

Doctoral Dissertation

Stefanie Reinhardt

The importance of snow for
mountain vegetation in the
Hardangervidda area
(Southern Norway):
plant distribution,
plant phenology,
plant diversity,
and effects of
global climate change



Telemark University College
Faculty of Arts and Sciences

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The importance of snow for mountain vegetation in the
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Thesis for the degree of Doctor Philosophiae

Telemark University College
Faculty of Arts and Sciences



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A bouquet of mountain flowers to all!!

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Summary

Snow is one of the most important factors for mountain vegetation. In mountain landscapes a varying topography and its interaction with climatic factors causes a heterogeneous distribution of snow. This snow distribution and snowmelt patterns are relatively consistent from year to year, and are clearly reflected in vegetation composition.

The main aim of this dissertation was to enhance the knowledge of the impact that snow has on alpine plant species and rich mountain vegetation types. The vegetation studied was stratified to rich vegetation types as an extension of earlier studies that had been conducted in poor vegetation. Vegetation was analysed in 2008 including vascular plants, mosses and liverworts, and lichens. The randomly selected study plots covered major snow layer duration and topography gradients. Environmental variables including altitude, exposition, and slope were measured, and soil samples were taken. Soil temperature, snow depth, and snowmelt date were monitored for three years (2009-2011). For the phenological study (Paper V), onset of flowering was observed for all species in 66 study plots over the same three years (2009-2011).

Field work was conducted on the Hardangervidda mountain plateau in southern Norway. Sites in the surroundings of Finse and Haukeliseter where base-rich bedrocks occurred were selected. A total of 117 study plots were established; 67 plots at Haukeliseter, and 50 plots at Finse. The number of plots included in the different papers varies. For the diversity study (Paper III), an additional 187 study plots from earlier studies were included.

The statistical methods used are TWINSpan classification, DCA (Detrended Correspondence Analysis), CCA (Canonical Correspondence Analysis), PCA (Principal Component Analysis), RDA (Redundancy Analysis), CVA (Canonical Variate Analysis), Kruskal-Wallis and Mann-Whitney U tests, regression, WA (weighted averaging), GLMs (Generalized Linear Models), and GLMMs (Generalized Linear Mixed Models). The statistical analyses were conducted with Minitab, CANOCO, and R.

In the study, 440 taxa (215 vasculars, 130 mosses, 61 liverworts, 34 lichens) were found. DCAs of the vegetation data with post-hoc introduced environmental variables show that axis 1 represents a complex altitudinal gradient, also indicating plant productivity, and axis 2 represents a snow gradient. Using TWINSpan classification the vegetation was grouped into exposed, leese, and snowbed vegetation which are the three main classes usually used to describe mountain vegetation. Comparisons with studies on poor vegetation show a higher species richness and higher levels of soil nutrients in the present study of rich vegetation.

Of 268 plant species tested (present in > 3 study plots), 160 showed significant responses to the snowmelt date, and snow indicator (SI) values on a scale from 1 (strictly chionophobic) to 9 (strictly chionophilous) were assigned to these species. Comparisons with results from a study that assigned SI values to species occurring in poor vegetation showed that of 54 species that received SI values in both studies, most species received the same or similar SI values (SI deviation < 2).

Snow cover was found to be correlated with soil nutrients and soil temperatures which in turn affect plant species. Soil temperature was found to differ between small-scale vegetation groups.

Relative altitude was a poor predictor for plant species richness and vascular plant species richness was a poor predictor of liverwort richness. Vascular plant species richness was highest at sites showing intermediate snowmelt dates, while liverwort richness was highest towards both ends of the snowmelt gradient.

Onset of flowering was generally related to the snowmelt date, but some species needed more time between snowmelt and onset of flowering in the year when snowmelt occurred earlier. Fewer significant annual differences were found in the onset of flowering in relation to soil temperature sums after snowmelt, than in relation to snowmelt.

SI values can be used to assess vegetation changes in relation to climate change. The application of SI values on resampled vegetation types shows a decrease in average SI values indicating that snowbeds melt out earlier today compared to the past. Mountain summit vegetation shows a slight increase in average SI values. Both the average SI values for the resampled vegetation types and predicted DCA axis positions of the study plots (1 °C increase in summer temperature and 5 days earlier snowmelt) suggests a vegetation homogenization in the future. Chionophilous species and snowbed vegetation types are found to be most threatened by future climate change.

Sammendrag

Snø er en av de viktigste faktorene for fjellvegetasjon. I fjellet forårsaker den varierende topografien og dens interaksjon med klimatiske faktorer en ujevn fordeling av snøen. Fordeling av snø og snøsmeltingsmønsteret er relativt konsistente fra år til år, og er tydelig reflektert i vegetasjonens komposisjon.

Hovedmålet med denne studien var å kvantifisere snøens påvirkning av edafisk kravfulle alpine planter og vegetasjonstyper. Data innsamlingen ble stratifisert til rike vegetasjonstyper definert som samfunn der mer enn 2 calcifile planter ble funnet, og er en utvidelse av tidligere studier utført i fattige samfunn. Vegetasjonen ble analysert i 2008, og inkluderte karplanter, moser og levermoser, og lav. Innsamlingen av data ble utført slik at samfunn med ulik framsmeltingstidspunkt og ulike topografiske gradienter skulle inngå. Miljøvariabler, som høyde over havet, eksposisjon og helning ble estimert, og jordprøver ble innsamlet i alle analyserutene. Jordtemperaturdata ble målt og snødybde og snøsmeltingstidspunkt ble overvåket i årene 2009-2011. I fenologistudiet ble blomstringstidspunktet observert for arter i 66 ruter i en treårsperiode (2009-2011).

Feltarbeidet ble utført på Hardangervidda i Sør-Norge. Områder rundt Finse og Haukelisetter med baserik berggrunn ble valgt ut. Totalt ble 117 analyseruter etablert, 67 ruter på Haukelisetter og 50 ruter på Finse. Antall ruter inkludert i de ulike artiklene varierer. I diversitets-studien (Artikkel III) ble i tillegg 187 ruter fra tidligere studier brukt.

Statistiske metoder brukt inkluderer TWINSpan klassifisering, DCA (Detrended Correspondence Analysis), CCA (Canonical Correspondence Analysis), PCA (Principal Component Analysis), CVA (Canonical Variate Analysis), Kruskal-Wallis og Mann-Whitney tester, regresjon, WA (weighted averaging), GLMs (Generalized Linear Models), og GLMMs (Generalized Linear Mixed Models). Statistiske analyser ble utført med Minitab, CANOCO, og R.

440 taxa (215 karplanter, 130 moser, 61 levermoser, 34 lav) ble registrert. DCA'er av vegetasjonsdataene med post-hoc introduserte miljøvariabler viser at akse 1 representerer en kompleks høydegradient som også indikerer planteproduktivitet, mens akse 2 representerer en snøgradient. TWINSpan klassifisering skilte mellom følgende hovedgrupper: eksponert-, leside-, og snøleivevegetasjon, som er de tre hovedklassene som normalt brukes til å beskrive fjellvegetasjon. Sammenlignet med studier av fattig vegetasjon viser de nyinnsamlede rutene klart høyere artsriktighet, og også høyere næringsstoffinnhold i jorda.

Av de 268 planteartene som ble testet (forekomst i > 3 ruter), viste 160 arter signifikante responser til snøsmeltingsdato. De ble gitt snøindikator (SI) verdier på en skala fra

1 (strengt chinofobe) til 9 (strengt chinofile). Sammenligning med resultater fra en studie som tildelte SI-verdier til arter som forekom i fattig vegetasjon, viste at av 54 arter som fikk SI-verdier i begge studier (den nåværende og den tidligere), fikk de fleste artene den samme eller en lignende SI-verdi (SI-avvik < 2).

Snødekket ble funnet å være korrelert med jords næringsstoffinnhold og jordtemperatureren, som igjen påvirker planteartene. Jordtemperaturforholdene varierte mellom småskala vegetasjonsgrupper.

Artsrikheten var lite korrelert med relativ høyde over have og karplanterikheten var ikke signifikant relatert til levermoserikdom. Rikhet av karplantearter var høyest ved midlere snøsmeltingsdatoer, mens rikhet av levermoser var høyest der snøen smeltet sent.

Blomstringstidspunktet er generelt relatert til snøsmeltingsdato, men de fleste arter behøvde mer tid mellom snøsmelting og blomstring i år hvor snøsmeltingen skjedde tidligere. Det var få signifikante forskjeller mellom årene i blomstringstidspunktet i forhold til temperatursummen etter snøsmelting.

SI-verdier kan brukes til å vurdere vegetasjonsendringer i relasjon til klimaendringer. Bruken av SI-verdier på re-samplede vegetasjonstyper viser en nedgang i gjennomsnittlige SI-verdier, noe som indikerer at snøleier smelter ut tidligere i dag enn før. Fjelltoppvegetasjon viser en liten økning i gjennomsnittlige SI-verdier. Både de gjennomsnittlige SI-verdiene for de re-samplede vegetasjonstypene og predikerte DCA-akse posisjonene til studierutene (1 °C økning i sommertemperatur og 5 dagers tidligere snøsmelting) indikerer at vi i fremtiden kan få en homogenisering av vegetasjonen i dette området. Snøkrevende arter og snøleiesamfunn er funnet å være mest truet av fremtidige klimaendringer.

List of papers

- I. **Reinhardt, S., Odland, A.** Soil temperature variation in calciphile mountain plant communities in Southern Norway. *Oecologia Montana* 21 (2013): 21-35.
- II. **Reinhardt, S., Odland, A., Pedersen, A.** Distribution of calciphile alpine plants and vegetation types in Southern Norway: importance of snow and possible effects of climate change. *Phytocoenologia* xx: xx-xx.
- III. **Odland, A., Reinhardt, S., Pedersen, A.** Differences in richness of vascular plants, mosses, and liverworts in S Norwegian alpine vegetation. Revised manuscript submitted to *Plant Ecology & Diversity*.
- IV. **Reinhardt, S., Odland, A., Grytnes, J.-A., Pedersen, A.** Plants as indicators of snow layer duration in Southern Norwegian mountains – calciphile vegetation. Submitted to *Ecological Indicators*.
- V. **Reinhardt, S., Odland, A.** Flowering phenology of 43 mountain plant species in response to snowmelt date and soil temperature conditions during a three year period. Manuscript.

Declaration

- I.** Soil temperature variation in calciphile mountain plant communities in Southern Norway.

Reinhardt, S.: Study design, field work, data processing, statistical analyses, writing, editing.

Odland, A.: Study design, field work, statistical analyses, co-writing, editing.
- II.** Distribution of calciphile alpine plants and vegetation types in Southern Norway: importance of snow and possible effects of climate change.

Reinhardt, S.: Study design, field work, laboratory work, data processing, statistical analyses, co-writing, editing.

Odland, A.: Study design, field work, statistical analyses, writing, editing.

Pedersen, A.: Field work, bryophyte identification.
- III.** Differences in richness of vascular plants, mosses, and liverworts in S Norwegian alpine vegetation.

Odland, A.: Study design, field work, statistical analyses, writing, editing.

Reinhardt, S.: Study design, field work, laboratory work, data processing, statistical analyses, editing.

Pedersen, A.: Field work, bryophyte identification.
- IV.** Plants as indicators of snow layer duration in Southern Norwegian mountains – calciphile vegetation.

Reinhardt, S.: Study design, field work, data processing, statistical analyses, writing, editing.

Odland, A.: Study design, field work, editing.

Grytnes, J.-A.: Statistical analyses, editing.

Pedersen, A.: Field work, bryophyte identification.
- V.** Flowering phenology of 43 mountain plant species in response to snowmelt date and soil temperature conditions during a three year period.

Reinhardt, S.: Study design, field work, data processing, statistical analyses, writing, editing.

Odland, A.: Study design, field work, editing.

1. Introduction

1.1. Snow-plant interaction in mountain areas

Snow is often considered to be the most important factor for mountain vegetation, either directly or indirectly having a major impact on alpine vegetation composition and distribution (e.g. Gjærevoll 1956, Friedel 1961, Gjærevoll 1990, Kudo and Ito 1992, Walker et al. 1993, Stanton et al. 1994, Körner 1999, Walker et al. 2001), plant species richness (Chapin and Körner 1995, Körner and Spehn 2002), plant metabolism and productivity (Billings and Bliss 1959, Körner and Larcher 1988, Walker et al. 1994, Walker et al. 2001), and on alpine plant phenology (Holway and Ward 1965, Canaday and Fonda 1974, Wijk 1986, Pantgey et al. 1990, Molau 1996, Körner 1999, Dunne et al. 2003, Molau et al. 2005, Kudo et al. 2006, Borner et al. 2008, Ellebjerg et al. 2008, Pudas et al. 2008, Ramming et al. 2009, Wipf 2010, Cooper et al. 2011, Abeli et al. 2012).

Snow distribution in alpine areas is heterogeneous, due to topographical variation in interaction with meteorological factors (Hiemsta et al. 2002). Snow is blown away from exposed sites and transported to lee-slopes and depressions. This snow distribution becomes particularly visible in spring and early summer when some locations have already melted out while other areas are still covered with a great depth of snow (Fig. 2B). Snow distribution and snowmelt patterns are relatively consistent from year to year, while the overall winter snowfall and the average snowmelt date varies between years, also formulated as the law of “constancy of spatial patterns despite varying temporal patterns” (Friedel 1961). The snowmelt patterns are clearly reflected in vegetation composition, allowing a classification into exposed, leese, and snowbed vegetation (Gjærevoll 1956, Körner 1999, Fremstad 1997, Direktoratet for Naturforvaltning 2007). This classical “snow zonation” (Fig. 1) has been slightly modified by Halvorsen et al. (2009) with a separation into six different zones.

The spatial and temporal distribution of snow cover in relation to alpine plants has been a classic topic in mountain plant ecology for a long time, starting with the study of Vestergren (1902). In Scandinavia major contributions to our knowledge on the effects of snow have especially been given by Nordhagen (1943), Gjærevoll (1956), and Dahl (1956). These studies inferred snow gradients mainly indirectly. Measurements of snow thickness, snow layer duration, and its effects on soil temperatures and soil quality were rarely included. The study of Baadsvik (1974) included also measurements of snow cover.

A snow depth between 50 and 80 cm, depending on snow density, insulates the ground from low air temperatures and causes stable soil temperatures at around 0 °C (Dahl 1956,

Salisbury 1985). These relatively high temperatures under snow might reduce the need for plants to invest in cryoprotective measures and protects them from thaw-freeze episodes in spring, which are particularly challenging for the plants (Tranquillini 1964, Christersson and Fircks 1990, Körner 2003, Taschler and Neuner 2004). Snow not only protects plants from low winter temperatures, but also from ice blast and solar radiation. Ice frozen to the vegetation may increase wind-induced mechanical forces; a snow cover of 30 cm has the same effect on light conditions as a dense carpet and the environment under is completely dark (Marchland 1991).

Due to the insulating effects of snow, snow cover duration is often assumed to determine the growing season length (Kudo 1991). Shortening of the growing season is one of the few restraints snow may have for alpine plants, and this limitation is only obvious at sites with relative long snow cover duration (Odland 2011). Snowbed pathogens, meltwater seepage and water logging, ground ice formation and possible anoxia in and above the soil, mechanical pressure and shearing effects on slopes, and below snow rodent activity are other indirect effects that snow can have on alpine plants (Körner 2003, Björk and Molau 2007).

1.2. Rich mountain vegetation in Norway

In Norway, 32 % of the landmass is situated in the alpine zone (Moen 1999) which is defined as the area above the climatic forest limit and subdivided into low alpine (willow-scrub, heath vegetation), middle alpine (heath, graminoids vegetation), and high alpine (lacking a continuous cover of vascular plants) zones (Kilander 1965).

In alpine landscapes a pronounced topographical variation implicates a large variation in plant species composition over short distances (Scherrer and Körner 2011). Classification of alpine vegetation occurs mainly along two gradients, a snowmelt gradient and an acidic to base-rich bedrock gradient (Nordhagen 1943, Gjærevoll 1956, Fremstad 1997, Moen 1999, Direktoratet for Naturforvaltning 2007). Besides these two main gradients there are numerous other gradients that might be of importance such as e.g. soil moisture content, soil stability, altitude, and human impacts.

The availability of mineral nutrients is an important ecological factor for mountain vegetation and results a distinction between poor vegetation in base-poor areas (soils poor in calcium and/ or poor in magnesium) and rich vegetation where these elements are available in relatively large quantities. The amount of mineral nutrients released from bedrock varies widely at different mountain sites in Norway. In all phytosociological investigations of

mountain vegetation in Scandinavia, the main distinction has been based on floristical differences related to presence or absence of calciphile species (Nordhagen 1943, Gjærevoll 1956, Bringer 1961, Fremstad 1997, Direktoratet for Naturforvaltning 2007). Even though vegetation types have been described as either calciphile or acidic and in other cases as eutrophic/ high productivity or oligotrophic/ low productivity, it can be assumed that mountain plant species are continuously distributed along the soil richness gradient. There is normally a major change in species composition along the soil richness gradient due to the fact that species have different optima for particularly Ca and pH (soil reaction) in mountain areas (e.g. Ellenberg et al. 1992). Gjærevoll (1956) distinguished between sites rich and poor in calciphiles, and data on pH from different plant communities are available. Typical alpine plant species of rich and poor vegetation types are shown in Fig. 1.

In the southern part of the Scandinavian mountains there have been few studies on the ecology of rich vegetation (Odland 2012). However, *Dryas octopetala* communities have attracted the interest of botanists, ecologists and phytogeographers in Scandinavia because they often have high species richness and are often associated with rare species.

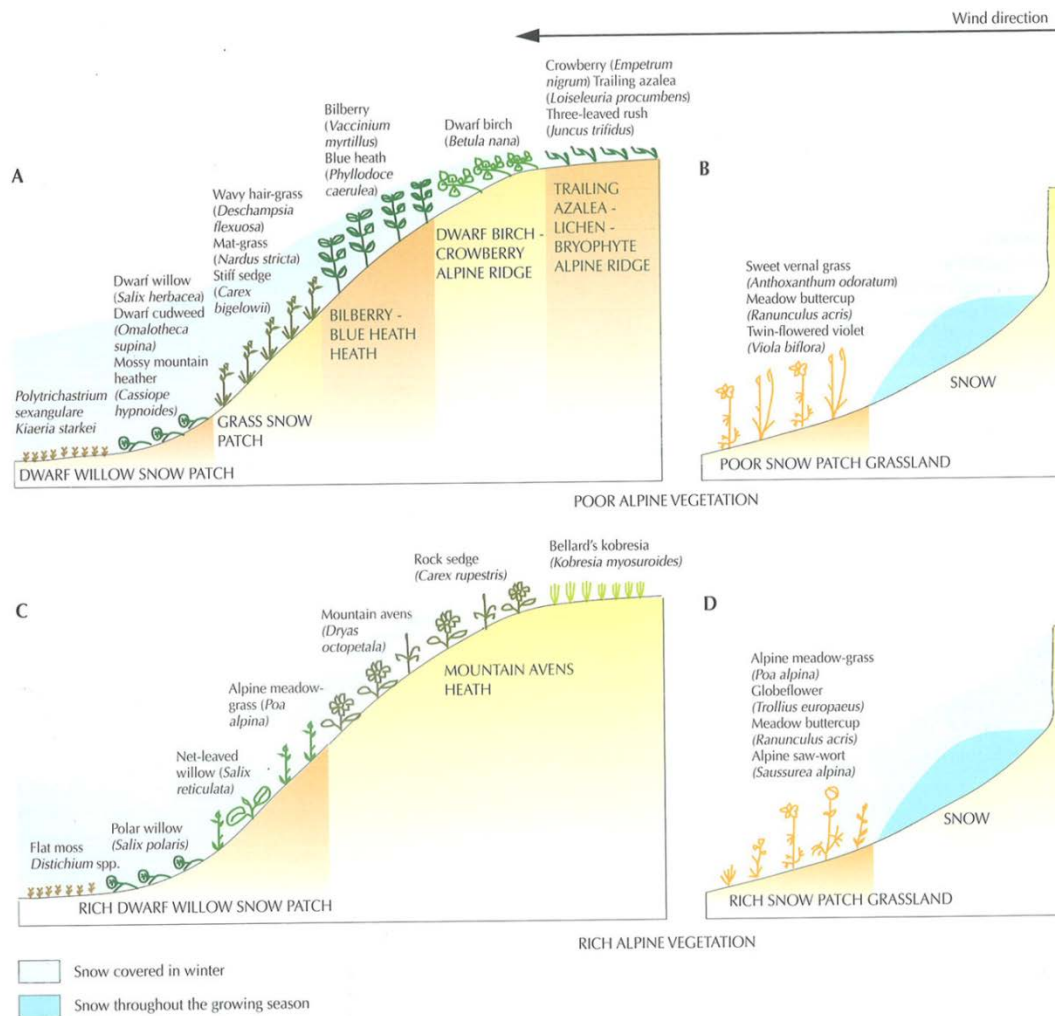


Fig. 1 Examples of alpine plant species and their distribution along the snowmelt gradient and classified into poor and rich vegetation (Moen 1999).

