the growing season (Kershaw, 1983). Porada et al. (2016) modelled the cooling effects of lichen and bryophyte vegetation on permafrost soils and found that it was stronger in alpine areas than on other types of terrain and led to lower active layer thicknesses. In areas where the lichen cover has been disturbed or removed, the soils warmed more quickly and soil temperatures decrease earlier than in areas with undisturbed lichen vegetation (Peth & Horn, 2006).

1.5.5. Soil Temperatures and Plant Growth

Soil temperature has a direct effect on plant species composition and can partially explain the distribution of plants in alpine areas (Scherrer & Körner, 2011; Reinhardt & Odland, 2012). Root zone temperature has a strong influence on plant phenology; low temperatures lead to decreases in growth and metabolism of plants and to short growing seasons (Holtmeier, 2009). The most important factor governing plant growth in cold climates occur belowground, meaning that changes in the root zone of plants are more important than those occurring above the soil surface (Ferrari et al., 2016). Increased winter soil temperatures could lead to an increase in N mineralization but there is also a greater chance of N loss through leaching (Schimel & Mikan, 2005). Karlsson & Nordell (1996) found that variations in both nitrogen uptake and growth of mountain birch (*Betula pubescens ssp. tortuosa*) are more strongly affected by increases in soil temperature than by fertilization. Brooker & van der Wal (2003) found significant increases in the above-ground biomass of arctic plants exposed to warmer soils; the increase was greatest in grasses. An increase in soil temperature could have roughly the same effect on seedlings as an increase in nutrient supply due to better root uptake of nitrogen (Weih & Karlsson, 2001). Jägerbrand et al. (2006) found that lichen species diversity decreased in lichen-dominated heaths exposed to increased temperatures and fertilization.

1.6. Relationships Between Alpine Soils and Vegetation

There are many ways in which soils influence the species composition of alpine sites. Studies have shown that lichen-dominated communities are associated with relatively deep soils resting on moraine material (Nordhagen, 1943; Dahl, 1957). There is often a 1-2 cm litter layer upon a humus layer 2-10 cm thick below the lichen surface mats. This can be followed by a bleached soil upon a red or red-brown horizon. These soils are often limited in fertility and are generally acidic. Factors such as pH, N and P availability, and moisture content can be decisive. Soil pH is possibly the most important (Gough et al., 2000) since it can affect the availability of nutrient ions. Arnesen et al. (2007) found that P availability was second only to pH in importance in describing floristic gradients in mountain areas in Troms, northern Norway. Lichens are adapted to growth in N-limited areas and are quickly outcompeted in areas where N levels are higher (Hauck, 2010). Factors such as precipitation and the presence/absence of snow have also been shown to have an influence on alpine soils. Reinhardt & Odland (2012), working in calcium-rich sites, found a strong correlation between snow, soil temperature, soil fertility, and vegetation. Vegetation cover can also have an influence on soil fertility; DeLuca & Zackrisson (2007) found that soils growing under juniper (*Juniperus communalis*) had higher concentrations of nitrogen than surrounding soils. Lichen litter can also contribute to podsol development in alpine areas (Stützer, 1999), a process which was earlier believed to occur only in forested areas.

Topography along the ridge-snowbed gradient also affects the availability of water and nutrients. Litaor et al. (2005) found that P availability was highest in relatively flat snowbed sites. Odland and Munkejord (2008b) found that, on poorer sites, snowbed soils tended to have a higher pH value than soils elsewhere along the ridge-snowbed gradient. Yao et al. (2013) found significant differences in both C and N across snow-depth gradients in alpine areas. Onipchenko et al. (1998) found that, on the landscape scale, decreases in vegetation diversity and soil fertility were related, but the relationship was negligible at the plot scale. Theodose & Bowman (1997) found that species diversity increases with nutrient additions to poor sites while Natali et al. (2012) found that winter warming led to higher N availability. Higher soil temperatures in winter can also increase leaching of inorganic N compounds during snowmelt (Kaste et al., 2008).

2. Study Areas and Methods

2.1. Study Areas

Three mountain areas in southern Norway were chosen: Haukeli, Imingfjell, and Lesja (Figures 1-4). The study sites were selected to include some geographic distance and different climate conditions. According to Moen (1999), Haukeli lies within a weakly oceanic section, Imingfjell in an indifferent section, and Lesja in a slightly continental section.

Figure 1: Study area locations.

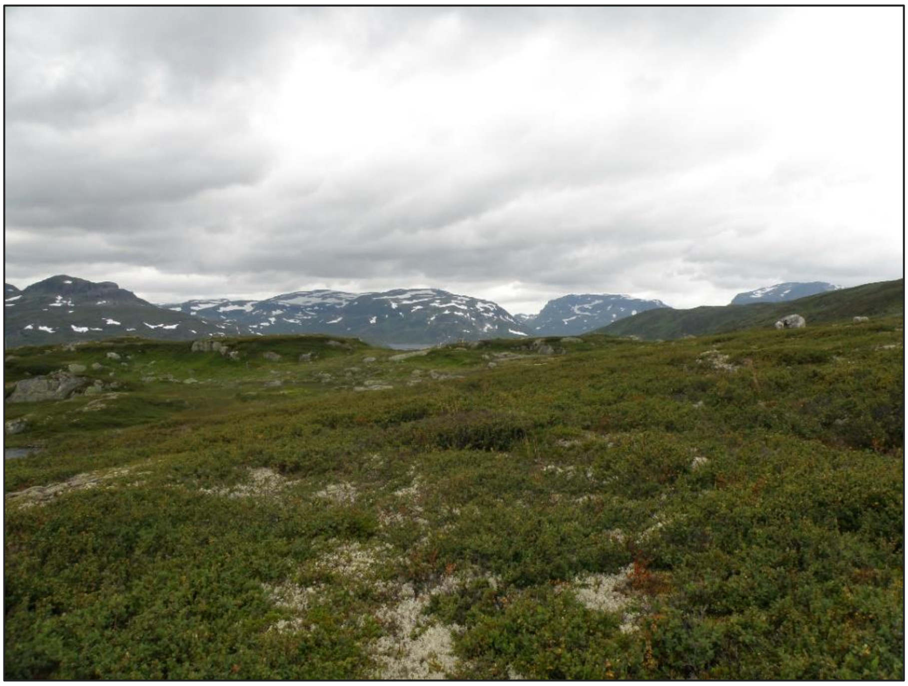

Figure 2: The Haukeli study area.

Figure 3: The Imingfjell study area.

Figure 4: The Lesja study area.

2.2. Vegetation Sampling

In each area, 3 or 4 main gradients were subjectively selected where the vegetation changes indicated major variations in snow accumulation patterns. Vegetation gradients are often divided into six zones (Odland & Munkejord 2008b, Halvorsen, 2015): 1- exposed heath, 2- snow protected heath, 3- lee-side, 4- early snow bed, 5- late snow bed and 6- extreme snow bed. Lichens are mainly confined to the first four zones; therefore sampling was limited to these. The distribution limits of the different zones could be identified by their characteristic species or species groups (plant functional types).

The gradients were analyzed along mountain slopes starting with exposed lichen-dominated heaths, and continued downwards in elevation through the different vegetation communities. 3 or 4 sampling plots were selected along each gradient, depending upon the rate of vegetation change (Table 1). A stratified sampling procedure where one sampling plot was selected within each vegetation zone was applied

Table 1. Gradient length, location, and elevation change for all three study areas. Areas beginning with H = Haukeli, I = Imingfjell, and L = Lesja; the gradients were named A-D.

Study area gradient name	Gradient length (m)	Top coordinates (UTM)	Bottom coordinates (UTM)	Top elevation (masl)	Bottom elevation (masl)
		Haukeli			
HA	91.4	59.814194, 7.218694	59.814472, 7.218278	1055	1048
HB	70.9	59.814694, 7.219167	59.814889, 7.218556	1052	1050
HC	92.9	59.814861, 7.220139	59.814972, 7.220972	1055	1051
HD	47.8	59.814139, 7.221833	59.813833, 7.221528	1054	1048
		Imingfjell			
IA	42.6	60.187472, 8.577722	60.187111, 8.577861	1153	1145
IB	111.4	60.188778. 8.582389	60.189583, 8.581778	1159	1155
IC	36.9	60.194333, 8.572278	60.194028, 8.572417	1178	1174
ID	75.9	60.189028, 8.573361	60.188528, 8.573833	1152	1140
		Lesja			
LA	236.0	62.036278, 8.968000	62.027583, 8.966306	1230	1218
LB	235.0	62.025917, 8.967194	62.024556, 8.965556	1228	1203
LC	256.8	62.022611, 8.970833	62.022889, 8.968528	1234	1216

(Figure 5). Distributions of the vegetation zones were highly variable both within and between the gradients, mainly due to differences in slope and aspect. A list of coordinates for every plot and distance matrices in meters can be found in the supplementary information section (§6).

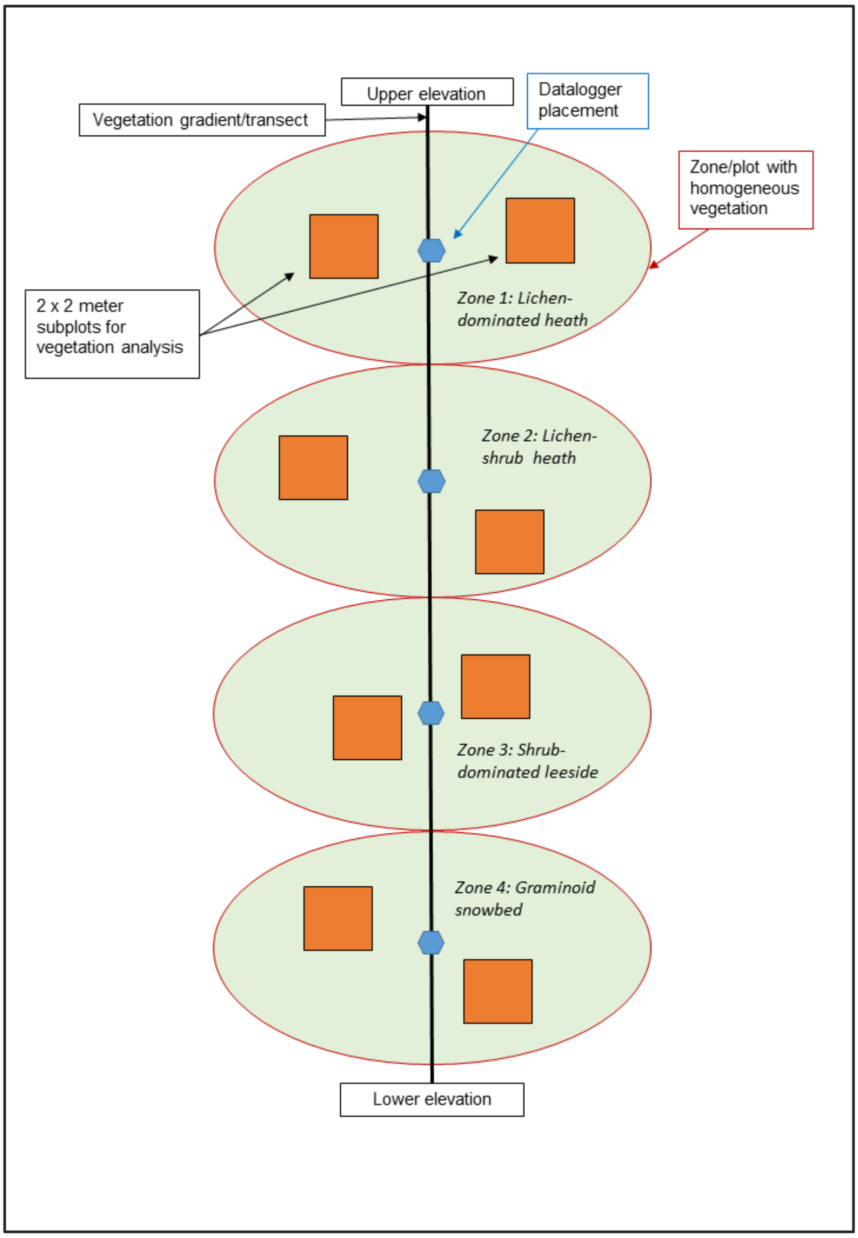

Figure 5: Schematic diagram showing the layout of transects, plots, and subplots, and placement of soil temperature recorders. The diagram is not to scale and is for illustration purposes only. Dataloggers were placed approximately in the center of the homogeneous zone, and vegetation analysis was carried out in 2 x 2 m. square plots located between 50 and 100 cm of the dataloggers.

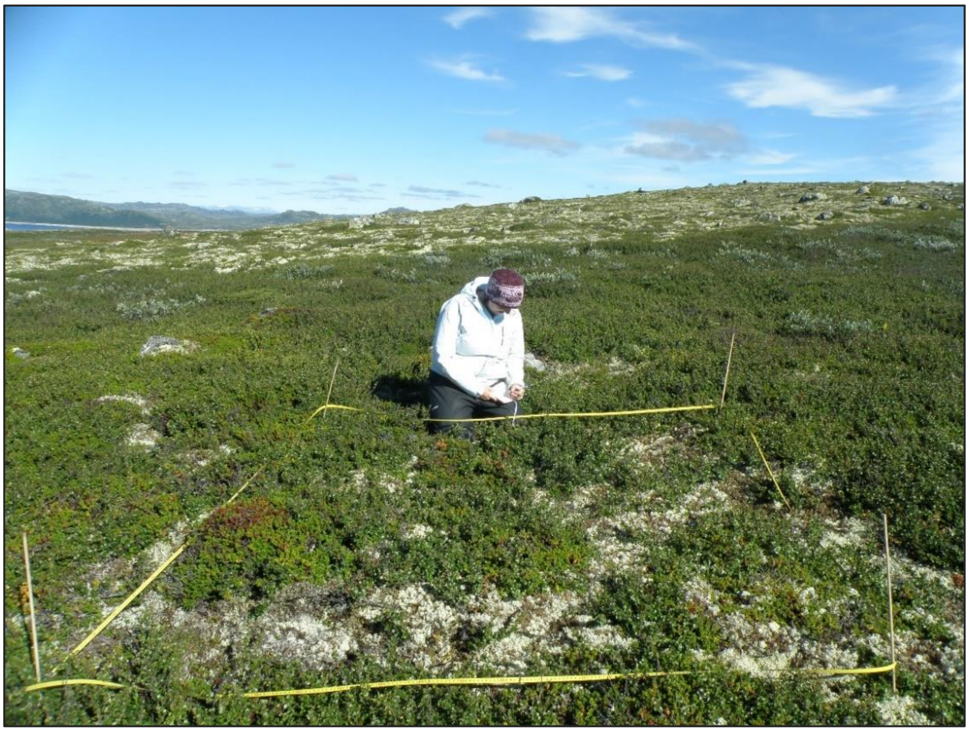

Figure 6: Vegetation analysis.

Vegetation analyses were performed in July, 2012 and 2013 (Figure 6) using two subplots measuring 2 X 2 meters, which were placed within 50 to 100 cm of the soil temperature recorders (§2.3). Only the vegetation analyses performed in 2013 were used. Vascular plants, terricolous lichens, and the most common mosses were identified, and their abundances were visually estimated in percentage. The total abundances of species belonging to five growth forms (lichens, mosses, shrubs, graminoids, and herbs) were also estimated. The observations from the two subplots were averaged to better capture the variation in community composition within the plots. Plant taxonomy is based on Mossberg et al. (2007); lichen taxonomy is based on Holien & Tønsberg (2008).

2.3. Soil Temperature Recording

LogTag© TRIX-8 temperature recorders ("dataloggers") (measuring range -40° to +85° C, resolution 0.1°) were packed into plastic freezer bags and installed in every plot at ca. five and 30 cm below the soil surface (Figure 7). The dataloggers were placed horizontally to minimize the disturbance to the soils above the recording sites. Soil temperatures were recorded at six-hour intervals (01:00, 07:00, 13:00, 19:00). One air temperature recording station was installed at each study area (Figure 8). Air temperatures were measured hourly at two m height using a Geotest and

Figure 7: Placement of a datalogger in the soil.

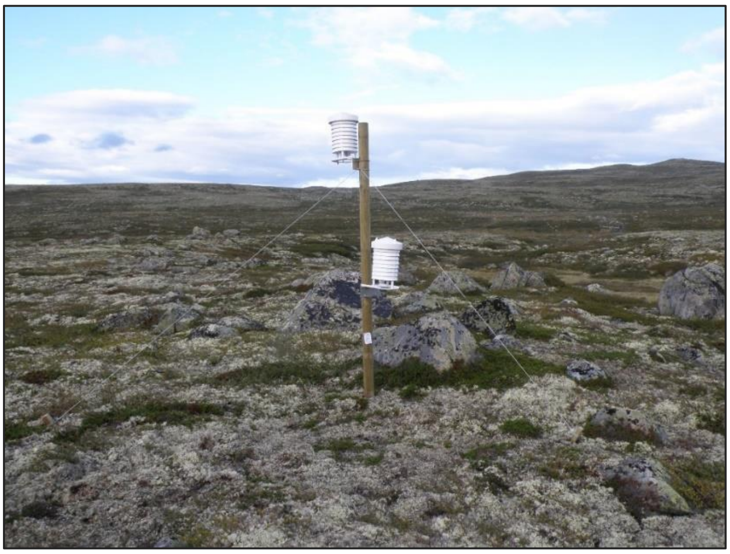

Figure 8: Air temperature recording station. Air temperatures were measured at 2 m; air temperature and relative humidity were recorded at 1 m. This station is at the Imingfjell study area.

SLF™ UTL-3 Scientific Datalogger (measuring range -30° to +40° C, accuracy 0.1° at ±20° and 0.2° at ±40°, resolution <0.1°). Air temperature and relative humidity (RH) were also recorded at one m above the surface using a LogTag™ Haxo-8 temperature and humidity recorder (measuring range 0-100% RH and -40° to 85° C, resolution 0.1% RH and 0.1° C). Buried dataloggers were replaced each summer; above-surface dataloggers were downloaded onsite and re-installed. Soil temperatures recorded at 5 cm between the 1st of October, 2011 and the 31st of July, 2014, (a total of 34 consecutive months) were used in the analyses; air temperature, humidity, and 30 cm soil temperature recordings were not used. Readings taken before or after this period (hereafter referred to as the "measurement period") were discarded. This gave us 4,140 individual readings of soil temperature per plot. The temperature readings from each plot were merged to give a continuous record over the entire analysis period. Temperature measurements were averaged to give a single measurement for each 24-hour period; these daily means were used in analyses. Temperature analyses and results are based upon data from the entire analysis period, which helped to minimize the effects of year-to-year variations in temperatures.

2.4. Soil Sampling and Analysis

Soil samples were collected in July, 2012. One sample was collected from the top 10 cm of mineral soils from each vegetation plot along the main gradients using a small shovel. These samples were then bulked, which resulted in one soil sample for every plot; there was a total of 38 soil samples from the vegetation plots.

Three soil profiles (Figure 9) located along extra gradients at each study area, for a total of 9 profiles. These were dug to a maximum depth of one meter or until bedrock or undifferentiated parent materials were reached. The profiles were located at three landscape positions as determined by vegetation community change; one profile in a lichen-dominated heath, one in a lichen-shrub heath or shrub-dominated leeside, and one in a graminoid snowbed. Soil samples were taken from each horizon and returned for analysis. There was a total of 39 samples taken from the soil profiles at the three study areas. The soil samples, both those from the vegetation plots in the main gradients and the horizons in the extra gradients, were dried at 105° then sifted and crushed to remove large stones and coarse woody debris prior to analysis. Organic matter content was determined by the loss on ignition technique at 550° C. Analyses of plant-available ions (P, K, Mg, and Ca) in the mineral soils were performed by the Soil Testing Laboratory at Telemark University College (now the University of South-Eastern Norway) by ammonium lactate extraction (Egnér et al., 1960) and atomic absorption spectrophotometry. Soil particle size distribution was analyzed using a laboratory sieve shaker. Sieve sizes were: 4.0 mm, 2.0 mm, 1.0 mm, 0.5 mm, 0.25 mm, 0.125 mm, and 0.063 mm. Texture class was assigned using an Excel macro downloaded from the United States Department of Agriculture Soil Conservation Website and were calculated without the 4.0 mm fraction. pH was measured on a 1:2.5 V/V water solution using a Hanna Instruments™ 8417 pH Meter. Total C, N, and H were analyzed by the Soil Testing

Figure *9*: One of the soil profiles that were excavated; this one was at Imingfjell.

Laboratory at The Norwegian University of Life Sciences at Ås using a LECO™ TruSpec CNH. Texture class determinations were made using an Excel download provided by the United States Department of Agriculture Natural Resources Conservation Service website.

2.5. Data Analysis

Statistical analyses (with the exception of some ordinations) were performed using R version 3.2.5. (R Core Development Team, 2016.). Ordinations were performed using CANOCO version 5.0 (Ter Braak & Smilauer, 2012) and using the vegan version 2.5-2 package in R (Oksanen et al., 2018). Generalized linear mixed models were performed using the lme4 package (Bates et al., 2015). R software was also used to create maps, distance matrices, and figures.

2.5.1. Analysis of Vegetation Data

Vegetation data for individual species were analyzed using Nonmetric Multidimensional Scaling (NMDS) on two axes with Bray-Curtis distance measures. The results of the NMDS were then rotated to Principal Components Analysis (PCA) axes for visualization. NMDS was performed on untransformed abundance data to identify similarities among species along environmental gradients; only species that occurred on at least two of the three study areas were included in the NMDS ordination, and the percent cover was averaged for the two subplots prior to analysis. A Detrended Correspondence Analysis (DCA) was also performed on the species data, again to detect similarities along gradients and to confirm the results of the NMDS, and again using only species that occurred at least two of the three study areas. Species abundance data were square-root transformed for DCA analyses. The two ordinations (unrotated NMDS and DCA) were then compared using Procrustes rotation, a process where two different ordinations are rotated to match configurations as best as possible (Ter Braak & Smilauer, 2012). With Procrustes rotation, a disagreement measure between 0 and 1 is given, with zero meaning that there is no disagreement between ordinations and 1.0

indicating complete disagreement. This procedure allows for verification and confirmation of the ordination results. Axes from the two ordinations were also compared via Pearson correlation tests. Abundances of the plant functional types were analyzed by Principal Components Analysis (PCA) with soil temperature variables as supplemental variables. A Redundancy Analysis (RDA) with forward selection followed by Monte Carlo permutation tests was then performed to determine which of the temperature variables were best correlated with type abundance.

2.5.2. Soil Temperature Variables and the Weighted Average Snow Index

Daily mean soil temperatures for the entire period were calculated, and these were used to generate temperature variables to represent different below-ground conditions. Only the temperatures recorded at 5 cm were used for variable calculation. The variables were designed to capture both warm-season and cold-season conditions; they included start of growing season (GSS), end of growing season (EGS), thaw date (TD), growing season length (GSL), warming time (WT), frost sum (FS), heat sum (HS), mean soil temperature (MST), and frost days (FD). GSS was defined as the fifth consecutive day of soil temperatures > 5° C. EGS was defined as the fifth consecutive day of soil temperatures < 5° C. GSL was the interval between GSS and EGS. TD was the day of the year when soil temperatures reached 1° C. and was used as a proxy for snowmelt. WT was the interval between TD and GSS. FS is the sum of all soil temperatures below 0° C, and HS is the sum of soil temperatures above 5° C. MST was the arithmetic mean of all soil temperatures measured each day during a one-year period, which was again averaged for the three years of measurements. FD was the number of days the soil temperature was < 0° C.

The weighted average snow index (WASI) was also calculated for each plot based upon the snow index of the vegetation, based on methods described by Odland and Munkejord (2008b). The WASI was then compared to the soil temperature variables using stepwise multiple regression in both directions (forward and backward).

2.5.3. Analysis of Soil Properties

The results of the soil sample analyses from the main gradients were compared to two of the soil temperature variables (FS and HS) using GLMM with transect as a random factor to control for spatial autocorrelation within study areas. These temperature variables were chosen because they are the most common temperature variables that are used and correspond to freezing degree days and growing degree days. The main gradient samples were also compared across the study areas using the non-parametric Kruskal-Wallis test with Dunn’s test applied post-hoc to identify significant differences. No statistical analyses were performed on the samples from the profiles along the extra gradients; the samples were taken for descriptive purposes only and not with the intention of being used for comparative studies.

3. Main Results and Discussion

This study focuses on the relationships between plant distribution and soil temperatures in alpine areas, with an emphasis on oligotrophic lichen heaths. Soil temperatures are determined by air temperatures and by the insulating effect of snow; it is therefore important to quantify the effects of snow cover duration on vegetation. Soil conditions are also affected by long periods of frozen temperatures; a lot of energy and time is needed to re-heat frozen soils (Odland & Munkejord, 2008a). Data on both snow duration and soil temperatures are therefore needed in order to understand the variations in regional and local distributions of lichen heaths in alpine areas. Soil temperatures are especially important, since plants are in close contact with the soil at all times, but snow causes a disconnect between plants from air temperatures for long periods, rendering them nearly irrelevant (Körner & Hiltbrunner, 2018). Effects of differing air temperature and precipitation patterns can be quantified by comparative studies from different climatic sections (Moen 1999).

It is therefore necessary to quantify effects of different temperature related factors affecting plant distribution. The soil temperature-related factors used here can be separated into two main categories:

- Cold-season variables, including frost sum (FS) and frost days (FD)
- Warm-season variables, including heat sum (HS), growing season start (GSS) and length (GSL), warming time (WT), and thaw date (TD).

However these variables are by necessity strongly correlated (Table 2); the deeper the frost a plot experiences, the longer it takes for the plot to thaw and to reach temperatures amenable to plant growth.

Table 2. Kendall's τ correlation matrix between the soil temperature variables. The closer the value of τ is to 1 (regardless of sign), the stronger the correlation. Matrix generated using the "cor()" command in R. (Significance levels: p < 0.001 ***, p < 0.01 **, p< 0.05 *)

	MAT	FD	FS	GSL	GSS	TD	WT
FD	-0.65***						
FS	0.65***	-0.58***					
GSL	0.69***	-0.47***	0.34*				
GSS	-0.44*	0.24*	-0.10	-0.68***			
TD	0.03	-0.06	0.32***	-0.20	0.43		
WT	-0.51***	0.43***	-0.48***	-0.46***	0.28*	-0.31*	
HS	0.69***	-0.48**	0.38*	0.81***	-0.61***	-0.07	-0.59

3.1. Snow Layer Duration and Soil Temperatures

Relative values for snow layer duration for the study plots have been quantified by the use of snow indicator values (WASI). Results in Article 2 show that WASI-value of the plots was significantly correlated with four of the soil temperature variables (FS, MST, HS, and GSS), while WT and TD were not. Of these FS was the most important contributor (40.3%, p = 0.003) followed closely by MAT (22.6%, p = 0.04), HS (19.4%, p = 0.03) and GSS (17.6%, p = 0.03). Increasing snow cover duration, as estimated by WASI, decreases soil frost, while the absence of snow leads to longer periods of frozen soil. Körner & Hiltbrunner (2018) call snow cover duration "crucial"; again because of the way that snow insulates vegetation from air temperatures and moderates soil temperatures. There were differences in soil temperatures within the gradients as well; Bilbrough et al. (2000) also had similar results. They found that soil temperatures in moist alpine meadows rarely fell below zero, while in snow-free lichen heaths they recorded sustained temperatures well below freezing, which is the same pattern recorded in the three studied areas. Lichen heaths at these study areas were nearly always frozen below the surface, while plots in lower landscape positions with different vegetation communities rarely froze.

3.2. Soil Temperature Variables and Vegetation

The study indicates that not all plant species and plant functional types appear to be influenced by soil temperatures. As shown in Article 1, Table 4, species with a wide distribution (*Juncus trifidus*, *Betula nana*, and *Cladonia uncialis*) and species associated with a relatively long-lasting snow cover (*Poa alpina*, *Salix herbacea* and *Carex vaginata*), were not significantly related to any of the studied temperature variables which implies that other factors drive the abundances of these species.

As shown in Article 1, Table 4, most lichen species were strongly associated with soil frost. Exceptions were *Cladonia stellaris, C. arbuscula*, and *C. rangiferina*; species which have relatively wide ecological ranges, and which are most often found in sites with a protective snow cover (Dahl 1957). Most shrubs and graminoids were not significantly associated with soil frost (Figure 10).

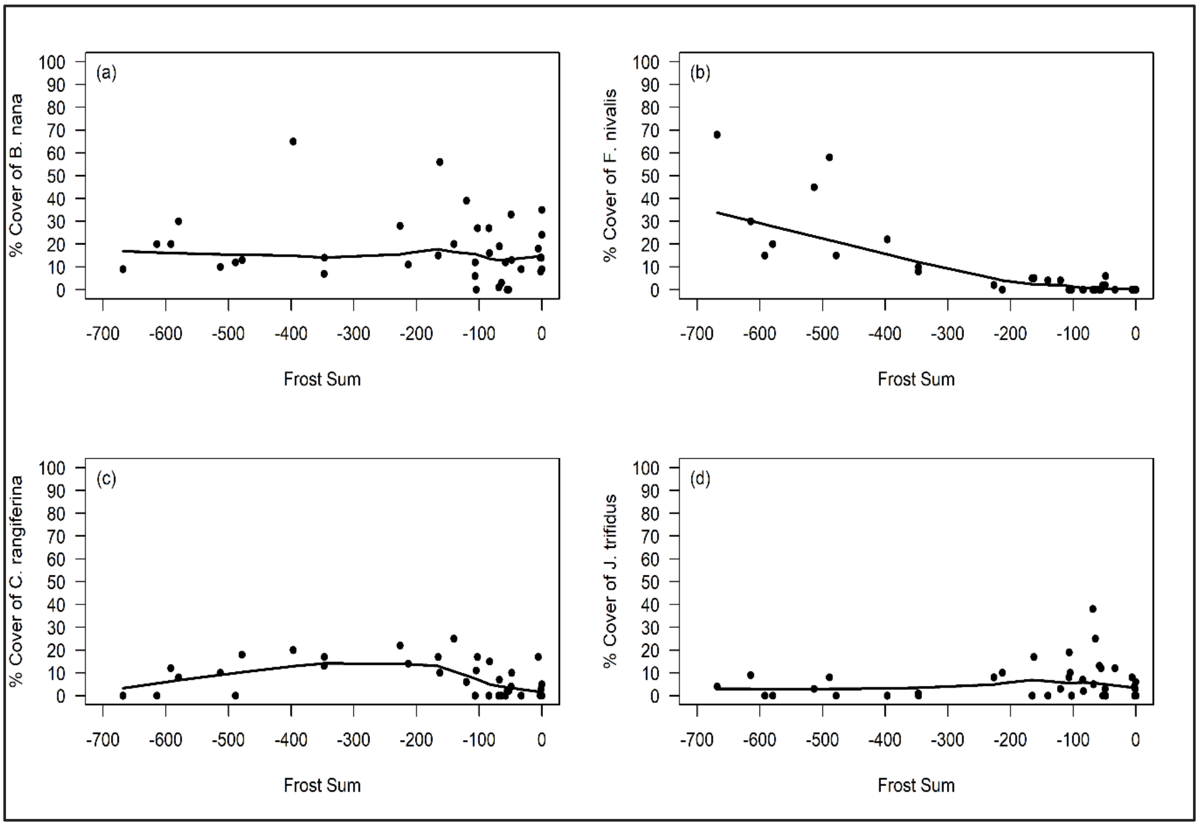

Figure 10. Plots of Betula nana (a), Flavocetraria nivalis (b), Cladonia rangiferina (c), and Juncus trifidus (d) against FS. Lowess regression lines are drawn. These were among the most common species at all three study areas.