1.3. Plant species as environmental (snow-) indicators

Plants have been recognized as biological indicators for environmental conditions for a very long time. Originally this knowledge was of traditional character, and in the past scientists used the occurrences and abundances of different plant species to assign indicator values to the species (e.g. Ellenberg 1974, Landolt 1977, Ellenberg et al. 1992, Landolt et al. 2010). These indicator values are often ranked on a scale from 1 to 9 with 1 for the lowest and 9 for the highest amount of the environmental factor.

Long established vegetation can provide a sensitive integrated measure of the environment (Hill and Carey 1997, Diekmann 2003), but in order to make useful generalizations about vegetation composition autecological data for relatively large numbers of species is necessary. Species optima and tolerances along environmental gradients have to

be estimated. Generally it is assumed that if species data is sampled over a sufficiently wide environmental range, species frequency or abundance will follow a Gaussian unimodal response model with different shapes of the model curves (Ter Braak and Looman 1986, Lawesson and Oksanen 2002). Absence of significant responses in relation to a particular environmental variable may indicate that this variable does not influence plants' distribution or that the data is sampled over too short a gradient.

The application of indicator values is popular because they reflect environmental conditions surprisingly well without using technically sophisticated and expensive equipment (Ellenberg et al. 1992), but indicator values are also criticized because they depend on field experience and not on objective measurements. Indicator values have been developed for environmental conditions such as acidity, moisture, nitrogen content of the soil, the plants preferences for light, temperature, and continental or oceanic weather conditions (Ellenberg 1974). Since snow is an important factor for mountain plant species we estimated indicator values for alpine plant species' snow preferences (Paper IV). Traditionally plant species have either been classified as chionophilous (snowbed species), chionophobous (exposed site species) or indifferent to the snow layer duration (e.g. Gjærevoll 1956, Dahl 1956, Jonasson 1981, Walker 1993). A weakness of this earlier classification has been that the relation between plant species distribution and snow has, in most cases, not been tested statistically and the tolerances of the species have not been estimated. Odland and Munkejord (2008a) studied the responses of mountain plant species in relation to the snowmelt date and found 103 species with statistically significant GLMs (Generalized Linear Models). As a parallel to the Ellenberg indicator values nine SI (snow indicator) classes were used to classify the species, with value 1 for strictly chionophobous species and value 9 for strictly chionophilous species. Odland and Munkejord (2008a) focused on mountain vegetation at sites with soils poor in nutrients while our study is based on vegetation types from base-rich sites, rich in soil nutrients.

Ecological indicators in combination with changes in species composition over time can be used to assess environmental changes (e.g. Dale and Beyeler 2001, Niemi and McDonald 2004, Kapfer et al. 2011) and SI values have already previously been used to assess vegetation changes in relation to snowmelt (Felde et al. 2012, Odland and Munkejord 2008a).

1.4. Plants and soil temperatures in the alpin

Weather conditions in mountain areas seem generally to be harsh and challenging for living organisms due to strong winds and low temperatures. However, microclimate at specific sites can be totally different from the overall macroclimate. Surface and soil temperatures are highly affected by topography (Barry 2008, Wundram et al. 2010, Scherrer and Körner 2011, Lenoir et al. 2013) and differences in soil temperature due to micro topography can be significantly larger within short horizontal distances (Dahl 1956, Greenland and Losleben 2001, Odland and Munkejord 2008b, Scherrer and Körner 2010) than between sites of the same vegetation type, but at well separated elevations or geographical areas (Körner et al. 2003, Wada et al. 2006, Wundram et al. 2010). Mean seasonal soil temperatures at high altitude treelines are found to be 6-7 °C worldwide (Mook and Vorren 1996, Körner and Paulsen 2004, Gehrig-Fasel et al. 2008). In vegetation studies interpolated temperature data from weather stations is often used. The adiabatic lapse rate varies from -0.98 °C/ 100 m for dry air to -0.4 °C/ 100 m for saturated air with a cooling average of -0.65 °C/ 100 m (Dodson and Marks 1997). Weather stations provide a relatively poor representation of regional climate patterns and the standard interpolation methods to different altitudes are seen as questionable approaches to assigning the temperature conditions alpine plants experience (Körner 2003, Fleming et al. 2000, Scherrer and Körner 2010). Temperatures, measured some centimeters below ground are assumed to reflect the microclimatic temperature conditions alpine plants experience better (Scherrer and Körner 2011) and are easier to measure than air temperatures because radiation can be ignored.

Soil temperatures measured in summer on a bright, sunny day can be higher in the alpine zone than in the boreal zone of the same area because there are no shading trees (Karlsson and Weih 2001, Körner et al. 2003). Solar radiation, slope and exposure, soil characteristics and heat capacity, and plant stature are the factors that determine the microclimate conditions of a site in summer (Körner 2003). In winter, most sites are covered by snow that insulates the soil from overall air temperatures. A snow cover of 30-40 cm (suggested by Cline 1995) to 50-80 cm (Goodrich 1982, Salisbury 1985) is sufficient to stabilize soil temperatures at 0 °C while the overall air temperatures drop far below the freezing point. Not only snow depth, but also snow density plays a major role for the insulation capacity. Fresh-fallen snow with a low density insulates more than compact old snow (Marchland 1991, Rixen et al. 2008). Because of highly varying snow distributions, soil temperature conditions differ markedly between exposed sites and snowbeds (e. g. Körner 2003, Weih and Karlsson 2002, Takahashi 2005, Odland and Munkejord 2008a, Schwöb et al.

2009, Morgner et al. 2010, Wundram et al. 2010, Scherrer and Körner 2011) and soil temperature may be very low at sites without snow cover (Fig. 2a). Extremely low soil temperatures (-30 °C at -2 cm soil depth) were measured near Toolik Lake, Alaska, in a *Dryas octopetala-Selaginella sibirica* windblown slope with minimal snow cover (Walker et al. 2001).

In sites that are covered with snow, measured soil temperatures may accurately indicate the date of snowmelt, by rising abruptly from stable approximate 0 °C to higher temperatures (Emerick and Webber 1982) (Fig. 2b), assuming high ambient air temperatures. At exposed sites snowmelt date can usually not be inferred from the soil temperatures. Here soil temperatures reflect the length of the frozen soil period and the occurrence of thaw-freeze events, both of which will have consequences for the soil ecosystem and vegetation (e.g. Edwards et al. 2007, Rixen et al. 2008, Vestgarden and Austnes 2009).

When measuring soil temperatures, the depth of the measurements have to be considered since the substrate condition influences the vertical temperature gradient (Ballad 1972, Mook and Vorren 1996, Schaetzl and Tomczak 2001, Wundram et al. 2010). Winter temperatures, measured just below the surface are generally lower and may have higher daily temperature variability than temperatures measured at deeper levels (Schaetzl and Tomczak 2001); summer soil temperatures also vary more when measured closer to the surface and show a more prompt reaction to air temperature oscillations (Hillel 1982).

Soil temperatures are important for plants because they influence plant growth and phenology in addition to having major effects on soil processes, such as mineralization and decomposition (Higgins and Spomer 1976, Kirschbaum 1995, Brooks et al. 1996, Weih and Karlsson 2002). Low soil temperatures limit nitrogen mineralization, but soil temperatures around 0 °C as in snowbeds are high enough to maintain biological activity in the soil (Litaor 2002, Mikan et al. 2002, Schimel et al. 2004). At soil temperatures below 5-7 °C plants net growth and/or nutrient uptake is very low (e.g. Kaspar and Bland 1992, Karlsson and Nordell 1996, Rabenhorst 2005, Alvarez-Uria and Körner 2007). When soil temperatures drop below 0 °C, the water uptake of plants is stopped and so are the plants' metabolic processes.

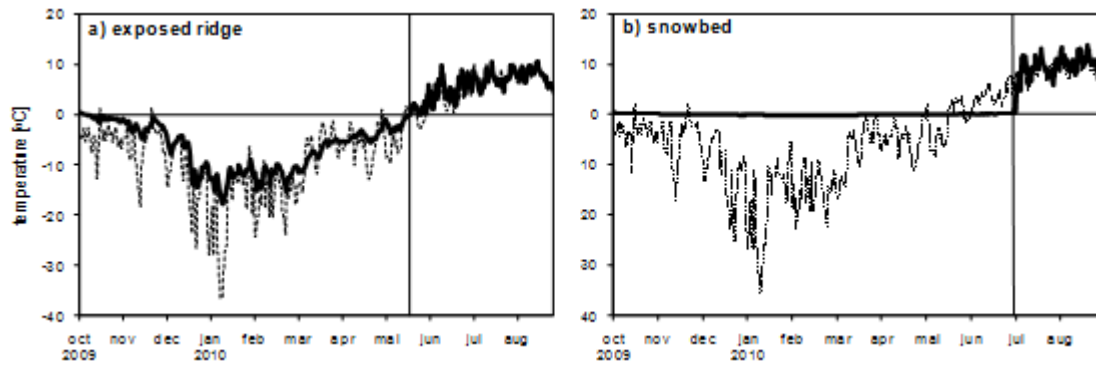


Fig. 2a and b. Seasonal courses of soil temperatures (continuous line) and according air temperatures (dashed line), using typical plots as examples to represent exposed ridges and snowbeds at Finse. The vertical line marks the snowmelt date. Soil temperatures were recorded twice a day from October 2009 to August/ September 2010. Air temperature data was received from nearby weather stations and extrapolated to the respective altitude of each study plot (Paper I).

1.5. Phenology of mountain plants in a changing climate

Plant phenology is the study of the seasonal timing of plant development events and how plants respond to seasonal changes in their environment (Lieth 1974). The ability of different plant species to adjust their phenology makes phenological observations highly valuable for climate change research (Studer et al. 2005, Menzel and Sparks 2006). Alpine ecosystems are considered to be particularly sensitive to climate change (Beniston et al. 1997, IPCC 2007), and many studies try to simulate possible climate change conditions by experimental warming to simulate earlier snowmelt on one hand (Molau and Edlund 1996, Arft et al. 1999) and delayed snowmelt by snow distribution manipulation using snow fences (e.g. Cooper et al. 2011) or manually adding snow (e.g. Wipf 2010) on the other hand. Warming experiments have recently been claimed to underpredict phenological responses of alpine plants (Wolkovich et al. 2012), making phenological *in-situ* observations even more important. Since plants are not able to move to better living conditions, they might respond to higher temperature by phenological adjustment (e.g. Körner and Basler 2010) or by metabolic and physiologic stress when the temperature optima are exceeded (Parsons 1990, Ciais et al. 2005). Climate change will not only lead to increasing temperatures, but will also cause changes in the snow cover regime (Hanssen-Bauer et al. 2009). Snowmelt date determines soil temperature conditions (Paper I) and is often considered to determine the length of alpine plants' growing season (e.g. Kudo 1991, Galen and Stanton 1995). Many studies have shown

a snowmelt-phenology correlation (Holway and Ward 1965, Canaday and Fonda 1974, Pantghey et al. 1990, Molau 1996, Körner 2003, Dunne et al. 2003, Molau et al. 2005, Kudo et al. 2006, Borner et al. 2008, Ellebjerg et al. 2008, Pudas et al. 2008, Ramming et al. 2009, Wipf 2010, Cooper et al. 2011, Abeli et al. 2012). Plants' phenological responses to snowmelt are species-specific (Theurillat and Schlüssel 2000, Miller-Rushing and Inouye 2009, Cooper et al. 2011, Abeli et al. 2012). Plant species with different optima along the snow gradient, i.e. snow depth and snowmelt date, are expected to show different phenological responses to the snowmelt date (Molau 1993, Venn and Morgan 2007). Once chionophilous plants are melted out, they may experience mid-summer weather conditions (Paper I), and may flower almost immediately, thereby not wasting any of the very short growing season in snowbeds (Bjørk and Molau 2007). Chionophilous plants are adapted to short growing seasons, inter alia by development of leaf and flowerbuds in the previous season and a higher prevalence of apomixis and vivipary (Molau 1993). They might also be able to grow at sites that melt out earlier, but would be displaced by other more competitive plants (Heegaard and Vandvik 2004). Phenological differences may be not only inter-specific, but also intra-specific (Wielgolaski 2002, Ladinig and Wagner 2005) with individuals growing at the extremes of the species preferred snow cover range responding differently to the snowmelt date than individuals of the same species growing at the species optimum (Körner 2003, Odland and Munkejord 2008a). Phenological phases may also be influenced differently by snowmelt date, with early phases being more controlled by snowmelt than later ones (Wipf 2010).

Alpine plants commonly start growing within 10 days before or after snowmelt and reach peak growth rates quickly (Körner 2003). However, an early onset of the growing season due to an early snowmelt can have numerous consequences, for example extension of the photosynthetic period. In alpine areas where water shortage may be a problem an earlier snowmelt may lead to increased summer drought because snowmelt water becomes unavailable (Giménez-Benavides et al. 2007). Temperature conditions, photoperiod (Hülber et al. 2006, Keller and Körner 2003), and soil moisture (Walker et al. 1995) are also considered to be crucial for alpine plants phenology. Usually these factors are correlated with each other and are highly dependent on snow cover conditions. Winter weather conditions such as short extreme winter warming events may play a major role (Bokhorst et al. 2008). Altitude is found not to influence phenological patterns of alpine plants (Iversen et al. 2009, Ziello et al. 2009) because the overall weather is subordinate to local temperature conditions that may vary greatly within very short horizontal distances due to high topographic variation in mountainous landscapes (Scherrer and Körner 2011, Paper I).

2. Objectives

The overall aim of this study was to extend the knowledge of the impact of snow on rich mountain vegetation types and the importance of snow for mountain plant species distribution, diversity, and flowering phenology with focus on the relationship between snow cover and soil temperatures. The aims of this study can be summarized as follows:

Investigate relationships between mountain plant species and species richness and the snowmelt date and soil temperature conditions (Paper III, IV, and V).

- Model the relationship between snowmelt date and abundances and distributions for mountain plant species.
- Develop a system of ordinal SI (snow indicator) values corresponding to the Ellenberg Indicator value system ranging from 1 to 9.
- Determine flowering onset in response to the snowmelt date and soil temperature.
- Find optima of species richness for different species groups (vasculars, mosses, and liverworts) in relation to the snowmelt date.

Investigate correlations between rich mountain plant communities, the snowmelt date, and soil temperature conditions (Paper I, II, III, and IV).

- Determine the main floristic gradients in the data and explain these gradients by sampled environmental variables.
- Test if there are significant differences in soil temperature parameters for different vegetation groups.
- Test if average SI values applied on previously sampled vegetation types reflect the snowmelt conditions of the sites.

Analyse the importance of snow and possible effects of climate change for rich mountain vegetation (Paper II, III, and IV).

- Estimate changes of average SI values in resampled vegetation types.
- Discuss possible threats to endangered species and endangered vegetation types as a result of climate change.

3. Material and methods

3.1. Overview of fieldwork and methods

Our study included vegetation analyses, phenological observations, manual snow measurements, soil temperature recordings, soil samplings, and air temperature and precipitation data (provided by the Norwegian Meteorological Institute). Field work was conducted on the Hardangervidda mountain plateau (Fig. 4 and 5). A summary of methods used in the different papers is given in Table 1. Detailed descriptions of data sampling and statistical methods are given in the respective papers.

Table 1. Overview of number of plots, and methods applied for the different papers (VA= vegetation analyses, ST = soil temperatures, SV = snow variables, SS = soil samples, PO = phenological observations). Statistical analyses (DCA = Detrended Correspondence Analysis, PCA = Principal Component Analysis, RDA = Redundancy Analysis, GLM = Generalized Linear Models, WA = weighted averaging, GLMM = Generalized Linear Mixed Models, Kruskal-Wallis and Mann Whitney U tests, and regressions) were conducted in Minitab, Canoco, and R.

| Paper | n plots (Finse/Haukeli) | field methods | soil variables | data analyses |
|-------|---------------------------------|----------------|----------------------------------|---|
| I | 60 (23/37) | VA, ST, SV | - | TWINSPAN, DCA, Kruskal-Wallis, Mann Whitney U, PCA, CVA |
| II | 106 (47/59) | VA, ST, SV, SS | VolW, LOI, P, K, Mg, Ca | TWINSPAN, DCA, CCA, CVA, Regressions |
| III | 304 (50/206) (Imingfjell 48) | VA, ST, SV, SS | P, K, Mg, Ca | PCA, RDA, Regressions, Mann Whitney U |
| IV | 117 (50/67) | VA, ST, SV, SS | Ca | DCA, GLM, WA |
| V | 67 (38/29) | PO, ST, SV | - | GLMM, Mann Whitney U |

Vegetation analyses were conducted in summer 2008. The plots, quadrats of 2x2 m were stratified randomly selected and covered major snow layer duration and topography gradients. Each plot was georeferenced by a GPS unit (Garmin) and permanently marked. Because the present study complements the studies of Odland and Munkejord (2008a and b) who sampled vegetation types on sites poor in nutrients with low pH, the present study was stratified to sites rich in calcium (as defined by the occurrence of two or more calciphile species sensu Nordhagen 1943, Gjærevoll 1956) and relatively high pH. The vegetation analyses included vascular plants, bryophytes (mosses and liverworts), and lichens. Species cover was given as percentage. Additional environmental variables sampled are shown in

Table 1. Altitude, exposition, and slope were estimated at the same time as the vegetation analyses. A photograph of each study plot was taken to make later identification easier and to allow monitoring of site changes in future studies. Soil samples were taken in 2008 after a period with relatively little precipitation. Meteorological data was available from nearby weather stations (provided by the Norwegian Meteorological Institute). Soil temperature data was recorded by data loggers (LogTag TRIX-8) at approximately 40 selected plots (Fig. 2A and B) and sampled manually in the other plots in 2008-2009. 2009-2011 soil temperature was recorded in all plots (n=67) where plants phenology was observed. Snow depth and snowmelt were monitored each spring 2009-2011 (Fig. 3C).



Fig. 3 Field work. A: Study plot of 4m² with a temperature data logger to dig down in the upper left corner. B: The author and her field assistant digging out a data logger after one year measurement duration in a study plot on an exposed site at Finse with patchy snow distribution which is typical for mountain areas during spring in the background. C: Snow measurement in the beginning of April.

3.2. Study locations

The Hardangervidda is located in Southern Norway (Fig. 4 and 5). As Europe's largest mountain plateau it covers an area of approximately 10,000 km². Altitude varies between 1100 and 1300 m a.s.l. with mountain peaks reaching up to 1900 m a.s.l. (Østbye et al. 1975). Climatic conditions at the Hardangervidda are influenced by the North Atlantic causing temperature to be higher than it would otherwise be at the same latitude, resulting in a pronounced climatic gradient from the western to the eastern parts of the plateau, as oceanic climate of the coastal areas and the continental inland climate intersect. According to Moen (1999) the climate is described as slightly oceanic at Haukelisetter and intermediate (oceanic-continental) at Finse. At Haukelisetter normal mean temperatures in July and January are 10 °C and -8 °C respectively and normal annual precipitation is 840 mm (weather station at 1019

m a.s.l.); at Finse the normal mean temperatures in July and January are 7 °C and -10.3 °C respectively and normal annual precipitation is 990 mm (weather station at 1210 m a.s.l.).

Most of the Hardangervidda area is dominated by Precambrian rocks, resulting in acidic, nutrient-poor soils (Østbye et al. 1975). The present study focuses on nutrient-rich vegetation sites and therefore the areas around Finse and Haukeliseter were selected. Bedrocks such as phyllite, marble, amphibolite, and calcareous breccia occur at Finse (Askvik 1994, Dahl 1997), and phyllite, amphibolite, basalt, and schist occur around Haukeliseter (Naterstad 1988). These bedrocks give calcareous and nutrient-rich soils that provide the basis for species-rich vegetation types with nutrient-demanding plant species and generally high species richness. Soil cover is often thin and patchy moraine with considerable areas of bare rock.

Important herbivores at the Hardangervidda are reindeer (*Rangifer tarandus tarandus* L.) and small rodent species such as lemming (*Lemmus lemmus*) and root vole (*Microtus oeconomus*). Domestic sheep grazing has impact on the vegetation too.

In the present study we established in total 117 plots, 67 plots in the Haukeliseter area (Fig. 4) and 50 plots in the Finse area (Fig. 5). The plots at Haukeliseter are distributed over a relatively wide east-west distance of approximately 24 km, with nine plots at Vågsli and five plots in the Rølldal area. The study plots at Finse were located relatively close to each other (approximately 4.3 km east-west distance), excepting five plots at Myrdal (distance Myrdal-Finse: approximately 26 km).

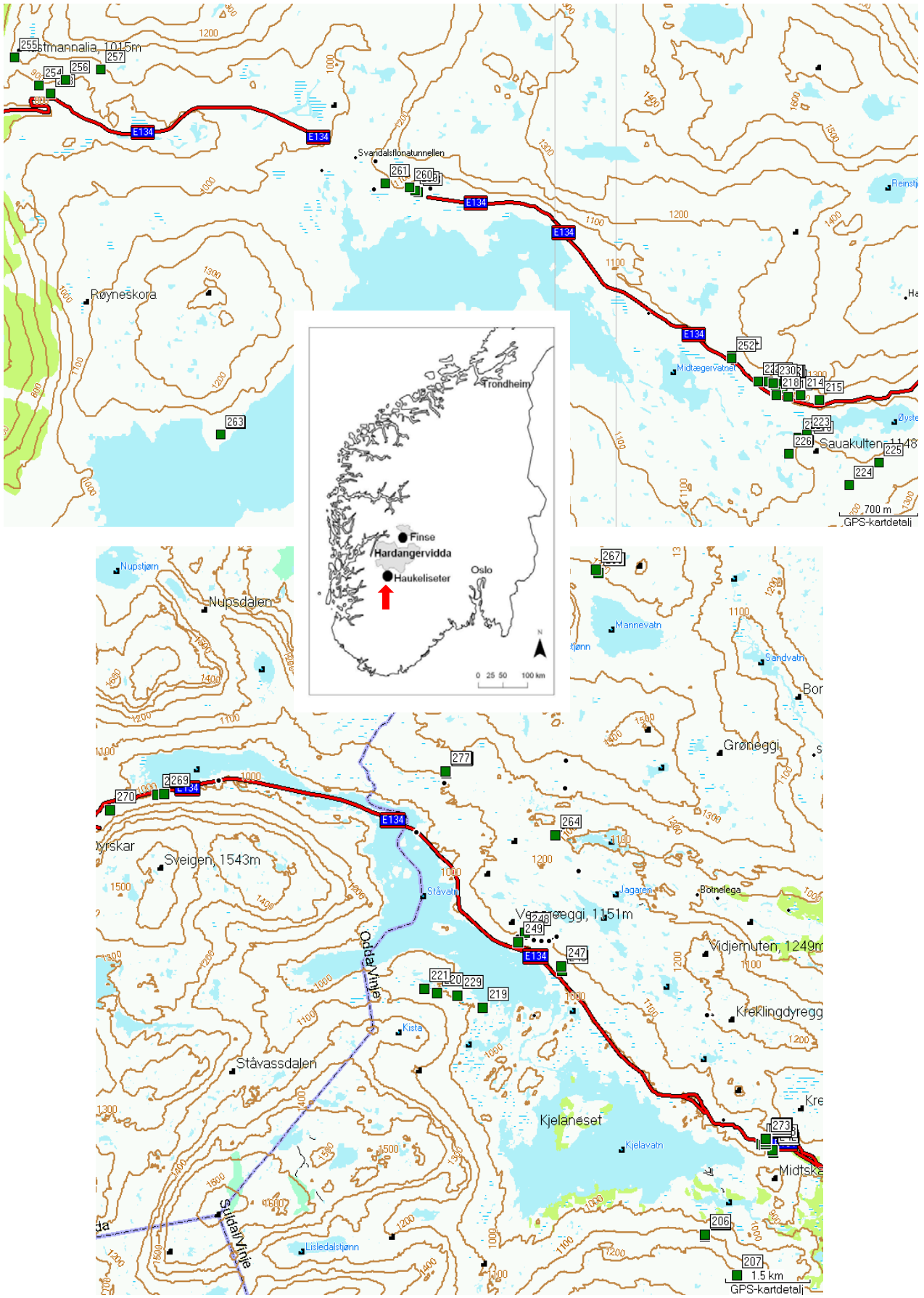


Fig. 4 Study plots (green quadrats) at Haukelisetet, Røldal, and Vågslid

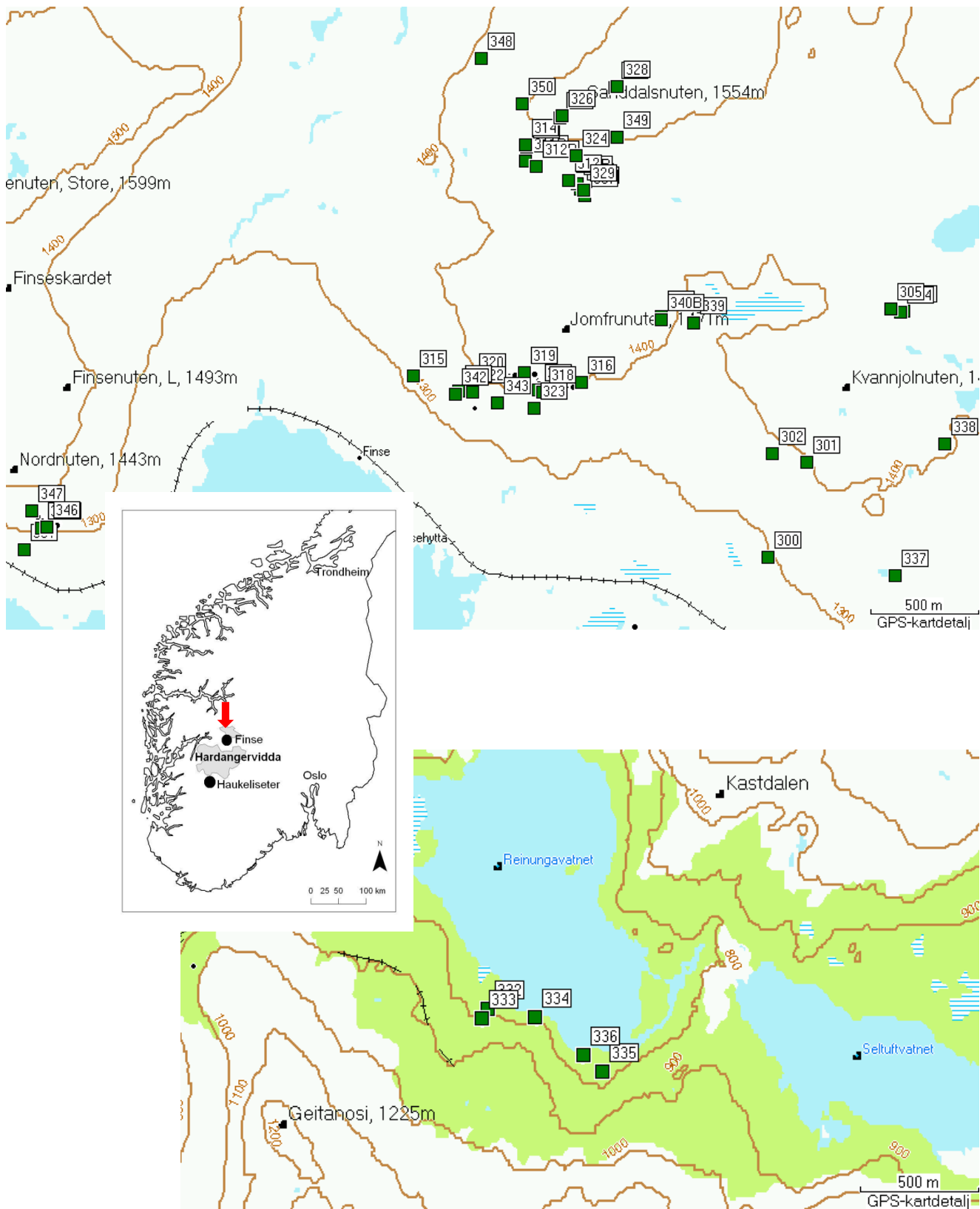


Fig. 5 Study plots (green quadrats) at Finse (upper map) and Myrdal (lower map)

4. Results and discussion

4.1. Main vegetation gradients

In the study 440 taxa (215 vascular plants, 130 mosses, 61 liverworts, 34 lichens) were found (Appendix 1). However, the number of species differs for the Papers I-V due to a variable number of study plots included. Additionally, other species, mainly from Røldal and Imingfjell (Paper III: Fig. 1, Appendix), are included in Paper III. A DCA plot gives an overview over most of the studied species (species present in > 3 study plots) and study plots (Paper II: Fig. 2; Paper IV: Appendix) in relation to post-hoc introduced environmental variables (Paper II: Fig. 5; Paper IV: Appendix). DCA axis 1 represents a complex altitudinal gradient, also indicating plant productivity, while DCA axis 2 represents a snow gradient.

We used TWINSPLAN to classify the study plots into vegetation clusters (Paper I and II). Paper I and II are based on unequal numbers of study plots included (Table 1), due to the number of temperature data loggers (Paper I), and in the TWINSPLAN analyses different levels were chosen, resulting in a different number of vegetation clusters (Paper I: Fig. 2, Table 2; Paper II: Fig. 2, Table 4). DCA and TWINSPLAN classifications (Paper I, Paper II) suggested separation of three main classes: exposed sites, leesides, and snowbeds, supporting previous classifications of Norwegian mountain vegetation types, by numerical methods and phytosociological classifications (Gjærevoll 1956, Dahl 1956, Fremstad 1997, Elven 2001, Halvorsen et al. 2009).

Odland (2012) studied the variation of 218 previously described rich vegetation communities from different parts of Fennoscandia, and even though his study was based on numerical analyses of plant communities, the results showed strong similarities to the present study. Species optima along the two main DCA axes were almost identical (Paper II: Fig. 4) and the optima of the communities formed a similar triangular structure with tall herb communities, snowbeds and exposed communities representing the edges, also reflected in the positions of certain plant species: *Aconitum lycoctonum*, *Dryas octopetala*, and *Phippsia algida* (Paper II: Fig 3; Odland 2012: Fig 3). A comparison between the two studies shows that the gradient length was slightly larger in the present study. The difference might be partly explained by a down-weighting of rare species in the previous study. In both studies relative altitude and pH were significantly correlated with DCA axis 1 (Table 2). There was no data on “snow” in the previous community descriptions, but one may assume that snow layer duration and maximum snow thickness were strongly correlated with DCA axis 2 also in that study.

Table 2 Comparison of the present study with Odland (2012)

| | Present study (106 plots) | | | Fennoscandia (218 communities) (Odland 2012) | | |
|------------------------------|---------------------------|-------|-------|---|-------|-------|
| | DCA 1 | DCA 2 | DCA 3 | DCA 1 | DCA 2 | DCA 3 |
| Eigenvalue | 0.67 | 0.4 | 0.32 | 0.62 | 0.33 | 0.16 |
| Gradient length | 6.65 | 2.95 | 3.15 | 5.22 | 4.15 | 3.23 |
| Correlation with altitude | 0.6 | 0.13 | | 0.62 | 0.07 | |
| Correlation with pH | 0.53 | 0.43 | | 0.24 | 0.03 | |

Table 3 Comparison of rich vegetation (Paper II) with poor vegetation (Odland and Munkejord 2008b)

| | Rich vegetation (106 plots) | | | | Poor vegetation (186 plots) | | | |
|-----------------------|-----------------------------|-------|--------|------|-----------------------------|------|-------|-----|
| | mean | SD | max | min | mean | SD | max | min |
| No Vasculars | 25.5 | 7.9 | 44.0 | 7.0 | 11.3 | 5.5 | 34.0 | 0.0 |
| No liverworts | 3.0 | 2.6 | 13.0 | 0.0 | 3.1 | 2.8 | 16.0 | 0.0 |
| No mosses | 8.4 | 3.4 | 17.0 | 2.0 | 4.5 | 2.4 | 12.0 | 0.0 |
| Total richness | 36.8 | 10.1 | 63.0 | 14.0 | 18.8 | 8.2 | 47.0 | 4.0 |
| pH | 5.6 | 0.5 | 7.2 | 4.5 | 4.5 | 0.4 | 5.4 | 3.7 |
| P (mg/100g dry soil) | 1.9 | 1.9 | 12.6 | 0.3 | 1.4 | 0.9 | 5.0 | 0.0 |
| K (mg/100g dry soil) | 20.2 | 16.9 | 113.3 | 1.4 | 10.7 | 4.6 | 26.0 | 0.0 |
| Mg (mg/100g dry soil) | 17.4 | 12.0 | 61.3 | 2.0 | 5.7 | 2.4 | 13.0 | 0.0 |
| Ca (mg/100g dry soil) | 242.8 | 194.5 | 1090.0 | 18.0 | 36.4 | 20.9 | 213.0 | 1.0 |

In earlier studies of poor vegetation, DCA axis 1 represents the snow gradient (Odland 2005, Odland and Munkejord 2008a and b). In the studies of rich vegetation, mountain birch forest tall herb vegetation was included while in the poor vegetation studies the equivalent tall-fern woodland was not included. We expect this to be the reason for the snow gradient to be represented on different axes in the present study of rich vegetation and the poor vegetation study respectively. There were also clear differences between vascular plant species richness and moss species richness. The soil nutrient variables, except phosphorus, showed significantly higher values in the study of rich vegetation (Table 3).

4.2. Relationship between snow and soil variables

We found several correlates of snow cover among both soil nutrient variables and soil temperatures. In mountain areas, snow cover determines soil temperatures over long periods of the year. During winter, soil temperatures at exposed sites may drop far below 0 °C, mainly following air temperatures, while soil temperatures in snowbeds remain at approximately 0

°C, decoupled from the overall air temperatures. Winter soil temperature conditions at leesides vary more and may either stay at approximately 0 °C or drop below 0 °C, depending on snow conditions and ambient air temperatures at the site (Paper I: Fig. 3). The thawing period which we defined as the time between snowmelt and the date when the threshold of 6 °C soil temperature is reached was as expected highly correlated with the snowmelt date (Paper II: Table 3). Sites melting out early are exposed to low ambient air temperatures, while sites melting out late are immediately exposed to summer temperature conditions that lead to a fast warming of the soil. It also takes more time to warm up deeply frozen soils than soils that remain close to 0 °C. There are some major differences between exposed communities on acidic and calcareous soils. The exposed plots on acidic soils were dominated by lichens and dwarf shrubs, often with a thick humus layer (Odland and Munkejord 2008b). In the present study (calcareous sites) the exposed communities were mostly dominated by *Dryas octopetala*, with thin topsoil and with almost no humus, resulting in major differences of soil freezing in winter. The thawing period in exposed sites was generally shorter than in exposed sites of the previous study (Odland and Munkejord 2008b). This may be explained by the thick humus layer often found in oligotrophic heaths, containing a higher amount of water. The soil analyses have shown that sites that melt out late in the year are significantly poorer in soil nutrients (calcium, magnesium, and potassium) (Paper II: Table 3). Snowbeds have generally a relatively sparse vegetation cover and because of the short growing season, biomass production is relatively low (Björk and Molau 2007). The amount of cations is usually highest in soils with a high amount of organic material.

The high correlation between the thawing period and pH and calcium might be explained by the location of the sites with a long thawing period at the highest elevation at the summits at Finse which also showed the highest pH values (Appendix 2). The same is reflected in the significant correlation between altitude and pH.

As expected, plots in the present study have higher values for metal cations and pH than the plots in the study of Odland and Munkejord (2008b) (Table 3). The variation in snow variables was similar. The higher soil pH in the present study has resulted in different trends in the pH variation along environmental gradients. In the study on poor vegetation the pH was strongly positively correlated with snowmelt date, which was interpreted as an effect of low production of organic material and therefore also low production of humic acids in the snowbeds (Odland and Munkejord 2008 b). In the present study no correlation could be found. This might partly also be explained by high pH values at the highest summits at Finse, with very low snow depths (Appendix 2).

Soil richness seems not to affect the estimation of indicator values. Species do not show different snow affiliations at sites with different soil richness. Of 54 plant species that received SI values in both the present (Paper IV) and the study of poor vegetation (Odland and Munkejord 2008a), 21 species showed exactly the same value in both studies and 25 received a similar one (SI deviation ± 1).

Vascular plant species richness increased significantly and linearly with increasing calcium content and pH while it showed a significant humped (quadratic) relation to the snowmelt date. The effect of high pH values at the mountain summits at Finse seems to be alleviated since more study plots are included in Paper III.

4.3. Importance of snowmelt date for mountain plant species distribution, richness, and phenology

In this study 160 species out of 268 (present in > 3 study plots) showed a statistically significant relationship with the snowmelt date (Paper IV: Table 2). Of the 160 species, 53 were strongly to moderately chionophobic and 40 species were strongly to moderately chionophilous. The vegetation types also showed a clear relation to the snowmelt date, with snowbed types melting out on average between day of the year 161 and 196, leesides melting out between day of the year 117 and 163 on average and exposed ridges between day of the year 110 and 131 (174 if vegetation type E4 is included) (Paper II: Table 4). The vegetation type E4 was classified as exposed site due to the TWINSpan analysis and as snowbed in literature (Nordhagen 1943, Gjørevoll 1956, Fremstad 1997). However, the DCA diagram shows that E4 lies just between the typical exposed types and the typical snowbed types (Paper II: Fig. 2) (see also Chapter Methodological Considerations). Moen (1999) and Halvorsen et al. (2009) pointed out that the clear snow gradient that reflects species composition in the low alpine and northern boreal zone becomes blurred in the middle alpine zone, with species that usually are affiliated to a typical snow condition then being found over the whole gradient. Another explanation might be that the sites concerned were affected by solifluction. However, it is also noticeable that one of the study plots in this group showed for snowbeds atypically low winter soil temperatures (Paper I: Fig. 7, Tab. 5).

At lower altitudes, the separation between exposed and leeside vegetation can also be difficult. Groups named N, M, and H in Paper I, or E1, E2, and L1 in Paper II include both *Dryas octopetala* and several typical leeside species such as *Solidago virgaurea*, *Salix lanata*, and *Geranium sylvaticum* (Paper I: Appendix; Paper II: Appendix). *Dryas octopetala* received an SI value of 2 (Paper IV: Table 2), indicating an early snowmelt at the growing sites. The

unimodal models of *Dryas octopetala* reveal wide tolerances (29 days in the abundance data and 37 days in the presence-absence data, showing that *Dryas octopetala* also can be found at later melting sites. Although often described as typical exposed ridge species (Fremstad 1997, Direktoratet for Naturforvaltning 2007), this species is frequently found at sites with later snowmelt (Baadsvik 1974, Odland 2012).

Studies of snow and alpine plant species distribution sometimes only consider snow depth and not the snowmelt date, as snow depth, mostly measured in early spring (Dahl 1956, Poore and McVean 1957, Jonasson 1981, Kyllönen 1988, Razzhivin 1994, Hejcman et al. 2006), or measured each month (McVean 1958), or separated into snow-depth classes (Flock 1978, Walker et al. 1993). Measuring snow depth is usually less time-consuming than date of snowmelt because the latter has to be monitored over a period in early spring and summer. We found that snow depth as measured in the beginning of April and date of snowmelt were significantly correlated ($p < 0.001$, $r^2 = 0.88$), but date of snowmelt was more correlated with the main floristic gradient in the dataset (Paper IV: Appendix). The actual snow depth is not important for plants, as long as a snow depth of > 50 cm is reached. Plants are then effectively insulated from low air temperatures, no radiation penetrates through the snow, and wind protection is given. Thus it does not matter if the plants are covered by 100 cm of snow or by 300 cm. Date of snowmelt occurs significantly earlier when the snow depth is less, but a site with more snow may melt out earlier than a site with little snow when the site with thin snow cover has an unfavourable exposure.

The distribution of vegetation types is highly affected by soil temperature conditions, dependent on snow cover. Paper I has shown that not only the general vegetation types, such as exposed sites, leesides, and snowbeds show their own soil temperature course throughout the year, in relation to the prevailing snow conditions, but also small-scale vegetation types had variable soil temperature conditions.

Snowmelt date has an impact not only on species distribution but also on species richness. Total plant species richness is highest at sites with an intermediate snowmelt date. Vascular plant species richness showed a significant humped (quadratic) response along the snowmelt gradient while number of liverworts increased and bryophytes species richness is more evenly distributed along the gradient (Paper III: Fig. 6). Vascular plant species richness was generally a poor predictor for liverwort richness (Paper II: Table 2). Number of vascular plants in snowbeds is in accordance with data presented by Björk and Molau (2007), i.e. often 5-10 vascular plant species per m^2 .

The number of species with snow indicator values at intermediate level (SI 5) was higher than species with low or high values (SI 1 or 9), also indicating that an intermediate date of snowmelt may result in high species richness (Paper IV: Fig. 4). At sites with a thin snow cover in winter that are snow free early, plants are exposed to low and variable temperatures and at sites with deep snow cover plants are challenged by a short growing-season. Only species adapted to the particular conditions can grow at these sites. Earlier studies have shown that alpine plant species richness is highest at sites with intermediate snow depth, but without classifying the plants into different species groups (Chen et al. 2008). Other factors of importance for species richness are temperature and pH (Volanthen et al. 2006).

The mean flowering day of the year of each of the studied species in the years 2009, 2010, and 2011 is shown in Fig. 6. We found statistically significant responses of many of the studied plant species to the snowmelt date (Paper V: Table 5), supporting earlier studies of flowering phenology related to the snowmelt date (e.g. Abeli et al. 2012). However, snow cover duration generally is a poor predictor of the start and length of the growing season (Odland 2011). Our study shows also that an earlier snowmelt, as in 2011 (snowmelt occurred 10 days earlier than in 2009 and 2010) (Paper IV: Fig. 3) does not automatically result in an earlier flowering date. The opposite was the case, in 2011 33 plant species needed on average more days to start flowering after snowmelt, indicating that other factors such as photoperiod or temperature conditions might be of importance. When the onset of flowering for each species was compared by years, the summarized soil temperature sums between snowmelt and flowering, differed least, compared to onset of flowering in relation to snowmelt (Paper V: Table 4).