The role of both the thaw date and the lapse between the soil defrosting and warming to growing season temperatures (thaw time) has also been investigated. This lapse has been reported earlier by Odland & Munkejord (2008a), but the ecological significance of the thaw period has not been widely investigated. However, for several species growing in apparently similar conditions (Odland, 2005), the thaw factors were important separators. One example is with matgrass (*Nardus stricta*) which is found almost exclusively in snowbeds. Löffler (2005) describes this species as "[able to] survive extreme conditions with wet but warm and short vegetation periods". It was found only in plots that defrosted late in the year and warmed up to growing temperatures very quickly, while other snowbed species such as dwarf willow (*Salix herbacea*) were less strongly correlated with thaw conditions. Several other species, most notably dwarf birch (*Betula nana*), had no relationships with any of the soil temperature variables. Differences in the abundance and distribution of the plant functional types were also strongly associated with differences in soil temperatures, again primarily soil frost (Article 2). Warming time was also significant for many lichen and vascular plant species. WT is a quantification of time needed for soil temperatures to reach the threshold temperature, and is short in sites with a thick and long-lasting snow-cover.

In conclusion, the studies indicate that degree of soil frost and length of the frozen soil period appear to be strongly related to the distribution of most alpine plant species, plant function types, and in particular the lichen heaths. There is a growing body of evidence showing that the cold season is as influential on plant community structure and function as is the warm season, if not more so (Kreyling et al., 2010; Morgner et al., 2010; Bjerke et al., 2015; Hollesen et al., 2015). Choler (2018) also investigated the relationships between soil frost and alpine vegetation, and used only two variables; freezing degree days (FDD), which corresponds to FD for these studies, and growing degree days (GDD), which correspond to HS for these studies. These two were found to be the key separators of alpine vegetation communities in his research sites in the French Alps; however this study has shown that at the areas investigated in southern

Norway, the cold-season variables were the main separators. A FS of -250 is the threshold that separates lichen-dominated plots from those with higher proportions of vascular plants (Figure 11).

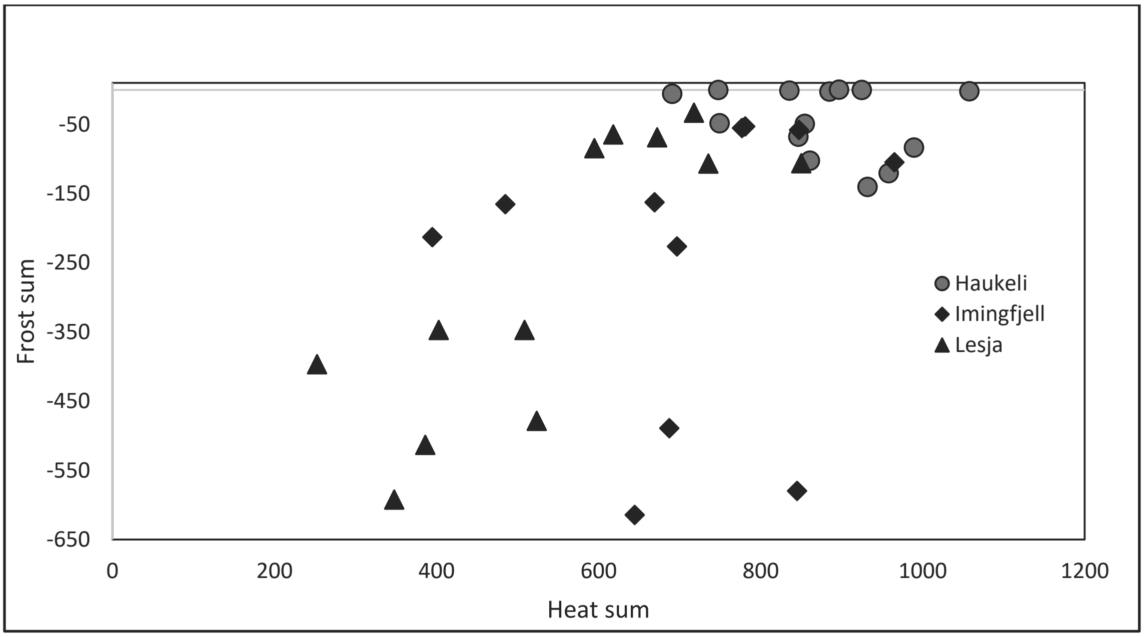

Figure 11. Mean of HS plotted against FS for each plot, showing the thermal patterns. The plots with FS about -250 or above are generally dominated by vascular plants while those with FS under -250 are dominated by lichens.

3.3. Growing Season Characteristics

The warm-season variables GSL, HS, and MAT are correlated with each other, and are negatively correlated with FS, FD, and WT (Article 2, Figure 2).

Neither GSL nor GSS were significantly correlated with the distribution of the majority of the plant species (Article 1, Table 4), nor with the abundances of the plant functional types (Article 2, Table 3). This was surprising because it has generally been assumed that because snowbed species are associated with long-lasting snow, and are therefore adapted to short vegetation periods. However the growing season does not necessarily start immediately after the snow has disappeared. The exposed ridges, if they have any snow cover at all, are snow-free early in the year; however the hard frost experienced in these areas hinders plant growth for a number of weeks (Odland & Munkejord 2008a).

Snowbeds, however, warm to temperatures amenable to growth within days of snowmelt, which leads to these habitats having roughly the same GSL as the ridges.

In conclusion, GSL and GSS were only significantly correlated with the distribution and abundance of few of the studied plant species. The species and types differed much more in their responses to soil frost than in their responses to warm-season variables such as HS and GSL, which was often reflected in their occurrences at the different landscape positons. Thus, in these alpine areas, it is the relationship between snow and soil frost that are important determinants of the presence or absence of lichen-dominated communities.

3.4. Relationships between soils, soil temperatures, and vegetation

Since lichen-dominated vegetation communities are often considered poor competitors for resources it is often assumed that they are only found on shallow soils. The soils in these areas, however, were deep and fairly well-developed at every location along the gradients, and many of them had characteristics associated with podzols (Article 3). Deep soils in areas with little to no snow cover in the winter are subject to long periods of frost, which limits the establishment and survival of vascular plants with deep roots and favors instead the development of lichen-dominated vegetation.

Total N was very low in the study plots, and the HS was found to be the best predictor of N content, available P, C:N ratio, and organic matter content (Article 3). All of these were higher in plots with higher HS values. Low soil temperatures have previously been correlated with low N availabilities (Weih & Karlsson, 1999) and with low uptake of N (Karlsson & Nordell, 1996). The C:N ratio was also similar to those measured by Hinneri et al. (1975) in lichen heaths on Hardangervidda, and can be indicative of low levels of plant-available N compounds and low decomposition rates. Total N, available Ca and

Mg, and pH also increased with increasing depth in the profiles; this is a common finding in previous research (Ellis, 1985; Freppaz et al., 2011; Tian et al., 2017).

In conclusion, the soils under alpine lichen heaths are deeper and better developed than has previously been assumed. Although a number of studies use microcosms to describe differences in soil nutrition along temperature gradients, this study has shown some ways in which temperatures are related to soil nutrition in situ. Seasonally frozen soils were poorer in nutrient ions than soils without seasonal frost, which can again limit the ability for vascular plants to establish in colder soils. Since lichens do not have roots, and acquire their macro- and micronutrients through the air, they are not constrained by the lack of fertility presented by colder soils. Increasing snow cover, with the associated increases in soil temperature, could lead to increased biological activity in the upper layers of the soils, which would have consequences for nutrient cycling activity.

3.5 Regional Climate Differences

Previous studies have shown that there are major regional differences in the distribution of alpine lichens heaths, and that this is explained by climatic differences (Moen 1999). The three study areas lie in different climatic sections, and the main climatic differences are shown in Article 2, Table 1. The Haukeli area has higher annual precipitation, higher temperatures, and more snow than other two. This study shows that the areas have also differences in soil temperature patterns and snow layer durations. These are mainly present on the exposed ridges. The soils at Lesja and Imingfjell are colder than those at Haukeli, where several of the plots remained unfrozen throughout the entire study period. Chinophilous lichen species are far less common at Haukeli than at Imingfjell or Lesja, while the more generalist species in the *Cladonia* genus are common at all three areas (Article 2, Table 2 and Figure 3).

In conclusion this study emphasizes the role of regional climate patterns in determining the distribution of alpine lichen heaths. Changes in climate that lead to increasing oceanity, including increases in temperature and precipitation, can eventually lead to decreases in the presence of lichen heaths.

To summarize, the relationships between soil temperature and vegetation community distribution have been described at these three study areas. In the majority of cases it was the winter temperature patterns, specifically those relating to the duration and intensity of soil frost, that were most strongly associated with vegetation abundances. With regards to future changes in climate, the results presented in Articles 1 and 2 show that if the predictions of increased precipitation and snow depths in alpine areas are correct the result would be higher winter soil temperatures and a general reduction in the extent of frozen soils. Should this occur, coupled with snow accumulations in areas that are normally snow-free, lichen heaths can be diminished and strongly chinophobic species could struggle.

3.6 Integration of Results

This study was an attempt to create a better understanding of the interactions between a number of environmental and biological factors that are associated with alpine lichen heaths, and with the patterns of vegetation change along gradients commonly found in mountain plateau areas. Each of the first three articles focus on different aspects of these areas: individual species, functional types, and soil characteristics. The common thread linking all three is the soil temperature variables, which affect both species, groups, and soil nutrition in differing, albeit interrelated, ways.

These results show that although groups of vegetation may respond to their environment in one way (Article 2), individual species within those groups can have completely different responses, or may not respond at all (Article 1). It is therefore important to have information about both individual and group responses when modelling responses to environmental changes. Because plants experience the environment both above and below the soil surface it is also important to take below-ground temperatures and processes into account as well. Changes in soil temperatures, as affected by factors including vegetation community type and snow, are also associated with changes in soil fertility (Article 3), which again also relates to vegetation community structure and function. This work has shown the importance of soil temperatures, and contributes to the increasing body of work which integrates below-ground temperatures with above-ground vegetation processes.

4. Conclusions and Future Perspectives

This project is the investigation of the relationships between soil temperatures and both individual plant and lichen species (Article 1) and functional groups of vegetation (Article 2). The soils of alpine lichen heaths have also been described, and the relationships between soil physical and chemical properties and soil temperature were investigated (Article 3). And finally, the previous knowledge of lichen ecology in alpine settings was compared to these and other recent findings and several predominant assumptions were challenged (Article 4).

The following conclusions can also be drawn from this research:

- **Winter conditions are better predictors of vegetation patterns in alpine areas than warm-season conditions**. In this study the warm-season variables were generally not correlated with the abundance patterns of any individual species or functional group. (Main aims #1 & 2)
- **Soil temperatures are better predictors of distribution patterns than air temperatures.** Air temperatures only represent a fraction of the environment experienced by plants, especially in alpine areas where plants tend to have large portions of their total biomass below the ground. (Main aim #2)
- **Alpine lichen heaths are associated with relatively deep soils resting on moraine materials.** The soils and the moraine materials freeze during winter, and they need a long period to thaw during the spring. This in turn has an influence on plant community composition. (Main aims #1-4)
- **Changes in soil temperature patterns can present a threat to lichen heaths in Norway.** Changes that can lead to increased N availability and warmer soils can be favorable to vascular plants and unfavorable to lichens. Although they are not directly connected to soils through roots, lichen dominance is dependent upon a certain set of environmental conditions. (Main aims #2 & 3)
- **Regional climate differences have major impacts on both species distributions and on soil properties.** If climate change continues at its current pace, the

conditions at the Imingfjell and Lesja areas could soon resemble those that are dominant at the Haukeli area. (Main aims #1 & 3)

Long-term monitoring studies should be carried out to evaluate the extent and health of lichen heaths on Norwegian mountain plateaus. These areas are not only interesting botanically but are important grazing resources for reindeer. Further investigation into the edaphic factors that characterize these areas should also be performed. A greater knowledge of below-ground conditions will help to improve predictions of above-ground changes.

In summary, alpine lichen heaths are found in areas with deep, well-developed soils, which can often be classified as podzols. These soils are nutrient poor, yet have a high organic matter content and low decomposition rates as evidenced by the high C:N ratios. They are most likely limited in both N and P, depending upon the geology of the underlying rocks. Mat-forming lichens are dominant where snow is absent and decrease in number and species diversity with increasing snow depth; they are generally absent in late snowbeds. The factors that were most closely associated with high lichen abundances were the frost sum, number of days with frozen soil, and the amount of time the soil needed to thaw in the spring. Environmental changes that lead to higher soil temperatures (such as increased snowfall), decreased albedo (such as grazing), or increased availability of N and P (such as deposition), can lead to decreases in lichen abundances; changes in all of these could create feedbacks that could cause major changes in the vegetation structure of alpine areas in southeastern Norway (Figure 12).

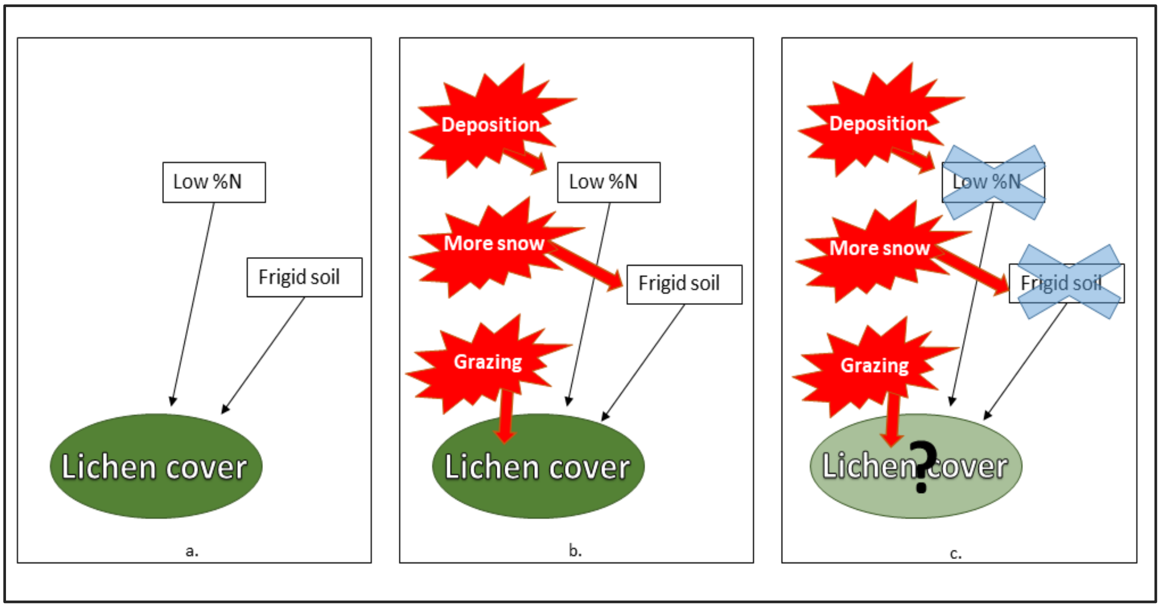

Figure 12. Conditions favorable to the development of lichen heaths (a), and threats to these areas (b). Increasing N through atmospheric deposition, coupled with warmer soils through increased snowfall, could lead to reductions in the extent of lichen heaths in the future (c).

5. Literature Cited

Ahti, T. 1999. Nordic lichen flora : Vol. 1 : Introductory parts, calicioid lichens and fungi. SBF-förlaget, Lund.

Ahti, T. and J. Oksanen. 1990. Epigeic lichen communities of taiga and tundra regions. Vegetation **86**:39-70.

Arnesen, G., P. S. A. Beck, and T. Engelskjøn. 2007. Soil acidity, content of carbonates, and available phosphorus are the soil factors best correlated with alpine vegetation: evidence from Troms, North Norway. Arctic, Antarctic, and Alpine Research **39**:189-199.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software **67**: 1-48.

Benestad, R. E. 2004. Tentative probabilistic temperature scenarios for northern Europe. Tellus **56A**:89-101.

Beringer, J., F. S. Chapin III, C. C. Thompson, and A. D. McQuire. 2005. Surface energy exchanges along a tundra-forest transition and feedbacks to climate. Agricultural and Forest Meterology **131**:143-161.

Bilbrough, C. J., J. M. Welker, and W. D. Bowman. 2000. Early Spring Nitrogen Uptake by Snow-Covered Plants: A Comparison of Arctic and Alpine Plant Function under the Snowpack. Arctic, Antarctic, and Alpine Research **32**:404-411.

Bjerke, J. W., H. Tømmervik, M. Zielke, and M. Jørgensen. 2015. Impacts of snow season on ground-ice accumulation, soil frost and primary productivity in a grassland of sub-Arctic Norway. Environmental Research Letters **10**.

Bjerkely, H. J. 2008. Norske naturtyper - økologi og mangfold. Universitetsforlaget, Oslo.

Blume-Werry, G., S. D. Wilson, J. Kreyling, and A. Milbau. 2016. The hidden season: growing season is 50% longer below than above ground along an arctic elevation gradient. New Phytologist **209**:978-986.

Bonan, G. B. 1989. A computer model of the solar radiation, soil moisture, and soil thermal regimes in boreal forests. Ecological Modelling **45**:275-306.

Bonan, G. B., and H. H. Shugart. 1989. Environmental Factors and Ecological Processes in Boreal Forests. Annual Review of Ecology and Systematics **20**:1-28.

Brooker, R. and R. van der Wal. 2003. Can soil temperature direct the composition of high arctic plant communities? Journal of Vegetation Science **14**:535-542.

Büdel, B. and C. Scheidegger. 2008. Thallus morphology and anatomy. Pages 40-68 Lichen Biology, Second Edition.

Cadotte, M. W. 2017. Functional traits explain ecosystem function through opposing mechanisms. Ecology Letters **20**:989-996.

Choler, P. 2018. Winter soil temperature dependence of alpine plant distribution: Implications for anticipating vegetation changes under a warming climate. Perspectives in Plant Ecology, Evolution and Systematics **30**:6-15.

Cohen, J., J. Pullianen, C. B. Menard, B. Johansen, L. Oksanen, and K. Luojos. 2013. Effect of reindeer grazing on snowmelt, albedo and energy balance based on satellite data analyses. Remote Sensing of the Environment **135**:107-117.

Cornelissen, J. H. C., T. V. Callaghan, J. M. Alatalo, A. Michelsen, E. Graglia, A. E. Hartley, D. S. Hik, S. E. Hobbie, M. C. Press, C. H. Robinson, G. H. R. Henry, G. R. Shaver, G. K. Phoenix, D. Gwynn Jones, S. Jonasson, and F. S. Chapin III. 2001. Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? Journal of Ecology. **89**:984-994.

Crabtree, D. and C. J. Ellis. 2010. Species interactions and response to wind speed alter the impact of projected temperature change in a montane system. Journal of Vegetation Science **21**:744-760.

Dahl, E. 1957. Rondane: Mountain Vegetation in South Norway and its Relation to the Environment. Skrifter Norske Videnskapsakademi i Oslo, Matematisk-naturvidenskapelig Klasse **3**: 1-374.

Dahl, E., G. Gulden, and H. J. B. Birks. 1998. The phytogeography of northern Europe : (British Isles, Fennoscandia, and adjacent areas). Cambridge University Press, Cambridge.

Davies, J. A. 1963. Albedo investigations in Labrador-Ungava. Archiv für Meteorologie, Geophysik und Bioklimatologie, Serie B **13**:137-151.

DeLuca, T. and O. Zackrisson. 2007. Enhanced soil fertility under Juniperus communis in arctic ecosystems. Plant and Soil **294**:147-155.

Díaz, S., J. G. Hodgson, K. Thompson, M. Cabido, J. H. C. Cornelissen, A. Jalili, G. Montserrat-Martí, J. P. Grime, F. Zarrinkamar, Y. Asri, S. R. Band, S. Basconcelo, P. Castro-Díez, G. Funes, B. Hamzehee, M. Khoshnevi, N. Pérez-Harguindeguy, M. C. Pérez-Rontomé, F. A. Shirvany, F. Vendramini, S. Yazdani, R. Abbas-Azimi, A. Bogaard, S. Boustani, M. Charles, M. Dehghan, L. De Torres-Espuny, V. Falczuk, J. Guerrero-Campo, A. Hynd, G. Jones, E. Kowsary, F. Kazemi-Saeed, M. Maestro-Martínez, A. Romo-Díez, S. Shaw, B. Siavash, P. Villar-Salvador, and M. R. Zak. 2004. The plant traits that drive ecosystems: Evidence from three continents. Journal of Vegetation Science **15**:295-304.

During, H. J. and B. F. V. Tooren. 1990. Bryophyte interactions with other plants. Botanical Journal of the Linnean Society **104**:79-98.

Dyrrdal, A., T. Saloranta, T. Skaugen, and H. Bache. 2013. Changes in snow depth in Norway during the period 1961-2010. Hydrology Research **44**:169-179.

Edwards, C. A., R. Scalenghe, and M. Freppaz. 2007. Changes in the seasonal snow cover of alpine regions and its effect on soil processes: a review. Quartenary International **162-163**:172-181.

Egnér, H., H. Riehm, and W. R. Domingo. 1960. Untersuchungen über die chemische Bodenanalyse als Grunlage für die Beurteilung des Nährstoffzustandes der Böden. II. Chemische Extraktionsmethoden zur Phosfor- und Kaliumbestimmung. Kungliga Lantbrukshögskolans Annaler **26**:199-215

Ellis, S. 1985. An altitudinal sequence of pozdolic soils, Hardangervidda, southern Norway. Norsk geografisk tidsskrift **39**:141-154.

Epstein, H. E., M. P. Calef, M. D. Walker, F. S. Chapin III, and A. M. Starfields. 2004. Detecting changes in arctic tundra plant communities in response to warming over decadal time scales. Global Change Biology **10**:1325-1334.

Eugster, W., W., R. Rouse, R. A. Pielke Sr, J. P. McFadden, D. D. Baldocci, T. G. F. Kittel, F. S. Chapin III, G. E. Liston, P. L. Vidale, E. Vaganov, and S. Chambers. 2000. Land-atmosphere energy exchange and boreal forests: available data and feedbacks to climate. Global Change Biology **6 (Supplement 1)**:84-115.

Fauria, M. M., T. Helle, A. Niva, H. Posio, and M. Timonen. 2008. Removal of the lichen mat by reindeer enhances tree growth in a northern Scots pine forest. Canadian Journal of Forest Research **38**:2981-2993.

Ferrari, A., F. Hagedorn, and P. A. Niklaus. 2016. Experimental soil warming and cooling alters the partitioning of recent assimilates: evidence from a 14C-labelling study at the alpine treeline. Oecologia **181**:25-37.

Flock, J. W. 1978. Lichen-bryophyte distribution along a snow-cover-soil-moisture gradient, Niwot Ridge, Colorado. Arctic and Alpine Research **10**:31-47.

Fraser, R. H., T. C. Lantz, I. Olthof, S. V. Kokelj, and R. A. Sims. 2014. Warming-induced shrub expansion and lichen decline in the Western Canadian Arctic. Ecosystems **17**:1151-1168.

Fremstad, E. 1997. Vegetasjonstyper i Norge - NINA Temahefte 12. 2. edition. NINA Norsk institutt for naturforskning, Trondheim.

Freppaz, M., G. Filippa, A. Caimi, G. Buffa, and E. Zanini. 2011. Soil and plant characteristics in the alpine tundra (NW Italy). Pages 81-110 *in* Tundras: Vegetation, Wildlife and Climate Trends.

Fryday, A. M. 2001. The lichen vegetation associated with areas of late snow-lie in the Scottish Highlands. Lichenologist **33**:121-150.

Galloway, D. J. 2008. Lichen biogeography. Pages 315-335 *in* Lichen Biology, Second Edition.

Gjærevoll, O. 1956. The plant communities of the Scandinavian alpine snow-beds. Skrifter (Det Kongelige norske videnskabers selskab) **1956**:1-405.

Gjærevoll, O. 1992. Plantegeografi. Tapir forlag, Trondheim, Norway.

Gornall, J. L., I. S. Jónsdóttir, S. J. Woodin, and R. Van Der Wal. 2007. Arctic mosses govern below-ground environment and ecosystem processes. Oecologia **153**:931-941.

Gornall, J. L., S. J. Woodin, I. S. Jónsdóttir, and R. van der Wal. 2011. Balancing positive and negative plant interactions: how mosses structure vascular plant communities. Oecologia **166**:769-782.

Gough, L., G. R. Shaver, J. Carroll, D. L. Royer, and J. A. Laundre. 2000. Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH. Journal of Ecology. **88**:54-66.

Graae, B. J., P. de Frenne, A. Kolb, J. Brunet, O. Chabrerie, K. Verheyen, N. Pepin, T. Heinken, M. Zobel, A. Shevtsova, I. Nijs, and A. Milbau. 2012. On the use of weather data in ecological studies along altitudinal and latitudinal gradients. Oikos **121**:3-19.

Green, T. G. A., T. H. Nash, III, and O. L. Lange. 2008. Physiological ecology of carbon dioxide exchange. Lichen Biology. 2nd ed. edition. Cambridge University Press, Cambridge, pp. 152-181.

Halvorsen, R. 2015. Grunnlag for typeinndeling av natursystem-nivået i NiN - analyser av generaliserte artslistedatasett. Natur i Norge.

Hanssen-Bauer, I. 2005. Regional temperature and precipitation series for Norway: analyses of time-series updated to 2004. Climate Report 15/2005. Norwegian Meterological Institute, Oslo.

Hanssen-Bauer, I., E. J. Førland, J. E. Haugen, and O. E. Tveito. 2003. Temperature and precipitation scenarios for Norway: comparison of results from dynamical and empirical downscaling. Climate Research **25**:15-27.

Hauck, M. 2010. Ammonium and nitrate tolerance in lichens. Environmental Pollution **158**:1127-1133.

Heggberget, T. M., E. Gaare, and J. P. Ball. 2002. Reindeer (Rangifer tarandus) and climate change: importance of winter forage. Rangifer **22**:13-31.

Heggenes, J., A. Odland, T. Chevalier, J. Ahlberg, A. Berg, H. Larsson, and D. K. Bjerketvedt. 2017. Herbivore grazing—or trampling? Trampling effects by a large ungulate in cold high-latitude ecosystems. Ecology and Evolution **7**:6423-6431.

Hinneri, S., M. Sonesson, and A. K. Veum. 1975. Soils of Fennoscandian IBP Tundra Ecosystems. Pages 31-40 *in* F. E. Wielgolaski, P. Kallio, and T. Rosswall, editors. Fennoscandian tundra ecosystems : Pt 1 : Plants and microorganisms. Springer, Berlin.

Holien, H. and T. Tønsberg. 2008. Norsk lavflora, 2. utgave. Tapir akademisk forlag, Trondheim, Norway.

Hollesen, J., A. Buchwal, G. Rachlewicz, B. U. Hansen, M. O. Hansen, O. Stecher, and B. Elberling. 2015. Winter warming as an important co-driver for Betula nana growth in western Greenland during the past century. Global Change Biology **21**:2410-2423.

Holten, J. and E. I. Aune. 2011. Altitudinal distribution patterns of alpine plants: studies along a coast-inland transect in southern Scandes, northern Europe. Tapir Academic Press, Trondheim, Norway.

Holtmeier, F.-K. 2009. Mountain Timberlines: Ecology, Patchiness, and Dynamics. Springer Verlag, Berlin.

Jonas, T., C. Rixen, M. Sturm, and V. Stoeckli. 2008. How alpine plant growth is linked to snow cover and climate variability. Journal of Geophysical Research: Biogeosciences **113**.

Jägerbrand, A. K., K. E. M. Lindblad, R. G. Björk, J. Alatalo, and U. Molau. 2006. Bryophyte and lichen diversity under simulated environmental change compared with observed variation in unmanipulated alpine tundra. Biodiversity and Conservation **15**:4453-4475.

Karlsson, P. S. and K. O. Nordell. 1996. Effects of soil temperature on the nitrogen economy and growth of mountain birch seedlings near its presumed low temperature distribution limit. Ecoscience **3**:183-189.

Kaste, Ø., K. Austnes, L. S. Vestgarden, and R. F. Wright. 2008. Manipulation of snow in small headwater catchments at Storgama, Norway: effects on leaching of inorganic nitrogen. Ambio **37**:29-37.

Kershaw, K. A. 1983. The thermal operating-environment of a lichen. Lichenologist **15**:191-207.

Kershaw, K. A. 1985. Physiological ecology of lichens. Cambridge University Press, Cambridge.

Keyser, A. R., J. S. Kimball, R. R. Nemani, and S. W. Running. 2000. Simulating the effects of climate change on the carbon balance of North American high-latitude forests. Global Change Biology **6**:185-195.

Klanderud, K. 2008. Species-specific responses of an alpine plant community under simulated environmental change. Journal of Vegetation Science **19**:363-372.

Klein, D. R. and M. Shulski. 2009. Lichen recovery following heavy grazing by reindeer delayed by climate warming. Ambio **38**:11-16.

Klein, D. R. and M. Shulski. 2011. The role of lichens, reindeer, and climate in ecosystem change on a Bering Strait Island. Arctic **64**:353-361.

Klimaservicesenter. 2015. Klima i Norge 2100. 2/2015, Norsk Klimaservicesenter, Oslo.

Kohler, J., O. Brandt, M. Johansson, and T. V. Callaghan. 2006. A long-term Arctic snow depth record from Abisko, northern Sweden, 1913-2004. Polar Research **25**:91-113.

Kollas, C., C. Körner, and C. F. Randin. 2013. Spring frost and growing season length co-control the cold range limits of broad-leaved trees. Journal of Biogeography:doi:10.1111/jbi.12238.