Often, a 6 °C threshold is used to define the start of the growing season. However, our study shows that some species, such as *Saxifraga oppositifolia* even start to flower before the 6 °C threshold is reached. A classic developmental adjustment of these “fast” plants is the preformation of leaf- and flowerbuds in the previous season. *Saxifraga oppositifolia* did not receive a SI value, neither in the present study (Paper IV) nor in the earlier study of oligotrophic vegetation (Odland and Munkejord 2008a), indicating that this plant species has a wide tolerance regarding the snowmelt date. A generalized start of the growing season for all species is not correct, it is rather a varying start depending on the plant species. Some plants might even become biological active when still covered with snow and soil temperatures around 0 °C (Körner 2003).

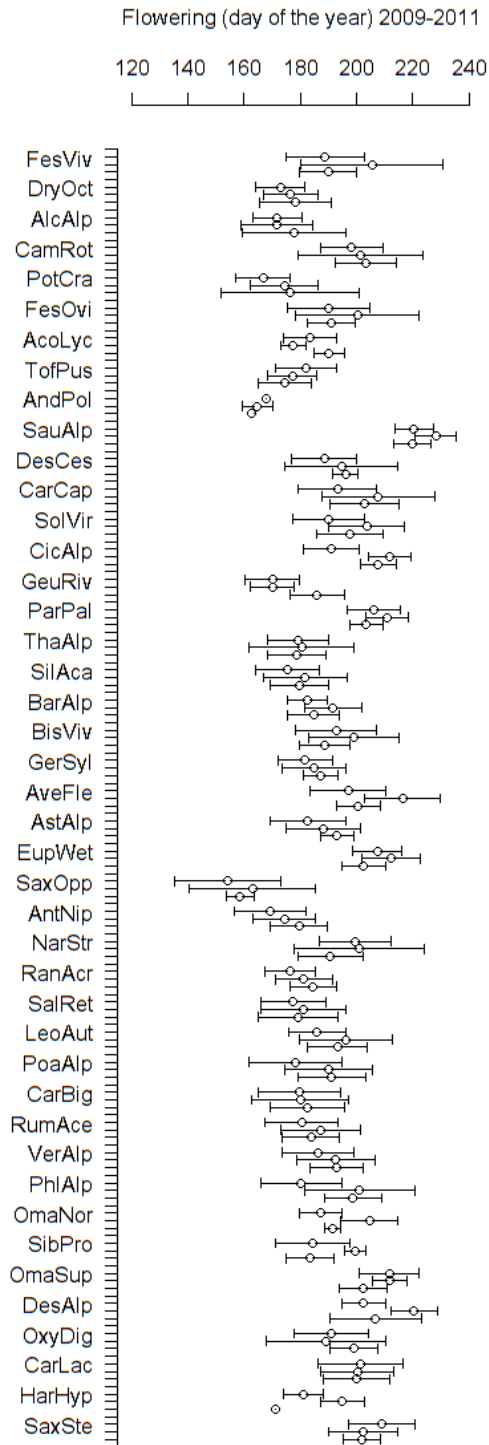


Fig. 6 Mean onset of flowering dates (day of the year) and standard deviations estimated for all species in the study plots they were observed in the year 2009 (highest bar per species), 2010 (middle bar per species), and 2011 (lowest bar per species). The species are ranked after their mean snowmelt date estimated for the study plots they occurred in the whole three year period, ranging from chionophobic to chionophilous species (see Paper V: Fig.3, species code see: Paper: Table 2).

4.4. Possible effects of climate change

Ecosystems in mountain areas are often considered to be particularly vulnerable to climate change (Beniston et al. 1997, IPCC 2007), since limited elevation levels inhibit plants ascending higher when weather conditions become unfavourable at their actual growing sites (Sætersdal et al. 1998). On the other hand, climatic conditions are highly variable within short horizontal distances resulting in a diverse number of vegetation types (Paper I). The high topographical and consequential micro thermal variability (Paper I, Scherrer and Körner 2010, Lenoir et al. 2013) might allow plant species to find thermally suitable niches, making alpine landscapes to safer places than lowland landscapes are (Scherrer and Körner 2011). However, monitoring and long-term observations of vegetation and plant species distribution are needed to trace effects of climate change in the complex alpine ecosystems (Beniston et al. 1997, Theurillat and Guisan 2001).

Our study shows that the vegetation at the Hardangervidda mountain plateau has been and will be affected by climate change (Paper I-V). Modeling scenarios for Norway indicate a shorter snow cover duration (e.g. Vikahamar-Schuler et al. 2006, Brown and Mote 2009, Hanssen-Bauer et al. 2009) that will affect alpine vegetation composition due to close relationships between snowmelt date and vegetation types (Paper II). Snowbed vegetation types and chionophilous plant species seem to be most threatened due to an increase of typical leeside vegetation and a general homogenization of the vegetation composition with respect to snow conditions (Paper II). The same results were found by the application of SI values to demonstrate changes in vegetation in relation to the snowmelt date. While average SI values estimated for resampled vegetation types on mountain summits only showed small changes, the changes in resampled snowbed vegetation types were more pronounced. Exposed sites showed a slight increase in average SI values, while snowbeds showed a decrease in average SI values, indicating that snowmelt in snowbeds occurred earlier compared to historic studies (Paper IV). SI values have already previously been found to be a helpful tool to assess vegetation changes in relation to snowmelt (Felde et al. 2012, Odland and Munkejord 2008a). Odland and Munkejord (2008a) found the same pattern as we did in the present study, with average SI values only slightly changing in exposed vegetation and clearly decreasing in snowbeds.

In addition to changes in species composition, species richness will also be affected by climate change. Vascular plant species richness is highest at sites with an intermediate snowmelt (Paper III: Fig. 6) and an earlier snowmelt would enhance vascular plant species richness at snowbed sites, but reduce the overall vascular species richness for the whole area,

since typical snowbed species will disappear. Liverwort species richness will probably decrease (Paper III) as a consequence of increased vascular plant cover. Vascular plants, mosses, and liverworts, generally show a different response in species richness along the snowmelt gradient. Mosses and vascular plants are shown to have their richness optima at intermediate snowmelt dates while number of liverwort species increases slightly towards the ends of the gradient (Paper III: Fig. 6).

In our study we found species, such as *Saxifraga rivularis* (SI 9), *Ranunculus pygmaeus* (SI 8), *Racomitrium fasciculare* (SI 9), *Brachytecium glaciale* (SI 8), and *Phippsia algida* (SI 9) to be threatened by climate change. These poorly competitive, but highly specialised species might be outcompeted by more competitive species that are dependent on a longer growing season (Heegard and Vandvik 2004).

In Norwegian mountain areas, 23 % of the bryophytes and 16 % of the vascular plants are considered threatened or near threatened. 58 species or almost 40 % of these species are considered to be negatively affected by climate change, and 65 % of these are vascular plants (Austrheim et al. 2010). Species and plant communities confined to calcium-rich substrates have a limited distribution in Southern Scandinavia, and they are therefore particularly vulnerable to different types of impact (Direktoratet for Naturforvaltning 2007). Several species confined to calcareous mountain sites are registered in the Norwegian red list (Kålås et al. 2010). The following red-listed species (Kålås et al. 2010) were found within the analysed plots (number of occurrences): *Comastoma tenellum* (5), *Draba cacumineum ssp. cacuminum* (1), *Kobresia simpliciuscula* (2), *Phippsia algida* (5), *Pseudorchis albida* (2), *Silene wahlbergella* (1), and *Saxifraga tenuis* (1) (Paper II and Appendix 1). The classification and ordination results show that the threatened species are confined to three out of all 15 vegetation types (Paper II). *Phippsia algida* is found at sites associated with a thick and long-lasting snow cover, while *Comastoma tenellum*, *Draba cacumineum*, and *Kobresia simpliciuscula* are found at sites associated with a thin and unstable snow cover and early date of snowmelt, and a relatively long thawing period. The red-listed species are often confined to sample plots that lie in the margins of the ordination diagram (Paper II: Fig. 2, Fig. 3).

Our phenological study shows that an earlier snowmelt does not automatically imply an earlier flowering date, but may even delay the onset of flowering for some plant species (Paper V). Plant species experiencing an earlier snowmelt and by that relatively low pre-flowering temperatures may even flower later in relation to snowmelt. However phenological responses to the snowmelt date and temperature conditions are species specific (Paper V: Fig. 4, Fig. 5; Theurillat and Schlüssel 2000, Venn and Morgan, 2007, Miller-Rushing and Inouye

2009, Hülber et al. 2010, Cooper et al. 2011, Abeli et al. 2012) and phenological field observations of particular species are important to predict possible effects of climate change, also because warming experiments are lately considered to not being a replacement for observational data (Wolkovich et al. 2012).

4.5. Methodological considerations

Vegetation

In this study tall herb birch forest vegetation types were included although they do not belong to the alpine zone. In this vegetation the impact of snow becomes less important than it is in the alpine (Körner 2003). The varying distribution of snow in forests is not as pronounced because trees shield the impact of wind. Leaving out the tall herb vegetation type would also make it more directly comparable to the studies of Odland and Munkejord (2008 a and b). However, results of Odland (2012) were reproduced, since the vegetation type was included there.

The phenological study was quite time consuming. Many species were included in the sampling, which was very instructive for my plant identification skills. However, a limited number of species, representing exposed ridges as well as leesides and snowbeds would have been sufficient. It was very time consuming to approach the two widely separated study areas, thus if doing the study again, I would have restricted the phenology study to only one area and instead visited the sites more often, even though covering different study areas may contribute to more representative results. Species abundances of each study plot should be included in the analysis and also if the plot represents the species optimum of the snow gradient or the edges.

Environmental variables

In the first study year we only used data loggers in 40 study plots. In all other plots we measured snowmelt date and soil temperature manually by visiting the plots and then interpolated the measured data. The use of data loggers to estimate date of snowmelt is less time consuming and consequently much cheaper than measuring snow depth manually in the field. Manual measurements of soil temperature may also give misleading results, because the measurements at different sites are not carried out simultaneously.

Concerning snowmelt date the following question arises: Is it possible to estimate the date of snowmelt by only measuring soil temperature by data loggers? In snowbed vegetation types, soil temperature shows a clear rise from constantly approximately 0 °C to higher

temperatures at the snowmelt date. In exposed sites soil freezes and remains frozen over a more or less long period after snowmelt (Paper I). Therefore manual snowmelt measurements cannot be compensated for in exposed sites.

Temperature data loggers were dug down in the upper left corner of each study plot (Fig. 3A) and therefore not exactly represent the temperature and snow conditions of the entire study plot. In our study this was compensated for by manual observations, noting if the logger was located at a part of the plot, melting out early or late.

In the phenology study we used temperature sums after the snowmelt date. It would be interesting to use temperature sums after the 6 °C threshold date is reached too. Clearer results (less differences between the years) would be expected between temperature conditions and phenology since plants are often (though not always) expected to mainly stay dormant until a 6 °C threshold is reached (Odland 2011).

Statistical methods

Paper IV is an extension of an earlier estimation of SI values for oligotroph mountain plant species (Odland and Munkejord 2008a), with a similar study design. However, in our study we did not use intercept values for species with significant linear GLMs as Odland and Munkejord (2008a) did, because the graphs slope coefficients vary depending on species amount of coverage. In our study, particularly some of the snowbed species such as e.g. *Phippsia algida*, *Saxifraga rivularis*, and *Oxyria digyna* occur with very low abundances (see Paper IV: Fig. 2) and therefore would show relatively high intercept values compared to other chionophilous species. However, in oligotrophic vegetation types, species often cover an area in high abundances and therefore it seems not to be a problem to use the intercept there (Munkejord and Odland 2008a). The comparison of species that occurred and received SI values in both studies showed a high accordance (Paper IV: chapter 4.2), indicating that the methods that were used gave reliable results.

Prior to correlation, only calcium and snow maximum values were log-transformed in Paper IV. The other environmental variables were not transformed. Log-transformation leads to relatively lower differences between high values than between low values. Therefore log-transformation is appropriate for variables where differences in high values are of less importance than low values.

Terms and definitions

We used the term “*snow maximum*” (abbreviated SnMax or Smax) for the snow depth measured in the end of March, beginning of April. At this time snow might already have started to melt or been packed. “*Snow maximum*” might therefore not give the maximum

snow depth of the site. However, in our study maximum snow depth represented the initial snow depth measurement of our measurement series to trace the snowmelt date. The term “*snow maximum*” might also be misleading because at some sites we were not able to measure the actual maximum snow depth since the snow layer was thicker than our measurement poles were long (> 2.7 m).

“*Thawing period*” was defined as the time span between snowmelt date and the date when a soil temperature threshold of 6 °C was reached. This time span is not really reflected by the term “*thawing period*” because sites with a thick snow cover did not thaw at all, soil temperatures already being stable around 0 °C. At exposed sites fluctuating temperatures with thaw-freeze events are common and the term “*thawing period*” may be appropriate.

We used the terms “*calciphile*” and “*acidic*”, which only refer to the pH and the calcium content, and “*eutrophic*” and “*oligotrophic*”, often associated with phosphor and nitrogen levels and not with calcium. It would be better to simply use “*nutrient rich*” and “*nutrient poor*” to refer to the whole all nutrient status.

In the first four papers (Paper I-IV) we used the term “*Julian day*” (e.g. Julian day of snowmelt) instead of “*day of the year*”. In Paper V we followed McVicar and Körner (2013). The same is the case for their definition of “*altitude*” and “*elevation*”, where “*altitude*” is “the vertical distance between an object and a reference point (...) where the object is not in direct contact with the mean sea level or the land surface (...)” and “*elevation*” is “the vertical distance between a point on the land surface and a reference point, usually taken to be the mean sea level”. We often used “*altitude*” synonymous to “*elevation*”. Concerning temperature differences McVicar and Körner (2013) recommend the use of K rather than °C to avoid confusions. However, since a temperature change of 1 K is exactly the same as a temperature change of 1 °C we continued to use °C also for changes in temperature.

5. Conclusions

- The main floristic gradients of the dataset are a complex altitudinal gradient, also indicating plant productivity (DCA axis 1), and a snow gradient (DCA axis 2).
- The vegetation could be classified into the three main vegetation groups (exposed-, leese-, and snowbed vegetation) that usually are used to arrange alpine vegetation.
- Gradients in the data support an earlier study of rich mountain vegetation (Odland 2012). Species optima along DCA axes 1 and 2 were similar to those in the earlier study and vegetation communities also showed a similar position in the diagrams.
- In earlier studies of poor vegetation the snowmelt gradient lies on axis 1 (Odland and Munkejord 2008b). The snowmelt gradient on axis 2 in the present study of rich vegetation might be explained by the inclusion of tall herb birch forest vegetation, while the equivalent tall fern woodland was not included in the study of poor vegetation.
- Snow cover, soil variables, and soil temperatures were significantly correlated.
- Soil temperature patterns throughout the year differ between the three main vegetation groups and also between small-scale vegetation groups and plants species composition was significantly correlated with soil temperature conditions.
- Out of 440 taxa (215 vascular plants, 130 mosses, 61 liverworts, 34 lichens) that were found, 268 plant species (present in > 3 study plots) were tested for relations between their abundances and the snowmelt date. Of these, 160 species showed significant GLMs and SI (snow indicator) values, on a scale from 1 (strictly chionophobic) to 9 (strictly chionophilous) were assigned to these species.
- Comparisons with the results of Odland and Munkejord (2008a) showed that of 54 species that received SI values in both studies, most species received the same or similar SI values (SI deviation ≤ 1).
- Application of SI values on vegetation samples of previous studies reproduced the snowmelt patterns fairly well.
- Relative altitude was a poor predictor of plant species richness in this study.
- Vascular plant species richness was a poor predictor of liverwort richness in this study. Vascular plant species richness is highest at intermediate snowmelt date, while liverwort richness is highest towards the ends of the snowmelt gradient.
- Onset of flowering of alpine plant species is species specific.

- Onset of flowering is generally positively related to the snowmelt date, but some species needed more time between snowmelt and onset of flowering in years when they were melted out significantly earlier.
- Soil temperature sums between snowmelt and flowering showed less inter-annual variation than the time span between flowering and snowmelt.
- The application of SI values on resampled vegetation types shows a decrease of average SI values in snowbeds, indicating that snowbeds melt out earlier today, compared to the past. Mountain summit vegetation shows a slight increase in average SI values.
- Both the average SI values for the resampled vegetation types and predicted DCA axis positions of the study plots (1 °C increase in summer temperature and 5 days earlier snowmelt) suggest a vegetation homogenization in the future.
- Chionophilous species and snowbed vegetation types are most threatened by future climate change.

6. References

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Appendix 1

Species list

| species names | abbreviation | n plots |
|------------------------------------|--------------|------------|
| Liverworts | | |
| <i>Anastrophyllum minutum</i> | AnaMinut | 4 |
| <i>Aneura pinguis</i> | AneuPing | 3 |
| <i>Anthelia julacea</i> | AnthJula | 2 |
| <i>Anthelia juratzkana</i> | AnthJura | 12 |
| <i>Barbilophozia attenuata</i> | BarbAtt | 1 |
| <i>Barbilophozia barbata</i> | BarbBar | 2 |
| <i>Barbilophozia floerkei</i> | BarbFloe | 11 |
| <i>Barbilophozia hatcheri</i> | BarbHatc | 14 |
| <i>Barbilophozia kunzeana</i> | BarbKunz | 3 |
| <i>Barbilophozia lycopodioides</i> | BarbLyco | 50 |
| <i>Barbilophozia quadiloba</i> | BarbQuad | 16 |
| <i>Barbilophozia rubescens</i> | BarbRub | 2 |
| <i>Blepharostoma trichophyllum</i> | BlepTric | 9 |
| <i>Cephalozia bicuspidata</i> | CephBicu | 1 |
| <i>Cephalozia pleniceps</i> | CephPlen | 5 |
| <i>Cephaloziella arctica</i> | CephArct | 8 |
| <i>Chiloscyphus minor</i> | ChilMin | 9 |
| <i>Chiloscyphus pallescens</i> | ChilPall | 3 |
| <i>Chiloscyphus polyanthos</i> | ChilPoly | 1 |
| <i>Chiloscyphus profundus</i> | ChilProf | 3 |
| <i>Gymnocolea inflata</i> | GymInfl | 1 |
| <i>Gymnomitrium concinnatum</i> | GymnConc | 2 |
| <i>Gymnomitrium corallioides</i> | GymCora | 3 |
| <i>Harpanthus flotovianus</i> | HarpFlot | 2 |
| <i>Hygrobiella laxifolia</i> | HygLaxi | 2 |
| <i>Jungermannia exsertifolia</i> | JungExse | 2 |
| <i>Jungermannia polaris</i> | JungPola | 1 |
| <i>Jungermannia pumila</i> | JungPum | 5 |
| <i>Lophozia bantriensis</i> | LophBant | 1 |
| <i>Lophozia collaris</i> | LophColl | 9 |
| <i>Lophozia excisa</i> | LophExci | 3 |
| <i>Lophozia heterocolpos</i> | LophHete | 8 |
| <i>Lophozia incisa</i> | LophInci | 2 |
| <i>Lophozia obtusa</i> | LophOptu | 7 |
| <i>Lophozia sudetica</i> | LophSude | 8 |
| <i>Lophozia ventricosa</i> | LophVentr | 1 |
| <i>Lophozia wenzelii</i> | LopWenz | 1 |
| <i>Marchantia aquatica</i> | MarcAqua | 1 |