Kreyling, J., C. Beierkuhnlein, and A. Jentsch. 2010. Effects of soil freeze–thaw cycles differ between experimental plant communities. Basic and Applied Ecology **11**:65-75.

Kullman, L. 2007. Tree line population of Pinus sylvestris in the Swedish Scandes, 1973-2005: implication for tree line theory and climate change ecology. Journal of Ecology. **95**:41-52.

Körner, C. 2003. Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems, Second Edition. Springer Verlag, Berlin.

Körner, C. and J. Paulsen. 2004. A world-wide study of high alttitude treeline temperatures. Journal of Biogeography **31**:713-732.

Körner, C. and E. Hiltbrunner. 2018. The 90 ways to describe plant temperature. Perspectives in Plant Ecology, Evolution and Systematics **30**:16-21

Lang, S. I., J. C. Cornelissen, G. R. Shaver, M. Ahrens, T. V. Callaghan, U. Molau, C. F. Ter Braak, A. Hölzer, and R. Aerts. 2012. Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. Global Change Biology **18**:1096-1107.

Laughlin, D. C. 2014. The intrinsic dimensionality of plant traits and its relevance to community assembly. Journal of Ecology **102**:186-193.

Litaor, M. I., T. R. Seastedt, M. D. Walker, M. Carbone, and A. Townsend. 2005. The biogeochemistry of phosphorus across an alpine topographic/snow gradient. Geoderma **124**:49-61.

Longton, R. E. 1988. The biology of polar bryophytes and lichens. Cambridge University Press, Cambridge.

Löffler, J. 2003. Micro-climatic determination of vegetation patterns along topographical, altitudinal, and oceanic-continental gradients in the high mountains of Norway. Erdkunde **57**:249.

Löffler, J. 2005. Snow cover dynamics, soil moisture variability and vegetation ecology in high mountain catchments of central Norway. Hydrological Processes **19**:2385-2405.

McFadden, J. P., G. E. Liston, M. Sturm, R. A. Pielke Sr., C. III, and F. S. 2001. Interactions of shrubs and snow in arctic tundra: measurements and models. Soil-Vegetation-Atmosphere Transfer Schemes and Large-Scale Hydrological Models: Proceedings of a symposium held during the Sixth IAHS Scientific Assembly. IAHS Publication 270, Maastricht, The Netherlands.

Moberg, A., H. Tuomenvirta, and Ø. Nordli. 2005. Recent Climatic Trends.*in* M. Seppälä, editor. The Physical Geography of Fennoscandia. Oxford University Press, Oxford.

Moen, A. 1999. National Atlas of Norway: Vegetation. Norwegian Mapping Authority, Hønefoss.

Morgner, E., B. Elberling, D. Strebel, and E. Cooper. 2010. The importance of winter in annual ecosystem respiration in the High Arctic: effects of snow depth in two vegetation types. Polar Research **29**:58-74.

Mossberg, B., T. Karlsson, S. Moen, S. Båtvik, B. Mossberg, and L. Stenberg. 2007. Gyldendals store nordiske flora. Rev. og utvidet utg. edition. Gyldendal, Oslo.

Myers-Smith, I. H., and D. S. Hik. 2013. Shrub canopies influence soil temperatures but not nutrient dynamics: An experimental test of tundra snow-shrub interactions. Ecology and Evolution **3**:3683-3700.

Myrvold, L. L. 2013. Variasjon i lavbiomasse mellom ulike naturtyper og geografiske regioner i tre sørnorske fjellområder. Telemark University College, Bø i Telemark.

Nash, T. H. 2008. Lichen Biology. 2nd ed. edition. Cambridge University Press, Cambridge.

Natali, S. M., E. A. G. Schuur, and R. L. Rubin. 2012. Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. Journal of Ecology. **100**:488-498.

Nordhagen, R. 1943. Sikilsdalen og Norges fjellbeiter: en plantesosiologisk monografi. A. S. John Greigs boktrykkeri, Bergen, Norge.

Odland, A. 2005. Oligotrophic and mesotrophic vegetation in southern Scandinavian mountains. Gradients in species and community distribution extracted by numerical analyses of earlier published vegetation descriptions. Phytocoenologia **35**:985-1018.

Odland, A. 2011. Estimation of the growing season length in alpine areas: effects of snow and temperatures.*in* J. G. Schmidt, editor. Alpine Environment: Geology, Ecology, and Conservation. Nova Science Publishers, Hauppauge, New York, USA.

Odland, A., T. Høitomt, and S. L. Olsen. 2010. Increasing vascular plant richness on 13 high mountain summits in southern Norway since the early 1970s. Arctic, Antarctic, and Alpine Research **42**:458-470.

Odland, A. and H. K. Munkejord. 2008a. The importance of date of snowmelt for the separation of different oligotrophic and mesotrophic mountain vegetation types in Southern Norway. Phytocoenologia **38**:3-21.

Odland, A. and H. K. Munkejord. 2008b. Plants as indicators of snow layer duration in southern Norwegian mountains. Ecological Indicators **8**:57-68.

Odland, A., S. M. Sandvik, D. K. Bjerketvedt, and L. M. Myrvold. 2014. Estimation of lichen biomass with emphasis on reindeer winter pastures at Hardangervidda, S Norway. Rangifer **34**:95-110.

Oechel, W. C. and K. Van Cleve. 1986. The role of bryophytes in nutrient cycling in the Taiga. Pages 121-137 *in* K. Van Cleve, F. S. Chapin III, P. W. Flanagan, L. A. Vierick, and C. T. Dyrness, editors. Forest ecosystems in the Alaskan Taiga. Springer-Verlag, New York.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. 2018. Vegan: Community Ecology Package. R package version 2.5-2. https://CRAN.R-project.org/package=vegan

Onipchenko, V. G., O. S. Vertelina, and M. I. Makarov. 1998. Spatial Heterogeneity of High-Altitude Phytocenoses and Soil Properties. Eurasian Soil Science **31**:622-628.

Pajunen, A. M., J. Oksanen, and R. Virtanen. 2011. Impact of shrub canopies on understorey vegetation in western Eurasian tundra. Journal of Vegetation Science **22**:837-846.

Peth, S. and R. Horn. 2006. Consequences of Grazing on Soil Physical and Mechanical Properties in Forest and Tundra Environments. Pages 217-242 *in* B. C. Forbes, M. Bölter, L. Müller-White, J. Hukkinen, F. Müller, N. Gunslay, and Y. Konstantinov, editors. Ecological Studies 184: Reindeer Management in Northernmost Europe. Springer, Berlin.

Porada, P., A. Ekici, and C. Beer. 2016. Effects of bryophyte and lichen cover on permafrost soil temperature at large scale. Cryosphere **10**:2291-2315.

Qian, B., E. G. Gregorich, S. Gameda, D. W. Hopkins, and X. L. Wang. 2011. Observed soil temperature trends associated with climate change in Canada. Journal of Geophysical Research **116**:D02016.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Rabenhorst, M. C. 2005. Biologic zero: a soil temperature concept. Wetlands **25**:616-621.

Reinhardt, S. and A. Odland. 2012. Soil temperature variation in calciphile plant communities in Southern Norway. Oecologia Montana **21**:21-35.

Scherrer, D. and C. Körner. 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. Journal of Biogeography **38**:406-416.

Schimel, J. P. and C. Mikan. 2005. Changing microbial substrate use in Arctic tundra soils through a freeze-thaw cycle. Soil Biology and Biochemistry **37**:1411-1418.

Schuur, E. A. G., J. Bockheim, J. G. Canadell, E. Euskirchen, C. B. Field, S. V. Goryachkin, S. Hagemann, P. Kuhry, P. M. Lafleur, H. Lee, G. Mazhitova, F. E. Nelson, A. Rinke, V. E. Romanovsky, N. Shiklomanov, C. Tarnocai, S. Venevsky, J. G. Vogel, and S. A. Zimov. 2008. Vulnerability of permafrost carbon to climate change: Implications for the global carbon cycle. BioScience **58**:701-714.

Snapp, S. 2017. Agroecology: Principles and Practice. Pages 33-72 Agricultural Systems: Agroecology and Rural Innovation for Development: Second Edition.

Stenroos, S., R. Moberg, T. Ahti, and F. Nordisk Lichenologisk. 2013. Nordic lichen flora : Vol. 5 : Cladoniaceae. SBF-förlaget, Lund.

Stoy, P., L. E. Street, L. V. Johnson, A. Prieto-Blanco, and S. A. Ewing. 2012. Temperature, heat flux, and reflectance of common subarctic mosses and lichens under field conditions: might changes to community composition impact climate-relevant surfact fluxes? Arctic, Antarctic, and Alpine Research **44**:500-508.

Stützer, A. 1999. Podzolisation as a soil forming process in the alpine belt of Rondane, Norway. Geoderma **91**:237-248.

Tarnocai, C. 2009. The impact of climate change on Canadian peatlands. Canadian Water Resources Journal **34**:453-466.

Ter Braak, C. J. F. and P. Smilauer. 2012. Canoco reference manual and user's guide: software for ordination (Version 5.0). Microcomputer Power, Ithaca, NY, USA.

Thannheiser, D., H. Tømmervik, and J. Wehberg. 2005. The vegetation changes and recent impact on the mountain birch forest during the last 40 years. Pages 235-254 *in* F. E. Wielgolaski, editor. Plant Ecology, Herbivory, and Human Impact in Nordic Mountain Birch Forests. Springer Verlag, Berlin.

Theodose, T. A. and W. D. Bowman. 1997. Nutrient availability, plant abundance, and species diversity in two alpine tundra communities. Ecology **78**:1861-1872.

Tian, L., L. Zhao, X. Wu, H. Fang, Y. Zhao, G. Yue, G. Liu, and H. Chen. 2017. Vertical patterns and controls of soil nutrients in alpine grassland: Implications for nutrient uptake. Science of the Total Environment **607-608**:855-864.

Tikkanen, M. 2005. Climate.*in* M. Seppälä, editor. The Physical Geography of Fennoscandia. Oxford University Press, Oxford.

Turunen, M., P. Soppela, H. Kinnunen, M.-L. Sutinen, and F. Martz. 2009. Does climate change influence the availability and quality of reindeer forage plants? Polar Biology **32**:813-832.

Tømmervik, H., B. Johansen, I. Tombre, D. Thannheiser, K. A. Høgda, E. Gaare, and F. E. Wielgolaski. 2004. Vegetation changes in the nordic mountain birch forest: The influence of grazing and climate change. Arctic, Antarctic, and Alpine Research **36**:323-332.

USDA-NRCS. 2018. Soil texture calculator. https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/?cid=nrcs142p2_054167.

Violle, C., M. L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! Oikos **116**:882-892.

Virtanen, R., A. Eskelinen, and E. Gaare. 2003. Long-term Changes in Alpine Plant Communities in Norway and Finland. Pages 411-422 *in* L. Nagy, G. Grabherr, C. Körner, and D. B. A. Thompson, editors. Ecological Studies 167: Alpine Biodiversity in Europe. Springer, Berlin.

Walker, D. A., W. D. Billings, and J. G. d. Molenaar. 2001. Snow-Vegetation Interactions in Tundra Environments.*in* H. G. Jones, J. W. Pomeroy, D. A. Walker, and R. W. Hoham, editors. Snow ecology : an interdisciplinary examination of snow-covered ecosystems. Cambridge University Press, Cambridge.

Walther, A. and H. W. Linderholm. 2006. A comparison of growing season indices for the Greater Baltic area. International Journal of Biometeorology **51**:107-118.

Weih, M. and P. S. Karlsson. 1999. The nitrogen economy of mountain birch seedlings: implications for winter survival. Journal of Ecology. **87**:211-219.

Weih, M. and P. S. Karlsson. 2001. Growth response of mountain birch to air and soil temperature: is increasing leaf-nitrogen content an acclimation to lower air temperature? New Phytologist **150**:147-155.

Yao, F., U. Vik, A. K. Brysting, T. Carlsen, R. Halvorsen, and H. Kauserud. 2013. Substantial compositional turnover of fungal communities in an alpine ridge-to-snowbed gradient. Molecular Ecology **22**:5040-5052.

Zimov, S. A., E. A. G. Schuur, and F. S. I. Chapin. 2005. Permafrost and the global carbon budget. Science **312**:1612-1613.

6. Supplementary Information

Table S1. Coordinates and elevations for every study plot. Coordinates were recorded where the dataloggers were buried. Plot names beginning with H = Haukeli; I = Imingfjell, and L = Lesja.

Plot Name	Longitude (DD, UTM)	Latitude (DD, UTM)	Elevation (masl)
HA1	7.219056	59.814194	1055
HA2	7.218694	59.814250	1053
HA3	7.218361	59.814333	1053
HA4	7.218278	59.814472	1048
HB1	7.219167	59.814694	1052
HB2	7.219056	59.814750	1052
HB3	7.218556	59.814889	1050
HC1	7.220139	59.814861	1055
HC2	7.220444	59.814917	1052
HC3	7.220972	59.814972	1051
HD1	7.221833	59.814139	1054
HD2	7.221861	59.814028	1052
HD3	7.221861	59.813833	1051
HD4	7.221528	59.813833	1048
IA1	8.577722	60.187472	1153
IA2	8.578000	60.187389	1150
IA3	8.577861	60.187111	1145
IB1	8.582389	60.188778	1159
IB2	8.582333	60.189028	1158
IB3	8.581778	60.189583	1155
IC1	8.572278	60.194333	1178
IC2	8.572306	60.194472	1178
IC3	8.572417	60.194028	1174
ID1	8.573361	60.189028	1152
ID2	8.573417	60.188806	1147
ID3	8.573833	60.188528	1140
LA1	8.968000	62.026278	1230
LA2	8.967417	62.026750	1225
LA3	8.966944	62.027167	1220
LA4	8.966306	62.027583	1218
LB1	8.967194	62.025917	1228
LB2	8.96675	62.025667	1221
LB3	8.966222	62.025167	1213
LB4	8.965556	62.024556	1203
LC1	8.970833	62.022611	1234
LC2	8.970028	62.022611	1227
LC3	8.969306	62.022889	1218
LC4	8.968528	62.022889	1216

Article 1

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Responses of alpine vascular plants and lichens to soil temperatures

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Plant abundance and distribution patterns have mostly been explained in terms of air temperatures, yet a great deal of vascular plant biomass is located below ground. Winter soil temperatures, which are related to both air temperature and snow cover, may therefore be important determinants of species composition in alpine areas. Epigeic lichens, however, have no underground biomass, and they often dominate at sites that are inhospitable to vascular plants, such as those that experience sustained periods of sub-freezing temperatures. In this study, effects of several warm- and cold-season soil-temperature variables on individual plant and lichen species common to oligotrophic alpine heaths was investigated using linear regression and ordination. The differences in growing season length as measured by soil temperatures were compared. Warm season variables were found to have less influence than cold season variables on individual species abundances in these areas. Changes in winter snow cover depth and duration, such as those that are predicted in Norway, can result in changes to soil temperature patterns, to the possible benefit of some species and detriment of others.

Introduction

Vascular plants and lichens are organisms with highly different life strategies (Grime 1977). Lichens have no roots, and environmental and edaphic conditions in the soil have therefore at best limited direct effects on their abundances. Vascular plants, however, live in contact with two different ecosystems, the aerial parts (the atmosphere) and the soil parts (the rhizosphere), and ecological conditions within both of these affect plant life. Unfavourable conditions experienced by one of the parts can have serious consequences for the whole plant. Vascular plants are dependent on uptake of water and nutrients from the soil, and plants exposed to high air temperatures on frozen soil can therefore be subject to drought stress. It has previously been demonstrated that initiation of alpine plant growth may be more strongly controlled by soil temperature than by air temperature (Holway & Ward 1965, Bliss 1971, Chapin *et al.* 1979, Sveinbjörnsson 1983). Soils provide a thermal buffer through absorption and subsequent release of heat throughout the day and night hours (Larcher 2012). Brooker and van der Waal (2003) found that different functional groups of alpine plants responded differently to increased soil temperatures, with grasses increasing the most rapidly, even with unchanged air temperatures (*see* e.g., Bjerke *et al*. 2015). Nevertheless, studies of alpine plant autecology have most often been based on air temperature data (Billings *et al*. 1961, Bliss 1971, Abeli *et al*. 2012) or snow melt data (Kudo 1991, Jonas *et al*. 2008, Odland & Munkejord 2008a). Delimitations of vegetation zones are also usually related to air temperature variables, especially average July temperature, while hardiness depends on average winter air temperatures.

Soil frost may be seasonal or permanent, and there are several factors determining the extent of soil freezing. Permafrost occurs mainly in arctic areas where average air temperatures are lower than –2 °C (King 1986, Harris *et al*. 2008), while in sub-arctic alpine areas frosts are generally seasonal. The distribution and depth extent of soil frost is determined mainly by three factors: winter air temperatures, snow cover (thickness and duration), and occurrence of a moist and humus-rich soil. According to Sofronov *et al*. (2004), soil thawing depth is affected by organic layers of mosses and lichens that densely cover the ground surface. Similarly, Odland and Munkejord (2008b) found that in exposed lichen alpine heaths with a thick, moist humus layer in southern Norway, soils needed more than one month longer to reach a soil temperature of 5 °C than snow-cover demanding lee-side communities. Exposed heaths without lichens or a thick humus layer show little to no delay in soil temperature increase in the spring (Reinhardt *et al*. 2013). The lack of snow cover reduces the degree of insulation and results in extensive soil freezing (Groffman *et al*. 1999, Freppaz *et al*. 2008). A closed lichen cover reflects more sunlight during the snow-free season than does other vegetation (Cohen *et al*. 2013) and keeps the subsurface temperatures lower during the growing season. Therefore, a layer of lichen vegetation can play a key role in many ecological processes.

Factors such as start and length of the growing season and frost and heat sums are essential variables determining species distribution. Growing season estimations are most often based on air temperature means rather than soil temperatures (Odland 2011). Differentiating between air and soil surface temperatures (2 cm depth) during the growing season has been stressed in arctic and alpine studies, nevertheless a literature survey has shown that even recent studies have used air temperature data to assess soil surface processes (Brooker and van der Wal 2003, Graae *et al*. 2012). A soil temperature threshold of 5 °C has often been used as a biological zero (Rabenhorst 2005) below which vegetative growth is stopped. Bjerke *et al*. (2015), in an analysis of winter air and soil temperatures, found that including soil temperature measurements to their models resulted in better classification of snow season types. Given the differences between soil and air temperatures that can occur during the spring thaw, and the general instability of air temperatures, soil temperatures offer an alternative means by which the initiation of vegetative growth and other phenological events can be estimated (Bjerke *et al*. 2015).

We assume that plant and lichen abundances in oligotrophic, alpine areas are strongly affected by snow thickness and duration, and their effects on soil temperatures. We hypothesize that cold season temperature variables, as influenced by snow cover and landscape position, are more important and have a stronger influence on the abundance and distribution of alpine vegetation than warm season variables.

Methods

Study areas

Three study areas in southeastern Norway were chosen along a climate gradient from semi-oceanic in the southwest to semi-continental in the northeast: Haukeli, Imingfjell, and Lesja (Fig. 1). The study areas are in the low alpine zone and are all considered oligotrophic, due to low levels of soil solution Ca (first author's pers. obs.). Haukeli is a mountain area in Telemark County, in the southern part of the Hardangervidda plateau. The study area was located at 59°48´N, 7°13´E and the plots ranged in elevation from 1048–1055 m above sea level (a.s.l.). The climate is categorized as slightly oceanic (Moen 1999) and a nearby station (Møsstrand II, Norwegian Meteorological Institute (NMI)) recorded 738 mm precipitation in 2012. Imingfjell is located in Buskerud County at 60°1´N, 8°34´E and plot elevations ranged from 1140 to 1178 m a.s.l. Here, the climate is categorized as indifferent (Moen 1999) and the nearby Tunhovd station (NMI) recorded 644 mm precipitation in 2012. The northernmost site is at Lesja in Oppland County, located at 62°1´N, 8°57´E . Plot elevations at Lesja ranged from 1203–1234 m a.s.l. and 540 mm of precipitation was recorded at the Prestulen station (NMI). The climate at Lesja is semi-continental (Moen 1999). Grazing by sheep and cattle occurs at all three sites, but neither of these graze on lichens.

Vegetation sampling and temperature recordings

The data were collected along transects running from exposed lichen heaths downward on the mountain slopes. In each of the study areas, three or four transects were subjectively selected. The transects (11 in total) were located along topographic gradients from windy, lichen-dominated ridges downward the slopes, where vegetation composition indicated increasing snow cover duration, and down to early snow bed communities. Due to topographic differences, transect lengths varied between 37 and 250 m. Randomly placed 2 × 2-m plots were selected for vegetation analyses and soil temperature measurements along each transect. Soil temperatures were recorded at 38 plots, and two vegetation analyses were performed from subplots located at a distance of 1 m from each soil temperature site. Vegetation analyses were performed in July 2013. Vegetation community composition was visually estimated and recorded by functional group (lichen, moss, shrub, graminoid, other vascular) and by species. LogTag TRIX-8 temperature recorders (measuring range –40 to +85 °C, resolution 0.1) were installed horizontally 5 cm below the soil surface. These recorded temperatures at 6-hour intervals beginning at 01:00 which gave us four readings per day. The recorders were installed in the summer of 2011 and removed in the summer of 2014. Measurements taken between 1 October 2011 and 31 July 2014 were analysed in this study. All temperature variables are based on averages for the three-year measurement period.

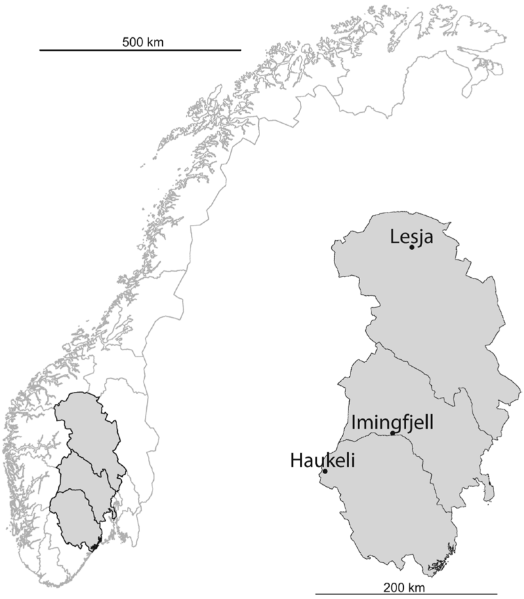

Fig. 1. Map showing the locations of the study areas.

Data analysis

Daily mean soil temperatures for the entire period were calculated first, and the temperature variables used in this study were based upon the daily means (Table 1). Start of Growing Season (SGS), End of Growing Season (EGS), and Thaw Date (TD) were determined by analysing the data for each plot and recording the day of the year (DOY) at which they occurred. Growing Season Length (GSL) and Thaw Time (TT) were then calculated based on the values of SGS, EGS, and TD. Abundance data (percent cover) for individual species was modelled as dependent variables against soil temperature variables using simple linear models (LM). Only species that appeared on at least two of the three sites were used in the LMs and the percent cover was averaged for the two sub-plots within each plot before analysis was performed. The r^2 values for vegetation functional groups were plotted for comparison.

Vegetation data were analysed using Nonmetric Multidimensional Scaling (NMDS) on two axes with Bray-Curtis distance measures. The results of the NMDS were then rotated to Principal Components Analysis (PCA) axes for visualization. The NMDS was performed on untrans-

Table 1. Definitions of soil temperature variables analysed in this study.

Variable	Definition
Start of growing season (SGS)	Day of the year which is the 5th in the series of five consecutive days when soil temperatures at 5 cm are ≥ 5 °C
End of growing season (EGS)	Day of the year which is the 5th in the series of five consecutive days when soil temperatures at 5 cm are ≤ 5 °C
Growing season length (GSL)	Interval between SGS and EGS
Thaw date (TD)	Day of the year where soil temperatures at 5 cm are ≥ 1 °C
Thaw time (TT)	Interval between TD and SGS
Heat sum (HS)	The sum of all soil temperatures above 5 °C at 5 cm
Frost sum (FS)	The sum of all soil temperatures below 0 °C at 5 cm

formed abundance data to identify similarities among species along environmental gradients. Detrended Correspondence Analysis (DCA) was also performed on the vegetation data, again to detect similarities along gradients and to confirm the results of the NMDS. Vegetation data were square-root-transformed for DCA. The two ordinations (unrotated NMDS and DCA) were then compared using Procrustes rotation, a process wherein two different ordinations are rotated to match configurations as best as possible (ter Braak & Smilauer 2012). With Procrustes rotation, a disagreement measure between 0 and 1 is given, with zero meaning that there is no disagreement between ordinations and 1.0 indicating complete disagreement. This procedure allows for verification and confirmation of the ordination results. Axes from the two ordinations were also compared using Pearson's correlation. Weighted average snow index values were estimated for each plot (Odland & Munkejord 2008a, 2008b).

Statistical analyses (with the exception of ordinations) were performed using R ver. 3.2.5. (R Core Development Team, 2016.) Ordinations were performed using CANOCO ver. 5.0 (Ter Braak & Smilauer 2012).

Table 2. Mean ± SD thaw date (TD), warming time (WT), start of growing season (SGS), growing season length (GSL) for all three study areas based on soil temperatures. DOY = day of year.

Site	TD (DOY)	TT (days)	SGS (DOY)	GSL (days)
Haukeli	147 ± 19	16 ± 9	163 ± 15	108 ± 16
Imingfjell	145 ± 9	25 ± 11	170 ± 14	89 ± 14
Lesja	151 ± 14	30 ± 16	180 ± 16	75 ± 20

Results

Variation in soil temperature variables between the study sites

The mean ± SD values of TD, TT, SGS, and GSL varied among the three study areas (Table 2). GSL decreased along the climate gradient from the southernmost, most humid study area (Haukeli) to the driest, northernmost study area (Lesja). The Haukeli study area thawed earlier in the year, the soils warmed to 5 °C more quickly, and the GSS was on average 17 days earlier than at Lesja. The average values, based on all plots within each of the three study areas, were highly variable, probably because of differences in snow cover, precipitation and air temperatures.

Species composition in the different plots in relation to the temperature variables

In the NMDS ordination (Fig. 2), the first axis represents a gradient from the warmest to the coldest soils and axis two represents the shift from sites that thaw slowly to those that thaw rapidly. The first two ordination axes cumulatively explained 75.5% of the variation in species abundances. The ordination axes for the DCA analysis were similar to those of the NMDS. Comparison of the two ordinations by Procrustes rotation resulted in a disagreement measure of 0.19 which suggests that these gradients are indeed important in describing vegetation abundances. The first and second ordination axes for the two ordinations were very strongly correlated (Pearson's $r = 0.97$, $p < 0.001$; and 0.80, $p < 0.001$; respectively).

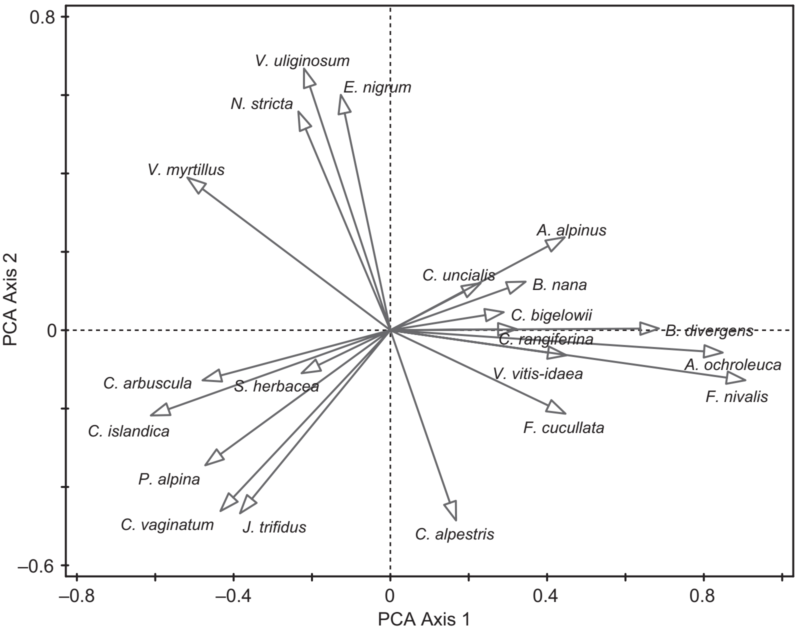

Fig. 2. NMDS ordination of species by plots, projected onto PCA axes. Axis 1 represents winter soil temperature gradient and Axis 2 represents a thaw gradient. Arrows indicate species responses to temperature variables.

Species DCA axis one scores were correlated (linear regression: $r^2 = 67.5$, $p < 0.0001$) with their snow indicator values (SI) values (Odland & Munkejord 2008b) (Table 3) which underscores the influence of snow cover and its insulating effect on alpine vegetation communities.

Species responses to different soil temperature variables

Abundances of the different species were modelled in relation to soil temperature variables (Table 4). In general, lichen species were positively associated with decreasing FS (colder soils). Species with the strongest positive response included *Alectoria ochroleuca*, *Flavocetraria nivalis*, and *Bryocaulon divergens*. However, some lichen species, including *Cladonia arbuscula* and *Cetraria islandica*, were positively associated with increasing FS (slightly warmer soils). Of the vascular plants, only *Arctous alpinus* responded positively to increasing FS, while *Vaccinium myrtillus* and *V. uliginosum* had positive associations with decreasing FS. In other words, *Arctous alpinus* was most common on the coldest sites, while the cover of *Vaccinium* increased as winter soil temperatures increased. TT was also an important factor for many of the lichen species; *Alectoria ochroleuca* and *Flavocetraria nivalis* were positively

Table 3. Mean species cover (Cover, %), number of plots where the species was recorded (*n*), DCA axis 1 scores, and snow indicator (SI) values for the species analysed in this study. SI values are based on data from Odland and Munkejord (2008b). ns = no score.

Species	Cover (%)	*n*	DCA 1	SI
Alectoria ochroleuca	15	10	3.50	1
Arctous alpinus	4	6	3.16	1
Betula nana	19	35	1.69	3
Bryocaulon divergens	6	5	3.77	1
Carex bigelowii	4	25	1.80	6
Carex vaginatum	5	4	–0.81	ns
Cetraria islandica	6	22	–0.13	ns
Cladonia alpestris	24	17	2.25	2
Cladonia arbuscula	18	34	0.51	2
Cladonia rangiferina	11	26	2.01	2
Cladonia uncialis	5	16	2.04	2
Empetrum nigrum	24	31	1.06	3
Flavocetraria cucullata	12	7	2.94	1
Flavocetraria nivalis	18	18	3.16	1
Juncus trifidus	9	25	0.52	ns
Nardus stricta	27	5	–1.21	7
Poa alpina	8	5	–0.82	ns
Salix herbacea	4	2	–0.79	8
Vaccinium myrtillus	6	19	–0.26	5
Vaccinium uliginosum	17	18	0.10	3
Vaccinium vitis-idaea	3	18	2.48	2

related to longer TTs while *Cladonia alpestris*, *C. rangiferina*, *Nardus stricta*, *V. myrtillus*, *V. uliginosum*, and *Empetrum nigrum* were positively associated with shorter TTs. *Nardus stricta* in particular was correlated with the shortest TT and the latest TD; it was most common in plots that warmed to 5 °C shortly after snowmelt. *Vaccinium vitis-idaea*, *Cladonia rangiferina*, and *C. alpestris* were negatively correlated with TD; they were found on sites that thawed earliest in the season. There were differences in response to the temperature variables between functional groups as well (Fig. 3), however there were several cases where a member of one functional group responded differently from the other members of that group.

Discussion

Responses to soil temperatures

The study shows that lichen and vascular plant species responded differently to soil temperature variables, and differences in soil temperatures were probably mainly associated with differences in winter temperatures, and with snow layer thickness and duration. The study plots within each study area were situated relatively close to each other and they differed very little in altitude (≤ 38 m), so differences in air temperatures had no direct effects on the distribution of the plants. Use of air temperatures and snow data to explain plant abundance patterns and developmental events may be useful at sites where there is a temperature-insulating snow cover, preventing extensive soil frost. For example, Jonas *et al*. (2008) found that plant growth started roughly two weeks after snowmelt in snow-covered alpine grasslands in the Swiss Alps. In their study, air temperature and precipitation were the best predictors of the beginning of the vegetation period. In wind exposed areas, the snow may be blown away, and there is virtually no snow cover at all during the winter. During periods with low air temperatures there may be extensive soil frost, and plants growing in these areas are at a greater risk of frost damage than those in areas with deeper snow cover (Larcher *et al*. 2010). Studies of effects of snow removal

Table 4. Linear regression's r^2 values for the relationships between soil temperature variables and species common to all three sites. GSL= growing season length; SGS = start of growing season; TD = thaw date, TT = thaw time, HS= heat sum, and FS = frost sum.

Species	GSL	SGS	TD	TT	HS	FS
Alectoria ochroleuca	0.069	0.016	0.076	0.173	0.077	0.597
Arctous alpinus	0.019	0.035	0.067	0.004	0.009	0.141
Betula nana	0.005	0.000	0.065	0.073	0.022	0.014
Bryocaulon divergens	0.024	0.005	0.047	0.088	0.037	0.446
Carex bigelowii	0.030	0.010	0.004	0.320	0.024	0.083
Carex vaginatum	0.002	0.004	0.006	0.004	0.004	0.027
Cetraria islandica	0.031	0.017	0.020	0.079	0.047	0.201
Cladonia alpestris	0.230	0.165	0.000	0.214	0.277	0.028
Cladonia arbuscula	0.112	0.129	0.039	0.033	0.076	0.170
Cladonia rangiferina	0.021	0.005	0.143	0.213	0.112	0.044
Cladonia uncialis	0.013	0.009	0.027	0.005	0.000	0.054
Empetrum nigrum	0.114	0.125	0.000	0.148	0.090	0.084
Flavocetraria cucullata	0.025	0.002	0.052	0.076	0.048	0.184
Flavocetraria nivalis	0.083	0.021	0.114	0.250	0.110	0.665
Juncus trifidus	0.013	0.006	0.079	0.038	0.000	0.041
Nardus stricta	0.008	0.060	0.387	0.143	0.066	0.056
Poa alpina	0.019	0.015	0.055	0.011	0.001	0.020
Salix herbacea	0.002	0.012	0.013	0.048	0.023	0.012
Vaccinium myrtillus	0.001	0.012	0.314	0.205	0.031	0.177
Vaccinium uliginosm	0.290	0.178	0.017	0.104	0.180	0.200
Vaccinium vitis-idaea	0.005	0.037	0.144	0.033	0.002	0.095

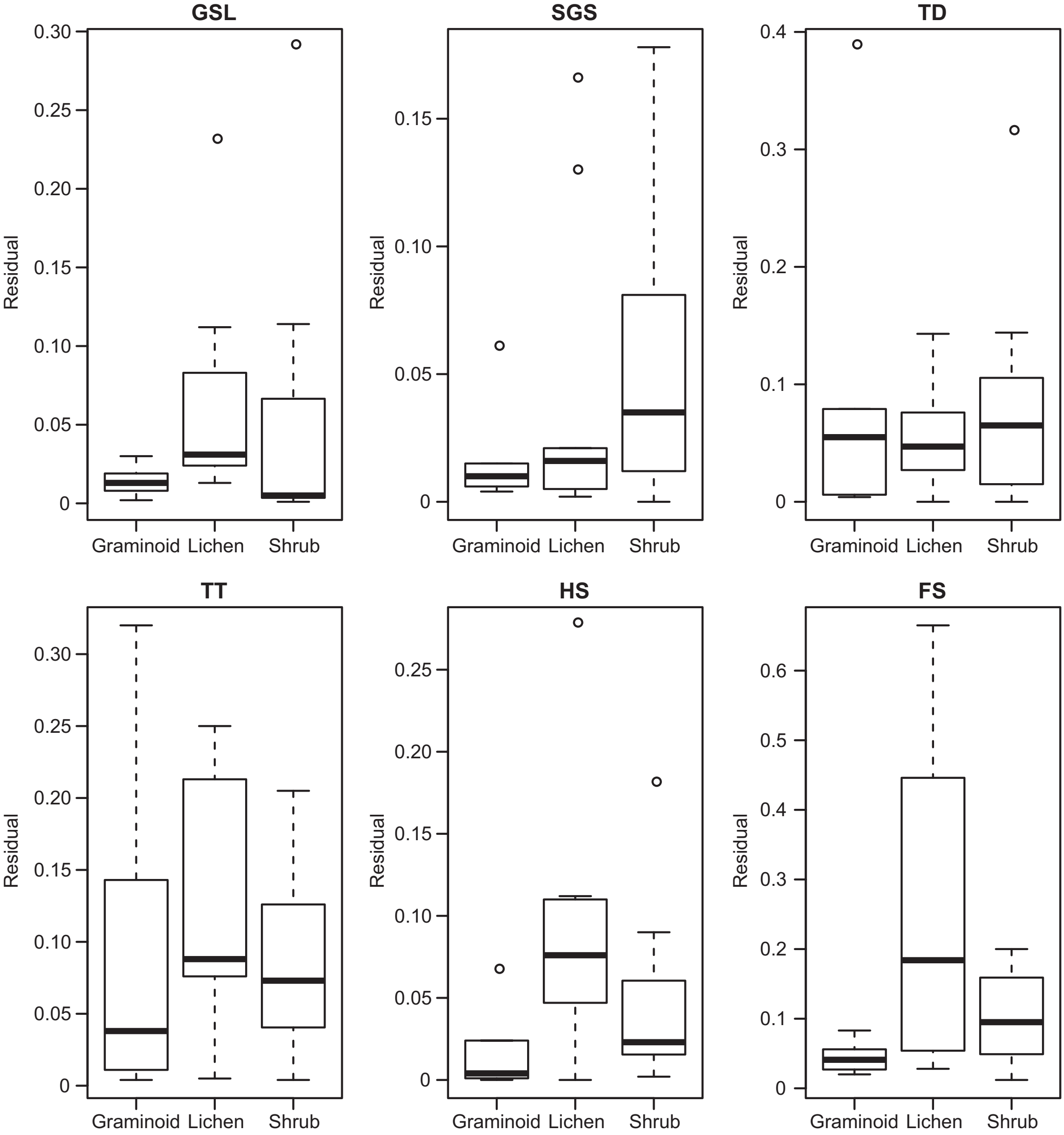

Fig. 3. Box-and-whiskers plots of r^2 values for functional groups and soil temperature variables (ines inside boxes are median values, boxes indicate 25th and 75th percentiles, whiskers indicate outliers). GSL= growing season length; SGS = start of growing season, TD = thaw date, TT = thaw time, HS = heat sum, and FS = frost sum.

have shown decreasing soil temperatures (Kaste *et al*. 2008), leading to delays in flowering (Petraglia *et al*. 2014) and reduced leaf area and flower number in *Vaccinium myrtillus* (Gerdol *et al*. 2013). Deeply frozen soils need more time and energy to thaw which can lead to delays in the start of the growing season and reductions in plant productivity (Bjerke *et al*. 2015). Studies also show that moss-lichen layers function as an important “thermal insulator”, and strongly determine conditions of the summer soil temperature. Although summer temperatures often exceed 40 °C just above the surface of the moss-lichen layers, frozen soils still occur under this cover type. This is primarily due to the low heat conductivity of the moss-lichen layers, especially under dry conditions (Oechel & Van Cleve 1986). Cohen *et al*. (2013) found that albedo was lower on the Norwegian side of a border fence than on the Finnish side during the snowmelt period, due to the presence of shrubs that stuck out from the snow surface. However, during the snow-free period, the Norwegian side had higher albedo, which was attributed to the presence of lichens and lack of disturbance. The high albedo of lichens contributes to their insulating effect and keeps soil temperatures lower than in adjacent areas without lichen cover.

Variations in GSL and SGS

In this study, the longest recorded growing season was at Haukeli in 2013 where the lower-lying plots had average GSL of 199 days based on the 5 °/5-day rule as described by Kollas *et al*. (2013). The shortest GSL was 40 days in an exposed plot at Lesja in 2012. At Haukeli, soil temperatures reached 2 °C in early- to mid-June, while at Lesja, the northernmost site, this temperature was reached later in the same month. In the lower-lying plots with little to no lichen component, the temperature tended to climb rapidly after snowmelt. Temperatures would often jump from 0 °C to 5 °C or above in just one day. Larcher (2012) defined the "climatically potential growing season" as the period between spring snowmelt and air temperatures below freezing in the autumn and assigned it a duration of 100–120 days in the Alps. Reinhardt and Odland (2012) set the growing season as the period from when the soil temperature exceeds 6 °C in spring until the temperatures fell below 5 °C the following autumn. Körner and Paulsen (2004) set a temperature threshold of 3.2 °C at 10 cm depth below the soil surface at the treeline, while Körner *et al*. (2003) defined the growing season in the alpine zone as beginning with the "obvious and sharp warming" above two degrees in the spring, and ending when the temperatures fell below 2 °C in autumn. So for plots with winter snow cover, Körner *et al*.'s (2003) 2 °C definition can be a useful indicator. However, in the lichen-dominated plots, which were much colder in the winter months, much more time is needed to come up to 5 °C and soil temperatures in the early summer were more unstable and variable. Growing seasons were generally longer at the lower-lying plots, despite having started later in the year; they also had much shorter warming times. The greatest limitation in estimating GSL from air temperatures is that it is impossible to take into account variations in surface and subsurface microclimate (Graae *et al*. 2012). Generally speaking, colder sites thaw earlier in the year than warmer sites yet it takes more time for them to warm up to temperatures conducive to plant growth. This can be attributed to the lack of snow at cold sites; the soils are exposed to direct solar radiation earlier in the year than the snow-covered sites, yet because of the lack of insulation reach much lower temperatures in winter. Thaw date is dependent upon the presence and depth of snow and on air temperatures, and varies from year to year.

Small topographical differences affect many factors, such as snow depth and exposure to direct solar radiation. These in turn have direct effects on the vegetation microclimate. Air temperatures can be well above 5 °C while the soils are still frozen; the time lag between higher air temperatures and soil thawing should not be discounted. At Haukeli, the most oceanic area, the average SGS according to air temperatures was on day 144. The mean soil temperature for all of the plots at Haukeli on day 144 was 2.5 °C and ranged from 0.0 to 8.5 °C. At Imingfjell, the mean SGS based on air temperatures was at day 145; the mean soil temperature on this day was 1.6 °C and ranged from –0.1 to 6.8 °C. At Lesja, the mean SGS based on air temperatures was on day 147. The mean soil temperature on this day was 1.7 °C and ranged from –0.1 to 6.5 °C. So while it is possible that vegetative growth had begun at some of the warmer microsites, it is unlikely that it had begun for these areas in general, considering that some of the soils were still frozen and the mean temperatures were well below 5 °C. The effects of spatial and topographic variations makes soil temperature a much better predictor of GSL than air temperature.

Species abundance in relation to frost sum

Vegetation communities in the three study areas can be assigned to one of the two phytosociological groups: the *Loiseleurio-Arctostaphylion* association in the lichen-dominated ridges, and the *Nardio-Caricion bigelowii* association in the lower landscape positions (Nordhagen 1936, Odland 2005). Three main plant abundance response patterns were found: (a) increasing with increasing frost, (b) increasing with decreasing frost, and (c) species with no significant response. Individual plant species have differing responses to soil temperatures, which are often related to their usual position in the landscape. *Nardus stricta* is a good example; it is generally found in snowbeds characterized by late-lying snows. In this study, we found that *N. stricta* is most closely correlated with short warming times, which are typical of snow-beds, which rarely have soil temperatures below 0 °C in the winter, and which can warm from 0 to 5 °C in less than 24 hours. For *Vaccinium uliginosum* in particular soil thaw has been found to be an important factor in the initiation of growth (Palacio *et al*. 2015) so a shorter thaw interval would be beneficial. Several lichen species and one vascular plant species were associated with the coldest soils and lowest FS; these species are generally found on ridge habitats, which are usually snow-free in the winter and which take the most time to defrost. In our study, *Vaccinium vitis-idaea* was negatively correlated with thaw date, yet Palacio *et al*. (2015) found that this species (along with *Loiseleuria procumbens* and *Calluna vulgaris*) was among the most frost-resistant of the ericaceous shrubs common to alpine areas. HS was significant for four species: *Cladonia alpestris*, *C. rangiferina*, *Nardus stricta* and *Vaccinium uliginosum*, but was generally less important, even for these species, than the cold-season variables. Wagner *et al*. (2012) also found that HS was generally not a good predictor of plant phenology, since temperatures at the plant surface often exceed air and soil temperatures. Several species of vascular plants and one species of lichen (*Cladonia uncialis*) were not dependent on any temperature factor. These species, which also include *Betula nana*, are usually found across the entire landscape on alpine sites, ranging from windy ridges to lee-sides, although their proportions in different habitat types can vary. It is therefore unsurprising to find that the species with the most general ranges have no soil temperature preferences. Nordhagen (1943) described *B. nana* as the “mountain enfant terrible” because he could not find any causal relationship for its abundance pattern. Schei *et al*. (2015) recently surveyed vegetation changes in the Rondane Massif in central Norway and found that *B. nana* had not changed in abundance. Two other species which had no significant relationship to soil temperature variables (*Carex bigelowii* and *Juncus trifidus*) had decreased and increased in abundance, respectively, which implies that other factors are responsible for the long-term changes in these two species.

Effects of soil frost on the floristic composition

The strong correlation between the two ordinations indicates that they represent the floristic and environmental gradients found in the study areas quite closely. These results would suggest that soil temperature is an important determinant of plant community composition in two ways; both the winter temperature patterns and the speed of the transition from winter frost to summer growth conditions are influential. Additionally, the DCA axis 1 scores were closely correlated in most cases to the SI values that have previously been established for alpine species (Odland & Munkejord 2008b). The limitation of SI is that it is only a useful indicator when the species is present in large amounts; a few scattered individuals of a plant with a high SI (for example *Carex bigelowii*) can occur even on sites that are generally snow-free or have little snow. Our DCA axis one scores were also similar to those of Bjerke *et al*. (2015), where they were able to separate types of snow seasons by soil frost duration, which again emphasises the importance of soil frost to ecological processes year-round. The DCA analysis also showed that these study areas had no true snowbeds; very few species had SI values higher than 5 and most were 1 or 2. Sites that have the mildest winter soil temperatures and shortest warming times are those that are generally snow-covered in winter, while colder sites with longer thaw times are snow-free. Long-term changes in snow depth and duration such as those predicted by both the IPCC (Christensen *et al.* 2007) and more local models (Dyrrdal *et al.* 2013) could contribute to permanent changes in the winter and spring soil temperature patterns at alpine sites and favour some vegetation types over others. Specifically, increases in snow cover that extend to areas that were previously snow-free can have an effect on vegetation communities, potentially eliminating frost-dependent species in favour of those that prefer milder winter soil temperatures.

According to Karlsson (1985), evergreen and semi-evergreen trees and dwarf shrubs may be heavily damaged if the ground remains frozen for a long time after snow melt. This is also consistent with effects of the ongoing global warming, which has been shown to increase shrub cover both in arctic and alpine areas (Sturm *et al.* 2001, Hallinger *et al.* 2010).

Conclusions

This study shows that cold-season soil temperatures affect the abundance of many alpine plant species and vegetation composition. Species responded differently to different soil temperature variables. Frost sum (FS) and thaw time (TT) were the variables that best explained the variations in abundance of the species, especially whether the individual species of lichen or vascular plant responded positively or negatively. Response of only three species to differences in growing season length (GSL) was significant, which could indicate that possible changes in this variable are of less concern than changes in winter frost regimes and snow depths. A long growing season found in the most oceanic study area was associated with a very low abundance of lichens. This indicates that a long growing season in an alpine area strongly reduces lichen heath distribution. Species associated with extensive soil frost and long defrost times may be vulnerable to increasing air temperatures and precipitation rates with continued climate change. Lichens are poor competitors in areas where vascular plants can grow, and consequently environmental changes which improve vascular plant growth may adversely affect lichens. Extensive oligotrophic alpine lichen heaths appear to be strongly associated with sites lacking or having a relatively thin insulating snow layer where the soils freeze during winter and then thaw slowly. *Cladonia alpestris* was, however, not strongly associated with extensive soil frost and was associated with a long growing season and a protective snow cover. Several species (*Betula nana*, *Carex bigelowii*, *C. vaginatum*, *Cladonia uncialis*, *Poa alpina*, and *Salix herbacea*) were not significantly associated with any of the soil temperature variables. The frozen soil and slow thaw also prevent the establishment of most vascular plants, which can outcompete lichens in the long term.

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References

Abeli T., Rossi G., Gentili R., Mondoni A. & Cristofanelli P. 2012: Response of alpine plant flower production to temperature and snow cover fluctuation at the species range boundary. — *Plant Ecology* 213: 1–13.

Billings W.D., Clebsch E.E.C. & Mooney H.A. 1961: Effect of low concentrations of carbon dioxide on photosynthesis rates of two races of *Oxyria*. — *Science* 133: 1834.

Bjerke J.W., Tømmervik H., Zielke M. & Jørgensen M. 2015: Impacts of snow season on ground-ice accumulation, soil frost and primary productivity in a grassland of sub-Arctic Norway. — *Environmental Research Letters* doi:10.1088/1748-9326/10/9/095007.

Bliss L.C. 1971: Arctic and alpine life cycles. — *Annual Review of Ecological Systems* 2: 405–438.

Brooker R. & van der Waal R. 2003: Can soil temperature direct the composition of high arctic plant communities? — *Journal of Vegetation Science* 14: 535–542.

Chapin F.S.III, van Cleve K. & Chapin M.C. 1979: Soil temperature and nutrient cycling in the tussock form of *Eriophorum vaginatum*. — *Journal of Ecology* 67: 169–189.

Christensen J.H., Hewitson B., Busuioc A., Chen A., Gao X., Held I., Jones R., Kolli R.K., Kwon W.-T., Laprise R., Magaña Rueda V., Mearns L., Menéndez C.G., Räisänen J., Rinke A., Sarr A. & Whetton P. 2007: Regional climate projections. — In: Solomon S., Qin D., Manning M., Chen Z., Marquis M., Averyt K.B., Tignor M. & Miller H.L. (eds.), *Climate change 2007: the physical science basis*: 848–940. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge.

Cohen J., Pulliainen J., Menard C.B., Johansen B., Oksanen L., Luojus K. & Ikonen J. 2013: Effect of reindeer grazing on snowmelt, albedo and energy balance based on satellite data analyses. — *Remote Sensing of Environment* 135: 107–117.

Dyrrdal A., Saloranta T., Skaugen T. & Bache H. 2013: Changes in snow depth in Norway during the period 1961–2010. — *Hydrology Research* 44: 169–179.

Freppaz M., Celi L., Marchelli M. & Zanini E. 2008: Snow removal and its influence on temperature and N dynamics in alpine soils (Vallée D'Aoste, Italy). — *Journal of Plant Nutrition and Soil Science* 171: 672–680.

Gerdol R., Siffi C., Iacumin P., Gualmini M. & Tomaselli M. 2013: Advanced snowmelt affects vegetative growth and sexual reproduction of *Vaccinium myrtillus* in a sub-alpine heath. — *Journal of Vegetation Science* 24: 569–579.

Graae B.J., de Frenne P., Kolb A., Brunet J., Chabrerie O., Verheyen K., Pepin N., Heinken T., Zobel M., Shevtsova A., Nijs I. & Milbau A. 2012: On the use of weather data in ecological studies along altitudinal and latitudinal gradients. — *Oikos* 121: 3–19.

Grime J.P. 1977: Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. — *The American Naturalist* 111: 1169–1194.

Groffman P.M., Hardy J.P., Nolan S., Fitzhugh R.D., Driscoll C.T. & Fahey T.J. 1999: Snow depth, soil frost and nutrient loss in a northern hardwood forest. — *Hydrological Processes* 13: 2275–2286.

Hallinger M., Manthey M. & Wilmking M. 2010: Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. — *New Phytologist* 186: 890–899.

Harris C., Kern-Luetschg M., Murton J., Font M., Davies M. & Smith F. 2008: Solifluction processes on permafrost and non-permafrost slopes: results of a large-scale laboratory simulation. — *Permafrost and Periglacial Processes* 19: 359–378.

Holway J. & Ward R.T. 1965: Snow and meltwater effects in an area of Colorado alpine. — *American Midland Naturalist* 69: 189–197.

Jonas T., Rixen C., Sturm M. & Stoeckli V. 2008: How alpine plant growth is linked to snow cover and climate variability. — *Journal of Geophysical Research: Biogeosciences* 113, G03013, doi: 10.1029/2007JG000680.

Karlsson P.S. 1985: Photosynthetic characteristics and leaf carbon economy of a deciduous and an evergreen dwarf shrub: *Vaccinium uliginosum* L. and *Vaccinium vitis-idaea* L. — *Holarctic Ecology* 8: 9–17.

Kaste Ø., Austnes K., Vestgarden L.S. & Wright R.F. 2008: Manipulation of snow in small headwater catchments at Storgama, Norway: effects on leaching of inorganic nitrogen. — *Ambio* 37: 29–37.

King L. 1986: Zonation and ecology of high mountain permafrost in Scandinavia. — *Geografiska Annaler* 68A: 131–139.

Kollas C., Körner C. & Randin C.F. 2013: Spring frost and growing season length co-control the cold range limits of broad-leaved trees. — *Journal of Biogeography* 41: 773–783.

Kudo G. 1991: Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. — *Arctic & Alpine Research* 23: 436–443.

Körner C. & Paulsen J. 2004: A world-wide study of high altitude treeline temperatures. — *Journal of Biogeography* 31: 713–732.

Körner C., Paulsen J. & Pelaez-Reidl S. 2003: A bioclimatic characterization of Europe's Alpine Areas. — In: Nagy L., Grabherr G., Körner C. & Thompson D.B.A. (eds.), *Alpine Biodiversity in Europe*: 13–28. Ecological Studies 167, Springer, Berlin.

Larcher W. 2012: Bioclimatic temperatures in the High Alps. — In: Lütz C. (ed.), *Plants in alpine regions*: 21–27. Springer-Verlag, Wien.

Larcher W., Kainmüller C. & Wagner J. 2010: Survival types of high mountain plants under extreme temperatures. — *Flora: Morphology, Distribution, Functional Ecology of Plants* 205: 3–18.

Moen A. 1999: *National Atlas of Norway: Vegetation*. — Norwegian Mapping Authority, Hønefoss.

Nordhagen R. 1936: Versuch einer neuen Einteilung der subalpinen-alpinen Vegetation Norwegens. — *Bergens Museums Årbok i naturvidenskap Rekke* 7: 1–88

Nordhagen R. 1943: Sikilsdalen og Norges Fjellbeiter: En plantesosiologisk monografi. — *Bergens Museums Skrifter* 22: 1–607

Odland A. 2005: Oligotrophic and mesotrophic vegetation in southern Scandinavian mountains. Gradients in species and community distribution extracted by numerical analyses of earlier published vegetation descriptions. — *Phytocoenologia* 35: 985–1018.

Odland A. & Munkejord H.K. 2008a: The importance of date of snowmelt for the separation of different oligotrophic and mesotrophic mountain vegetation types in Southern Norway. — *Phytocoenologia* 38: 3–21.

Odland A. & Munkejord H.K. 2008b: Plants as indicators of snow layer duration in southern Norwegian mountains. — *Ecological Indicators* 8: 57–68.

Odland A. 2011: Estimation of the growing season length in alpine areas: effects of snow and temperatures. — In: Schmidt J.G. (ed.), *Alpine environment: geology, ecology, and conservation*: 85–134. Nova Science Publishers, Hauppauge, New York, USA.

Oechel W.C. & van Cleve K. 1986: The role of bryophytes in nutrient cycling in the Taiga. — In: van Cleve K., Chapin F.S.III, Flanagan P.W., Vierick L.A. & Dyrness C.T. (eds.), *Forest ecosystems in the Alaskan Taiga*: 121–137. Springer-Verlag, New York.

Palacio S., Lenz A., Wipf S., Hoch G. & Rixen C. 2015: Bud freezing resistance in alpine shrubs across snow depth gradients. — *Environmental and Experimental Botany* 118: 95–101.

Petraglia A., Tomaselli M., Petit Bon M., Delnevo N., Chiari G. & Carbognani M. 2014: Responses of flowering phenology of snowbed plants to an experimentally imposed extreme advanced snowmelt. — *Plant Ecology* 215: 759–768.

R Core Team 2016: *R: A language and environment for statistical computing*. — R Foundation for Statistical Computing, Vienna, Austria.

Rabenhorst M.C. 2005: Biologic zero: a soil temperature concept. — *Wetlands* 25: 616–621.

Randin C.F., Jaccard H., Vittoz P., Yoccoz N.G. & Guisan A. 2009: Land use improves spatial predictions of mountain plant abundance but not presence–absence. — *Journal of Vegetation Science* 20: 996–1008.

Reinhardt S. & Odland A. 2012: Soil temperature variation in calciphile plant communities in southern Norway. — *Oecologia Montana* 21: 21–35.

Reinhardt S., Odland A. & Pedersen A. 2013: Calciphile alpine vegetation in southern Norway: importance of snow and possible effects of climate change. — *Phytocoenologia* 43: 207–223.

Schei F.H., Kapfer J., Birks H.J.B. & Grytnes J.A. 2015: Stability of alpine vegetation over 50 years in central Norway. — *Folia Geobotanica* 50: 39–48.

Sofronov M., Volokitina V., Kajimoto T. & Uemura S. 2004: The ecological role of moss-lichen cover and thermal amelioration of larch forest ecosystems in the northern part of Siberia. — *Eurasian Forest Research* 7: 11–19.

Sturm M., Manthey M. & Wilmking M. 2001: Increasing shrub abundance in the Arctic. — *Nature* 411: 546–547.

Sveinbjörnsson B. 1983: Bioclimate and its effect on the carbon flux of mountain birch (*Betula pubescens* Her.) at its altitudinal treeline in the Torneträsk area, northern Sweden. — *Nordicana* 47: 111–122.

Svoboda J. 1977: Ecology of primary production of raised beach communities, Truelove Lowland. — In: Bliss L.C. (ed.), *Truelove Lowland, Devon Island, Canada: a High Arctic ecosystem*: 185–216. University of Alberta Press, Alberta.

ter Braak C.J.F. & Smilauer P. 2012: *Canoco reference manual and user's guide: software for ordination (Version 5.0)*. — Microcomputer Power, Ithaca, NY, USA.

Theurillat J.P. & Schlussel A. 2000: Phenology and distribution strategy of key plant species within the subalpine-alpine ecocline in the Valaisan Alps (Switzerland). — *Phytocoenologia* 30: 439–456.

Wagner J., Ladinig U., Steinacher G. & Larl I. 2012: From the flower bud to the mature seed: Timing and dynamics of flower and seed development in high-mountain plants. — In: Lütz C. (ed.), *Plants in alpine regions*: 135–152. Springer-Verlag, Wein.

Article 4

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Alpine lichen-dominated heaths: ecology, effects of reindeer grazing, and climate change. A review

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Abstract. Lichens are important forage for reindeer during winter, making evaluation of lichen biomass important for reindeer population management. Lichen heaths have a scattered distribution at high latitudes and altitudes in Fennoscandia. During the last few decades, their decrease has been attributed to reindeer grazing and trampling as well as climate change. Some consider this decrease to be the result of competition from vascular plants. However, we believe that this is a far too simple an explanation. In many studies the most important factor - deep soils with long-lasting frost - has not been considered. As a result, anticipated long-term effects of climate change and grazing should be reconsidered. Lichens have no roots, and therefore, environmental and edaphic conditions have limited direct effects on lichen abundance. Vascular plants live in contact with two different environments; the atmosphere and the rhizosphere, and ecological factors within both affect them. It is imperative to know which environmental factors increase the possibility of maintenance and development of extensive lichen heaths. In this review, we use current ecological knowledge to discuss the ecology of alpine lichen heath distribution and possible reasons for their decline, both at present and in the future.

Key words: lichen, temperature, thaw, snow, competition, soil frost

Introduction

Macro-lichens (often called reindeer lichens or even reindeer mosses) can dominate the vegetation in alpine, boreal, and arctic ecosystems. In addition to being an important food resource for reindeer during winter, macro-lichens are also important for the functioning and biodiversity of cold ecosystems (Cornelissen *et al.* 2001; Asplund and Wardle 2017).

Lichen heaths in alpine ecosystems are dominated by lichen species with podetia that can reach heights of 12-14 cm, and the most important species belong to the *Cladonia* or *Flavocetraria* genera. They are frequently abundant at high elevations and latitudes in Fennoscandia (the alpine and northern boreal zone (Ahti *et al.* 1968; Moen 1999). Patches of lichen-dominated vegetation may also be found under highly variable environmental conditions. In lowland areas, lichen-dominated vegetation is often patchy and restricted to exposed naked rocks with very thin soils where the vegetation is frequently exposed to drought (Kleiven 1959). Lichens can also be common on sand dunes, on raised bogs and newly exposed substrates (Ahti and Oksanen 1990). The floristic composition and ecology of such communities is quite different from alpine lichen heaths. In continental parts of Fennoscandia, pine forests dominated by lichens have a wide distribution. In the present review, we will mainly discuss the ecology of alpine lichen heaths.