| | | |
|--|------------|----|
| <i>Nardia geoscyphus</i> | NardGeo | 4 |
| <i>Nardia scalaris</i> | NardScal | 1 |
| <i>Pellia neesiana</i> | PellNees | 4 |
| <i>Plagiochila asplenioides</i> | PlagAspl | 1 |
| <i>Plagiochila porelloides</i> | PlagPore | 9 |
| <i>Pleurocladula albescens</i> | PleuAlb | 3 |
| <i>Porella cordaeana</i> | PoreCord | 4 |
| <i>Preissia quadrata</i> | PreiQuad | 3 |
| <i>Ptilidium ciliare</i> | PtilCili | 27 |
| <i>Radula lindenbergiana</i> | RaduLind | 2 |
| <i>Scapania curta</i> | ScapCurt | 4 |
| <i>Scapania gymnostomophila</i> | ScapGym | 6 |
| <i>Scapania hyperborea</i> | ScapHyp | 3 |
| <i>Scapania irrigua</i> | ScapIrri | 16 |
| <i>Scapania mucronata</i> | ScapMucr | 4 |
| <i>Scapania paludicola</i> | ScapPalc | 7 |
| <i>Scapania paludosa</i> | ScapPalu | 2 |
| <i>Scapania subalpina</i> | ScapSuba | 3 |
| <i>Scapania uliginosa</i> | ScapUlig | 3 |
| <i>Scapania undulata</i> | ScapUnd | 2 |
| <i>Tritomaria polita</i> | TritPoli | 7 |
| <i>Tritomaria quinquentata</i> | TritQuiqT | 3 |
| <i>Tritomaria scitula</i> | TritScit | 4 |
| Mosses | | |
| <i>Amblystegium serpens</i> | AmblSerp | 2 |
| <i>Aongstroemia longipes</i> | AongLong | 2 |
| <i>Aulacomnium palustre</i> | AulaPalu | 6 |
| <i>Bartramia ithyphylla</i> | BartIthy | 7 |
| <i>Blindia acuta</i> | BlinAcut | 5 |
| <i>Brachythecium glaciale</i> | BracGlac | 7 |
| <i>Brachythecium reflexum</i> | BracRefl | 26 |
| <i>Brachythecium latifolium</i> | BracLat | 1 |
| <i>Brachythecium oedipodium</i> | BracOed | 1 |
| <i>Brachythecium rivulare</i> | BracRiv | 1 |
| <i>Brachythecium salebrosum</i> | BracSale | 43 |
| <i>Brachythecium starkei</i> | BracStar | 18 |
| <i>Brachythecium turgidum</i> | BracTurg | 8 |
| <i>Bryoerythrophyllum recurvirostrum</i> | BryoRecu | 2 |
| <i>Bryum amblyodon</i> | BryAmbl | 11 |
| <i>Bryum capillare</i> | BryCap | 1 |
| <i>Bryum elegans</i> | BryEleg | 9 |
| <i>Bryum neodamense</i> | BryNeod | 1 |
| <i>Bryum pallens</i> | BryPallens | 5 |
| <i>Bryum pallescens</i> | BryPalls | 5 |

| | | |
|----------------------------------|------------|----|
| <i>Bryum pseudotriquetum</i> | BryPseu | 31 |
| <i>Bryum weigelii</i> | BryWeig | 1 |
| <i>Calliergonella lindbergii</i> | CallLind | 1 |
| <i>Campylium chrysophyllum</i> | CampChr | 3 |
| <i>Campylium protensum</i> | CampProt | 26 |
| <i>Campylium stellatum</i> | CampStel | 4 |
| <i>Campylophyllum halleri</i> | CampHall | 1 |
| <i>Climacium dendroides</i> | ClimDend | 8 |
| <i>Conostomum tetragonum</i> | ConoTetr | 3 |
| <i>Dichodontium pellucidum</i> | DichPell | 7 |
| <i>Dicranella palustris</i> | DicrnePal | 3 |
| <i>Dicranella schreberiana</i> | DicrneSchr | 1 |
| <i>Dicranella subulata</i> | DicrneSub | 1 |
| <i>Dicranoweisia crispula</i> | DicrwCris | 6 |
| <i>Dicranum bergeri</i> | DicrAffi | 2 |
| <i>Dicranum bonjeanii</i> | DicrBon | 2 |
| <i>Dicranum brevifolium</i> | DicrBrev | 1 |
| <i>Dicranum elongatum</i> | DicrElon | 3 |
| <i>Dicranum flexicaule</i> | DicrFlex | 2 |
| <i>Dicranum fuscescens</i> | DicrFusc | 9 |
| <i>Dicranum polysetum</i> | DicrPoly | 8 |
| <i>Dicranum scoparium</i> | DicrScop | 7 |
| <i>Dicranum spadiceum</i> | DicrSpad | 16 |
| <i>Distichium capillaceum</i> | DistCapi | 16 |
| <i>Ditrichum crispatissimum</i> | DitrCrisp | 5 |
| <i>Ditrichum flexicaule</i> | DitrFlex | 22 |
| <i>Encalypta alpina</i> | EncAlp | 3 |
| <i>Fissidens adianthoides</i> | FissAdia | 5 |
| <i>Fissidens osmundoides</i> | FissOsmu | 13 |
| <i>Grimmia anodon</i> | GrimAnod | 1 |
| <i>Grimmia muehlenbeckii</i> | GrimMuel | 2 |
| <i>Heterocladium dimorphum</i> | HetDimo | 3 |
| <i>Hygrohypnum ochraceum</i> | HygrOchr | 1 |
| <i>Hylocomiastrum pyrenaicum</i> | HyloPyre | 39 |
| <i>Hylocomiastrum umbratum</i> | HyloUmb | 1 |
| <i>Hylocomium splendens</i> | HylSple | 21 |
| <i>Hypnum bambergeri</i> | HypBam | 5 |
| <i>Hypnum callichroum</i> | HypCall | 2 |
| <i>Hypnum hamulosum</i> | HypHam | 5 |
| <i>Hypnum revolutum</i> | HypRevo | 1 |
| <i>Hypnum vaucheri</i> | HypVau | 2 |
| <i>Kiaeria falcata</i> | KiaeFalc | 2 |
| <i>Kiaeria starkei</i> | KiaeStar | 1 |
| <i>Lescurea incurvata</i> | LescIncu | 27 |

| | | |
|------------------------------------|----------|----|
| <i>Lescuraea radicata</i> | LescRadi | 13 |
| <i>Leucobryum glaucum</i> | LeucGlau | 1 |
| <i>Meesia uliginosa</i> | MeesUlig | 4 |
| <i>Mnium ambiguum</i> | MniuAmb | 3 |
| <i>Mnium blyttii</i> | MniuBlyt | 9 |
| <i>Mnium marginatum</i> | MniuMarg | 6 |
| <i>Mnium spinosum</i> | MniuSpin | 22 |
| <i>Mnium stellare</i> | MniuSte | 1 |
| <i>Mnium thomsonii</i> | MniuThom | 2 |
| <i>Myurella julacea</i> | MyuJul | 5 |
| <i>Oncophorus virens</i> | OncoVir | 12 |
| <i>Oncophorus wahlenbergii</i> | OncoWahl | 4 |
| <i>Palustriella commutata</i> | PaluComm | 10 |
| <i>Paraleucobryum enerve</i> | ParaEne | 1 |
| <i>Paraleucobryum sauteri</i> | ParaSau | 1 |
| <i>Philonotis caespitosa</i> | PhilCae | 5 |
| <i>Philonotis seriata</i> | PhilSeri | 4 |
| <i>Philonotis tomentella</i> | PhilTom | 10 |
| <i>Plagiothecium cavifolium</i> | PlagCavi | 9 |
| <i>Plagiothecium denticulatum</i> | PlagDent | 12 |
| <i>Pleurozium schreberi</i> | PleuSchr | 8 |
| <i>Pogonatum urnigerum</i> | PogoUrni | 5 |
| <i>Pohlia cruda</i> | PohlCrud | 5 |
| <i>Pohlia drummondii</i> | PohlDrum | 8 |
| <i>Pohlia filum</i> | PohlFil | 1 |
| <i>Pohlia nutans</i> | PohlNut | 1 |
| <i>Pohlia wahlenbergii</i> | PohlWahl | 5 |
| <i>Polytrichastrum alpinum</i> | PolyAlpi | 32 |
| <i>Polytrichum hyperboreum</i> | PolyHyp | 4 |
| <i>Polytrichum juniperinum</i> | PolyJuni | 24 |
| <i>Polytrichum piliferum</i> | PolyPili | 1 |
| <i>Polytrichastrum sexangulare</i> | PolySexa | 4 |
| <i>Pseudocalliergon turgescens</i> | PseuTurg | 1 |
| <i>Pterigynandrum filiforme</i> | PterFili | 1 |
| <i>Racomitrium canescens</i> | RacCane | 3 |
| <i>Racomitrium elongatum</i> | RacElon | 14 |
| <i>Racomitrium ericoides</i> | RacEric | 10 |
| <i>Racomitrium fasciculare</i> | RacFasc | 9 |
| <i>Racomitrium lanuginosum</i> | RacLanu | 15 |
| <i>Racomitrium macounii</i> | RacMac | 4 |
| <i>Racomitrium microcarpon</i> | RacMier | 2 |
| <i>Racomitrium sudeticum</i> | RacSude | 6 |
| <i>Rhizomnium pseudopunctatum</i> | RhizPseu | 3 |
| <i>Rhodbryum roseum</i> | RhodRos | 15 |

| | | |
|---|----------|----|
| <i>Rhytidiadelphus squarrosus</i> | RhytSqua | 7 |
| <i>Rhytidiadelphus subpinatus</i> | RhytSubp | 6 |
| <i>Rhytidium rugosum</i> | RhytRugo | 11 |
| <i>Saelania glaucescens</i> | SaeGlau | 1 |
| <i>Sanionia uncinata</i> | SaniUnci | 67 |
| <i>Schistidium dupretii</i> | SchiDupr | 1 |
| <i>Scorpidium cossonii</i> | ScorCoss | 9 |
| <i>Scorpidium revolvens</i> | ScorRevo | 2 |
| <i>Sphagnum capillifolium</i> | SphCap | 1 |
| <i>Sphagnum warnstorffii</i> | SphWarn | 1 |
| <i>Stegonia latifolia</i> | StegLat | 1 |
| <i>Syntrichia norvegica</i> | SynNorv | 14 |
| <i>Tayloria lingulata</i> | TaylLing | 5 |
| <i>Timmia austriaca</i> | TimmAust | 2 |
| <i>Tomentypnum nitens</i> | TomNit | 1 |
| <i>Tortella fragilis</i> | TortFrag | 7 |
| <i>Tortella tortuosa</i> | TortTort | 11 |
| <i>Tortula euryphylla</i> | TortAuri | 8 |
| <i>Trichostomum tenuirostre</i> | TricTenu | 11 |
| <i>Warnstorfia exannulata</i> | WarnExan | 3 |
| <i>Warnstorfia procera</i> | WarnProc | 3 |
| <i>Warnstorfia sarmentosa</i> | WarnSarm | 5 |
| Vascular plants | | |
| <i>Achillea millefolium</i> | AchiMill | 1 |
| <i>Aconitum lycoctonum</i> | AconLyco | 10 |
| <i>Agrostis capillaris</i> | AgroCapi | 22 |
| <i>Agrostis mertensii</i> | AgroMert | 13 |
| <i>Agrostis stolonifera</i> | AgroStol | 1 |
| <i>Ajuga pyramidalis</i> | AjugPyra | 1 |
| <i>Alchemilla alpina</i> | AlchAlpi | 16 |
| <i>Alchemilla glabra</i> | AlchGlab | 17 |
| <i>Alchemilla glomerolans</i> | AlchGlom | 24 |
| <i>Alchemilla spp.</i> | AlchSpp | 58 |
| <i>Alchemilla subcrenata</i> | AlchSubc | 2 |
| <i>Andromeda polifolia</i> | AndrPoly | 5 |
| <i>Angelica archangelica</i> | AngeArch | 6 |
| <i>Antennaria dioica</i> | AnteDioi | 24 |
| <i>Antennaria alpina</i> | AnteAlpi | 13 |
| <i>Anthoxanthum odoratum/nipponicum</i> | AnthOdor | 72 |
| <i>Arabis alpina</i> | ArabAlpi | 6 |
| <i>Arabis hirsuta</i> | ArabHirs | 2 |
| <i>Arctous alpinus</i> | ArctAlpi | 2 |
| <i>Astragalus alpinus</i> | AstrAlpi | 42 |
| <i>Athyrium distentifolium</i> | AthyDist | 10 |

| | | |
|--|-----------|----|
| <i>Atocion rupestre</i> | AtocRupe | 4 |
| <i>Avenella flexuosa</i> | AvenFlex | 51 |
| <i>Bartsia alpina</i> | BartAlpi | 54 |
| <i>Beckwithia glacialis</i> | BeckGlac | 2 |
| <i>Betula nana</i> | BetuNana | 4 |
| <i>Betula pubescens</i> | BetuPube | 10 |
| <i>Bistorta vivipara</i> | BistVivi | 83 |
| <i>Botrychium lunaria</i> | BotrLuna | 11 |
| <i>Calamagrostis phragmitoides</i> | CalaPhra | 7 |
| <i>Calluna vulgaris</i> | CallVulg | 12 |
| <i>Campanula rotundifolia</i> | CampRotu | 43 |
| <i>Cardamine pratensis ssp. angustifolia</i> | CardAngu | 2 |
| <i>Cardamine bellidifolia</i> | CardBell | 3 |
| <i>Carex adelostoma</i> | CareAdel | 1 |
| <i>Carex atrata</i> | CareAtra | 21 |
| <i>Carex atrofusca</i> | CareAtro | 1 |
| <i>Carex bigelowii</i> | CareBige | 47 |
| <i>Carex brunescens</i> | CareBrun | 2 |
| <i>Carex capillaris</i> | CareCapi | 21 |
| <i>Carex flava</i> | CareFlav | 3 |
| <i>Carex glacialis</i> | CareGlac | 2 |
| <i>Carex lachenalii</i> | CareLach | 10 |
| <i>Carex nigra</i> | CareNigr | 7 |
| <i>Carex norvegica</i> | CareNorv | 1 |
| <i>Carex pallescens</i> | CarePall | 4 |
| <i>Carex panicea</i> | CarePani | 9 |
| <i>Carex pilulifera</i> | CarePilu | 1 |
| <i>Carex rupestris</i> | CareRupe | 13 |
| <i>Carex saxatilis</i> | CareSaxa | 7 |
| <i>Carex serotina</i> | CareSero | 1 |
| <i>Carex vaginata</i> | CareVagi | 15 |
| <i>Cerastium alpinum</i> | CeraAlpi | 24 |
| <i>Cerastium cerastoides</i> | CeraCera | 16 |
| <i>Cerastium fontanum</i> | CeraFont | 21 |
| <i>Chamerion angustifolium</i> | ChamAngu | 4 |
| <i>Cicerbita alpina</i> | CiceAlpi | 5 |
| <i>Cirsium heterophyllum</i> | CirsHete | 7 |
| <i>Coeloglossum viride</i> | CoelViri | 10 |
| <i>Comastoma tenellum</i> | ComaTene | 5 |
| <i>Corydalis intermedia</i> | CoryInter | 1 |
| <i>Crepis paludosa</i> | CrepPalu | 1 |
| <i>Cystopteris fragilis</i> | CystFrag | 1 |
| <i>Deschampsia alpina</i> | DescAlpi | 18 |
| <i>Deschampsia cespitosa</i> | DescCesp | 36 |

| | | |
|-----------------------------------|-----------|----|
| <i>Draba cacuminum</i> | DrabCacu | 1 |
| <i>Draba fladnizensis</i> | DrabFlad | 1 |
| <i>Draba spp.</i> | DrabaSp | 4 |
| <i>Dryas octopetala</i> | DryaOcto | 27 |
| <i>Dryopteris expansa</i> | DryoExpa | 1 |
| <i>Diphasiastrum alpinum</i> | DiphAlpi | 6 |
| <i>Empetrum nigrum</i> | EmpeNigr | 32 |
| <i>Epilobium alsinifolium</i> | EpilAlsi | 2 |
| <i>Epilobium anagallidifolium</i> | EpilAnag | 16 |
| <i>Epilobium hornemannii</i> | EpilHorn | 7 |
| <i>Epilobium lactiflorum</i> | EpilLact | 3 |
| <i>Epilobium spp.</i> | EpilobSp | 4 |
| <i>Equisetum arvense</i> | EquiArve | 24 |
| <i>Equisetum fluviatile</i> | EquiFluvi | 2 |
| <i>Equisetum palustre</i> | EquiPalu | 3 |
| <i>Equisetum scirpoides</i> | EquiScir | 1 |
| <i>Equisetum sylvaticum</i> | EquiSylv | 6 |
| <i>Equisetum variegatum</i> | EquiVari | 10 |
| <i>Erigeron uniflorus</i> | ErigUnif | 17 |
| <i>Eriophorum angustifolium</i> | ErioAngu | 3 |
| <i>Eriophorum scheuchzeri</i> | ErioSche | 2 |
| <i>Eriophorum vaginatum</i> | ErioVagi | 1 |
| <i>Euphrasia wettsteinii</i> | EuphWett | 40 |
| <i>Festuca ovina</i> | FestOvin | 19 |
| <i>Festuca rubra</i> | FestRubr | 8 |
| <i>Festuca vivipara</i> | FestVivi | 21 |
| <i>Filipendula ulmaria</i> | FiliUlma | 7 |
| <i>Fragaria vesca</i> | FragVesc | 2 |
| <i>Galeopsis spp.</i> | GaleSp | 1 |
| <i>Gentiana nivalis</i> | GentNiva | 14 |
| <i>Gentiana purpurea</i> | GentPurp | 7 |
| <i>Gentianella campestris</i> | GentCamp | 5 |
| <i>Geranium sylvaticum</i> | GeraSylv | 50 |
| <i>Geum rivale</i> | GeumRiva | 26 |
| <i>Gymnadenia conopsea</i> | GymnCono | 3 |
| <i>Gymnocarpium dryopteris</i> | GymnDryo | 9 |
| <i>Harrimanella hypnoides</i> | HarrHypn | 4 |
| <i>Hieracium sec. Alpinum</i> | HierAlpi | 13 |
| <i>Hieracium sec. Vulgatum</i> | HierVulg | 19 |
| <i>Huperzia selago</i> | HupeSela | 16 |
| <i>Hypericum maculatum</i> | HypeMacu | 5 |
| <i>Juncus arcticus</i> | JuncArct | 1 |
| <i>Juncus biglumis</i> | JuncBigl | 9 |
| <i>Juncus castaneus</i> | JuncCast | 4 |

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|--------------------------------|-----------|----|
| <i>Juncus filiformis</i> | JuncFili | 1 |
| <i>Juncus trifidus</i> | JuncTrif | 20 |
| <i>Juncus triglumis</i> | JuncTrig | 2 |
| <i>Juniperus communis</i> | JuniComm | 11 |
| <i>Kobresia myosuroides</i> | KobrMyos | 3 |
| <i>Kobresia simpliciuscula</i> | KobrSimp | 2 |
| <i>Leontodon autumnalis</i> | LeonAutu | 36 |
| <i>Loiseleuria procumbens</i> | LoisProc | 1 |
| <i>Lotus corniculatus</i> | LotuCorn | 18 |
| <i>Luzula confusa</i> | LuzuConf | 2 |
| <i>Luzula multiflora</i> | LuzuMult | 29 |
| <i>Luzula pilosa</i> | LuzuPilo | 1 |
| <i>Luzula spicata</i> | LuzuSpic | 36 |
| <i>Luzula sudetica</i> | LuzuSude | 12 |
| <i>Lycopodium clavatum</i> | Lycoclav | 1 |
| <i>Maianthemum bifolium</i> | MaiaBifo | 3 |
| <i>Melica nutans</i> | MeliNuta | 6 |
| <i>Melampyrum sylvaticum</i> | MelaSylv | 6 |
| <i>Milium effusum</i> | MiliEffu | 6 |
| <i>Minuartia biflora</i> | MinuBifl | 5 |
| <i>Molinia caerulea</i> | MoliCaer | 7 |
| <i>Montia fontana</i> | MontFont | 2 |
| <i>Myosotis decumbens</i> | MyosDecu | 15 |
| <i>Nardus stricta</i> | NardStri | 38 |
| <i>Omalothea norvegica</i> | OmalNorv | 20 |
| <i>Omalothea supina</i> | OmalSupi | 15 |
| <i>Omalothea sylvatica</i> | OmalSylv | 1 |
| <i>Oxalis acetosella</i> | OxalAcet | 5 |
| <i>Oxyria digyna</i> | OxyrDygi | 9 |
| <i>Oxytropis lapponica</i> | OxytLapp | 5 |
| <i>Paris quadrifolia</i> | PariQuad | 2 |
| <i>Parnassia palustis</i> | ParnPalu | 24 |
| <i>Phegopteris connectilis</i> | PhegConn | 4 |
| <i>Phippisia algida</i> | PhipAlgi | 5 |
| <i>Phleum alpinum</i> | PhleAlpi | 41 |
| <i>Pinguicula vulgaris</i> | PingVulg | 15 |
| <i>Poa alpina</i> | PoaAlpi | 51 |
| <i>Poa glauca</i> | PoaGlau | 2 |
| <i>Poa nemoralis</i> | PoaNemo | 2 |
| <i>Poa pratensis</i> | PoaPrat | 4 |
| <i>Polygala vulgaris</i> | PolygVulg | 3 |
| <i>Polystichum lonchitis</i> | PolyLonc | 4 |
| <i>Potentilla crantzii</i> | PoteCran | 35 |
| <i>Potentilla erecta</i> | PoteErec | 13 |