Lichen heaths often have scattered, patchy occurrences on exposed windblown sites in alpine areas. Their main distribution is confined to the continental parts of Scandinavia, indicating that they favor areas with low winter temperatures and low precipitation. The alpine zone in Scandinavia includes areas above the forest limit (Ahti *et al.* 1968; Moen 1999). The position of the forest limit is highly variable as shown by iso-line maps (Aas and Faarlund 2000; Moen 1999; Heikkinen 2005). The highest limits lie in the southern parts of Norway, mainly between 1 100 and 1 300 m, decreasing in all directions due to both climatic factors and mountain height (Odland 2015).

Ecologists have tried to explain the lichen heath distribution, and several possible factors have been suggested. It has frequently been emphasized that the distribution of lichens is primarily controlled by their inability to compete with faster-growing vascular plants. Apparently, lichen-dominated vegetation develops only in environments where competition from higher plants is excluded or reduced (Kershaw 1978; 1985). Consequently, a key to understanding lichen distribution can be to investigate ecological conditions where vascular plants are not growing. Crittenden (2000) reviewed knowledge on mat-forming lichen biology and their ecological relationships with reindeer. His conclusion was that factors controlling the development of lichen-dominated terrain remain incompletely understood.

Vascular plant and lichen abundance is significantly negatively correlated (Odland *et al.* 2015). Vascular plants easily outcompete lichens except under the most harsh ecological conditions, and Corneliessen *et al.* (2001) found that the relationship between lichen biomass and vascular plants was consistently negative across alpine, subarctic and mid-arctic areas.

Lichens can survive extreme conditions, such as cold, heat, or drought. They grow in polar regions, high mountain areas, and arid deserts (Kappen *et al.* 1995; Körner 2003). Lichens can grow and metabolize at much wider ecological ranges than vascular plants, including at freezing or below-freezing temperatures, so long as the lichen thallus is sufficiently moist (Klein and Shulski 2011). In many ecosystems, such as on rocky coasts or otherwise bare mountaintops, lichens are often the most common and diverse organisms (Seaward 2008). This large lichen tolerance is an effect of being metabolically active only when wet; during dry periods, they can tolerate extreme temperature stress (Green *et al.* 2007).

Lichens are poikilohydric organisms, characterized by a high water absorption index, using atmospheric water as well as rain, dew and fog. Under the influence of evaporative forces, lichens lose water, becoming dry and largely metabolically inactive. After only 30 seconds of direct contact with water, the absorption exceeds the weight of the dry lichen biomass and maximum water absorption is reached during the first few minutes of exposure (Matwiejuk 2000).

Most lichen species require good light conditions. Light saturation for lichen photosynthesis is about 35 000 lux, which is higher than for vascular plants (20 000 – 30 000 lux) (Skre 1975). Lichens can begin photosynthesis early in spring, likely even before snowmelt. Lichens have a low optimum temperature for photosynthesis (between 7 and 10 ˚ C), depending on temperature pretreatment. Apparent photosynthesis can continue down to -5 to -10˚ C (Skre 1975). The growth rate of reindeer lichens is generally low (Kärenlampi 1971; Helle *et al.* 1983; den Herder *et al.* 2003).

Lichens produce a wide array of secondary compounds (Fahselt 1994; Molnár and Farkas 2010). Although the best studied lichen secondary compound is usnic acid (Cocchietto *et al.* 2002), there are countless other secondary compounds the functions of which are less well understood. Several laboratory studies have been executed to test allelopathic effects on plants and mosses (Huneck 1999; Sedia and Ehrenfeld 2003). Some studies indicate that substances inhibit growth of a variety of plants (Lawrey 1995), while other field studies have not shown any definitive effects (Kytöviita and Stark 2009).

Lichens are sensitive to different types of air pollution. Fertilization experiments show that the addition of approximately 150 kg N ha^{-1} produced a negative effect (23-73%) on a standing crop of *Cladina* spp. over a period of time exceeding eleven years compared to the control standing crop (Eriksson and Raunistola 1993).

Bryophytes and lichens are ubiquitous in cold ecosystems, and recently their roles in controlling energy fluxes have been studied in alpine and arctic areas (Petzold and Rencz 1975; Gornall *et al.* 2007; Peltoniemi *et al.* 2010). Studies show that moss-lichen layers function as important "thermal insulators," and strongly affect soil temperatures.

Development of mature lichen-dominated vegetation is a long-lasting process. It has been estimated that after a fire, it may take around 100 years for lichen stands to achieve the climax stage (Morneau and Payette 1989; Kumpula *et al.* 2000). In many cases, lichens fail to re-colonize sites after removal due to their inability to compete with faster-growing vascular species (Klein and Shulski 2011).

Lichen species are on the decline across the arctic, alpine and boreal (Joly *et al.* 2009; Fraser *et al.* 2014; Sandström *et al.* 2016), due to climate change and reindeer grazing (Joly *et al.* 2007). According to Bjerke (2011) and Bokhorst *et al.* (2012), lichen-dominated heaths appear to be one of the most vulnerable ecosystems in circumpolar regions. It is therefore important to have more information about which ecological factors are critical for lichen heath development, and which factors that threaten their future existence.

In this review, we will focus on the ecology of low alpine lichen heaths. Lichen-dominated heaths are characteristic for alpine landscapes, where they are considered to be a major winter food resource for wild and semi-domesticated reindeer. The following issues will be emphasized:

- Floristic variation of lichen-dominated heaths in Scandinavian alpine areas,
- Environmental factors associated with alpine lichen heath distribution and development,
- Effects of reindeer grazing, and
- Effects of ongoing climate change on the distribution of alpine lichen heaths

Alpine lichen heaths; distribution and flora

Distribution

Reindeer lichens have a wide circumpolar distribution and reach their maximum abundance in dry and oligotrophic sites around the coniferous timberline where competition with mosses, dwarf shrubs, and grass is low (Ahti and Oksanen 1990).

The distribution of lichen heaths is, however highly variable in the Scandinavian mountains. In general, lichen heaths are more common in the east than in the west, and they become more common toward the north (Du Rietz 1925; Ahti and Oksanen 1990). According to Moen (1999), alpine lichen heaths are mainly confined to the slightly continental and indifferent sections of Norway, characterized by an annual precipitation lower than 1 200 mm, and an air temperature frost-sum higher than 50 (Moen 1999; Odland *et al.* 2014; Falldorf *et al.* 2014; Sundstøl and Odland, 2017).

In oceanic areas, winter temperatures are generally warmer, and the winter conditions are often unstable. This gives important clues as to how environmental conditions are affecting the climatic tolerances of lichen-dominated heaths.

On the Hardangervidda mountain plateau (southern Norway), the chionophobous heaths where lichens are more or less dominant have been estimated to cover around 10% of the total area (Wielgolaski 1975; Hesjedal 1975; Rekdal *et al.* 2009). There are major geographic variations, with a strongly decreasing frequency toward the south and west (Moen 1999). According to Gaare and Skogland (1979), the cover of lichen heaths has been estimated to be 25% in the eastern region, and less than 1% in the snow-rich western region.

Studies of lichen heath elevation distribution in south central Norway (mostly on the Hardangervidda mountain plateau) show that they are mainly found at elevations between 1 150 and 1 400 m, in the low alpine zone (Fig. 1). A regression analysis of the data showed no significant trend within this elevational span.

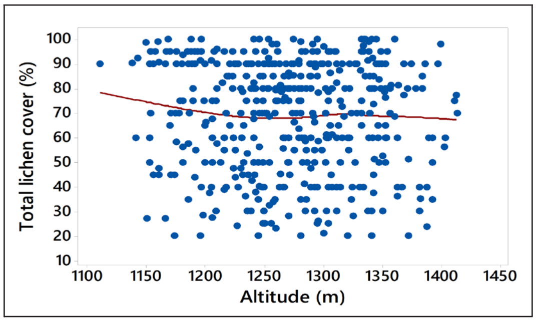

Fig. 1. Altitudinal distribution of lichen heath vegetation types around Hardangervidda. 437 plots where total lichen cover was higher than 20% have been plotted against altitude (data from Odland *et al.* 2014 and unpublished data). A Lowess smoother line (degree of smoothing = 0.8, number of steps = 2) is drawn.

Floristic variation

Lichens can be dominant in different types of vegetation. Alpine oligotrophic and chionophobous lichen-dominated vegetation types have been studied and described in Scandinavia for more than a century. The most ecologically successful terricolous lichens are mat-forming species within the genera *Cetraria*, *Cladonia*, *Flavocetraria*, *Stereocaulon*, and *Alectoria* (Ahti and Oksanen 1990). Lichens can also be dominant in alpine shrub vegetation dominated by *Salix glauca*, *Juniperus communis*, and *Betula nana* (DuRietz 1925; Nordhagen 1928; 1943; Jonasson 1981). Graminoids may also be abundant in lichen heaths, especially *Festuca ovina*, *Juncus trifidus*, and *Carex bigelowii* (Nordhagen 1943). Most commonly associated with lichen heaths are shrub species like *Loiseleuria procumbens*, *Arctous alpinus*, *Empetrum nigrum*, *Betula nana*, *Vaccinium uliginosum* and *Vaccinium vitis-idaea*.

In the northernmost parts of Fennoscandia, Haapasaari (1988) described different heath types where macro-lichens were dominant, e.g. Arctic *Empetrum-Cetraria nivalis* type, Arctic-hemiarctic *Myrtillus-Lichenes* type, Hemiarctic *Empetrum-Lichenes* type, and *Betula nana-Lichenes* scrub type.

In coastal areas (oceanic sections sensu Moen 1999) exposed sites in alpine areas are mainly dominated by vascular plants and bryophytes, while lichens are less abundant (Reistad, 1997). Vegetation on exposed alpine sites in oceanic areas have been described by Odland (1981), Huseby and Odland (1981), Røsberg (1981), Löffler (2003), and Tveraabak (2004). *Cladonia arbuscula* and *C. rangiferina* may locally be abundant, but species like *Bryocaulon divergens*, *Alectoria nigricans*, *A. ochroleuca*, *Coleocaulon aculeatum*, *Flavocetraria cucullata*, *F. nivalis* and *Cladonia stellaris* are mostly rare or absent in oceanic alpine areas. The most abundant vascular plants at these sites are *Carex bigelowii*, *Scirpus cespitosus*, *Molinia caerulea*, and *Juncus trifidus*, in addition to several dwarf shrub species (*Empetrum nigrum*, *Vaccinium uliginosum*, *Betula nana*, and *Calluna vulgaris*). Mosses are also often highly abundant, especially *Racomitrium lanuginosum* and *Dicranum* spp.

Pine forest floors, often completely dominated by *Cladonia stellaris* are abundant in the continental parts of Fennoscandia (Kielland-Lund 1981; Ahti and Oksanen 1990; Haapasaari 1988). *Betula pubescens* forests at high elevations or latitudes can also be dominated by *C. stellaris* (Nordhagen 1943; Haapasaari 1988; Kumpula *et al.* 2011). These are not included in this review.

Importance of substrate and soil

Most alpine soils have developed since the last glaciations, during the last 9 000 years. The importance of lichens for soil development processes is not well known, but some information can be gleaned from recent succession studies in the front of retreating glaciers. Macro-lichens can be dominant in both boreal forests and in low alpine heaths, and one should therefore expect their soil conditions to be different. Lichens can have many direct and indirect effects on the substrate where they grow. Sedia and Ehrenfeld (2006) found that many biotic soil factors were significantly different under naturally occurring lichen and moss mats than under other ground covers.

Role of lichens in primary successions

Lichens and mosses are assumed to be pioneer species on recently exposed, dry minerogenic sediments, and in the early stages of primary successions (Cooper 1953; Ahti and Oksanen 1990). Studies on primary succession of exposed glacier moraines show, however, that species dominant in alpine lichen heaths arrive relatively late, long after bryophytes and many vascular plants. Studies from retreating glaciers indicate that reindeer lichens have minor ecological impacts during the early stages of primary successions (Stork 1963; Vetaas 1994; Rydgren *et al.* 2014). According to Ahti and Hepburn (1967), reindeer lichens require at least a thin soil layer for attachment because they cannot colonize bare rock. The role of reindeer lichens during primary succession in the front of retreating glaciers has been studied in different parts of the world (Matthews 1992). During the first stages (often 0-50 years), cryptogams (primarily mosses) are most abundant, followed by dwarf shrub heath and woodland, while macro-lichens are sparse (e.g. Fægri 1934; Cooper 1953; Ahti and Oksanen 1990; Coxson and Marsh 2001).

Vetaas (1994; 1997) studied vegetation on moraines of different ages in front of a retreating glacier in west central Norway. The youngest moraine ridges studied had been exposed for 54 years, and were primarily dominated by mosses, especially *Racomitrium* spp., *Dicranum* spp., *Polytrichum* spp., *Pohlia* spp., hepatics, and vascular plants. The most abundant lichen was *Stereocaulon* spp., while *Cladonia* spp. occurred only sporadically. *Alectoria ochroleuca, Flavocetraria nivalis*, and *F. cucullata* were abundant on moraines exposed for between 84 and 186 years. *Cladonia rangiferina*, *C. arbuscula*, and *C. uncialis* had a wider span, occurring on moraines between 54 and 226 years old. *C. stellaris* was most abundant on moraines around 200 years old. Moraines more than 200 years old were mainly dominated by birch, shrubs, herbs, graminoids, and bryophytes. Lichens were very rare in plots on moraines older than 200 years, likely outcompeted by trees and shrubs. In addition, lichens had different distribution on the moraine ridges, mainly confined to the ridge tops. Vascular plants (mainly shrubs) and mosses dominated both the distal and proximal slopes, probably a result of increased snow downward the slopes. Soil development on the moraines is a slow process, particularly at the highest altitudes. Mosses, especially *Racomitrium* spp. were the main source for the humus development (Vetaas 1986). Viereck (1966) also notes that mosses were most important for the development of humus on exposed moraine ridges.

Hestmark *et al.* (2005) studied the population biology of *Flavocetraria nivalis* on a glacier foreland. They found that the largest thallus was 96 mm in diameter, on moraines exposed for approximately 240 years. The fastest growth occurred during the first 60 years. The density of individual thalli (in m^{-2}) increased nearly linearly with time, and reached 10 after 240 years. The height of the thalli never exceeded 60 mm. Development of lichen-dominated vegetation appears to be a long-lasting process. It has been estimated that after a fire, it may take 100 years for lichen stands to achieve the climax stage (Morneau and Payette 1989; Kumpula *et al.* 2000). In general, during primary successions, soil organic matter and nitrogen content will increase with time. This can favor vascular plant dominance and in turn can decrease lichen abundance (Stork 1963; Tisdale *et al.* 1966; Vetaas 1994; Rydgren *et al.* 2014).

Lichens are slow-growing and produce a low volume of organic matter compared to most vascular plants and mosses. On Svalbard, Uchida *et al.* (2006) found that lichen primary production was 5.1 g dry weight m^{-2}, and represented 29% of moss and 5% of vascular plant primary production. Consequently, lichens have a limited effect on the development of organic humus layers, and during early stages of vegetation development vascular plants probably contributed most to soil development. Lichens could only become dominant when the soil layers were deep enough to remain frozen for long periods during the spring and early summer.

Lichen heath soil types and soil depth

Lichen-dominated forest communities have mostly been found on regosols or podsols (Nordhagen 1943; Löffler *et al.* 2008). Plant growth generally results in accumulation of organic residues, developing an organic layer (the O- and A-horizons). After sufficient time, a distinctive organic layer forms with humus (the A-horizon) which rest on mineral soils. Eluviation is driven by a downward movement of soil water. In time, this can develop an E-horizon. Beneath the E-horizon lies the B-horizon, a zone where the downward moving material is accumulated. The C-horizon is the relatively unaltered parent material, usually brightly colored directly from parent rock.

In alpine areas, conditions for soil development are unfavorable, and the humus layers are often less than 2 cm thick (Nordhagen 1943; Dahl 1956). During the warm Holocene period forest limits were up to 200 m higher than at present, and sites presently lichen-dominated were probably within the Boreal forest region. Alpine lichen heaths have been found on podsols, and an example is shown in Fig. 2.

Fig. 2. Soil profile from a lichen-dominated heath at Slondalen, central Norway (cf. Table 1).

Previous studies of alpine heath communities have shown they are mainly found on sites with variable soil thickness, but often the depth to the underlying bedrock can be more than 0.5 m. Lichen heaths have frequently been recorded at sites with a growth substrate of more than 30 cm, often with a humus-rich upper layer (Nordhagen 1943; Dahl 1956; Odland and Munkejord 2008a). The humus layer (O) is mostly between 1 and 10 cm thick, underlain by a bleached soil layer (E) often 5-12 cm thick.

Nordhagen (1943) described soil profiles from different types of lichen-dominated vegetation types from Sikilsdalen, southeast Norway. In all profiles, there was a humus-rich layer with a thickness between 1 and 8 cm. In some, there was a bleached soil layer 4-5 cm thick, followed by a B-layer 15-20 cm thick, underlain by moraine material. Dahl (1956) studied soil conditions in low alpine Alectorieto-Arctostaphyletum communities (extreme exposed sites), and found a thin humus layer and a 2-12 cm bleached soil layer below. On Hardangervidda, lichen-dominated plant communities presented with a 0-8 cm humus layer, and a 40 cm thick B layer (Hinneri *et al.* 1975). Lichen cover degree and lichen biomass have been studied in sites with different soil thickness (Myrvold 2013; Odland *et al.* 2014). These measurements include the thickness of the moraine material (the C-horizons), and indicate that high lichen abundance was mainly associated with a soil thickness between 10 and 40 cm (Fig. 3). Sundstøl (unpublished) found podsol profiles in most lichen dominated types (cf. Tab. 1).

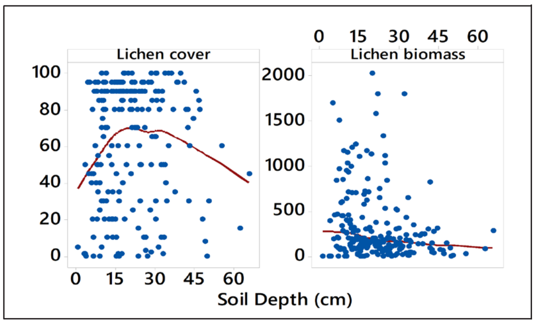

Fig. 3. Relationships between lichen cover (%), lichen biomass (g.m^{-2}) and soil depth (cm) (Based on data from Odland *et al.* 2014). Average lichen cover was 65±26%, average soil depth was 14.8±9.1 cm, and average lichen biomass was 533±405 g.m^{-2}. Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

Soil richness

Previous studies have shown that alpine lichen-dominated heaths are mostly confined to oligotrophic soils with a pH mostly below 5.0 (Dahl 1956; Ahti and Oksanen 1990; Odland and Munkejord 2008; Sundstøl *et al.* unpublished).

Fig. 4 shows a plot of relationship between soil pH (upper 10 cm) and total lichen cover (data from Reinhardt *et al.* 2013; Odland *et al.* 2014). The data indicates that high lichen cover is mainly associated with pH values between 4.0 and 4.5.

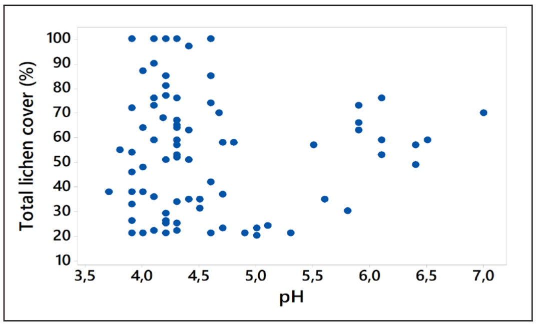

Fig. 4. Relationship between soil pH and total lichen cover (Based on data from Odland *et al.* 2014 and Reinhardt *et al.* 2013).

Soil horizon	Depth	pH	% Organic matter (loss on ignition)
Imingfjell, site 1 (ridgetop)			
OA	1-10	4.1	6.71
E	10-15	4.3	3.20
B1	15-26	4.9	1.00
B2	26-51	5.0	0.65
B3	51-68	5.2	0.34
BC	68+	5.1	0.33
Imingfjell, site 2 (midslope)			
O	0-8	3.7	56.40
E	8-14	4.0	1.92
Bs	14-29	4.7	5.48
Bh	29-40	4.7	9.69
BC	40+	5.2	0.88
Slondalen, site 1 (midslope)			
O	0-10	4.6	22.25
E	10-13	4.8	6.00
Bs	7-23	5.6	1.67
B2	23-43	5.8	1.62
C	43+	5.9	5.20
Slondalen, site 2 (snowbed)			
O	0-3	4.5	11.57
E	3-6	4.9	4.57
Bs	6-26	5.8	3.45
C	26+	6.1	2.60

Table 1. Data from four soil profile analyses in two alpine areas in S Norway (Data from Sundstøl *et al.* unpublished). Sites: I = Imingfjell (north-eastern part of Hardangervidda), L = Slondalen (Lesja mountain, Central Norway). Depth in cm, H = soil horizon. LOI = loss on ignition.

The substrate has mostly low amounts of N and P, and is often subjected to frequent episodes of acute drought (Crittenden *et al.* 1994; Crittenden 2000). Lichens are adapted to growth in N-limited habitats, are quickly outcompeted in areas where N levels are higher (Hauck 2010), and are therefore sensitive to air pollution and nitrogen deposition. In an experimental study, Britton and Fisher (2010) found a critical N load for terricolous lichen communities (<7.5 kg N ha^{-1} yr^{-1}) and suggest that concentrations of N may have detrimental effects on the growth of sensitive species. Theodose and Bowman (1997) found that species diversity increased with nutrient additions to poor sites, while Natali *et al.* (2012) found that winter warming led to higher N availability. Higher soil temperatures in winter can also increase leaching of inorganic N compounds during snowmelt (Kaste *et al.* 2008). In a study by Klanderud (2008), which simulated environmental changes, the five most common lichen species decreased in abundance, and in some cases disappeared completely, likely due to a combination of increased temperatures and N inputs. Alpine lichen-dominated heaths are rarely found on calcareous sites. In these sites, the soils are generally less than 10 cm thick and the lichen cover is usually lower than 20% (Bringer 1961a, 1961b; Nordhagen 1955; Baadsvik 1974; Reinhardt *et al.* 2013). Tab. 2 shows data from soil chemical analyses from the upper 10 cm soil layer in 13 plots dominated by lichens.

Mat-forming lichens are not dependent on soil conditions because they are able to sequester nutrients directly from atmospheric sources (Crittenden 1988; Ellis *et al.* 2004). They can efficiently recycle nutrients from senescent tissue to support growth, with high nutrient-use efficiency and residence times (Kytöviita and Crittenden 2007), and are physiologically able to survive long periods of desiccation (Kranner *et al.* 2008).

Lichen cover (%)	pH	Extractable P (mg/kg)	Extractable K (mg/kg)	Extractable Mg (mg/kg)	Extractable Ca (mg/kg)	Total C (%)	Total N (%)
95	4.4	0.6	2.5	3.8	18.4	4.4	0.2
100	4.1	1.4	3.1	3.2	20.0	3.7	0.2
75	4.2	0.6	0.9	2.4	19.8	4.3	0.2
78	3.8	2.0	16.9	10.8	48.0	8.9	0.3
60	3.9	0.9	2.8	2.4	22.6	4.8	0.2
73	4.3	0.6	3.0	3.2	17.9	5.0	0.3
83	4.2	1.0	2.5	2.9	20.1	3.3	0.2
95	4.3	0.6	3.3	5.2	24.2	3.3	0.2
90	5.2	0.9	3.1	15.0	129.0	4.8	0.3
95	4.4	0.7	2.2	6.5	28.8	3.1	0.2
85	4.4	0.9	6.6	10.5	35.8	8.3	0.4
80	4.4	1.9	8.6	12.0	51.3	9.6	0.6
73	4.7	0.7	6.8	18.3	55.0	5.2	0.3
AV	**4.3**	**1.0**	**4.8**	**7.4**	**37.8**	**5.3**	**0.3**
SD	**0.3**	**0.5**	**4.1**	**5.1**	**29.3**	**2.1**	**0.1**

Table 2. Results of soil chemical analyses from 13 lichen-dominated heaths (Data from Sundstøl *et al.* unpublished). LC = total lichen cover (%), P = phosphorous, K = Potassium, Mg = Magnesium, Ca = Calcium, C = Carbon, and N = nitrogen. AV = average values, SD = Standard deviation.

Importance of snow

Ecological gradients generated by spatial patterns of snow represent several correlated environmental factors influencing alpine plant life. Ecological effects of snow can be either direct or indirect, and these can have major impacts on both vegetation composition and grazing animals.

In Norway, snow can be quantified in different ways: maximum thickness, length of the snow cover period, timing of snow melt during spring, snow density, amount of water (snow water equivalent or SWE), and hardness. Snow has generally achieved maximum thickness and distribution during March/April, and by then most exposed sites are free from snow (Kohler *et al.* 2006: Odland and Munkejord 2008a; Löffler *et al.* 2008). Long periods with little snow resulted in extensive soil frost that can last until late June.

Estimation of the effect of snow is difficult because all variables change continuously during the snow season and from year to year. Long-term average values are the main factor defining vegetation distribution patterns that we can observe at present. According to Wahren *et al.* (2005) and Bidussi *et al.* (2016), direct effects of show depth, duration and quality on lichens in natural habitats are less recognized and only partly understood.

Lack of snow cover reduces the degree of insulation and results in low soil temperatures, extensive soil freezing, and increases in freeze/thaw cycles (Edwards and Cresser 1992; Groffman *et al.* 1999; Freppaz *et al.* 2008). Schimel *et al.* (2004) focused on the importance of early snow accumulation during autumn. Previous studies have mostly concluded that the main factors associated with the occurrence of alpine lichen-dominated heaths are snow thickness and its effect on soil temperatures (Dahl 1956; Odland and Munkejord 2008a).

Snow thickness

Snow thickness is a very important factor associated with lichen heath occurrence. Dahl (1956) measured snow thickness (early spring) on the Cetrarietum nivalis association to between 0 and 0.4 m, and between 0.4 and 2.0 m on the *Cladonietum stellaris* association. He found that a snow layer less than 50 cm results in extensive soil frost during autumn/winter, which was associated with largest lichen communities dominated by *Flavocetraria nivalis*, while *Cladonia stellaris* was associated with a thicker snow layer.

According to Löffler (2007), there was an increased snow thickness where *Alectoria ochroleuca* was growing (mostly totally without snow cover) in comparison to the thinner snow cover (5-10 cm) present where *Flavocetraria nivalis* grew. And that of *Cladonia stellaris* (10-30 cm). This gradient was associated with late melting of frozen soil.

Sulkava and Helle (1975) and Kumpula *et al.* (1998) showed that *Alectoria* sp. and *Bryoria* sp. were accessible to reindeer during the winter, and these account for the main portion of the lichen biomass found where snow thickness was less than 2 m.

The relationship between maximum recorded snow thickness (early April) and total lichen species cover (Fig. 5) clearly indicate that lichen-dominated heath types were closely related to sites where the maximum snow cover was less than 1.0 m thick (Odland and Munkejord 2008a).

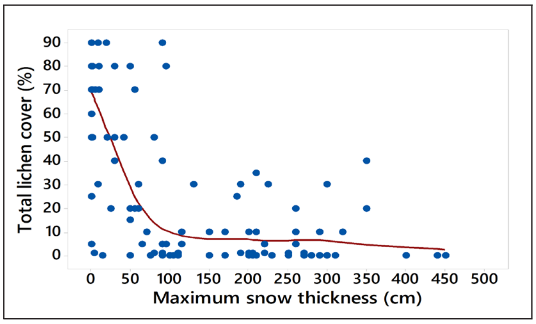

Fig. 5. Relationship between maximum recorded snow thickness (measured early April) and total lichen cover (Based on data from Odland and Munkejord 2008a). Lowess smoother line (degree of smoothing = 0.8, number of steps = 2) is drawn.

Snow layer duration

In general, length of the snow cover duration is closely related to maximum snow thickness ($r = 0.86$, $p < 0.001$, Odland and Munkejord 2008a); however, air temperatures and their variations due to differences in altitude and aspect are also important. Date of snow-melt can be defined in the field or based on the date when soil temperature exceeds 1° C (Sundstøl and Odland 2017). Relationships between day of snow-melt and the total cover of lichens and vascular plants are shown in Fig. 6. The investigation indicates that lichens have their highest cover degree in sites where the snow had melted earlier than day 100 (April 10), while total vascular plant cover was highest in sites where the snow was melted around day 130 (end of May).

The rate of snowmelt is variable. It is mainly a function of air temperature, but can also be modified by factors such as rain, slope, aspect, and elevation. The melt rate has generally been measured to lie between 3 and 4 cm day^{-1} (Odland and Munkejord 2008a).

Odland and Munkejord (2008b) have shown that some macrolichen species show statistically significant responses to snow layer duration (timing of snowmelt). Species with significant responses are listed in Table 3, where species with an indicator value of 1 are mainly found on sites with little or no snow cover (exposed early April). Species with an indicator value of 2 normally require a protective snow layer, and are mainly found on sites which are snow free 10 days later (before April 20). Species with higher indicator values are normally not abundant in lichen heaths.

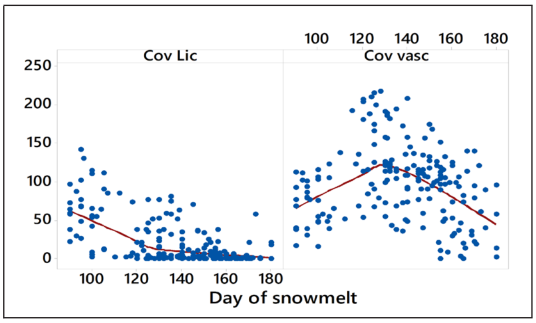

Fig. 6. Effects of snow layer duration (day of snowmelt) on the total cover of lichens (Cov Lic) and total vascular plant cover (Cov vasc) (Based on data from Odland and Munkejord 2008a). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

Weighted average snow indicator values (WaSI) can be estimated for different alpine plant communities based on indicator values for both lichens, bryophytes and vascular plants (Odland and Munkejord 2008b; Odland *et al.* 2014). The WaSI-values can range from close to 1.0 (the most exposed lichen heaths) to below 6 (snow bed communities mostly without lichens). As shown in Fig. 7, lichen total cover and lichen volume (lichen height*lichen cover) decrease with increasing WaSI-value. The thickest lichen mats, with the highest volume are found in communities with a WaSI-value around 2, and in such communities (often dominated by *Cladonia stellaris*) there is normally a protective snow layer.

Species/Taxon	**Snow Index (SI)**
Alectoria nigricans	1
Alectoria ochroleuca	1
Bryocaulon divergens	1
Flavocetraria cucullata	1
Flavocetraria nivalis	1
Thamnolia vermicularis	1
Cladonia uncialis	2
Cladonia rangiferina	2
Cetraria ericetorum	2
Cladonia stellaris	2
Cladonia arbuscula	2
Cladonia gracilis	2
Cladonia macrophylla	2
Cladonia spp. (unidentified species)	4
Stereocaulon spp. (unidentified)	4
Cladonia ecmocyna	7

Table 3. Indicator values for lichen species (SI) and lichen taxa that show significant responses to snow layer duration (from Odland and Munkejord 2008b). Differences between the SI-values are explained in Table 4.

Effects of snow layer duration on the total abundances of lichens and vascular plants can be expressed in terms of WaSI-values (cf. Tab. 4 and Odland and Munkejord 2008b) as shown in Fig. 7. Figs. 6 and 7 indicate, however, that lichen abundance is highest where a thin snow cover is present.

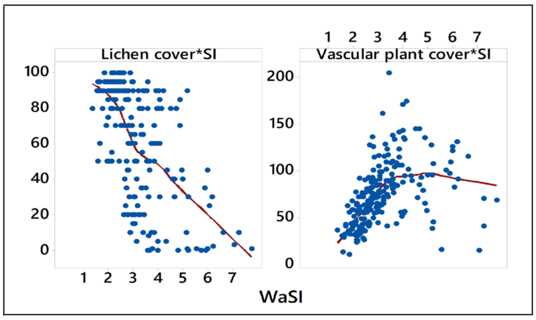

Fig. 7. Relationships between weighted average snow indicator values (WaSI), total lichen cover and vascular plant cover (Based on data from Odland *et al.* 2014) (cf. Table 4). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

Lichen biomass and lichen volume show major variation with estimated snow layer duration as estimated by WaSI. As shown in Fig. 8, the highest biomass and volumes have been found in sites with a WaSI-value between 2 and 3. Sites with low WaSI-values are mainly dominated by *Alectoria nigricans*, *A. ochroleuca*, *Bryocaulon divergens*, *Flavocetraria cucullata*, *F. nivalis*, and *Thamnolia vermicularis*. Lichen heaths dominated by *Cladonia species* (especially *C. stellaris*) have higher biomass. The large differences in lichen biomass and volume as shown in Fig. 8 are mainly effects of reindeer grazing and trampling.

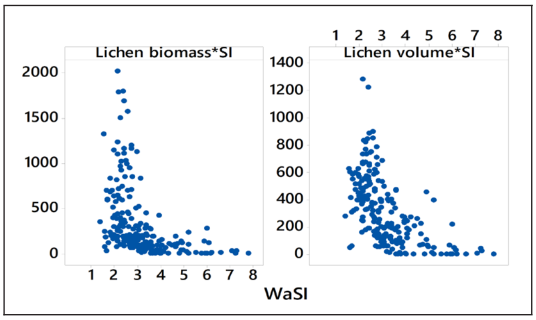

Fig. 8. Relationships between weighted average snow indicator values (WaSI), lichen biomass (g m^2) and lichen volume (lichen cover*lichen height) (cf. Table 4) (Based on data from Odland *et al.* 2014).

The gradient from the most exposed alpine sites mostly without a snow cover to sites with heavy snow loads are often separated into six zones (Odland 2012). Ecological characteristics between these zones have been quantified in Tab. 4. As shown in Figs. 7 and 8, lichens have their main abundances in zone 1 and 2, and these are mainly characterized by early snow-melt, WaSI-values lower than 3, a thin or missing snow cover and a long thaw period.

Bidussi *et al.* (2016) studied how increased snow accumulation affected lichen growth in dominant mat-forming arctic-alpine lichens. The species were transplanted for one year at different snow depths. Snow depth significantly affected lichen RGR (relative growth rate), but in species-specific ways. *A. ochroleuca* and F. nivalis, which are confined to sites with little or no snow, showed reduced RGR % when exposed to 120 cm of snow. *C. mitis* and *C. delicei* have a broader tolerance and showed relatively small reductions in RGR % when exposed to 200 cm snow. Their conclusion was that increased snow most likely reduces the abundance of dominant mat-forming lichens in alpine ecosystems of Scandinavia.

Vegetation zone	SI	WaSI	Snow melt date		Thaw-period	SGS Day	Snow thickness
			Day	Date			
1. Exposed ridge	1	<2	<99	Before April 9	>50	150	0–0.5 m
2. Snow protected heath	2	2-3	100–110	Before April 20	30-40	145	0.5–1 m
3. Lee-side	3	3-5	111–121	Before May 1	20	140-150	1.5–3 m
	4		122–127	Before May 7	15		
	5		128–135	Before May 15	10		
	6		136–146	Before May 26	6		
4. Early snow bed	7	5-6	147–153	Before June 2	5	155	3–4 m
5. Late snow bed	8	6-7	154–162	Before June 11	6	165	
6. Extreme snow bed	9	7-8	>162	Later than June 11	2	170	4–10 m

Table 4. Vegetation zonation along a snow gradient from an exposed lichen-dominated ridge, down to an extreme snow bed community. Six zones are separated (Odland 2012). SI = characteristic species indicator values (Odland and Munkejord 2008b). WaSI = Weighted average snow indicator values estimated from plant communities (Odland and Munkejord 2008b; Odland *et al.* 2014) (cf. Figs. 7 and 8). Snow-melt dates for different zones are given as day of the year (measured during 2004 which was a warm season when snow melt was approximately 2 weeks earlier than normal (Odland and Munkejord 2008b). The thaw period gives an average number of days between date of snow-melt and the start of the growing season determined by the day when soil temperature exceeded 6oC. Snow thickness gives values measured in early April. SGS = start of the growing season (day of the year).

Lichen heath albedo and insulating effects

Albedo

Albedo is the proportion of incident solar radiation that is reflected by the land surface. The reflected solar radiation averages 80 – 90% on snow-covered surfaces, and there is a significant and rapid drop from about 80% to 10% when snowmelt begins and the vegetative surface emerges.

Thus, albedo plays a critical role in the surface energy budget and is a direct feedback from vegetation to the climate system (Pitman 2003; Bala *et al.* 2007; Bonan 2008). Albedo varies substantially among different vegetation types, and changes with the development and senescence of the canopy. More specifically, the seasonal course of albedo is determined by the combined effect of seasonal changes in the reflectance of photosynthetically active (PAR, 400–700 nm wavelengths) and near-infrared (NIR) radiation. Lichen albedo has been measured at 0.31, mosses 0.24, and green vegetation 0.20 (Peltoniemi *et al.* 2010). This shows that lichens have high albedo compared to other vegetation surfaces. Where vegetation is sparse, the degree to which the soil warms up depends on its color, water and air content, and its structure (Larcher 1995).

The roles of bryophytes and lichens in controlling energy fluxes have been studied in alpine and arctic areas (Petzold and Rencz 1975; Gornall *et al.* 2007; Peltoniemi *et al.* 2010). With their high albedo and thermal conductivity, lichen mats also act as insulators that greatly impede the flux of heat into the underlying soil. A lichen mat 12 cm deep can reduce the soil heat flux by almost 50% and thereby significantly lower soil temperature (Bonan 1989). According to Kershaw (1985) and Gold *et al.* (2001), lichen mats will also reduce soil temperature during summer and dampen diurnal temperature fluctuations (cf. Figs 9 and 11). Reducing the lichen cover increases the heat flux between soil and the atmosphere, leading to higher soil temperatures in the summer and lower average soil temperatures in the winter (Olofsson *et al.* 2002). When the lichen canopy is disturbed, soils tend to warm up more quickly, especially at the beginning of the vegetation period, which could have positive feedback on plant growth since germination may begin earlier, thus lengthening the vegetation period.

Cohen *et al.* (2013) found that albedo was lower on the Norwegian side of a border fence than on the Finnish side during the snowmelt period, due to the presence of shrubs that stuck out from the snow surface. However, during the snow-free period, the Norwegian side had higher albedo which was attributed to the presence of lichens and lack of disturbance. Stoy *et al.* (2012), using satellite data, also found that the albedo in the snow-free season was higher on the less-intensively grazed Norwegian side of a border fence than on the overgrazed Finnish side.

Insulator effects

The effects of lichens and bryophytes as temperature insulators have been emphasized in several studies (Olofsson *et al.* 2002; Sofronov et al., 2004; Peth and Horn, 2006; Fauria *et al.* 2008; Klein and Shulski 2011; Stoy *et al.* 2012). Consequently, changes in lichen cover that result from trampling during summer grazing alters the soil microclimate (Stark *et al.* 2000).

Well-developed lichen mats have been found to strongly affect the moisture and thermal regimes of forest soils, thereby reducing drought stress (Kershaw 1985; Bonan and Shugart 1989; Fauria *et al.* 2008). It is possible that the ecological effects are similar in alpine lichen heaths.

Stoy *et al.* (2012) quantified the surface and subsurface temperatures and spectral reflectance of common moss and lichen species at field sites in Alaska and Sweden. Under alpine lichen heaths, temperatures were lowered by 10 to 11° C compared to bare soil. Similarly, cryptogams can also prevent warming of the soil. This is important for preventing permafrost from melting (van der Wal and Brooker 2004; Gornall *et al.* 2007). Field observations have revealed that at the beginning of June 2003, the soil underneath undisturbed lichen cover was still frozen at a depth of 30 cm, whereas no ice was encountered at that depth at the sites with moderately and heavily disturbed lichen cover. Similarly, Odland and Munkejord (2008a) found that in exposed lichen alpine heaths with a thick, moist humus layer in south Norway, soil temperatures needed more than two months to thaw on humus-rich soils. In exposed *Dryas octopetala* heaths without a thick humus layer, there was no delayed soil temperature increase during the spring (Reinhardt *et al.* 2013).

Effects of soil temperature and thaw period

Soil temperature

In Arctic tundra, lichens are commonly associated with permafrost and/or carbon-rich soils (Zimov *et al.* 2005; Schuur *et al.* 2008; Tarnocai *et al.* 2009). In Fennoscandia, previous lichen heath studies have reported that they are mainly found on sites with a seasonally frozen soil (Dahl 1956; Wielgolaski 1975). The amount and duration of soil frost has been associated with length of the thaw period, but this relationship has rarely been quantified. Soil temperature can be highly variable over very small distances, being dependent upon snow cover, type of vegetation cover and the heat capacity of the soil (Dahl 1956; Larcher 1995).

The presence or absence of snow determines the winter soil surface temperature (Dahl 1975; Löffler 2005), and snow acts as an insulator that influences both the temperature and the extent to which the soil is exposed to freeze-thaw events (Edwards *et al.* 2007). According to Kershaw (1985) and Rees (1993), studies of surface and subsurface temperatures and subsurface heat fluxes of bryophytes and lichens at the species level has rarely been undertaken. The relationship between air temperature and soil temperature is in itself fairly complex. Soil temperatures are dependent upon a number of factors such as moisture content, evaporation, albedo, and the thermal conductivity of the soil itself (Garcia-Suarez and Butler 2006) and is generally less variable than air temperatures (Gehrig-Fasel *et* *al.* 2008). Sundstøl and Odland (2017), investigated relationships between soil temperature and total lichen cover. Results (Fig. 9) show that a high lichen cover is associated with low soil temperatures, but also with relatively low summer soil temperatures. Total shrub cover correlated with differences in soil temperatures (Fig. 10), partly because some shrubs can be present in lichen heaths while other require a protective snow cover.

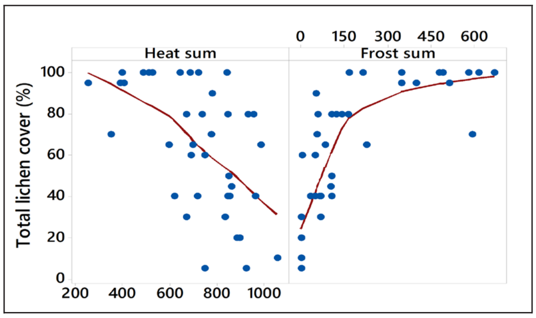

Fig. 9. Average lichen cover degree in relation to soil heat sum and soil frost sum measured during a three year period (Based on data from Sundstøl and Odland 2017). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

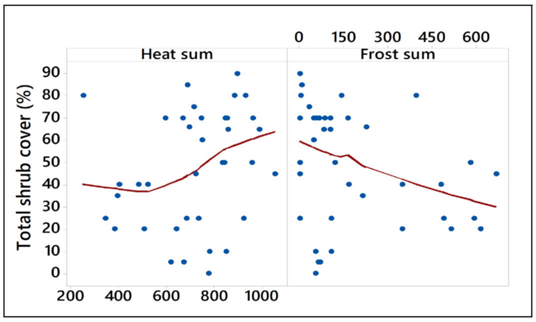

Fig. 10. Average shrub cover degree in relation to soil heat and frost sums measured during a three year period (Based on data from Sundstøl and Odland 2017). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

Different lichen and vascular plant species frequently found in alpine lichen heaths respond differently to the degree of frost sum (Sundstøl and Odland 2017). Lichen species characteristic of the most exposed heath types (cf. Tab. 2) such as *Alectoria ochroleuca*, *Bryocaulon divergens*, *Flavocetraria cucullata* and *F. nivalis* increase their abundance with increasing soil frost. *Cladonia arbuscula*, *C. rangiferina*, and *C. stellaris* however, decrease their abundance with increasing frost. *Betula nana* has a wide tolerance in relation to soil frost, while *Empetrum nigrum*, *Vaccinium myrtillus*, and *V. uliginosum* increase their abundance with decreasing frost sum. *Nardus stricta* was only found on sites with low or no frost while *Juncus trifidus* had a broad tolerance, but was most abundant where frost-sum was lower than 200. This indicates that many vascular plants do not tolerate high soil frost, and are therefore not competitors to lichen heaths so long as the soil frost remained unchanged.

Length of the growing season and the thaw period

The start and end of the vascular plant growing season are closely related to soil freezing and soil thawing (Ryden and Kostov 1980; Bonan and Shugart 1989). The start of the growing season during spring/summer has been defined in different ways (see review by Odland 2011). In general, biological activity is low when temperature is low, and, growing season start has frequently been defined by use of a soil temperature threshold of 5 - 6° C (Heikinheimo and Lappalainen 1997; Tuhkanen 1980; Karlsson and Weih 2001). This applies mainly for vascular plants with their roots in frozen soil where there is no available water. Low soil temperatures inhibit root elongation and increase water viscosity, inhibiting water uptake (Bonan and Shugart 1989). Lichens and bryophytes, however, have no roots, and they can grow when the substrate is frozen.

Thaw describes the change from a frozen solid to a liquid phase by gradual warming. The term "thaw period" has been defined in two ways: 1) On the most exposed sites without snow during most of the winter, the thaw period has been quantified as number of days from DOY 90 (day of the year) (April 1) which generally is the period when snow starts to melt (Odland and Munkejord 2008a). 2) In sites with a snow cover, start of the thaw period has been defined by timing of the event when soil temperatures reach + 1° C (Sundstøl and Odland, 2017). Odland and Munkejord (2008a) studied the distribution of oligotrophic alpine vegetation types in relation to length of the thaw period. Lichen-dominated types had thaw periods longer than 40 days, lee side vegetation less than ca. 20 days, and snow bed vegetation less than 8 days.

Thawing processes are highly influenced by the high heat capacity of water. Moist soil with a high heat capacity must be subjected to a long period of frost to freeze, but a long period with high temperatures is also needed to thaw the soil (Willis and Power 1975). Effects of air temperature on soil temperature are strongly influenced by the species composition of the surface and by soil (humus) water content. A relatively dry soil freezes more quickly and deeply than a wet soil, and thaws faster in the spring. Lichen cover reduces heat transfer to the soil below during warm periods because of its high albedo (Sofronov *et al.* 2004). Although summer temperatures often exceeded 40° C just above the surface of the moss-lichen layers, frozen soils remained under this coverage. The strong effect of lichen cover on soil temperatures is also evident from Fig 11. Sites with a high lichen cover were associated with lower winter and summer soil temperatures than sites where lichen cover was low.

Sofronov *et al.* (2004) showed that soil temperature increased from 0° C in an organic soil layer, to 8° C at the soil surface measured in August (in Larix forest in Siberia). Depth of the soil thawing was affected by surface vegetation dominated by mosses and lichens. There was a strong linear correlation between organic layer thickness and soil temperature.

Lichens and vascular plants have different responses in relation to the length of the thaw period (Fig. 12). Lichens have their highest cover degree where the thaw period is longer than 15 days, while vascular plant cover decreases when the thaw period is longer than 15 days. Betula nana, Arctous

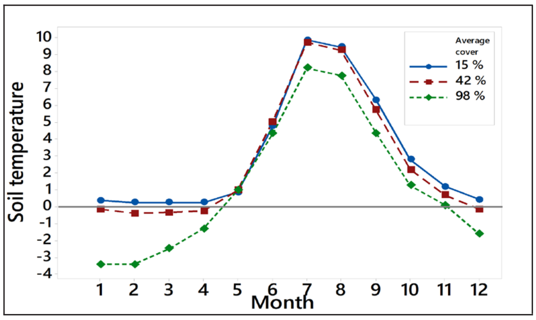

Fig. 11. Effects of variable average lichen cover in relation to average monthly soil temperatures. Sampled study sites were divided into three groups where lichen cover was >80% (average in 13 plots was 98%), cover 30 -50% (average in 7 plots was 42%), and cover <30% (average in 6 plots was 15%). Sites with a high lichen cover were associated with lower winter and summer soil temperatures than sites where lichen cover was low (Data from Sundstøl and Odland 2017).

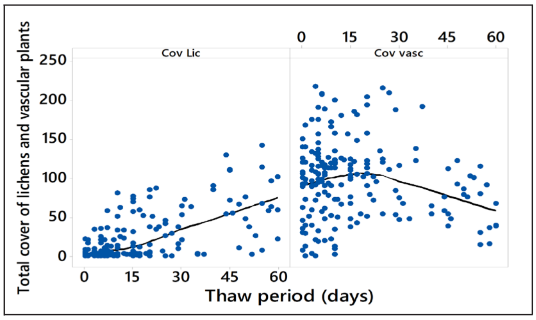

Fig. 12. Relationships between total lichen cover (Cov Lic) and total vascular plant cover (Cov vas) in relation to number of days needed to increase soil temperature from 1° C to 5° C. Start of the growing season is often defined as the day when soil temperature exceeds 5° C (Based on data from Odland and Munkejord 2008b and Sundstøl and Odland 2017). Lowess smoother lines (degree of smoothing = 0.8, number of steps = 2) are drawn.

alpinus, and Empetrum nigrum can however, tolerate a long thaw period (Sundstøl and Odland 2017).

A relatively deep soil (cf. Fig. 3) has a decisive impact on the start of the growing season and length of the growing period. A moist, humus-rich soil is essential for development of a long soil frost period. Water has a high specific heat capacity, meaning that the soil needs to be exposed to extensive frost to freeze, and that the frozen soil needs to be exposed to high temperatures for a long period to thaw. Exposed sites with lichen heaths may need more than 50 days to thaw (Odland and Munkejord 2008a). Exposed *Dryas octopetala* vegetation with a thin soil layer were, however, associated with less than 15-30 days to thaw (Reinhardt and Odland 2012; Reinhardt *et al.* 2013).

Even if the snow has melted on a site, vascular plants may not start to grow because the soil can be frozen. Lichens, however have no roots and can therefore initiate growth.

Lichen growth, biomass, and relationship to other plants

Lichen photobionts are concentrated in the apical part of the thalli (Nash *et al.* 1980). Experiments have shown that the relative growth rate of the apical parts is higher than that of the lower basal parts, which are constituted of fungal, sometimes senescent, tissues (Kärenlampi 1971; Kytöviita and Crittenden 2002; Gaio Oliveira *et al.* 2006).

The optimal growth temperature for lichens lie between 15-25° C, but in summer the temperature at the surface of lichen mats can reach 35-40° C without affecting their vitality (Tegler and Kershaw 1980; Coxson and Wilson 2004). Laboratory experiments show that lichens are extremely tolerant of freezing stress and of exposure to low temperatures. CO_2 exchange was already active at around -20° C, while the optimum temperature for net photosynthesis lies between 0 and 15° C.

Most vascular plants are not able to grow on sites with a long-lasting frozen soil. A precondition for lichen heaths is therefore a relatively thick and moist soil layer which will freeze solid. The great success of lichens in cold areas gives evidence of their physiological adaptation to areas with low temperatures. In general, lichens are able to persist through glacial periods, but extended snow cover and glaciation are limiting factors (Kappen *et al.* 1996).

Lichen growth and biomass

According to Ahti (1959), three growth stages exist throughout the reindeer lichen lifespan. The first stage, the growth-accumulation period, lasts an average of 10 years but can vary from 6 to 25 years. During this stage, size increases annually, and no part of the podetium dies. The internodes grow 10 to 15 times the height attained in the first year of life. During the second stage, podetium height still increases, but internode death occurs at the base. Despite some internode decay, height growth continues. This stage may continue for several decades and can exceed 100 years. During the third stage, the withering period, the podetium decays at the base faster than internodes lengthen. This stage of growth lasts some 10 to 20 years.

Maximum reindeer lichen height is around 12 cm, which is found when the top zone growth equals the rate of death and decomposition in the bottom zone (Morneau and Payette 1989). In old undisturbed lichen stands reaching heights of 12 cm, the lowermost 1-2 cm of the podetia are dead or decaying (Odland *et al.* 2014).

Lichen growth follows a logistic or sigmoidal curve with a maximum growth rate at an intermediate lichen height (Kumpula *et al.* 2000; Heggberget *et al.* 2002). Different methods have been used to determine the growth rate of reindeer lichens (see discussions in Kumpula *et al.* 2000), resulting in growth rates ranging from 2 to 6 mm year^{-1}. Kumpula *et al.* (2000) found that the maximum thickness increase in the living part of the whole lichen stand was only 1.5-1.6 mm year^{-1}, and the estimated biomass increase was 11% year^{-1}.

Standing biomasses in oligotrophic lichen heaths at Hardangervidda have been estimated to be 61, 7, and 380 g m^{-2} respectively for vascular plants, mosses and lichens (Wielgolaski 1975). Annual production in lichen heaths was 88 and 182 g m^{-2} year^{-1} respectively for lichens and vascular plants.

In Kevo, north Finland, the lichen biomass production was estimated to be 77 g m^{-2} $year^{-1}$ and for vascular plants it was 375 g m^{-2} $year^{-1}$ (Kallio 1975). The highest annual increase in lichen biomass has been estimated at approximately 120 kg ha^{-1} $year^{-1}$ in a lichen mat with a biomass of ca. 800 kg ha^{-1} (Helle *et al.* 1990). According to Kumpula *et al.* (2000), the maximum lichen production has been estimated to be 170 kg dry matter ha^{-1} $year^{-1}$ measured in a lichen stand that was around 40 year old, with a standing living biomass of nearly 3 000 kg dry matter ha^{-1}.

Estimations of lichen production in heath communities often include vascular plants growing in the heaths. In some cases, total production has been found to be as high as 250 – 300 g m^{-2} $year^{-1}$ (Kjelvik and Kärenlampi 1975). When dominated totally by lichens, the total production was only around 100 g m^{-2} $year^{-1}$ even in dense lichen heaths. The production to biomass ratio in lichen at Hardangervidda was estimated to be ca. 0.2 (Wielgolaski 1975). Lichen productivity was calculated from an estimated growth rate of 0.23 g g^{-1} $year^{-1}$ (Kjelvik 1978).

Relationships to vascular plants

It is generally considered that lichens are very poor competitors (Grime 1977), growing in places where vascular plants and bryophytes are less successful. In areas where their competitors are suppressed by severe climate, lichens would expand to new habitats due to competitive release (Ahti and Oksanen 1990). It can therefore be assumed that lichens are in greatest abundance at sites where the establishment of vascular plants is difficult or unsuccessful. The main factor critical to most vascular plant growth is, as described, soil frost and a long period with frozen soil (Karlsson 1985; Sofronov *et al.* 2004). Several studies have emphasized the negative effects of low soil temperatures for the growth of vascular plants (Tranquilini 1979). There are, however, only a few vascular plant species which are able to grow on frozen soil together with lichens (Odland and Munkejord 2008b). Unfrozen soil is a prerequisite factor for the initiation of springtime root-zone processes and recovery of photosynthetic capacity (Karlsson and Nordell 1996; Sutinen *et al.* 2009).

Decrease of lichen poplations has frequently been described as an effect of strong competition from the expanding shrub cover due to increased leaf litter and subsequent shading which prevents the re-establishment of lichen cover (Gaare 1997; Heggberget *et al.* 2002; Fraser *et al.* 2014). These views are not in accordance with the conclusions above. Some alpine lichen heath communities can have a co-dominance of vascular plants, but the data shown in Fig. 13 indicates a negative correlation between total lichen cover and total vascular plant cover. Species with snow indicator values of 1 (cf. Table 3) rarely have a high cover of shrub species. *Cladonia* species with snow indicator values of 2 or higher, which have a relatively thin snow layer during the winter, can have a high cover of *Betula nana* which also has a snow indicator index of 2.

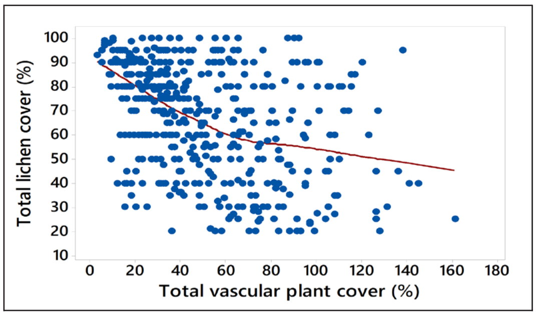

Fig. 13. The relationship between total vascular plant cover and total lichen cover from 471 study plots at the Hardangervidda mountain plateau, south Norway. Only plots where total lichen cover was higher than 20% were included (Based on data from Odland *et al.* 2014 and unpublished data). Lowess smoother line (degree of smoothing = 0.8, number of steps = 2) are drawn.

Effects of reindeer grazing

Reindeer grazing and trampling can locally be the most important factor affecting the state of lichen pastures. Reindeer prefer certain lichen species to others, and this selective grazing can change the species composition of lichen pastures. Lichen mats can be heavily affected by overgrazing and trampling which, in high-density populations, can cause substantial winter forage depletion and trigger large scale habitat shifts or population declines (Crittenden 2000; den Herder *et al.* 2003; Klein 1987; Manseau *et al.* 1996; Vistnes and Nelleman 2008; Falldorf *et al.* 2014, Heggenes *et al.* 2018).

Graminoids (grasses and sedges) have been found to increase under heavy grazing pressure from reindeer and caribou on lichen-dominated plant communities (Klein 1968; Thing 1984; Post and Klein 1999), and such species have also been predicted to increase under global warming scenarios (Chapin *et al.* 1995; Joly *et al.* 2009).

Intensive reindeer grazing reduces lichen biomass, being commonly 10% or even less of the biomass typical in un-grazed mature lichen associations (Mattila 1981; Tømmervik and Lauknes 1988; Kojola *et al.* 1995). On the Hardangervidda mountain plateau, lichen biomasses or volumes have been estimated to have decreased by more than 60% (Odland *et al.* 2014). Väre *et al.* (1996) found that grazing reduced lichen biomass from 790 to 86 g dw m^{-2}. Similarly, Akujärvi *et al.* (2014) found that the lichen cover was about five-fold greater and the biomass about fifteen-fold greater in the ungrazed (fenced) sites than in the grazed ones.

van der Wal (2006) reports that increased grazing pressure results in a transition to first a moss-dominated tundra and finally a graminoid-dominated vegetation. He suggested that lichens have to be protected by snow in winter to prevent overexploitation (cf. also Adamczewski *et al.* 1988; Ferguson *et al.* 2001). This may be valid for *Cladonia stellaris*-dominated forest vegetation but probably not for alpine lichen dominated vegetation. Increased snow would insulate the soil from extensive soil frost and thereby give vascular plants a chance to establish and outcompete lichens.

In the tundra, grazing by reindeer has been shown to reduce the cover of both lichens (Väre *et al.* 1995; den Herder *et al.* 2003; van der Wal *et al.* 2001) and dwarf shrubs (Olofsson *et al.* 2009; Dahlgren *et al.* 2009; den Herder *et al.* 2008). Stepwise transition from unproductive lichen-dominated vegetation to more productive moss and graminoid-dominated vegetation types have been hypothesized by Oksanen and Oksanen (2000), Zimov *et al.* 2005, and van der Wal (2006).

Destruction of cryptogamic vegetation by herbivore grazing and trampling can lead to extensive melting of permafrost, both directly and by accelerating the decomposition of organic matter, which in turn will increase soil temperatures (Woodin and Marquiss 1997; van der Wal and Brooker 2004). Sofronov *et al.* (2004) showed that the depth of soil thawing increased with a reduction in the moss-lichen layer thickness.

Effects of climate change

Reviews of effects of climate change on the winter food resources for reindeer (*Rangifer tarandus tarandus*), have been published by Suominen and Olofsson (2000), Heggberget *et al.* (2002), and Bernes *et al.* (2015). Most of these have, however, not included effects of soil frost and thaw period.

Ongoing climate change has had multiple effects on alpine lichen-dominated heaths. The main climate changes affecting lichen heaths can be assumed to be increased precipitation, both in the form of rain and snow, higher winter temperatures, and more unstable winter conditions. The general climate character will therefore be increasingly oceanic in most areas. Such changes have already resulted in both floristic and ecological changes, and those will probably be accelerated into the future.

Recent studies have found that the abundance of reindeer lichens have decreased in alpine heath communities. This has often been associated with increased dominance of shrub species (Cornelissen *et al.* 2001; Virtanen *et al.* 2003; van Wijk *et al.* 2003; Kullman 2005; Öberg 2002; Hudson and Henry 2009; Tømmervik *et al.* 2009; Pajunen *et al.* 2011; Danby *et al.* 2011; Fraser *et al.* 2014; Vuorinen *et al.* 2017). After resampling of *Loiseleuria procumbens* heaths, Virtanen *et al.* (2003) found that lichen abundance had decreased while *Empetrum nigrum* and mosses had increased. Other studies have also found that dense mats of lichens have been replaced by expanding *Empetrum nigrum* or other dwarf-shrubs (Kullman 2005; Öberg 2002).

Increased nutrient inputs combined with warming treatments have been found to decrease lichen abundance in northern Sweden (Jägerbrand *et al.* 2009), and a changing climate along with increased herbivory led to such losses of lichen cover in Arctic Canada that reintroduction was not viable (Klein and Shulski 2011).