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|---------------------------------|----------|----|
| <i>Prunella vulgaris</i> | PrunVulg | 3 |
| <i>Pseudorchis straminea</i> | PseuAlbi | 2 |
| <i>Pyrola minor</i> | PyroMino | 19 |
| <i>Pyrola rotundifolia</i> | PyroRotu | 2 |
| <i>Pyrola spp.</i> | PyrolaSp | 5 |
| <i>Ranunculus acris</i> | RanuAcri | 57 |
| <i>Ranunculus platanifolius</i> | RanuPlat | 6 |
| <i>Ranunculus pygmaeus</i> | RanuPygm | 4 |
| <i>Rhinantus minor</i> | RhinMino | 18 |
| <i>Rhodiola rosea</i> | RhodRose | 23 |
| <i>Rubus idaeus</i> | RubuIdae | 2 |
| <i>Rubus saxatilis</i> | RubuSaxa | 5 |
| <i>Rumex acetosa</i> | RumeAcet | 49 |
| <i>Sagina saginoides</i> | SagiSagi | 22 |
| <i>Salix glauca</i> | SaliGlau | 31 |
| <i>Salix hastata</i> | SaliHast | 7 |
| <i>Salix herbacea</i> | SaliHerb | 48 |
| <i>Salix lanata</i> | SaliLana | 26 |
| <i>Salix lapponum</i> | SaliLapp | 16 |
| <i>Salix myrsinites</i> | SaliMyrs | 3 |
| <i>Salix polaris</i> | SaliPola | 8 |
| <i>Salix reticulata</i> | SaliReti | 34 |
| <i>Salix spp.</i> | SalixSp | 3 |
| <i>Saussurea alpina</i> | SausAlpi | 66 |
| <i>Saxifraga aizoides</i> | SaxiAizo | 9 |
| <i>Saxifraga cespitosa</i> | SaxiCesp | 2 |
| <i>Saxifraga cernua</i> | SaxiCern | 2 |
| <i>Saxifraga nivalis</i> | SaxiNiva | 2 |
| <i>Saxifraga oppositifolia</i> | SaxiOppo | 15 |
| <i>Saxifraga rivularis</i> | SaxiRivu | 4 |
| <i>Saxifraga stellaris</i> | SaxiStel | 12 |
| <i>Saxifraga tenuis</i> | SaxiTenu | 1 |
| <i>Saxifraga adscendens</i> | SaxiAdsc | 2 |
| <i>Sedum acre</i> | SeduAcre | 2 |
| <i>Selaginella selaginoides</i> | SelaSela | 53 |
| <i>Sibbaldia procumbens</i> | SibaProc | 26 |
| <i>Silene acaulis</i> | SileAcau | 40 |
| <i>Silene dioica</i> | SileDioi | 11 |
| <i>Silene vulgaris</i> | SileVulg | 1 |
| <i>Silene wahlbergella</i> | SileWahl | 1 |
| <i>Solidago virgaurea</i> | SoliVirg | 34 |
| <i>Stellaria nemorum</i> | StelNemo | 10 |
| <i>Taraxacum spp.</i> | TaraxaSp | 46 |
| <i>Thalictrum alpinum</i> | ThalAlpi | 48 |

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|--------------------------------|-----------|----|
| <i>Tofieldia pusilla</i> | TofiPusi | 13 |
| <i>Trichophorum cespitosum</i> | TricCesp | 6 |
| <i>Trientalis europaea</i> | TrieEuro | 18 |
| <i>Trifolium repens</i> | TrifRepe | 1 |
| <i>Trisetum spicatum</i> | TrisSpic | 6 |
| <i>Vaccinium myrtillus</i> | VaccMyrt | 33 |
| <i>Vaccinium uliginosum</i> | VaccUlig | 31 |
| <i>Vaccinium vitis-idaea</i> | VaccViti | 21 |
| <i>Valeriana sambucifolia</i> | ValeSamb | 8 |
| <i>Veronica alpina</i> | VeroAlpi | 43 |
| <i>Veronica fruticans</i> | VeroFruc | 5 |
| <i>Veronica officinalis</i> | VeroOffi | 2 |
| <i>Veronica serpyllifolia</i> | VeroSerp | 2 |
| <i>Vicium sepium</i> | ViciSepi | 2 |
| <i>Viola biflora</i> | ViolBifl | 23 |
| <i>Viola canina</i> | ViolCani | 13 |
| <i>Viola palustris</i> | ViolPalu | 20 |
| <i>Viscaria alpina</i> | ViscAlpi | 4 |
| Lichens | | |
| <i>Alectoria ochroleuca</i> | AlecOchr | 2 |
| <i>Bryocaulon divergens</i> | BryoDive | 2 |
| <i>Cetraria cucullatum</i> | CetrCucu | 8 |
| <i>Cetraria delisei</i> | CetrDeli | 1 |
| <i>Cetraria ericetorum</i> | CetrEric | 16 |
| <i>Cetraria islandica</i> | CetrIsla | 30 |
| <i>Cetraria juniperina</i> | CetrJuni | 4 |
| <i>Cetraria nivalis</i> | CetrNiva | 16 |
| <i>Cladonia arbuscula</i> | CladArbu | 25 |
| <i>Cladonia coccifera</i> | CladCocc | 1 |
| <i>Cladonia furcata</i> | CladFurc | 1 |
| <i>Cladonia gracilis</i> | CladGrac | 3 |
| <i>Cladonia pyxidata</i> | CladPyxi | 4 |
| <i>Cladonia rangiferina</i> | CladRang | 8 |
| <i>Cladonia squarrosa</i> | CladSqua | 3 |
| <i>Cladonia subfurcata</i> | CladSubf | 5 |
| <i>Cladonia symphylicarpa</i> | CladSymp | 3 |
| <i>Cladonia uncialis</i> | CladUnci | 8 |
| <i>Cladonia spp.</i> | CladonSp | 4 |
| <i>Coelocaulon aculeatum</i> | CoelAcul | 4 |
| <i>Ochrolechia frigida</i> | OchrFrig | 4 |
| <i>Peltigera aphtosa</i> | PeltApht | 5 |
| <i>Peltigera canina</i> | PeltCani | 2 |
| <i>Peltigera praetextata</i> | PeltPrae | 1 |
| <i>Peltigera spp.</i> | PeltigSp. | 4 |

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|---------------------------------|----------|----|
| <i>Pertusaria panyrga</i> | PertPany | 1 |
| <i>Solorina saccata</i> | SoloSacc | 1 |
| <i>Stereocaulon alpinum</i> | SterAlpi | 1 |
| <i>Stereocaulon condensatum</i> | SterCond | 3 |
| <i>Stereocaulon paschale</i> | SterPasc | 2 |
| <i>Stereocaulon pileatum</i> | SterPili | 2 |
| <i>Stereocaulon spp.</i> | SterSp. | 9 |
| <i>Thamnotia vermicularis</i> | ThamVerm | 10 |

Appendix 2

Study plots with coordinates and environmental variables

| Study plot | Coordinates | Alt | RelAlt | Asp | Slope | Soilwat | DryMat | Ign | Vol | P | Ca | Mg | K | pH | SnMax | SnMelt | STemp | Phenology |
|------------|----------------------|------|--------|-----|-------|---------|--------|------|-----|-----|-------|-----|------|-----|-------|--------|-------|-----------|
| 201 | N59 46.755 E7 15.051 | 1135 | 55 | NW | 20 | 199.0 | 96.6 | 19.7 | 0.8 | 2.0 | 298.0 | 7 | 9 | 5.9 | 56 | 123 | 158 | |
| 202 | N59 46.759 E7 15.058 | 1135 | 55 | N | 30 | 159.0 | 96.9 | 14.4 | 0.9 | 2.0 | 295.0 | 6 | 7 | 5.8 | 65 | 125 | 158 | |
| 203 | N59 46.766 E7 15.053 | 1125 | 45 | NE | 20 | 166.0 | 94.9 | 32.7 | 0.4 | 1.0 | 249.0 | 4 | 7 | 6.3 | 0 | 100 | 164 | |
| 204 | N59 46.765 E7 15.057 | 1125 | 45 | N | 30 | 238.0 | 96.7 | 15.0 | 0.9 | 2.0 | 425.0 | 6 | 4 | 6.4 | 0 | 100 | 164 | |
| 205 | N59 46.398 E7 15.670 | 1185 | 105 | S | 15 | 129.0 | 99.0 | 6.0 | 1.1 | 2.0 | 308.0 | 3 | 4 | 7.2 | 117 | 149 | 154 | |
| 206 | N59 46.777 E7 15.043 | 1123 | 43 | NE | 30 | 149.0 | 93.7 | 51.8 | 0.3 | 1.0 | 92.0 | 10 | 13 | 5.1 | 74 | 150 | 154 | |
| 207 | N59 46.401 E7 15.661 | 1188 | 108 | S | 30 | 56.0 | 99.3 | 4.3 | 1.2 | 8.0 | 106.0 | 2 | 2 | 6.5 | 121 | 170 | 171 | |
| 208 | N59 50.047 E7 00.196 | 1119 | 39 | SE | 20 | 170.0 | 95.2 | 39.5 | 0.4 | 1.0 | 95.0 | 17 | 16 | 5.2 | 57 | 132 | 140 | |
| 209 | N59 50.064 E7 00.267 | 1143 | 63 | S | 30 | 139.0 | 98.1 | 11.7 | 0.9 | 5.0 | 50.0 | 17 | 14 | 4.9 | 188 | 150 | 155 | |
| 210 | N59 50.084 E7 00.245 | 1160 | 80 | S | 40 | 137.0 | 96.4 | 20.4 | 0.7 | 2.0 | 237.0 | 23 | 11 | 5.8 | 65 | 132 | 140 | x |
| 211 | N59 50.083 E7 00.237 | 1154 | 74 | S | 30 | 153.0 | 95.7 | 25.7 | 0.7 | 2.0 | 303.0 | 29 | 15 | 5.8 | 0 | 132 | 141 | x |
| 212 | N59 50.085 E7 00.228 | 1168 | 88 | S | 20 | 141.0 | 96.1 | 23.6 | 0.7 | 3.0 | 215.0 | 30 | 20 | 5.5 | 0 | 100 | 130 | x |
| 213 | N59 50.025 E7 00.313 | 1124 | 44 | SW | 40 | 111.0 | 96.4 | 22.3 | 0.7 | 1.0 | 138.0 | 21 | 22 | 5.7 | 133 | 149 | 151 | |
| 214 | N59 50.033 E7 00.437 | 1166 | 86 | SE | 40 | 120.0 | 96.1 | 20.4 | 0.9 | 2.0 | 221.0 | 14 | 15 | 6.3 | 0 | 100 | 130 | |
| 215 | N59 50.011 E7 00.615 | 1143 | 63 | S | 30 | 249.0 | 97.7 | 12.4 | 0.9 | 2.0 | 254.0 | 13 | 10 | 6.2 | 126 | 148 | 150 | |
| 216 | N59 49.823 E7 00.515 | 1097 | 17 | N | 20 | 108.0 | 97.3 | 20.3 | 0.8 | 2.0 | 102.0 | 11 | 19 | 5.4 | 78 | 144 | 150 | x |
| 217 | N59 50.046 E7 00.199 | 1114 | 34 | SW | 10 | 401.0 | 96.7 | 19.0 | 0.7 | 1.0 | 159.0 | 13 | 18 | 5.5 | 146 | 149 | 152 | |
| 218 | N59 50.035 E7 00.202 | 1113 | 33 | SE | 10 | 325.0 | 95.7 | 29.8 | 0.6 | 1.0 | 153.0 | 11 | 13 | 5.7 | 146 | 150 | 153 | |
| 220 | N59 49.046 E7 09.959 | 1015 | -65 | NE | 25 | 133.0 | 98.7 | 7.4 | 1.0 | 2.0 | 48.0 | 10 | 6 | 5.8 | 262 | 180 | 181 | |
| 221 | N59 49.079 E7 09.706 | 1026 | -54 | NE | 20 | 144.0 | 97.9 | 13.4 | 0.9 | 3.0 | 69.0 | 14 | 10 | 5.4 | 275 | 185 | 187 | |
| 222 | N59 49.834 E7 00.412 | 1073 | -7 | NW | 2 | 258.0 | 98.4 | 9.6 | 1.0 | 3.0 | 18.0 | 2 | 3 | 5.7 | 232 | 200 | 201 | x |
| 223 | N59 49.848 E7 00.498 | 1081 | 1 | N | 5 | 298.0 | 95.3 | 37.0 | 0.5 | 2.0 | 132.0 | 13 | 19 | 5.5 | 191 | 174 | 175 | x |
| 224 | N59 49.609 E7 00.898 | 1127 | 47 | NW | 30 | 315.0 | 97.9 | 14.4 | 0.9 | 2.0 | 148.0 | 13 | 14 | 5.5 | 218 | 181 | 182 | |
| 225 | N59 49.715 E7 01.187 | 1117 | 37 | N | 20 | 221.0 | 97.1 | 20.6 | 0.5 | 1.0 | 106.0 | 7 | 16 | 5.5 | 93 | 152 | 155 | |
| 226 | N59 49.758 E7 00.325 | 1080 | 0 | W | 10 | 207.0 | 98.5 | 8.2 | 1.0 | 2.0 | 26.0 | 3 | 9 | 5.5 | 137 | 158 | 159 | x |
| 227 | N59 50.099 E7 00.030 | 1117 | 37 | S | 30 | 243.0 | 96.8 | 20.6 | 0.5 | 2.0 | 117.0 | 18 | 13 | 5.3 | 154 | 150 | 154 | |
| 228 | N59 50.098 E7 00.129 | 1144 | 64 | S | 20 | 198.0 | 96.8 | 24.0 | 1.1 | 6.0 | 92.0 | 35 | 36 | 4.9 | 64 | 133 | 145 | |
| 229 | N59 49.022 E7 10.336 | 1002 | -78 | S | 10 | 389.0 | 95.1 | 35.8 | 0.5 | 2.0 | 133.0 | 7 | 10 | 5.3 | 175 | 165 | 167 | |
| 230 | N59 50.090 E7 00.175 | 1144 | 64 | S | 30 | 206.0 | 96.6 | 22.2 | 0.7 | 4.0 | 116.0 | 33 | 20 | 5.2 | 138 | 150 | 154 | |
| 240 | N59 47.573 E7 16.324 | 981 | -99 | S | 14 | 363.1 | 97.4 | 20.0 | 0.8 | 0.8 | 216.4 | 9.6 | 27 | 5.7 | 85 | 148 | 148 | x |
| 241 | N59 47.547 E7 16.353 | 973 | -107 | NE | 12 | 260.8 | 97.7 | 20.8 | 1.0 | 1.5 | 183.6 | 9.5 | 21.1 | 5.6 | 154 | 152 | 154 | x |
| 242 | N59 47.571 E7 16.344 | 978 | -102 | E | 5 | 331.2 | 96.0 | 33.8 | 0.6 | 1.4 | 272.5 | 13 | 39.3 | 5.7 | 119 | 149 | 151 | x |
| 243 | N59 47.630 E7 16.132 | 1007 | -73 | E | 18 | 211.2 | 98.0 | 17.1 | 1.0 | 0.8 | 132.2 | 7.5 | 16.7 | 5.5 | 123 | 150 | 152 | x |
| 244B | N59 47.623 E7 16.184 | 999 | -81 | S | 3 | 248.0 | 97.2 | 24.4 | 0.8 | 1.2 | 181.6 | 9.3 | 19 | 5.2 | 37 | 121 | 135 | x |
| 245 | N59 47.624 E7 16.207 | 997 | -83 | SE | 5 | 454.1 | 97.3 | 21.2 | 0.9 | 0.4 | 162.0 | 7.4 | 17.3 | 5.6 | 94 | 149 | 150 | x |

| | | | | | | | | | | | | | | | | | |
|-----|----------------------|------|--------|----|-------|------|------|-----|------|-------|-----|------|-----|-----|-----|-----|---|
| 246 | N59 49.255 E7 12.326 | 1021 | -59 SW | 14 | 473.0 | 97.1 | 21.9 | 0.6 | 2.4 | 119.3 | 19 | 25.1 | 5.2 | 107 | 142 | 145 | |
| 247 | N59 49.296 E7 12.312 | 1029 | -51 SW | 19 | 423.6 | 98.1 | 16.0 | 0.8 | 1.2 | 189.6 | 18 | 17.4 | 5.3 | 74 | 136 | 142 | |
| 248 | N59 49.605 E7 11.631 | 1102 | 22 S | 35 | 261.4 | 96.5 | 32.4 | 0.7 | 5.3 | 73.7 | 27 | 39.9 | 4.7 | 133 | 130 | 130 | |
| 249 | N59 49.520 E7 11.493 | 1019 | -61 S | 30 | 184.1 | 97.2 | 24.2 | 0.7 | 4.2 | 88.9 | 27 | 38.3 | 4.8 | 48 | 125 | 132 | |
| 250 | N59 50.910 E7 04.760 | 1018 | -62 NW | 18 | 284.4 | 97.4 | 18.3 | 0.8 | 1.4 | 204.5 | 39 | 20.4 | 5.1 | 127 | 157 | 170 | x |
| 251 | N59 50.216 E6 59.772 | 1117 | 37 S | 40 | 374.5 | 96.3 | 19.2 | 0.8 | 2.5 | 259.1 | 45 | 15.9 | 4.9 | 50 | 135 | 144 | |
| 252 | N59 50.208 E6 59.778 | 1120 | 40 W | 5 | 340.2 | 97.0 | 19.6 | 0.8 | 1.7 | 176.4 | 37 | 23 | 4.9 | 50 | 140 | 150 | |
| 253 | N59 51.453 E6 53.249 | 836 | -134 S | 20 | 421.7 | 94.4 | 42.9 | 0.5 | 1.5 | 119.7 | 16 | 32.3 | 5.1 | 93 | 138 | 139 | x |
| 254 | N59 51.491 E6 53.136 | 870 | -100 S | 35 | 174.0 | 97.2 | 20.4 | 0.8 | 1.0 | 249.5 | 38 | 49.5 | 5.6 | 18 | 117 | 118 | x |
| 255 | N59 51.619 E6 52.900 | 946 | -24 S | 38 | 156.8 | 97.1 | 22.1 | 0.9 | 1.9 | 241.2 | 39 | 31.1 | 5.5 | 12 | 116 | 117 | x |
| 256 | N59 51.515 E6 53.393 | 895 | -75 SE | 30 | 333.7 | 97.4 | 18.5 | 0.8 | 1.6 | 190.0 | 21 | 21.5 | 5.4 | 12 | 116 | 118 | |
| 257 | N59 51.566 E6 53.731 | 964 | -6 SW | 38 | 282.3 | 97.7 | 18.3 | 0.9 | 1.0 | 154.4 | 23 | 25.5 | 5.2 | 77 | 148 | 149 | |
| 258 | N59 50.989 E6 56.771 | 1064 | -16 SE | 15 | 496.0 | 96.9 | 21.8 | 0.6 | 0.7 | 431.2 | 11 | 15.8 | 5.8 | 113 | 148 | 149 | x |
| 259 | N59 50.996 E6 56.744 | 1068 | -12 S | 20 | 342.8 | 95.4 | 37.0 | 0.4 | 3.8 | 401.1 | 35 | 41.2 | 5.2 | 117 | 143 | 148 | x |
| 260 | N59 51.010 E6 56.684 | 1076 | -4 S | 20 | 492.1 | 92.6 | 46.2 | 0.4 | 0.5 | 641.8 | 21 | 42.2 | 5.7 | 90 | 143 | 146 | x |
| 261 | N59 51.030 E6 56.454 | 1024 | -56 SW | 30 | 386.8 | 97.5 | 15.7 | 0.9 | 1.1 | 75.2 | 14 | 24.3 | 4.9 | 107 | 140 | 143 | x |
| 262 | N59 49.843 E6 54.886 | 1046 | -34 SW | 10 | 220.7 | 97.5 | 20.5 | 0.7 | 0.7 | 144.6 | 22 | 15.9 | 5.2 | 60 | 125 | 135 | x |
| 263 | N59 49.849 E6 54.874 | 1051 | -29 SE | 25 | 110.8 | 98.4 | 10.0 | 1.1 | 0.8 | 104.5 | 12 | 9.4 | 5.9 | 3 | 113 | 121 | x |
| 264 | N59 50.521 E7 12.196 | 1132 | 52 S | 15 | 431.0 | 93.7 | 51.2 | 0.3 | 3.5 | 545.6 | 24 | 52.7 | 4.5 | 139 | 162 | 166 | |
| 265 | N59 52.980 E7 13.042 | 1303 | 223 SW | 15 | 167.3 | 98.0 | 19.0 | 0.9 | 2.8 | 102.9 | 24 | 27.8 | 5.2 | 155 | 161 | 163 | |
| 266 | N59 52.983 E7 13.017 | 1295 | 215 SW | 30 | 245.7 | 97.3 | 20.4 | 0.8 | 0.7 | 186.0 | 35 | 27.8 | 5.9 | 169 | 160 | 162 | |
| 267 | N59 53.009 E7 12.978 | 1303 | 223 SW | 30 | 126.7 | 98.9 | 9.1 | 1.0 | 0.4 | 91.4 | 14 | 9.7 | 5.7 | 92 | 143 | 150 | |
| 268 | N59 50.899 E7 04.634 | 1017 | -63 N | 10 | 333.5 | 96.3 | 19.1 | 0.8 | 2.1 | 195.7 | 59 | 21.5 | 5 | 68 | 145 | 160 | x |
| 269 | N59 50.911 E7 04.763 | 1018 | -62 N | 20 | 305.7 | 96.6 | 22.3 | 0.6 | 1.5 | 330.9 | 41 | 17.6 | 5.2 | 108 | 154 | 170 | |
| 270 | N59 50.753 E7 03.732 | 1042 | -38 NW | 5 | 317.2 | 98.5 | 4.7 | 1.1 | 0.7 | 47.4 | 11 | 5.2 | 4.8 | 275 | 184 | 184 | x |
| 271 | N59 47.651 E7 16.211 | 1003 | -77 SE | 10 | 464.9 | 97.5 | 23.6 | 0.8 | 1.0 | 144.6 | 9.3 | 18.1 | 5.3 | 100 | 146 | 148 | x |
| 272 | N59 47.687 E7 16.230 | 1017 | -63 S | 15 | 245.0 | 98.2 | 14.3 | 1.0 | 0.8 | 85.9 | 4.3 | 10.8 | 5.3 | 133 | 150 | 151 | x |
| 273 | N59 47.675 E7 16.212 | 1014 | -66 SE | 15 | 268.8 | 97.7 | 20.2 | 1.1 | 0.7 | 136.3 | 7.3 | 17.8 | 5.3 | 133 | 154 | 156 | x |
| 274 | N59 51.111 E7 10.140 | 1118 | 38 S | 15 | 445.7 | 96.3 | 28.4 | 0.8 | 3.1 | 306.1 | 20 | 32.9 | 5.1 | 199 | 163 | 164 | |
| 275 | N59 51.104 E7 10.136 | 1115 | 35 S | 5 | 524.1 | 96.1 | 28.7 | 0.6 | 4.0 | 353.9 | 27 | 36.9 | 5.2 | 165 | 164 | 166 | |
| 276 | N59 51.124 E7 10.118 | 1125 | 45 SW | 5 | 416.6 | 92.0 | 67.5 | 0.2 | 11.7 | 697.5 | 44 | 94.4 | 5.4 | 81 | 144 | 149 | |
| 277 | N59 51.118 E7 10.113 | 1120 | 40 S | 25 | 401.4 | 91.0 | 77.9 | 0.1 | 12.6 | 812.5 | 61 | 113 | 5.5 | 111 | 144 | 149 | |
| 300 | N60 35.847 E7 32.329 | 1300 | 150 SW | 5 | 550.9 | 94.1 | 45.2 | 0.4 | 2.6 | 863.6 | 20 | 45.5 | 6.1 | 115 | 156 | 162 | |
| 301 | N60 36.085 E7 32.528 | 1402 | 252 SW | 25 | 291.5 | 96.3 | 31.4 | 0.4 | 1.5 | 388.2 | 18 | 31.6 | 5.6 | 107 | 154 | 158 | |
| 302 | N60 36.107 E7 32.352 | 1385 | 235 SW | 15 | 474.5 | 97.4 | 20.5 | 0.8 | 0.9 | 145.9 | 9.8 | 18.8 | 5 | 50 | 141 | 157 | |
| 303 | N60 36.462 E7 33.024 | 1459 | 309 SW | 25 | 322.8 | 98.7 | 10.6 | 1.0 | 0.5 | 170.0 | 8.4 | 7.8 | 5.9 | 37 | 132 | 143 | |
| 304 | N60 36.459 E7 33.004 | 1457 | 307 S | 15 | 418.4 | 97.5 | 20.4 | 0.6 | 0.7 | 308.2 | 15 | 11.3 | 6.1 | 2 | 113 | 140 | |
| 305 | N60 36.467 E7 32.958 | 1455 | 305 SW | 25 | 346.9 | 96.9 | 22.0 | 0.6 | 0.4 | 417.5 | 16 | 13.4 | 5.9 | 19 | 130 | 145 | |
| 306 | N60 36.758 E7 31.401 | 1466 | 316 S | 25 | 302.1 | 98.2 | 12.0 | 0.9 | 1.5 | 212.4 | 22 | 8.6 | 5.9 | 6 | 114 | 141 | x |
| 307 | N60 36.750 E7 31.395 | 1460 | 310 S | 25 | 345.0 | 95.4 | 32.0 | 0.4 | 1.3 | 437.8 | 36 | 27.9 | 5.6 | 77 | 154 | 159 | x |