Effects of changes in snow cover

So far, precipitation has increased in most parts of Fennoscandia. Increased rain, especially during the winter (rain on snow) has multiple effects on lichens, especially rate of snow-melt, soil temperatures, and soil thaw. Increased precipitation combined with low temperatures will increase snow depths. However, despite increased precipitation, the snow layer duration has decreased in most low-alpine areas. This is mainly an effect of faster snowmelt due to increased air temperature.

A reduction in snow depth could also lead to an increase in the depth and extent of frozen soil, which would have effects on biogeochemical and microbial processes and could result in direct injuries to roots (Hülber *et al.* 2011). However, in Norway, most models predict an increase in snow depths at higher elevations, coupled with a shorter snow season (Dyrrdal 2013; Klimaservicesenter 2015). Snow depth increases of about 2 cm per decade since the early 1900s have been recorded at Abisko in northern Sweden, despite there being no changes in snow season duration (Kohler *et al.* 2006). According to Bidussi *et al.* (2016), increasing snow depths will likely reduce the abundance and distribution of dominant mat-forming lichens in Scandinavian alpine ecosystems.

Autumn and winter climate change due to changes in snow regime and temperatures can have major impacts on northern plant communities. Vascular plants, particularly shrubs, appear to be most prone to damage while lichens appear tolerant (Bokhorst *et al.* 2012).

Turunen *et al.* (2009) suggested that increased winter precipitation, the occurrence of ice layers, deeper snow cover, and the appearance of molds beneath the snow cover may reduce the availability and/or quality of reindeer forage, but prolongation of snowless periods might have the opposite effect.

Effects of soil warming

Changes in the snow cover and higher air temperatures have been reported to increase soil temperatures and thereby the length of the growing season. This can change the competition between lichens and vascular plants. According to Sturm *et al.* (2001b, 2005), Bret-Harte *et al.* (2002), and Mack *et al.* (2004), the potential impacts of shrub expansion are warmer winter soils, enhanced nutrient cycling, and altered plant communities.

According to Lemke *et al.* (2007), the amount of seasonally frozen ground has decreased by about 7% during the last one hundred years. Henry (2006), reporting on data from weather stations across Canada, found that warmer winters resulted in fewer soil freezing days, associated with reductions in snow depth and number of days with snow on the ground.

Macias Fauria *et al.* (2008) found large differences in soil temperature values and dynamics between grazed and un-grazed heaths. Soils in the grazed part warmed up faster in spring, thawed 2–4 weeks earlier, and cooled down faster in autumn at all depths. Soil in the grazed parts reached lower winter temperatures, and higher summer temperatures at all depths. Indeed, significantly higher growing season degree-days were found in the grazed part of the stand at depths of –5 and –20 cm.

Porada *et al.* (2016) estimated average cooling effects of the bryophyte and lichen cover of 2.7° C on temperature in the topsoil for the region north of 50° N under the current climate. Locally, a cooling of up to 5.7° C was found. These results suggest that the reducing effect of the bryophyte and lichen ground cover on soil temperature should be accounted for in studies which aim at quantifying feedbacks between permafrost soil temperature and climate change.

Results from experimental warming suggest that lichens may become less competitive due to climate warming (Lang *et al.* 2012). According to Cornelissen *et al.* (2001), macrolichens in climatically milder Arctic ecosystems may decline if and where climate changes cause vascular plants to increase in abundance. They suggested that climate warming and/or increased nutrient availability leads to decline in macrolichen abundance as a function of increased abundance of vascular plants.

A decline in lichen biomass or abundance in artificially warmed fertilized ecosystems has been reported repeatedly in subarctic and mid-Arctic studies (Jonasson 1992; Chapin *et al.* 1995; Molau and Alatalo 1998; Press *et al.* 1998; Graglia *et al.* 2001). This was suggested to be a response to increased shading by the taller vascular plants or the litter that they produce. Studies, both in situ and experimentally, have shown that warming increased height and cover of deciduous shrubs and graminoids, and decreased cover of mosses and lichens (Lang *et al.* 2012). Shrub abundance influences the summer albedo, and the effects of increasing shrub abundance on albedo will contribute to changes in the surface energy balance (te Beest *et al.* 2016).

General discussion and conclusions

It is of vital ecological importance to bear in mind that lichens are very poor competitors (Grime 1979), and that the distribution of alpine lichen heaths are primarily controlled by their inability to compete with fast-growing vascular plants (Kershaw 1985). Apparently, lichen heaths are mainly developed in environments where competition from vascular plants is excluded or reduced (Bonan 1989). As indicated in previous studies, the main factor associated with alpine lichen heath distribution is determined by the degree of soil frost and the length of the thaw period. It has been suggested that wind speed is the main factor for lichen heath distribution in alpine areas (Crabtree and Ellis 2010), but in our opinion, wind is an indirect factor which blows the snow cover away.

Lichen heath ecology

As shown above, alpine lichen heaths are developed on sites with a thick substrate and a humus layer on top, which is generally more than 5 cm thick. Based on results reviewed in the current paper, important factors influencing the distribution on an exposed low alpine ridge may be presented in a schematic way as shown in Fig. 14. The most exposed sites (zone 1) are dominated by species like *Bryocaulon divergens*, *Alectoria nigricans*, *A. ochroleuca*, *Coleocaulon aculeatum*, *Flavocetraria cucullata*, and *F. nivalis*. In zone 2 (snow protected heath), *Cladonia stellaris*, *C. arbuscula*, and *C. rangiferina* are more important. In zone 3 (lee sides), dwarf shrubs graminoids, and herbs dominate but *Cladonia* species can be important.

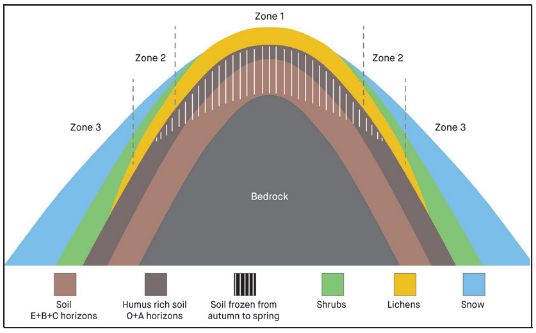

Fig. 14. Schematic drawing of an exposed low alpine ridge with important ecological factors influencing the distribution of lichens. The zones are described in Table 4.

Any factor that changes the period with frozen soil will reduce the lichen abundance. Reindeer grazing and/or climate will change the surface albedo. The high albedo of a lichen mat decreases the heat influx to the soil, both during winter and summer. Consequently, a reduction of the lichen cover due to grazing and trampling will increase soil thawing during spring, and increase soil temperature during the summer and autumn. As a result, the growing season (defined as the period when soil temperature exceeds 5° C), will increase and this will again favor the growth of vascular plants.

Relationships to vascular plants

Numerous studies have recently reported decreasing lichen abundances in boreal, alpine and Arctic areas. This trend has often been explained by an increased dominance of vascular plants. In general, the total cover degree of vascular plants and lichens have opposite trends, and this can be explained by their different responses to snow and soil temperatures.

Ongoing climate change involves changes in several environmental factors which can be critical to lichens. Numerous studies have concluded that vascular plants, especially shrubs, have increased as an effect of ongoing climate change. Few studies have linked this change to the underlying critical factor: soil temperatures have to be increased before vascular plants can outcompete lichens in the most exposed heaths. However, Brooker and van der Wal (2003) concluded that factors influencing soil temperature such as climate change or herbivory may also direct changes in vascular plant community composition. Fauria *et al.* (2008) and Porada *et al.* (2016) have also emphasized the negative effects of soil temperatures on lichens in a warmer climate.

Low temperatures and long-lasting soil frost may restrict vascular plant growth directly by limiting the rate of tissue respiration (Semikhatova *et al.* 1992) and thus nutrient uptake. Indirectly, soil frost slows the rate of soil decomposition and thus reduces the availability of essential nutrients (Jonasson 1983; Rustad *et al.* 2001). Frozen soils give vascular plants reduced soil water supply leading to tissue water deficits, especially if air temperatures increase before the soil is thawed (Gold and Bliss 1995). Winter desiccation happens when plants are rooted in frozen ground, but are trying to continue their metabolic processes anyway. Low soil temperature inhibits root growth as well as water uptake, and thus affects seedlings' water absorption and nutrient uptake rates (Mellander *et al.* 2004). This indicates that most vascular plants will probably not be able to invade lichen-dominated heaths, even if they have been well grazed before the frozen soil period has increased to a certain threshold.

Changed alpine lichen heath distribution

Climate change may modify the geographical distribution of lichen heaths in the future. Lichen heaths have their main distribution within the low-alpine zone in the continental parts of Fennoscandia where precipitation is relatively low, and winter temperatures and frost sum are low. An assumed general effect of climate change is that the climate character in Scandinavia will become increasingly oceanic, with more precipitation and less frost, even in continental regions. Consequently, the abundance of alpine lichen heaths in the future may become similar to the present situation in oceanic parts of Norway.

It has been suggested that lichen heaths may "move upward" as an effect of climate change (Heggberget *et al.* 2002). According to Moen *et al.* (2004), plant studies simulating climatic change indicate that a warmer and wetter climate may cause an altitudinal upward shift of macrolichens. This can result in an increased potential for lichen growth at high altitudes. At lower elevations, there may be increased competition from taller, faster-growing vascular plants, e.g. *Betula nana*. In our view, this is not a probable scenario, at least not in the near future. Lichen heaths are associated with a relatively thick soil layer, and in the mid-alpine zone (more than ca. 300 m above the forest limit), soils are shallow. Total thickness of organic and moraine substrate where the lichen cover was higher than 20% varied between 5 and 60 cm (average was 14.8±9.1 cm). Secondly, the snow amount may increase in high elevations due to increased precipitation and low temperatures.

Recent climate models indicate that the climate may become increasingly oceanic. Future climate in continental parts of Fennoscandia may then be similar to conditions in the western parts of Norway. In these areas, the distribution of alpine lichens heaths are generally small, and lichen abundance low.

Effects of grazing

Relationships between abundances of lichens and effects of reindeer grazing and climate have been discussed in several studies. It has frequently been reported that lichen abundances have decreased because of increased competition from expanding vascular plants, but this has rarely been verified by relevant studies. Certainly, lichen biomass will decrease with reindeer grazing and trampling, but the long-term effects remain unclear. Ecological effects of grazing have been discussed in several papers, however without reference to the importance of soil frost (e.g. Gaare 1997; Heggberget *et al.* 2002).

Cohen *et al.* (2013) suggested that effects of reindeer grazing with subsequent shrub expansion could cause climatic feedback through changed albedo. Similar feedback loops that couple vegetation changes, change in albedo and climatic feedback processes have been presented in other studies, particularly from Arctic areas (Hinzman *et al.* 2005; Sturm *et al.* 2005a; Chapin *et al.* 2005; Wookey *et al.* 2009; Myers-Smith and Hik 2013).

Sofronov *et al.* (2004) found that growth rates of young larch (*Larix* spp.) trees declined due to the reduction of the average soil thawing depth resulting from a recovery of the moss-lichen layer. This indicates that we cannot generally assume that vascular plants will outcompete and replace lichens. If vascular plants are to replace lichens, soil frost and thaw length must decrease first.

According to this, we suggest a possible explanation of lichen heath ecology, impacts of reindeer grazing, climate change, changed albedo, and soil temperature change (Fig. 15). Combined effects of extensive reindeer grazing and climate changes may result in feedback effects that in time may increase soil temperatures and thereby significantly decrease the distribution of the oligotrophic, chionophobous alpine lichen heaths.

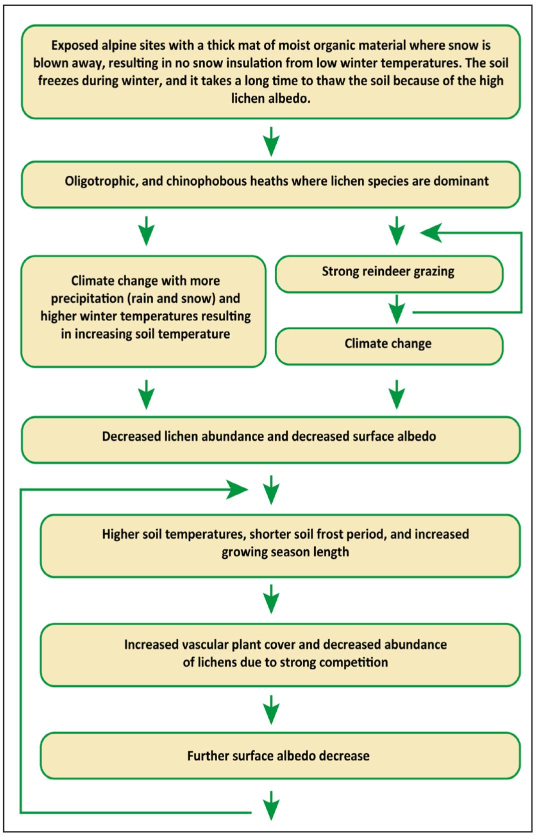

Fig. 15. Pathways for assumed relationships between lichen heath ecology, impacts of reindeer grazing, changes in climate, albedo, and soil temperatures. Feedback from reduced lichen cover result in reduced albedo and increasing soil temperatures. This may in turn give vascular plants favorable growth in the lichen heaths. Long-term impacts of lichen heaths without effects of climate changes are so far not known. As indicated, reindeer grazing may not necessary result in permanent loss of lichen heaths. A lichen-dominated heath can possibly be naturally reestablished if there are no effects of climate change.

References

Aas, B., and Faarlund, T. 2000: Forest limits and the sub-alpine birch belt in northern Europe with a focus on Norway. *AmS-Varia,* **37**:103-147.

Adamczewski, J.Z., Gates, C.C., Soutar, B.M. and Hudson, R.J. 1988: Limiting effects of snow on seasonal habitat use and diets of caribou (*Rangifer tarandus groenlandicus*) on Coats Island, Northwest territories, Canada. *Canadian Journal of Zoology,* **66**:1986-1996.

Ahti, T. 1959: Studies on the caribou lichen stands of Newfoundland. Societas zoologica botanica Fennica "Vanamo", Helsinki.

Ahti, T., and Hepburn, R. L. 1967: Preliminary studies on woodland caribou range, especially on lichen stands, in Ontario. Research branch, Ontario Department of Lands and Forests, Ontario.

Ahti, T., Hämet-Ahti, L. and Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici*, **5**:169-211.

Ahti, T., and Oksanen, J. 1990: Epigeic lichen communities of taiga and tundra regions. *Vegetatio*, **86**:39-70.

Akujärvi, A., Hallikainen, V., Hyppönen, M., Mattila, E., Mikkola, K. and Rautio, P. 2014: Effects of reindeer grazing and forestry on ground lichens in Finnish Lapland. *Silva Fennica*, **48**: article id 1153

Asplund, J., and Wardle, D.A. 2017: How lichens impact on terrestrial community and ecosystem properties. *Biological Reviews*, **92**:1720-1738.

Baadsvik, K. 1974: Phytosociological and ecological investigations in an alpine area at Lake Kamtjern, Trollheimen Mts, Central Norway: vegetation, snow and soil conditions. Universitetsforlaget, Trondheim.

Bala, G., Caldeira, K., Wickett, M., Phillips, T.J., Lobell, D.B., Delire, C. and Mirin, A. 2007: Combined climate and carbon-cycle effects of large-scale deforestation. *Proceedings of the National Academy of Sciences of the United States of America*, **104**:6550-6555.

Bernes, C., Brathen, K.A., Forbes, B.C., Speed, J.D. and Moen, J. 2015: What are the impacts of reindeer/caribou (*Rangifer tarandus* L.) on arctic and alpine vegetation? A systematic review. *Environmental Evidence*, **4**:4.

Bernier, P.Y., Desjardins, R.L., Karimi-Zindashty, Y., Worth, D., Beaudoin, A., Luo, Y. and Wang, S. 2011: Boreal lichen woodlands: A possible negative feedback to climate change in eastern North America. *Agricultural and Forest Meteorology*, **151**:521-528.

Bidussi, M., Solhaug, K.A. and Gauslaa, Y. 2016: Increased snow accumulation reduces survival and growth in dominant mat-forming arctic-alpine lichens. *The Lichenologist*, **48**:237-247.

Bjerke, J.W. 2011: Winter climate change: Ice encapsulation at mild subfreezing temperatures kills freeze-tolerant lichens. *Environmental and Experimental Botany*, **72**:404-408.

Blok, D., Sass-Klaassen, U., Schaepman-Strub, G., Heijmans, M.M.P.D., Sauren, P. and Berendse, F., 2011a. What are the main climate drivers for shrub growth in Northeastern Siberian tundra? *Biogeosciences*, **8**:1169-1179.

Blok, D., Schaepman-Strub, G., Bartholomeus, H., Heijmans, M.M.P.D., Maximov, T.C. and Berendse, F. 2011b: The response of Arctic vegetation to the summer climate: Relation between shrub cover, NDVI, surface albedo and temperature. *Environmental Research Letters*, **6**(3): 035502.

Bojariu, R., Garcia-Herrera, R., Gimeno, L., Zhang, T. and Frauenfeld, O.W. 2008: Cryosphere-atmosphere interactions related to variability and change of Northern Hemisphere Annular Mode. *Trends and Directions in Climate Research: Annals of the New York Academy of Sciences,* **1146**:50-59.

Bokhorst, S.F., Bjerke, J.W., Tømmervik, H., Preece, C. and Phoenix., G.K. 2012: Ecosystem response to climatic change: The importance of the cold season. *Ambio*, **41**:246-255.

Bokhorst, S.F., Bjerke, J.W., Tømmervik, H., Callaghan, T.V. and Phoenix, G.K. 2009: Winter warming events damage sub-Arctic vegetation: Consistent evidence from an experimental manipulation and a natural event. *Journal of Ecology*, **97**:1408-1415.

Bonan, G.B. 1989: A computer model of the solar radiation, soil moisture, and soil thermal regimes in boreal forests. *Ecological Modelling*, **45**:275-306.

Bonan, G.B. 2008: Ecological climatology : concepts and applications. 2nd ed. edition. Cambridge University Press, Cambridge.

Bonan, G.B., and Shugart, H.H. 1989: Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics*, **20**:1-28.

Bret-Harte, M.S., Shaver, G.R. and Chapin Iii, F.S. 2002: Primary and secondary stem growth in arctic shrubs: Implications for community response to environmental change. *Journal of Ecology*, **90**:251-267.

Bringer, K-G. 1961a: Den lågalpina *Dryas*-hedens differentiering och ståndortekologi inom Torneträsk-områden I. *Svensk Botanisk Tidsskrift*, **55**:349-375.

Bringer, K.-G. 1961b. Den lågalpina Dryas-hedens differentiering och ståndortekologi inom Torneträsk-områden II. *Svensk Botanisk Tidsskrift*, **55**:551-584.

Britton, A.J., and Fisher, J.M. 2010: Terricolous alpine lichens are sensitive to both load and concentration of applied nitrogen and have potential as bioindicators of nitrogen deposition. *Environmental Pollution*, **158**:1296-1302.

Brooker, R.B. and van der Wal, R. 2003: Can soil temperature direct the composition of high arctic plant communities? *Journal of Vegetation Science*, **14**: 535-542.

Chapin III, F.S., Shaver, J.M., Giblin, A.E. Nadelhoffer, K.J. and Laundre, J.A. 1995: Response of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**:694-711.

Chapin III, F.S. and Shaver, G.R. 1996: Physiological and growth responses of arctic plants to a field experiment simulating climatic change. *Ecology*, **77**:822-840.

Chapin III, F.S., Sturm, M., Serreze, M.C., McFadden, J.P. Key, J.R. Lloyd, A.H,. McGuire, A.D., Rupp, T.S., Lynch, A.H., Schimel, J.P., Beringer, J., Chapman, W.L., Epstein, H.E., Euskirchen, E.S., Hinzman, L.D., Jia, G., Ping, C.L., Tape, K.D., Thompson, C.D C., Walker, D.A. and Welker, J.M. 2005: Role of land-surface changes in arctic summer warming. *Science*, **310**:657-660.

Cocchietto, M., Skert, N., Nimis, P. and Sava, G. 2002: A review on usnic acid, an interesting natural compound. *Naturwissenschaften*, **89**:137-146.

Cohen, J., Pullianen, J., Menard, C.B., Johansen, B., Oksanen, L. and Luojos, K. 2013: Effect of reindeer grazing on snowmelt, albedo and energy balance based on satellite data analyses. *Remote Sensing of the Environment*, **135**.

Cooper, R. 1953: The Role of lichens in soil formation and plant succession. *Ecology,* **34**:805-807.

Cornelissen, J.H.C., Callaghan, T.V., Alatalo, J.M., Michelsen, A., Graglia, E., Hartley, A.E., Hik, D.S., Hobbie, S.E., Press, M.C., Robinson, C.H., Henry, G.H.R., Shaver, G.R., Phoenix, G.K., Gwynn Jones, D., Jonasson, S. and Chapin III., F.S. 2001: Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology*, **89**:984-994.

Coxson, D.S., and Marsh, J. 2001: Lichen chronosequences (postfire and postharvest) in lodgepole pine (*Pinus contorta*) forests of northern interior British Columbia. *Canadian Journal of Botany*, **79**:1449-1464.

Coxson, D.S. and Wilson, J.A. 2004: Carbon gain in *Cladina mitis* from mixed feather moss mats in a sub-alpine spruce-fir forest: The role of soil respiratory carbon dioxide release. *Symbiosis*, **37**:307-321.

Crabtree, D. and Ellis, C.J. 2010: Species interactions and response to wind speed alter the impact of projected temperature change in a montane system. *Journal of Vegetation Science*, **21**:744-760.

Crittenden, P.D. 1988: Nitrogen relations of mat-forming lichens. In: *Nitrogen, phosphorus, and sulphur utilization by fungi: Symposium of the British Mycological Society held at the University of Birmingham, April 1988* (eds. L. Boddy, R. Marchant and D.J. Read, editors), pp. 243-268. Cambridge University Press, Cambridge.

Crittenden, P.D. 2000: Aspects of the ecology of mat-forming lichens. *Rangifer,* **20**:127-139.

Crittenden, P.D., Kalucka, I. and Oliver, E. 1994: Does nitrogen supply limit the growth of lichens? *Cryptogamic Botany,* **4**:143-155.

Dahl, E. 1956: Rondane: Mountain Vegetation in South Norway and its Relation to the Environment. Skrifter Norske Videnskapsakademi i Oslo, *Matematisk-naturvidenskapelig Klasse*, **3**: 1-374.

Dahlgren, J., Oksanen, L., Olofsson, J., and Oksanen, T. 2009: Plant defences at no cost? The recovery of tundra scrubland following heavy grazing by grey-sided voles, myodes rufocanus. *Evolutionary Ecology Research*, **11**:1205-1216.

Danby, R.K., Koh, S., Hik, D.S. and Price, L.W. 2011: Four decades of plant community change in the alpine tundra of southwest Yukon, Canada. *Ambio,* **40**:660-671.

den Herder, M., Kytöviita, M.-M. and Niemelä, P. 2003: Growth of reindeer lichens and effects of reindeer grazing on ground cover vegetation in a Scots pine forest and a subarctic heathland in Finnish Lapland. *Ecography*, **26**:3-12.

den Herder, M., Virtanen, R., and Roininen, H. 2008: Reindeer herbivory reduces willow growth and grouse forage in a forest-tundra ecotone. *Basic and Applied Ecology*, **9**:324-331.

Du Rietz, G. 1925: Zur kenntis der Flechtenreichen Zwergstrauchheiden im kontinentalen Südnorwegen. *Svenska växtsociologiska sällskapets handlingar,* **4**:19-79.

Dyrrdal, A., Saloranta, T., Skaugen, T. and Bache, H. 2013: Changes in snow depth in Norway during the period 1961-2010. *Hydrology Research*, **44**:169-179.

Edwards, A.C., and Cresser, M.S. 1992: Freezing and its effect on chemical and biological properties of soil. In: *Advances in Soil Science.* (ed. B.A. Stewart), pp. 59-79. Springer New York, New York, NY.

Edwards, C.A., Scalenghe, R. and Freppaz, M. 2007: Changes in the seasonal snow cover of alpine regions and its effect on soil processes: a review. *Quartenary International*, **162-163**:172-181.

Ellis, C.J., Crittenden, P.D. and Scrimgeour, C.M. 2004: Soil as a potential source of nitrogen for mat-forming lichens. *Canadian Journal of Botany*, **82**:145-149.

Eriksson, O., and Raunistola, T. 1993: Impact of forest fertilizers on winter pastures of semi-domesticated reindeer. *Rangifer*, **13**:203-214.

Fahselt, D. 1994: Secondary biochemistry of lichens. *Symbiosis*, **16**:117-165.

Falldorf, T., Strand, O. Panzacchi, M. and Tømmervik, H. 2014: Estimating lichen volume and reindeer winter pasture quality from Landsat imagery. *Remote Sensing of Environment*, **140**:573-579.

Fauria, M.M., Helle, T., Niva, A., Posio, H. and Timonen, M. 2008: Removal of the lichen mat by reindeer enhances tree growth in a northern Scots pine forest. *Canadian Journal of Forest Research*, **38**:2981-2993.

Ferguson, M.A.D., Gauthier, L. and Messier, F. 2001: Range shift and winter foraging ecology of a population of Arctic tundra caribou. *Canadian Journal of Zoology,* **79**:746-758.

Fraser, R.H., Lantz, T.C., Olthof, I., Kokelj, S.V. and Sims, R.A. 2014: Warming-induced shrub expansion and lichen decline in the Western Canadian Arctic. *Ecosystems*, **17**:1151-1168.

Freppaz, M., Celi, L., Marchelli, M. and Zanini, E. 2008: Snow removal and its influence on temperature and N dynamics in alpine soils (Vallée D'Aoste, Italy). *Journal of Plant Nutrition and Soil Science*, **171**:672-680.

Fægri, K. 1934: Über die Längenvariationen einiger Gletscher des Jostedalsbre und die daduch bedingten Pflanzensukzessionen. *Bergens museums aarbok*, **1933**:7.

Gaare, E. 1997: A hypothesis to explain lichen-Rangifer dynamic relationships. *Rangifer*, **17**:3-7.

Gaare, E., and Skogland, T. 1975: Wind reindeer food habitats and range use at Hardangervidda. In: *Fennoscandian tundra ecosystems: Pt 2. Animals and systems analysis* (ed. F.-E. Wielgolaski), pp. 195-205. Springer, Berlin.

Gaare, E., and Skogland, T. 1979: Grunnlaget for villreinforvaltningen. *Jakt, fiske, friluftsliv*, **4**:16-19.

Gaio-Oliveira, G., Moen, J., Danell, O. and Palmqvist, K. 2006: Effect of simulated reindeer grazing on the regrowth capacity of mat-forming lichens. *Basic and Applied Ecology*, **7**:109-121.

Garcia-Suarez, A.M., and Butler, C.J. 2006: Soil temperatures at Armagh Observatory, Northern Ireland, from 1904 to 2002. *International Journal of Climatology*, **26**:1075-1089.

Gehrig-Fasel, J., Guisan, A. and Zimmermann, N.E. 2008: Evaluating treeline indicators based on air and soil temperature using and air-to-soil temperature transfer model. *Ecological Modelling*, **213**:345-355.

Gold W.G., Glew, K.A. and Dickson, L.G. 2001: Functional influences of cryptobiotic surface crusts in an Alpine tundra basin of the Olympic Mountains, Washington, U.S.A. *NorthWest Science*,**75**:3.

Gold, W.G. and Bliss, L.C. 1995: Water limitations and plant community development in a polar desert. *Ecology*, **76**:1558-1568.

Gornall, J.L., Jónsdóttir, I.S., Woodin, S.J. and Van Der Wal, R. 2007: Arctic mosses govern below-ground environment and ecosystem processes. *Oecologia*, **153**:931-941.

Graglia, E., Julkunen-Tiitto, R., Shaver, G.R., Schmidt, I.K., Jonasson, S. and Michelsen, A. 2001: Environmental control and intersite variations of phenolics in Betula nana in tundra ecosystems. *New Phytologist*, **151**:227-236.

Green, T.G.A., Schroeter, B. and Sancho, L.G. 2007: Plant Life in Antarctica. In: *Functional Plant Ecology.* (eds. F. Pugnaire, F. Valladares, and F. I. Pugnaire), pp. 389-434. CRC Press, Hoboken.

Grime, J.P. 1977: Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**:1169-1194.

Grime, J.P. 1979: Plant strategies and vegetation processes. Wiley, Chichester.

Groffman, P.M., Hardy, J.P., Nolan, S., Fitzhugh, R.D., Driscoll, C.T. and Fahey, T.J. 1999: Snow depth, soil frost and nutrient loss in a northern hardwood forest. *Hydrological Processes*, **13**:2275-2286.

Haapasaari, M. 1988: The oligotrophic heath vegetation of northern Fennoscandia and its zonation. *Acta Botanica Fennica*, **135**: 1-219.

Hadac, E. 1972: Notes on some plant communities in Blefjell, S. Norway. *Preslia*, **43**:202-217.

Hauck, M. 2010: Ammonium and nitrate tolerance in lichens. *Environmental Pollution*, **158**:1127-1133.

Heggberget, T.M., Gaare, E. and Ball, J.P. 2002: Reindeer (*Rangifer tarandus*) and climate change: importance of winter forage. *Rangifer*, **22**:13-31.

Heggenes, J., Odland, A. and Bjerketvedt, D.K. 2018: Are trampling effects by wild tundra reindeer understudied? *Rangifer*, **38**:1-11.

Heikinheimo, M., and Lappalainen, H. 1997: Dependence of the flower bud burst of some plant taxa in Finland on effective temperature sum: Implications for climate warming. *Annales Botanici Fennici*, **34**:229-243.

Heikkinen, O. 2005: Boreal forests and northern upper timberlines. In: *The Physical geography of Fennoscandia* (ed. M. Seppälä), pp. 185-200. Oxford University Press, Oxford.

Helle, T., Aspi, J. and Tarvainen, L. 1983: The growth rate of *Cladonia rangiferina* and *C. mitis* in relation to forest characteristics in Northeastern Finland. *Rangifer*, **3**:2-5.

Helle, T., Kilpelä, S.-S., and Aikio, P. 1990: Lichen ranges, animal densities and production in Finnish reindeer management. *Rangifer Special Issue,* **3**:115-121.

Henry, H.A.L. 2006: Climate change and soil freezing dynamics: historical trends and predicted changes. *Climactic Change*, **87**: 421-434.

Hesjedal, O. 1975. Vegetation mapping at Hardangervidda. Pages 74-81 in F.-E. Wielgolaski, editor. Fennoscandian tundra ecosystems : Pt 1 : Plants and microorganisms. Springer, Berlin.