| | | | | | | | | | | | | | | | | | |
|------|----------------------|------|---------|----|-------|------|------|-----|-----|--------|-----|------|-----|-----|-----|-----|---|
| 308 | N60 36.767 E7 31.374 | 1472 | 322 S | 15 | 311.5 | 96.0 | 33.2 | 0.4 | 0.5 | 709.7 | 40 | 23.6 | 6.4 | 1 | 108 | 148 | x |
| 309 | N60 36.779 E7 31.357 | 1463 | 313 W | 5 | 274.5 | 98.6 | 12.0 | 0.8 | 0.7 | 150.8 | 13 | 9.7 | 5.5 | 128 | 176 | 177 | x |
| 310B | N60 36.786 E7 31.317 | 1453 | 303 SW | 5 | 302.4 | 98.8 | 8.2 | 0.9 | 0.4 | 222.7 | 17 | 4.4 | 6.5 | 111 | 173 | 174 | x |
| 311B | N60 36.837 E7 31.096 | 1390 | 240 SW | 10 | 329.8 | 99.2 | 4.1 | 1.1 | 0.4 | 105.9 | 7.5 | 1.5 | 6.9 | 232 | 182 | 201 | x |
| 312B | N60 36.824 E7 31.147 | 1398 | 248 SW | 20 | 309.8 | 96.0 | 29.2 | 0.5 | 1.0 | 551.3 | 18 | 23.5 | 5.8 | 70 | 148 | 158 | x |
| 313 | N60 36.872 E7 31.100 | 1449 | 299 SW | 25 | 220.9 | 98.2 | 13.4 | 0.9 | 0.8 | 84.3 | 8.5 | 14.4 | 5 | 259 | 168 | 169 | x |
| 314 | N60 36.878 E7 31.092 | 1449 | 299 SW | 15 | 434.9 | 97.0 | 22.7 | 0.7 | 1.1 | 431.5 | 20 | 19.9 | 5.7 | 162 | 155 | 162 | x |
| 315 | N60 36.300 E7 30.524 | 1318 | 168 SW | 10 | 365.7 | 98.7 | 5.6 | 1.1 | 0.7 | 127.5 | 4.1 | 2.4 | 6.6 | 64 | 139 | 158 | |
| 316 | N60 36.284 E7 31.382 | 1396 | 246 S | 10 | 202.8 | 99.4 | 4.5 | 1.2 | 0.6 | 61.7 | 5.6 | 4.3 | 5.9 | 259 | 184 | 186 | |
| 317 | N60 36.265 E7 31.160 | 1396 | 246 SW | 2 | 566.4 | 93.5 | 57.2 | 0.3 | 1.6 | 858.1 | 20 | 23.1 | 6.1 | 0 | 100 | 159 | x |
| 318 | N60 36.262 E7 31.183 | 1391 | 241 S | 2 | 519.3 | 96.0 | 30.7 | 0.5 | 0.4 | 610.8 | 13 | 16.3 | 6.6 | 23 | 125 | 160 | x |
| 319 | N60 36.308 E7 31.088 | 1415 | 265 SW | 2 | 600.7 | 98.5 | 13.2 | 0.8 | 0.7 | 135.5 | 8.7 | 14.1 | 5.6 | 187 | 176 | 177 | |
| 320 | N60 36.294 E7 30.822 | 1392 | 242 S | 5 | 388.5 | 98.7 | 11.6 | 1.0 | 0.6 | 297.5 | 5.9 | 7.5 | 6.1 | 123 | 162 | 167 | x |
| 321 | N60 36.261 E7 30.817 | 1367 | 217 S | 15 | 589.1 | 97.9 | 15.0 | 0.9 | 0.7 | 300.5 | 8.1 | 11.5 | 6.1 | 143 | 161 | 165 | x |
| 322 | N60 36.260 E7 30.826 | 1366 | 216 S | 10 | 620.5 | 97.0 | 24.5 | 0.6 | 0.9 | 497.3 | 13 | 20.5 | 6 | 128 | 160 | 165 | x |
| 324 | N60 36.852 E7 31.354 | 1477 | 327 S | 5 | 244.1 | 98.4 | 13.2 | 0.9 | 0.6 | 195.1 | 8.6 | 7.9 | 5.8 | 170 | 167 | 170 | x |
| 325 | N60 36.944 E7 31.270 | 1542 | 392 SW | 15 | 214.7 | 98.6 | 10.5 | 1.1 | 0.6 | 223.2 | 10 | 7 | 6.4 | 0 | 100 | 143 | x |
| 326 | N60 36.950 E7 31.282 | 1547 | 397 SW | 5 | 266.1 | 98.3 | 10.0 | 1.0 | 0.4 | 173.2 | 7.7 | 5.3 | 6.1 | 3 | 113 | 140 | x |
| 327 | N60 37.021 E7 31.549 | 1555 | 405 SW | 25 | 326.5 | 98.0 | 12.5 | 0.9 | 0.3 | 291.9 | 13 | 10.7 | 6.1 | 35 | 140 | 168 | x |
| 328 | N60 37.022 E7 31.562 | 1556 | 406 S | 15 | 281.9 | 99.1 | 5.8 | 1.1 | 0.6 | 151.1 | 6.3 | 3.1 | 6.5 | 25 | 140 | 162 | x |
| 329 | N60 36.764 E7 31.393 | 1469 | 319 SE | 5 | 324.4 | 98.1 | 16.5 | 0.9 | 0.6 | 161.0 | 15 | 12.9 | 5.5 | 1 | 108 | 127 | x |
| 330 | N60 36.448 E7 31.785 | 1410 | 260 NE | 5 | 311.7 | 99.4 | 4.5 | 1.2 | 0.6 | 31.3 | 3.3 | 1.9 | 5.9 | 169 | 181 | 182 | x |
| 331 | N60 35.866 E7 28.542 | 1259 | 109 S | 25 | 536.4 | 94.8 | 37.1 | 0.4 | 4.7 | 367.7 | 23 | 41.6 | 5.3 | 266 | 175 | 178 | x |
| 332 | N60 44.198 E7 08.902 | 793 | -277 S | 30 | 289.4 | 96.8 | 24.2 | 0.7 | 3.1 | 200.6 | 31 | 31.3 | 5.2 | 109 | 143 | 148 | x |
| 333 | N60 44.177 E7 08.874 | 806 | -264 N | 15 | 323.8 | 95.8 | 23.9 | 0.7 | 0.8 | 45.5 | 5.5 | 3.7 | 5.3 | 141 | 150 | 159 | x |
| 334 | N60 44.178 E7 09.123 | 790 | -280 N | 25 | 365.3 | 96.0 | 22.1 | 0.8 | 0.5 | 264.1 | 22 | 20.8 | 5.6 | 70 | 135 | 138 | x |
| 335 | N60 44.056 E7 09.441 | 793 | -277 NE | 20 | 268.6 | 97.1 | 10.7 | 0.9 | 1.8 | 178.4 | 39 | 23.9 | 4.7 | 109 | 146 | 149 | x |
| 336 | N60 44.092 E7 09.348 | 779 | -291 NW | 5 | 313.3 | 97.6 | 12.4 | 0.9 | 3.4 | 89.3 | 23 | 25 | 4.8 | 90 | 135 | 149 | x |
| 337 | N60 35.802 E7 32.977 | 1363 | 213 SW | 2 | 294.0 | 99.1 | 4.2 | 1.2 | 0.6 | 85.4 | 3.5 | 2 | 6.4 | 251 | 197 | 197 | |
| 338 | N60 36.132 E7 33.233 | 1420 | 270 NW | 5 | 287.9 | 97.4 | 15.4 | 0.9 | 0.5 | 1090.0 | 15 | 8.5 | 7 | 73 | 146 | 168 | |
| 339 | N60 36.433 E7 31.951 | 1395 | 245 SE | 5 | 229.6 | 99.2 | 3.5 | 1.3 | 1.0 | 28.8 | 2.7 | 1.5 | 6 | 234 | 183 | 186 | x |
| 340B | N60 36.442 E7 31.788 | 1409 | 259 SE | 5 | 196.9 | 99.7 | 3.4 | 1.2 | 0.8 | 21.3 | 2.3 | 1.4 | 5.6 | 106 | 176 | 182 | x |
| 341 | N60 36.264 E7 30.751 | 1347 | 197 SW | 35 | 343.5 | 96.9 | 29.0 | 0.5 | 1.7 | 282.6 | 25 | 52.9 | 5.1 | 182 | 153 | 154 | x |
| 342 | N60 36.256 E7 30.737 | 1337 | 187 S | 25 | 376.7 | 95.4 | 41.1 | 0.5 | 3.9 | 440.1 | 16 | 51 | 5.3 | 125 | 153 | 154 | x |
| 343 | N60 36.234 E7 30.949 | 1355 | 205 S | 5 | 489.3 | 96.5 | 32.7 | 0.6 | 2.4 | 394.1 | 16 | 31.7 | 5.2 | 94 | 156 | 168 | x |
| 344 | N60 35.920 E7 28.627 | 1295 | 145 S | 30 | 304.6 | 95.4 | 30.9 | 0.5 | 3.4 | 509.4 | 32 | 29.1 | 5.5 | 174 | 160 | 164 | x |
| 345 | N60 35.921 E7 28.659 | 1301 | 151 S | 35 | 400.1 | 97.5 | 17.9 | 0.9 | 3.2 | 183.7 | 19 | 33 | 4.9 | 244 | 165 | 167 | x |
| 346 | N60 35.922 E7 28.657 | 1325 | 175 SW | 40 | 358.7 | 97.4 | 21.5 | 0.8 | 1.4 | 298.7 | 16 | 29.9 | 5.5 | 259 | 174 | 176 | x |
| 347 | N60 35.963 E7 28.577 | 1352 | 202 S | 25 | 108.9 | 95.5 | 41.3 | 0.3 | 4.8 | 478.1 | 25 | 58.8 | 5.2 | 101 | 156 | 158 | x |
| 348 | N60 37.094 E7 30.868 | 1413 | 263 NW | 15 | 195.2 | 99.4 | 3.5 | 1.2 | 0.5 | 77.1 | 5.4 | 2.1 | 6.4 | 275 | 202 | 203 | x |

| | | | | | | | | | | | | | | | | | |
|-----|----------------------|------|--------|----|-------|------|------|-----|-----|-------|-----|-----|-----|-----|-----|-----|---|
| 349 | N60 36.897 E7 31.561 | 1504 | 354 S | 7 | 289.2 | 97.5 | 12.9 | 0.9 | 0.5 | 130.2 | 9.4 | 8.4 | 5.7 | 153 | 178 | 179 | x |
| 350 | N60 36.981 E7 31.079 | 1505 | 355 NW | 17 | 254.8 | 98.7 | 9.3 | 1.0 | 0.4 | 167.8 | 5.7 | 5.6 | 6.3 | 93 | 172 | 173 | x |

Paper I-V

Paper I

Soil temperature variation in calciphile mountain plant communities in Southern Norway

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Abstract. Soil temperature dynamics are considered to be of great importance for alpine plant life. The aim of this study was to analyse differences in soil temperature parameters between and within exposed ridges, leesides, and snowbeds during one year. The study was performed in two mountain areas, north and south of the Hardangervidda mountain plateau (Norway). Data loggers recorded soil temperatures 5-10 cm below surface, twice daily in 60 study plots, stratified to calciphile vegetation. In each plot, species abundances were estimated in percentage ground cover, and snowmelt was monitored. TWINSpan classification was used to separate small-scale vegetation groups. Relationships between these small-scale vegetation groups and soil temperature parameters were tested by Detrended Correspondence Analysis, Principal Component Analyses, and Canonical Variates Analyses. The results demonstrate that the annual variation in soil temperatures not only differed significantly between exposed ridges, leesides, and snowbeds, but also between the small-scale vegetation groups. Plant species composition was highly correlated with soil temperature variables. To distinguish between small-scale vegetation groups, soil temperature conditions during the snowmelt period were most important, followed by growing season and winter soil temperatures. The winter half-year is also predicted to be most affected by future climate change in Norwegian mountains.

Key words: snowmelt, alpine vegetation, ordination, microclimate, altitude

Introduction

Soil temperatures are important parameters for alpine life conditions because they influence plant growth and phenology in addition to having major effects on soil processes (e.g. Higgins and Spomer 1976, Edwards *et al.* 2007). Soil temperatures match microclimates that mountain plants experience better than air temperatures extrapolated from weather stations (Scherrer *et al.* 2011), because many mountain plants are of

low stature and therefore decoupled from overall air temperatures (Körner 1999). Furthermore, soil temperatures are easier to measure at specific sites than air temperatures because radiation does not have to be considered. Soil temperatures determine the length of the frozen soil period and the occurrence of freezing/ thawing events, which both will have consequences for the soil ecosystem and vegetation (e.g. Rixen *et al.* 2008, Vestgarden and Austnes 2009).

Mountain vegetation can be separated into sharp bordered plant communities with micro habitats created by the varying mountain topography. It is well known that neighbouring sites can have a totally different plant species composition due to prevailing snow distribution (e.g. Gjørsvoll 1956, Dahl 1956, Friedel 1961, Dierßen 1996, Walker *et al.* 2001). Soil temperatures, which are influenced by snow cover, vegetation cover, exposure, and soil characteristics and heat capacity, may be highly different within short distances (Dahl 1956, Greenland and Losleben 2001, Odland and Munkejord 2008, Scherrer and Körner 2010). The annual as well as the diurnal courses of microhabitat soil temperatures show different trends according to topographic conditions (Scherrer and Körner 2010, Wundram *et al.* 2010) and varying snow exposure (Emerick and Webber 1982, Goodrich 1982). Hence the question arises how certain vegetation groups can be associated with specific soil temperatures.

Scherrer and Körner (2011) demonstrated that soil temperature conditions in an alpine landscape with varied topography are linked to local plant species distribution. Some large-scale studies have been performed to find soil temperature variables correlated with particular vegetation: Körner and Paulsen (2004) found that a seasonal mean root-zone temperature of 6.7 °C(±0.8) was fairly equal at the high altitude treeline worldwide. Also Gehrig-Fasel *et al.* (2008) estimated a root-zone temperature of 7.0 °C(±0.4) for the alpine treeline position. Similar soil temperatures during the growing season were measured in alpine grasslands across Europe (Körner *et al.* 2003). However there are only few soil temperature analyses that cover a range along the snow gradient from exposed ridges (ER), over leesides (LS), to snowbed (SB) vegetation in the same study area (e.g. May and Webber 1982, Takahashi 2005). Studies emphasizing differences between vegetation communities within ERs, LSs and SBs are even less frequent. But those that are available show soil temperature differences between small-scale vegetation types, e.g. soil temperatures in SBs (Schwöb *et al.* 2009), soil temperatures during

the growing season in the Swiss Alps (Scherrer and Körner 2011), and within different types of oligotrophic and mesotrophic mountain vegetation (Odland and Munkejord 2008).

In the present study, soil temperatures in calciphile mountain plant communities covering a snow gradient from ERs to SBs, were recorded during one year, to answer the following questions: (1) Are there significant differences in soil temperature parameters between ERs, LSs, and SBs? (2) Are there significant differences between small-scale vegetation groups within these main groups? (3) Which of the estimated soil temperature parameters are most important to distinguish between the small-scale vegetation groups?

Material and Methods

Study sites

This study was conducted at two locations at the Hardangervidda mountain plateau in Southern Norway: at Finse (60° 36' N, 7° 30' E) in the north, and at Haukelisetet (59° 49' N, 7° 12' E), in the south (Fig. 1). Both areas cover a west-east (oceanic-continent) gradient and the study plots range from the northern boreal (NB) zone, over the low alpine (LA) zone, to the middle alpine (MA) zone (Moen 1999). The sampling sites in the Haukelisetet area are located at altitudes between 836 and 1168 m a.s.l. (climatic birch forest limit: 970 – 1080 m a.s.l.). The sites at Finse are located at altitudes between 1259 and 1556 m a.s.l., with some sites at ca. 800 m a.s.l. (climatic birch forest limit: 1070 – 1150 m a.s.l.). According to Moen (1999) the climate is described as slightly oceanic at Haukelisetet (mean normal temperature July/January: 10 °C/-8 °C, normal annual precipitation: 840 mm), passing into the indifferent section at Finse (mean normal temperature July/January: 7 °C/-10.3 °C, normal annual precipitation: 1030 mm). In both study areas, winter 2009/2010 was relatively cold, with mean air temperatures that were until 6 °C lower than normal and considerable little precipitation from December to February compared to normal precipitation. Precipitation in January 2010 was 5.8 mm versus a normal January precipitation of 90 mm at Finse (data provided by the Norwegian Meteorological Institute, normal = 1961-1990).