Hestmark, G., Skogesal, O. and Skullerud, ∅. 2005: Growth, population density and population structure of *Cetraria nivalis* during 240 years of primary colonization. *Lichenologist*, **37**: 535-541.

Hinneri, S., Sonesson, M. and Veum, A.K. 1975. Soils of Fennoscandian IBP tundra ecosystems. In: *Fennoscandian tundra ecosystems: Pt 1. Plants and microorganisms* (eds. F. E. Wielgolaski, P. Kallio, and T. Rosswall), pp. 31-40. Springer, Berlin.

Hinzman, L.D., Bettez, N.D., Bolton, W.R., Chapin, F.S., Dyurgerov, M.B., Fastie, C.L., Griffith, B., Hollister, R. D., Hope, A., Huntington, H.P., Jensen, A.M., Jia, G.J., Jorgenson, T., Kane, D.L., Klein, D.R., Kofinas,G., Lynch,A.H., Lloyd, A.H., McGuire, A.D., Nelson, F.E., Oechel, W.C., Osterkamp, T.E., Racine, C.H., Romanovsky, V.E., Stone, R.S., Stow, D.A., Sturm, M., Tweedie, C.E., Vourlitis, G.L., Walker, M.D., Walker, D.A., Webber, P.J., Welker, J.M., Winker, K.S. and Yoshikawa, K. 2005: Evidence and implications of recent climate change in Northern Alaska and other Arctic regions. *Climatic Change*, **72**: 251-298.

Hudson, J.M.G. and Henry, G.H.R. 2009: Increased plant biomass in a high arctic heath community from 1981 to 2008. *Ecology*, **90**: 2657-2663.

Huneck, S. 1999: The significance of lichens and their metabolites. *Naturwissenschaften*, **86**: 559-570.

Huseby, K. and Odland, A. 1981: Botaniske undersøkelser i Vikedals-vassdraget, Vindafjord, Rogaland. Universitetet i Bergen, Botanisk inst., Bergen.

Hülber, K., Bardy, K. and Dullinger, S. 2011. Effects of snowmelt timing and competition on the performance of alpine snowbed plants. *Perspectives in Plant Ecology, Ecology, Evolution, and Systematics,* **13**: 15-26.

Joly, K., Jandt, R.K., Meyers, C.R. and Cole, M.J. 2007: Changes in vegetative cover on western arctic herd winter range from 1981-2005: potential effects of grazing and climate change. *Rangifer Special Issue*, **17**: 199-207.

Joly, K., Jandt, R.R. and Klein, D.R. 2009: Decrease of lichens in arctic ecosystems: the role of wildfire, caribou, competition, and climate in north-western Alaska. *Polar Research*, **28**: 433-442.

Jonasson, S. 1981: Plant communities and species distribution of low alpine *Betula nana* heaths in Northernmost Sweden. *Vegetatio*, **44**: 51-64.

Jonasson, S. 1983: Nutrient content and dynamics in north Swedish shrub tundra areas. *Ecography*, **6**: 295-304.

Jonasson, S. 1992: Plant responses to fertilization and species removal in tundra related to community structure and clonality. *Oikos*, **63**: 420-429.

Jägerbrand, A.K., Alatalo, J., Chrimes, D. and Molau, U. 2009: Plant community responses to 5 years of simulated climate change in meadow and heath ecosystems at a subarctic-alpine site. *Oecologia*, **161**: 601-610.

Kallio, P. 1975: Kevo, Finland. In: *Structure and function of tundra ecosystems: papers presented at the IBP Tundra Biome V. International Meeting on Biological Productivity of Tundra, Abisko, Sweden, April 1974.* (eds. T. Rosswall and O.W. Heal), Swedish Natural Science Research Council, Stockholm.

Kappen, L., Schroeter, B., Scheidegger, C., Sommerkorn, M. and Hestmark, G. 1996. Cold resistance and metabolic activity of lichens below 0° C. *Advances in Space Research*, **18**:119-128.

Kappen, L., Sommerkorn, M. and Schroeter, B. 1995: Carbon acquisition and water relations of lichens in polar regions - potentials and limitations. *The Lichenologist*, **27**: 531-545.

Karlsson, P.S. 1985: Photosynthetic characteristics and leaf carbon economy of a deciduous and an evergreen dwarf shrub: *Vaccinium uliginosum* L. and *Vaccinium vitis-idaea* L-. *Holarctic Ecology*, **8**: 9-17.

Karlsson, P.S., and Nordell, K.O. 1996: Effects of soil temperature on the nitrogen economy and growth of mountain birch seedlings near its presumed low temperature distribution limit. *Ecoscience*, **3**:183-189.

Karlsson, P.S., and Weih, M. 2001: Soil temperatures near the distribution limit of the mountain birch (*Betula pubescens* ssp. *czerepanovii*): Implications for seedling nitrogen economy and survival. *Arctic, Antarctic, and Alpine Research*, **33**: 88-92.

Kaste, ∅., Austnes, K., Vestgarden, K.L. and Wright, R.F. 2008: Manipulation of snow in small headwater catchments at Storgama, Norway: effects on leaching of inorganic nitrogen. *Ambio*, **37**: 29-37.

Kershaw, K.A. 1978: The role of lichens in boreal tundra transition areas. *The Bryologist*, **81**: 294-306.

Kershaw, K.A. 1985: Physiological ecology of lichens. Cambridge University Press, Cambridge.

Kielland-Lund, J. 1981: Die Waldgesellschaften SO-Norwegens. *Phytocoenologia*, **9**: 53-250.

Kjelvik, S. 1978: Plantens produksjon pǎ Hardangervidda. *Blyttia*, **36**: 87-90.

Kjelvik, S. and Kärenlampi, L. 1975: Plant biomass and primary production of Fennoscandian subarctic and subalpine forests of alpine willow and heath ecosystems. In: *Fennoscandian tundra ecosystems: Pt 1. Plants and microorganisms* (ed. F.-E. Wielgolaski), pp. 111-120. Springer, Berlin.

Klanderud, K. 2008: Species-specific responses of an alpine plant community under simulated environmental change. *Journal of Vegetation Science*, **19**: 363-372.

Klein, D.R. 1968: The introduction, increase, and crash of reindeer on St. Matthew Island. *Journal of Wildlife Management*, **32**: 350-367.

Klein, D.R. 1987: Interactions of *Rangifer tarandus* (reindeer and caribou) with their habitat in Alaska. *Finnish Game Research*, **30**: 289-293.

Klein, D.R. and Shulski, M. 2011: The role of lichens, reindeer, and climate in ecosystem change on a Bering Strait Island. *Arctic*, **64**: 353-361.

Kleiven, M. 1959: Studies on the xerophile vegetation in northern Gudbrandsdalen, Norway. *Nytt magasin for botanikk*, **7**: 1-60.

Klimaservicesenter 2015: Klima i Norge 2100. 2/2015, Norsk Klimaservicesenter, Oslo.

Kohler, J., Brandt, O., Johansson, M. and Callaghan, T.V. 2006: A long-term Arctic snow depth record from Abisko, northern Sweden, 1913-2004. *Polar Research*, **25**: 91-113.

Kojola, I., Helle, T., Niskanen, M. and Aikio, P. 1995: Effects of lichen biomass on winter diet, body mass and reproduction of semi-domesticated reindeer *Rangifer tarandus* in Finland. *Wildlife Biology*, **1**: 33-38.

Kranner, I., Beckett, R., Hochman, A. and Nash Iii, T.H. 2008: Desiccation-tolerance in lichens: A review. *The Bryologist*, **111**: 576-593.

Kullman, L. 2005: Old and new trees on Mt Fulufjället in Dalarna, central Sweden. *Svensk Botanisk Tidskrift,* **99**: 315-329.

Kumpula, J., Colpaert, A. and Nieminen, M. 1998: Reproduction and productivity of semidomesticated reindeer in northern Finland. *Canadian Journal of Zoology*, **76**: 269-277.

Kumpula, J., Colpaert, A. and Nieminen, M. 2000: Condition, potential recovery rate, and productivity of lichen (*Cladonia* spp.) ranges in the Finnish reindeer management area. *Arctic*, **53**: 9.

Kumpula, J., Stark, S. and Holand, Ø. 2011: Seasonal grazing effects by semi-domesticated reindeer on subarctic mountain birch forests. *Polar Biology*, **34**: 441-453.

Kytöviita, M.M. and Crittenden, P.D. 2007: Growth and nitrogen relations in the mat-forming lichens *Stereocaulon paschale* and *Cladonia stellaris*. *Annals of Botany*,

100: 1537-1545.

Kytöviita, M.M. and Stark, S. 2009: No allelopathic effect of the dominant forest-floor lichen *Cladonia stellaris* on pine seedlings. *Functional Ecology*, **23**: 435-441.

Kärenlampi, L. 1971: Studies on relative growth rate of some fruticose lichens. *Reports of the Kevo Subarctic Research Station*, **7**: 33-39.

Körner, C. 2003: Alpine plant life: Functional plant ecology of high mountain ecosystems, 2nd ed. Springer Verlag, Berlin.

Lang, S.I., Cornelissen, J.C., Shaver, G.R., Ahrens, M., Callaghan, T.V., Molau, U., Ter Braak, C.F., Hölzer, A. and Aerts, R. 2012: Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. *Global Change Biology*, **18**: 1096-1107.

Larcher, W. 1995: Physiological plant ecology: ecophysiology and stress physiology of functional groups. 3rd ed. Springer, Berlin.

Lawrey, J.D. 1995: Lichen allelopathy: A review. In: *Allelopathy: organisms, processes, and applications* (eds. Inderjit, K.M.M. Dakshini and F.A. Einhellig). American Chemical Society, Washington.

Lemke, P., Ren, J., Alley, R.B., Allison, I., Carrasco, J., Flato, G., Fujii, Y., Kaser, G., Mote, P., Thomas, R.H. and Zhang, T. 2007: Observations: Changes in Snow, Ice, and Frozen Ground., Cambridge, United Kingdom and New York, United States of America.

Löffler, J. 2003: Micro-climatic determination of vegetation patterns along topographical, altitudinal, and oceanic-continental gradients in the high mountains of Norway. *Erdkunde*, **57**: 249.

Löffler, J. 2005: Snow cover dynamics, soil moisture variability and vegetation ecology in high mountain catchments of central Norway. *Hydrological Processes*, **19**: 2385-2405.

Löffler, J. 2007: The influence of micro-climate, snow cover, and soil moisture on ecosystem functioning in high mountains. *Journal of Geographical Sciences*, **17**: 3-19.

Löffler, U.C.M., Cypionka, H. and Löffler, J. 2008. Soil microbial activity along an arctic-alpine altitudinal gradient from a seasonal perspective. *European Journal of Soil Science*, **59**: 842-854.

Mack, M.C., Schuur, E.A.G., Bret-Harte, M.S., Shaver, G.R. and Chapin Iii, F.S. 2004: Ecosystem carbon storage in arctic tundra reduce by long-term nutrient fertilization. *Nature*, **431**: 440-443.

Manseau, M., Huot, J. and Crête, M. 1996: Effects of summer grazing by caribou on composition and productivity of vegetation: Community and landscape level. *Journal of Ecology*, **84**: 503-513

Matthews, J.A. 1992: The ecology of recently-deglaciated terrain: a geoecological approach to glacier forelands and primary succession. Cambridge University Press, Cambridge.

Mattila, F. 1981: Survey of reindeer winter ranges as part of the Finnish national forest inventory 1976-1978. *Communicationes Instituti Forestalis Fenniae*, **99**: 1-74.

Matwiejuk, A. 2000: Water content in terricolous lichens. *Acta Societatis Botanicorum Poloniae*, **69**: 55-63.

Mellander, P.-E., Bishop, K. and Lundmark, T. 2004: The influence of soil temperature on transpiration: a plot scale manipulation in a young Scots pine stand. *Forest Ecol ogy and Management*, **195**: 15–28.

Moen, A. 1999: National Atlas of Norway: Vegetation. Norwegian Mapping Authority, Hønefoss.

Moen, J., Aune, K., Edenius, L. and Angerbjörn, A. 2004: Potential effects of climate change on treeline position in the Swedish mountains. *Ecology and Society*, **9**: 16.

Molau, U. and Alatato, J. M. 1998: Responses of subarctic-alpine plant communities to simulated environmental change: Biodiversity of bryophytes, lichens, and vascular plants. *Ambio*, **27**: 322-329.

Molnár, K. and Farkas, E. 2010: Current results on biological activities of lichen secondary metabolites: A review. *Zeitschrift fur Naturforschung - Section C Journal of Biosciences*, **65**: 157-173.

Morneau, C. and Payette, S. 1989: Postfire lichen-spruce woodland recovery at the lmit of the boreal forest in northern Quebec. *Canadian Journal of Botany*, **67**: 2770-2782.

Myers-Smith, I.H. and Hik, D.S. 2013: Shrub canopies influence soil temperatures but not nutrient dynamics: An experimental test of tundra snow-shrub interactions. *Ecology and Evolution*, **3**: 3683-3700.

Myrvold, L.M. 2013: Variasjon i lavbiomasse mellom ulike naturtyper og geografiske regioner i tre sørnorske fjellområder. Master thesis, Telemark University College.

Nash, T.H., Moser, T.J. and Link, S.O. 1980: Nonrandom variation of gas exchange within arctic lichens. *Canadian Journal of Botany*, **58**: 1181-1186.

Natali, S.M., Schuur, E.A.G. and Rubin, R.L. 2012: Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. *Journal of Ecology*, **100**: 488-498.

Nordhagen, R. 1928: Die Vegetation und Flora des Sylenegebietes. Eine Pflanzen-soziologische Monografie. Skrifter Det Norske videnskaps-akademi, Oslo.

Nordhagen, R. 1943: Sikilsdalen og Norges fjellbeiter: en plantesosiologisk monografi. A.S. John Greigs boktrykkeri, Bergen, Norge.

Nordhagen, R. 1955: Kobresieto-Dryadion in Northern Scandinavia. *Svensk Botanisk Tidskrift*, **49**: 63-87.

Odland, A. 1981: Botaniske undersøkelser i Ørsta-vassdraget. Universitetet i Bergen, Botanisk inst., Bergen.

Odland, A. 2011: Estimation of the growing season length in alpine areas, Effects of snow and temperatures. In: *Alpine Environment, Geology, Ecology and Conservation*. (ed. J.G Schmidt),pp. 85-134. Nova Science Publishers Inc., New York.

Odland, A. 2012: Variation in Fennoscandian calciphile alpine vegetation. Are previous phytosociological classifi cations reproduced by numerical analyses. *Phytocoenologia*, **42**: 203-220.

Odland, A. 2015. Effect of latitude and mountain height on the timberline (*Betula pubescens* ssp. *czerpanovii*) elevation along the central Scandinavian mountain range. *Fennia*, **193**: 260-270.

Odland, A. and Munkejord, H.K. 2008a: The importance of date of snowmelt for the separation of different oligotrophic and mesotrophic mountain vegetation types in Southern Norway. *Phytocoenologia*, **38**: 3-21.

Odland, A. and Munkejord, H.K. 2008b: Plants as indicators of snow layer duration in southern Norwegian mountains. *Ecological Indicators*, **8**: 57-68.

Odland, A., Reinhardt, S. and Pedersen, A. 2015: Differences in richness of vascular plants, mosses, and liverworts in southern Norwegian alpine vegetation. *Plant Ecology and Diversity*, **8**: 37-47.

Odland, A., Sandvik, S.M., Bjerketvedt, D.K. and Myrvold, L.M. 2014: Estimation of lichen biomass with emphasis on reindeer winter pastures at Hardangervidda, S Norway. *Rangifer*, **34**: 95-110.

Oksanen, L. and Oksanen, T. 2000: The logic and realism of the hypothesis of exploitation ecosystems. *American Naturalist*, **155**: 703-723.

Olofsson, J., Moen, J. and Oksanen, L. 2002: Effects of herbivory on competition intensity in two arctic-alpine tundra communities with different productivity. *Oikos*, **96**: 265-272.

Olofsson, J., Oksanen, L., Callaghan, T., Hulme, P.E., Oksanen, T. and Suominen, O. 2009: Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology*, **15**: 2681–2693

Pajunen, A.M., Oksanen, J. and Virtanen, R. 2011: Impact of shrub canopies on understorey vegetation in western Eurasian tundra. *Journal of Vegetation Science*, **22**: 837-846.

Peltoniemi, J.I., Manninen, T., Suomalainen, J., Hakala, T., Puttonen, E. and Riihelä, A. 2010: Land surface albedos computed from BRF measurements with a study of conversion formulae. *Remote Sensing*, **2**: 1918-1940.

Peth, S. and Horn, R. 2006: Consequences of grazing on soil physical and mechanical properties in forest and tundra environments. In: *Ecological Studies 184: Reindeer Management in Northernmost Europe* (eds. B.C. Forbes, M. Bölter, L. Müller-White, J. Hukkinen, F. Müller, N. Gunslay, and Y. Konstantinov), pp. 217-242. Springer, Berlin.

Petzold, D.E. and Rencz, A.N. 1975: The albedo of selected sub arctic surfaces. *Arctic and Alpine Research*, **7**: 393-398.

Pitman, A.J. 2003: The evolution of, and revolution in, land surface schemes designed for climate models. *International Journal of Climatology*, **23**: 479-510.

Porada, P., Ekici, A. and Beer, C. 2016: Effects of bryophyte and lichen cover on permafrost soil temperature at large scale. *The Cryosphere*, **10**: 2291-2315.

Post, E. and Klein, D.R. 1999: Caribou calf production and seasonal range quality during a population decline. *Journal of Wildlife Management*, **63**: 335-345.

Press, M.C., Potter, J.A., Burke, M.J.W., Callaghan, T.V. and Lee, J.A. 1998: Responses of a subarctic dwarf shrub heath community to simulated environmental change. *Journal of Ecology*, **86**: 315-327.

Rees, W.G. 1993: Infrared emissivities of arctic land cover types. *International Journal of Remote Sensing,* **14**: 1013-1017.

Reinhardt, S. and Odland, A. 2012: Soil temperature variation in calciphile plant communities in Southern Norway. *Oecologia Montana*, **21**: 21-35.

Reinhardt, S., Odland, A. and Pedersen, A. 2013: Calciphile alpine vegetation in Southern Norway: importance of snow and possible effects of climate change. *Phytocoenologia*, **43**: 207-223.

Reistad, I. 1997: Horisontale gradientar i lavrik rabbevegetasjon frå innland til kyst ved Sognefjorden. I.Reistad, Bergen.

Rekdal, Y., Angeloff, M. and Hofsten, J. 2009: Vegetasjon og beite på Hardangervidda. Skog og landskap oppdragsrapport: 1-50.

Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., Cornelissen, J.H.C., Gurevitch, J., Alward, R., Beier, C., Burke, I., Canadell, J., Callaghan, T., Christensen, T.R., Fahnestock, J., Fernandez, I., Harte, J., Hollister, R., John, H., Ineson, P., Johnson, M.G., Jonasson, S., John, L., Linder, S., Lukewille, A., Masters, G., Melillo, J., Mickelsen, A., Neill, C., Olszyk, D.M., Press, M., Pregitzer, K., Robinson, C., Rygiewiez, P.T., Sala, O., Schmidt, I.K., Shaver, G., Thompson, K., Tingey, D.T., Verburg, P., Wall, D., Welker, J. and Wright, R. 2001: A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**: 543-562.

Ryden, B.E. and Kostov, L. 1980: Thawing and freezing in tundra soils. *Ecological Bulletins (Sweden)*, **30**: 251-281.

Rydgren, K., Halvorsen, R., Töpper, J.P. and Njøs, J.M. 2014: Glacier foreland succession and the fading effect of terrain age. *Journal of Vegetation Science*, **25**(6): 1367–1380.

Røsberg, I. 1981: Flora og vegetasjon i Yndesdals-vassdraget. Universitetet i Bergen, Botanisk inst., Bergen.

Sandström, P., Cory, N., Svensson, J., Hedenås, H., Jougda, L. and Borchert, N. 2016: On the decline of ground lichen forests in the Swedish boreal landscape: Implications for reindeer husbandry and sustainable forest management. *Ambio*, **45**: 415-429.

Schimel, J.P., Bilbrough, C. and Welker, J.M. 2004: Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology and Biochemistry*, **36**: 217-227.

Schuur, E.A.G., Bockheim, J., Canadell, J.G., Euskirchen, E., Field, C.B., Goryachkin, S.V., Hagemann, S., Kuhry, P., Lafleur, P.M., Lee, H., Mazhitova, G., Nelson, F.E., Rinke, A., Romanovsky, V.E., Shiklomanov, N., Tarnocai, C., Venevsky, S., Vogel, J.G. and Zimov, S.A. 2008: Vulnerability of permafrost carbon to climate change: Implications for the global carbon cycle. *BioScience*, **58**: 701-714.

Seaward, M. 2008: Environmental role of lichens. In: *Lichen Biology* (ed. T.H. Nash III), pp: 276-300. Cambridge University Press, Cambridge.

Sedia, E. G., and J. G. Ehrenfeld. 2003. Lichens and mosses promote alternate stable plant communities in the New Jersey Pinelands. Oikos 100: 447-458.

Sedia, E.G. and Ehrenfeld, J.G. 2006: Differential effects of lichens and mosses on soil enzyme activity and litter decomposition. *Biology and Fertility of Soils*, **43**: 177-189.

Semikhatova, O.A., Gerasimenko, T.V. and Ivanova, T.I. 1992: Photosynthesis, Respiration and Growth of Plants in the Soviet Arctic. In: *Arctic ecosystems in a changing climate: an ecophysiological perspective* (eds. F.S.I. Chapin, R.L. Jefferies, J.F. Reynolds and J. Svoboda), pp. 169-192. Academic Press, San Diego, California.

Skre, O. 1975: CO_2 exchange in Norwegian tundra plants studied by infrared gas analyzer technique. In: *Fennoscandian tundra ecosystems pt 1*. (ed. F.E. Wielgolaski), pp: 168-183. Springer, Berlin.

Sofronov, M., Volokitina, V., Kajimoto, T. and Uemura, S. 2004: The ecological role of moss-lichen cover and thermal amelioration of larch forest ecosystems in the northern part of Siberia. *Eurasion Forest Research*, **7**: 11-19.

Stark, S., Wardle, D.A., Ohtonen, R., Helle, T. and Yeates, G.W. 2000: The effect of reindeer grazing on decomposition, mineralization and soil biota in a dry oligotrophic Scots pine forest. *Oikos*, **90**: 301-310.

Stork, A. 1963: Plant immigration in front of retreating glaciers, with examples from the Kebnekajse area, Northern Sweden. *Geografiska Annaler*, **45**: 1-22.

Stoy, P., Street, L., Johnson, A., Prieto-Blanco, A. and Ewing, S. 2012: Temperature, heat flux, and reflectance of common subarctic mosses and lichens under field conditions: Might changes to community composition impact climate-relevant surface fluxes? *Arctic, Antarctic, and Alpine Research*, **44**: 500-508.

Sturm, M., Douglas, T., Racine, C. and Liston, G.E. 2005: Changing snow and shrub conditions affect albedo with global implications. *Journal of Geophysical Research,* **110**: G01004.

Sturm, M., McFadden, J.P., Liston, G.E., Stuart Chapin Iii, F., Racine, C.H. and Holmgren, J. 2001a: Snow-shrub interactions in Arctic Tundra: A hypothesis with climatic implications. *Journal of Climate*, **14**: 336-344.

Sturm, M., Manthey, M. and Wilmking, M. 2001b: Increasing shrub abundance in the Arctic. *Nature*, **411**: 546-547.

Sulkava, S. and Helle, T. 1975: Range ecology of the domesticated reindeer in the Finnish coniferous area. *Biological Papers of the University of Alaska Special Report*, **1**: 308-315.

Sundstøl, S.A. and Odland, A. 2017: Responses of alpine vascular plants and lichens to soil temperatures. *Annales Botanici Fennici*, **54**: 17-28.

Suominen, O. and Olofsson, J. 2000: Impacts of semi-domesticated reindeer on structure of tundra and forest communities in Fennoscandia: A review. *Annales Zoologici Fennici*, **37**: 233-249.

Sutinen, R., Vajda, A., Hänninen, P. and Sutinen, M.L. 2009: Significance of snowpack for root-zone water and temperature cycles in subarctic lapland. *Arctic, Antarctic, and Alpine Research*, **41**: 373-380.

Tarnocai, C. 2009: The impact of climate change on Canadian peatlands. *Canadian Water Resources Journal*, **34**: 453-466.

Te Beest, M., Sitters, J., Ménard, C.B. and Olofsson, J. 2016: Reindeer grazing increases summer albedo by reducing shrub abundance in Arctic tundra. *Environmental Research Letters*, **11**: 125013

Tegler, B. and Kershaw, K.A. 1980: Studies on lichen-dominated systems. XXIII. The control of seasonal rates of net photosynthesis by moisture, light, and temperature in *Cladonia rangiferina*. *Canadian Journal of Botany*, **58**: 1851-1858.

Theodose, T.A. and Bowman, W.D. 1997: Nutrient availability, plant abundance, and species diversity in two alpine tundra communities. *Ecology*, **78**: 1861-1872.

Thing, H. 1984: Feeding ecology of the West Greenland caribou (*Rangifer tarandus groenlandicus*) in the Sisimiut-Kangerlussuaq region. *Danish Review of Game Biology*, **12**.

Tisdale, E.W., Fosberg, M.A. and Poulton, C.E. 1966: Vegetation and soil development on a recently glaciated area near Mount Robson, British Columbia. *Ecology*, **47**: 517-523.

Tranquillini, W. 1979: Physiological ecology of the alpine timberline: tree existence at high altitudes with special reference to the European Alps. Springer, Berlin.

Tuhkanen, S. 1980: Climatic parameters and indices in plant geography. *Acta Phytogeographica Suecica*, **67**.

Turunen, M., Soppela, P., Kinnunen, H., Sutinen, M.-L. and Martz, F. 2009: Does climate change influence the availability and quality of reindeer forage plants? *Polar Biology*, **32**: 813-832.

Tveraabak, L.U. 2004: Atlantic heath vegetation at its northern fringe in Central and Northern Norway. *Phytocoenologia*, **34**: 5-31.

Tømmervik, H., Johansen B., Riseth, J.Å., Karlsen, S.R., Solberg, B. and Høgda, K.A. 2009: Above ground biomass changes in the mountain birch forests and mountain heaths of Finnmarksvidda, northern Norway, in the period 1957-2006. *Forest Ecology and Management*, **257**: 244-257.

Tømmervik, H. and Lauknes, I. 1988: Inventory of reindeer winter pastures by use of Landsat-5 TM data. Page 1223 in Digest - International Geoscience and Remote Sensing Symposium (IGARSS).

Uchida, M., Nakatsubo, T., Kanda, H. and Koizumi, H. 2006: Estimation of the annual primary production of the lichen *Cetrariella delisei* in a glacier foreland in the High Arctic, Ny-Ålesund, Svalbard. *Polar Research,* **25**: 39-49.

van der Wal, R. 2006: Do herbivores cause habitat degradation or vegetation state transition? Evidence from the tundra. *Oikos*, **114**.

van der Wal, R., Brooker, R., Cooper, E. and Langvatn, R. 2001: Differential effects of reindeer on high Arctic lichens. *Journal of Vegetation Science*, **12**: 705-710.

van der Wal, R. and Brooker, R.W. 2004: Mosses mediate grazer impacts on grass abundance in arctic ecosystems. *Functional Ecology*, **18**: 77-86.

van Wijk, M.T., Clemmensen, K.E., Shaver, G.R., Williams, M., Callaghan, T.V., Chapin III, F.S., Cornelissen, J.H.C., Gough, L., Hobbie, S.E., Jonasson, S., Lee, J.A., Michelsen, A., Press, M.C., Richardson, S.J. and Reuth, H. 2003: Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystems and plant type responses to global change. *Global Change Biology*, **10**: 105-123.

Vetaas, O.R. 1986: Økologiske faktorer i en primærsuksesjon på daterte endemorener i Bødalen, Stryn. O. R. Vetaas, Bergen.

Vetaas, O.R. 1994: Primary succession of plant assemblages on a glacier foreland - Bodalsbreen, southern Norway. *Journal of Biogeography*, **21**: 297-308.

Vetaas, O.R. 1997: Relationships between floristic gradients in a primary succession. *Journal of Vegetation Science*, **8**: 665-676.

Viereck, L.A. 1966: Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska. *Ecological Monographs*, **36**: 182-199.

Virtanen, R. 2003: The high mountain vegetation of the Scandes. In: *Alpine biodiversity in Europe* (eds. L. Nagy, G. Grabherr, C. Körner and D.B.A. Thompson), pp. 31-38.Springer, Berlin.

Vistnes, I.I. and Nellemann, C. 2008. Reindeer winter grazing in alpine tundra: Impacts on ridge community composition in Norway. *Arctic, Antarctic, and Alpine Research,* **40**: 215-224.

Väre, H., Ohtonen, R. and Mikkola, K. 1996: The effect and extent of heavy grazing by reindeer in oligotrophic pine heaths in northeastern Fennoscandia. *Ecography*, **19**: 245-253.

Väre, H., Ohtonen, R. and Oksanen, J. 1995: Effects of reindeer grazing on understorey vegetation in dry *Pinus sylvestris* forests. *Journal of Vegetation Science*, **6**: 523-530.

Wahren, C.-H.A., Walker, M.D. and Bret-Harte, M.S. 2005: Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, **11**: 537-552.

Wielgolaski, F.-E. 1975: Functioning of Fennoscandian tundra ecosystems. In: *Fennoscandian tundra ecosystems: Pt 2. Animals and Systems Analysis* (ed.F.E. Wielgolaski), pp. 300-326. Springer, Berlin.

Willis, W.O. and Power, J.F. 1975. Soil temperature and plant growth in the northern Great Plains. In: *Prairie: A Multiple View* (ed. M. Wali), pp. 209-219. USDA ARS, North Central Region.

Woodin, S.J., Marquiss, M. (eds.) 1997: Ecology of Arctic environments: 13th Special Symposium of the British Ecological Society. Blackwell, Oxford.

Wookey, P.A., Aerts, R., Bardgett, R.D., Baptist, F., Bråthen, K.A. and Cornelissen, J.H.C. 2009: Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology*, **15**: 1153-1172.

Zimov, S.A., Schuur, E.A.G. and Chapin, F.S.I.: 2005: Permafrost and the global carbon budget. *Science*, **312**: 1612-1613.

Öberg, L. 2002: Tree-limit dynamics on Mount Sånfjället, central Sweden. *Svensk Botanisk Tidskrift*, **96**: 177-185.

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