Study design

The investigation is based on manual measurements of snowmelt, and data-logger recordings of soil temperatures in different mountain vegetation types. To decrease the floristic variation in the data, the sampling was mainly stratified to homogeneous sites rich in calcium (occurrence of two or more calciphile species sensu Nordhagen 1943, Gjærevoll 1956). Data collection was carried out in 60 randomly selected sample plots (37 at Finse, 23 at Haukelisetet) of 2x2m in stands which cover major gradients in snow layer duration. The geographic positions and altitudes of all plots were recorded by a GPS unit. Vegetation analyses were conducted during summer 2008. The abundances of species of vascular plants, lichens, and bryophytes were estimated in

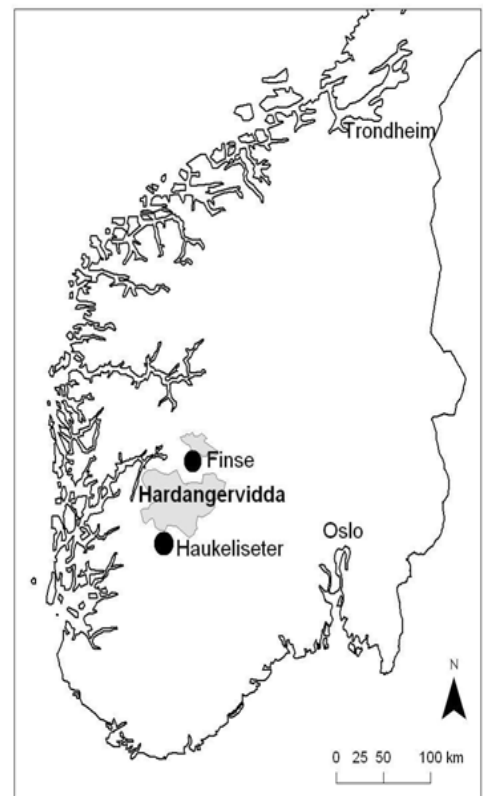


Fig. 1. Location of the study areas Finse and Haukelisetet in Southern Norway.

percentage cover. For vascular plants, the names of species followed Lid and Lid (2005). During spring 2010 the plots were visited frequently to estimate the date when they were completely free from snow. Air temperature and precipitation data were interpolated from the nearby weather stations Midtlæger (59° 83'38" N and 6° 99'15" E, altitude: 1079 m a.s.l.) and Finsevatn (60° 59'25" N and 7° 53'05" E, altitude: 1,210 m a.s.l.) (data provided by the Norwegian Meteorological Institute).

A data logger (LogTag TRIX-8, measurement range: -40 °C to +85 °C, resolution: <0.1 °C for temperatures between -40 °C and +40 °C) was placed in the upper left corner of each plot in the middle of August 2009. The loggers recorded soil temperatures twice daily (1 am and 1 pm) until the middle of August 2010. Each logger was buried 5-10 cm below ground.

The following temperature parameters were calculated from the data logger measurements in each plot: Maximum, minimum and mean temperatures were calculated for a winter period (November 1 to March 31) and a summer period (May 1 to August 31). And minimum and mean temperatures in April were calculated. April was treated separately from summer and winter because it was expected to be the month with most obvious differences between the vegetation communities.

Mean temperature was also calculated for the growing season period of each plot. To estimate growing season length it was assumed that growing season started when soil temperature exceeded 6 °C, and ended when mean air temperature of ten succeeding days dropped below 5 °C (Odland 2011).

Date of snowmelt was defined as Julian day when the study plot was completely snow free. Snowmelt is a gradual process, occurring between two visits, hence snow measurements had to be interpolated to determine the Julian day of snowmelt. A soil temperature of 1 °C was then found useful to determine the Julian day of snowmelt.

The required number of days after snowmelt to reach the soil temperature threshold of 6 °C, and the Julian day when autumn soil temperature dropped below 1 °C and remained there for the rest of the year, were estimated.

An overview with abbreviations of all soil temperature related parameters is given in Table 1.

Data analyses

The vegetation samples were classified by the use of the TWINSpan program (Hill 1979). Six pseudo-species cutlevels (0, 5, 10, 20, 40, 60) and four indicator species were selected.

Detrended Correspondence Analysis (DCA) was applied to the floristic data to estimate the compositional change along the main gradient as assessed by standard deviation (SD) units of turnover (detrending by segments, non-linear rescaling, and no downweighting of rare species). The dataset included 381 species. Species abundance data, measured as percent cover was square root transformed.

A Kruskal-Wallis test was conducted to test significant differences in soil temperatures between exposed ridges (ERs), leesides (LSs), and snowbeds (SBs) and a Mann-Whitney test was used to compare the types pairwise.

To explore the relationships between the small-scale vegetation groups classified by TWINSpan and the soil temperature variables, Principal Component Analyses (PCA) were conducted. All tempera-

ture based data was log transformed ($\log(x)$) and to data in °C, 21 was added before log transformation to avoid negative numbers.

Canonical Variates Analyses (CVA) were performed to estimate which soil temperature parameters discriminated best between the small-scale vegetation groups. Both forward selection and manual selection of the analyses were run.

Variation in soil temperatures and related parameters between and within LSs and SBs were overshadowed by the variation of the ERs. Therefore PCA and CVA were conducted twice, once including all small-scale vegetation groups and once only including small-scale vegetation groups belonging to LSs and SBs, excluding those of ERs.

All ordinations were performed by the use of CANOCO 4.5 (Ter Braak and Šmilauer 2002).

Results

Vegetation classification and floristic gradients

Based on the TWINSpan classification of the 60 study plots, 20 different small-scale vegetation groups were defined, representing different vegetation communities. The classified small-scale vegetation groups were arranged subjectively, according to their floristical composition, into the three main groups: ERs, LSs and SBs. This arrangement depended on the abundance of species typical for ERs (e.g. *Carex rupestris*, *Dryas octopetalla*, *Festuca ovina*), LSs (e.g. *Angelica archangelica*, *Geranium sylvaticum*, *Molinium caerulea*, *Salix lapponum*), and SBs (e.g. *Cerastium cerastoides*, *Phippsia algida*, *Salix herbacea*, *Saxifraga stellaris*, *Sibbaldia procumbens*) (cf. Nordhagen 1943, Gjørvoll 1956, Dierßen 1996).

The small-scale vegetation groups included one to eight study plots each. An overview of the

| Abbr. | Parameter | Unit |
|---------|---|----------------|
| Wmin | Minimum soil temperature during winter | °C |
| Wmea | Mean soil temperature during winter | °C |
| Wmax | Maximum soil temperature during winter | °C |
| Amin | Minimum soil temperature in April | °C |
| Amea | Mean soil temperature in April | °C |
| Smin | Minimum soil temperature during summer | °C |
| Smea | Mean soil temperature during summer | °C |
| Smax | Maximum soil temperature during summer | °C |
| GSmea | Mean soil temperature during growing season | °C |
| dsMELT | Day of the year when the study plot was melted out (threshold of 1°C soil temperature, in some cases adjusted to the observed date of snowmelt) | Julian day |
| dTR6 | Day of the year when soil temperature exceeded the threshold of 6°C | Julian day |
| dAUT | Day of the year when soil temperature dropped below the threshold of 1°C in autumn and remained there | Julian day |
| dSM-TR6 | Time period between snowmelt and the day when soil temperature exceeded the 6°C threshold | Number of days |
| dGSL | Growing season length | Number of days |

Table 1. Overview of all soil temperature parameters with abbreviations and measurement units used in the context of this study

| | Altitudinal range [m a.s.l.] | Vegetation description | |
|---|---------------------------------|--|----|
| A | 1073 | Late, wet <i>Deschampsia alpina</i> , <i>Eriophorum scheuzerii</i> snowbed | SB |
| B | 1395 - 1410 | Wet <i>Phippsia algida</i> snowbed | SB |
| C | 1390 - 1415 | Wet <i>Saxifraga rivularis</i> , <i>Ranunculus pygmaeus</i> snowbed | SB |
| G | 1453 - 1505 | Midalpine <i>Harimanella hypnoides</i> snowbed with <i>Silene acaulis</i> and <i>Salix herbacea</i> | SB |
| L | 1042 - 1449 | Early snowbed, graminoid dominated with <i>Salix herbacea</i> | SB |
| D | 1542 - 1547 | <i>Dryas octopetala</i> ridge with <i>Salix polaris</i> , and <i>Carex rupestris</i> | ER |
| E | 1555 - 1556 | <i>Dryas octopetala</i> ridge with <i>Oxytropis lapponum</i> | ER |
| F | 1396 - 1472 | <i>Dryas octopetala</i> ridge with <i>Kobresia myosuroides</i> , <i>Carex rupestris</i> , and <i>Festuca ovina</i> | ER |
| M | 1046 - 1051 | <i>Dryas octopetala</i> ridge with <i>Antenaria dioica</i> relatively poor in species | ER |
| H | 1097 - 1168 | Less exposed <i>Salix reticulata</i> ridge with <i>Dryas octopetala</i> | ER |
| I | 1347 - 1477 | Late herb meadow leeseide with <i>Bistorta vivipara</i> , <i>Parnassia palustris</i> , and <i>Salix reticulata</i> | LS |
| J | 1076 - 1449 | <i>Alchemilla</i> spp. with <i>Astragalus alpinus</i> and <i>Geranium sylvaticum</i> | LS |
| K | 1367 - 1392 | <i>Salix reticulata</i> , <i>Silene acaulis</i> , <i>Saussurea alpina</i> meadow | LS |
| O | 1068 - 1160 | Willow shrub with <i>Geranium sylvaticum</i> , <i>Saussurea alpina</i> and graminoids | LS |
| P | 1295 - 1325 | Willow shrub with tall herbs, <i>Geranium sylvaticum</i> , <i>Cirsium heterophyllum</i> and <i>Angelica archangelica</i> | LS |
| Q | 1024 - 1259 | Willow shrub with <i>Geranium sylvaticum</i> , <i>Alchemilla</i> spp. and <i>Ranunculus acris</i> | LS |
| N | 973 - 1017 | <i>Dryas octopetala</i> with <i>Nardus stricta</i> with a sparse tree canopy | LS |
| R | 870 - 946 | Tall herb meadow with <i>Aconitum lycotonum</i> and <i>Filipendula ulmaria</i> under a sparse tree canopy | LS |
| S | 779 - 806 | Tall herb, dense birch forest with <i>Aconitum lycotonum</i> and <i>Cicerbita alpina</i> | LS |
| T | 836 | Tall herb meadow <i>Aconitum lycotonum</i> under a sparse tree canopy | LS |

Table 2. Description of the classified TWINSpan groups (small-scale vegetation groups: A-T) with their altitudinal ranges and main classification into snowbeds (SB), exposed ridges (ER), and leesides (LS)

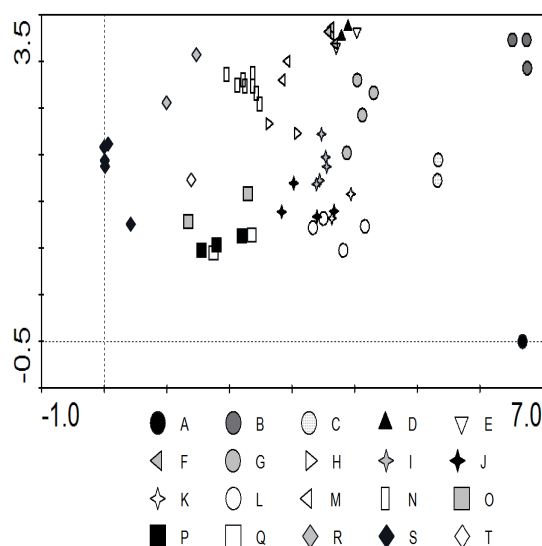


Fig. 2. Relative position of the studied plots (circles = snowbeds, triangles = exposed ridges, others = leesides), classified into 20 TWINSpan groups (small-scale groups: A-T), in relation to DCA axes 1 and 2. See Table 2 and Appendix for descriptions of the small-scale groups and for an overview of characteristic vascular plant species and snow gradient.

groups is given in Table 2. ERs included five small-scale groups D, E, F, H, and M, other five small-scale groups A, B, C, G, and L represented SBs and ten,

which were I, J, K, N, O, P, Q, R, S, and T were described as LS vegetation (Table 2 and Appendix).

A DCA was run to quantify the floristic variation and the main gradients in the dataset (Fig. 2). Gradient lengths and eigenvalues for DCA axes 1-3 were: 6.759/0.722, 3.374/0.428, and 2.907/0.300 respectively, with a total inertia of 9.307. The main vegetation gradient included mostly a variation from Northern Boreal tall herb birch forests and other LS vegetation groups close to the climatic forest limit over LSs at higher altitudes and ERs to chionophilous SB vegetation. SBs had relatively high scores on DCA axis one and ER had relatively high scores on DCA axis two. However, the vegetation transitions between ERs, LSs, and SBs appear to be continuous (Fig. 2).

Annual courses of soil temperatures

The annual courses of soil temperatures varied strongly between ERs, LSs and SBs as shown in Fig. 3.

During winter, soil temperatures fluctuated at ERs (Fig. 3a and e). The variation of winter soil temperatures followed air temperatures, although with smaller amplitudes. Soil temperatures did not drop as low as extreme low winter air temperatures. January 8 was the day when minimum soil temperature was measured in all plots at Finse, and February 22 in all plots at Haukelisetter (one exception: January 8 in the plot that reached lowest soil temperature at Haukelisetter, which was also the plot that melted out earliest and had the thinnest snow cover at Haukelisetter). The

increase in soil temperatures after snowmelt was, compared to SBs, relatively slow. During summer the courses of the soil temperature curves followed the variation in air temperatures.

Soil temperatures in LS vegetation plots remained either at ca. 0 °C (Fig. 3d) or dropped to until -5 °C (Fig. 3c) during winter. In those plots where soil temperatures dropped clearly below the freezing point, the days of minimum soil temperatures were February 21 and 22 at both Finse and Haukeliseter (one exception). Later in spring before snowmelt, the temperatures stabilised around 0 °C. After snowmelt soil temperatures in the LS plots increased rapidly. Soil temperatures in LS plots seemed to vary less during summer than soil temperatures in ERs and SBs.

In SB plots, soil temperatures remained at ca. 0 °C during the whole winter period and until the snow disappeared at the end of June or later (Fig. 3b and f). After snowmelt, soil temperatures increased rapidly and reached temperatures of >6 °C within three days (mean). During summer, soil temperature curves mostly followed the variation in air temperatures but soil temperatures could be clearly lower than air temperatures (Fig. 3f).

Soil temperature variations between ERs, LSs and SBs

All winter soil temperature parameters (Wmin, Wmax, Wmea, Amin, Amea, Smin) differed significantly between ERs, and SBs respectively LSs (Table 3, Fig. 4). This was most pronounced for Wmin (Fig. 4).

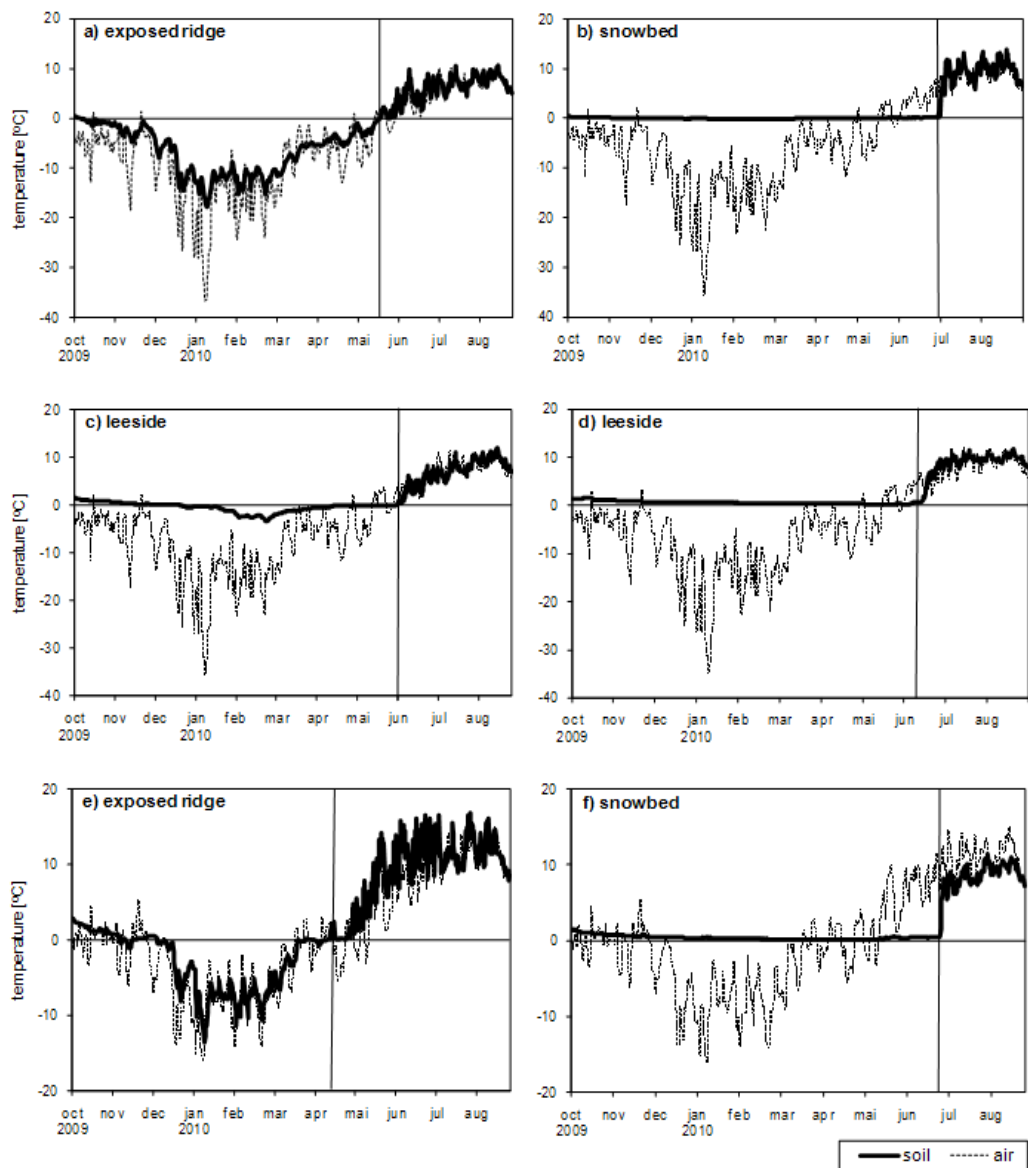


Fig. 3. Seasonal courses of soil temperatures (continuous line) and corresponding air temperatures (dashed line), using typical plots as examples to represent exposed ridges, leesides, and snowbeds at Finse (a-d) and at Haukeliseter (e-f). The vertical line marks the Julian day of snowmelt. Soil temperatures were recorded twice a day from October 2009 to August/ September 2010. Air temperature data was received from nearby weather stations and extrapolated to the respective altitude of each study plot.

The Julian day of snowmelt varied between the middle of April (Julian day 103) and the middle of July (Julian day 199) and was significantly different between ERs, LSs, and SBs (Table 3, Fig. 5 dSMELT).

Soil temperatures in SBs required a significantly shorter period to reach the 6 °C threshold after snowmelt than soil temperatures in ERs and LSs (Table 3). There was no significant difference between ERs and LSs but the time span tended to decrease gradually from ERs over LSs to SBs (Table 3, Fig. 5 dSM-TR6).

Mean growing season soil temperature was significantly highest in the LS vegetation but there was no significant difference in mean growing season soil temperature between ERs and SBs (Table 3, Fig. 4 GSmea). Maximum summer soil temperature showed the same trend, but without being significant (Table 3, Fig. 4 Smax). Mean summer soil temperature was significantly different between all groups and was lowest in SBs (Table 3, Fig. 4 Smea).

The growing season length lasted about three months (mean) in both, ER and LS vegetation. SBs had a significantly shorter growing season period of only two months (mean) (Table 3, Fig. 4 dGSL).

The Julian day when autumn temperature dropped permanently below 1 °C occurred significantly earlier in ERs and SBs than in LSs (Table 3, Fig. 5 dAUT).

PCA analyses of soil temperature parameters

A PCA was performed to show how soil temperature variables estimated for each plot were related to each other and to the different vegetation groups. Results based on soil temperature data from all study plots are shown in Fig. 6a. Eigenvalues for PCA axes 1-3 were 0.705, 0.208, and 0.062 respectively. PCA axis 1 was negatively correlated with soil winter temperatures

(e.g. Wmin). PCA axis 2 was negatively correlated with the variation in snowmelt date and positively correlated with the variation in growing season length. Most plots at ERs were associated with low winter temperatures. PCA axis 2 separated LSs and SBs. SBs were associated with late snowmelt and a short growing season, and LSs with an early snowmelt and a long growing season.

A PCA, where ERs were omitted, is shown in Fig. 6b. This analysis allowed a more detailed view on differences between plots and small-scale vegetation groups in SBs and LSs. The eigenvalues for axes 1-3 were 0.817, 0.092 and 0.035. PCA axis 1 included a gradient from long growing season to a late Julian day when soil temperature reached 6 °C, respectively the Julian day of snowmelt. In this analysis, winter temperatures were less relevant than in the PCA analysis which included ERs. All SBs were situated in the right, lower part of the PCA ordination diagram showing a late snowmelt, late Julian day when the threshold of 6 °C was reached, and a short time span between these two dates. The LS vegetation groups showed mainly a long growing season and a relatively early date of snowmelt.

For both PCA analyses, the study plots were labelled due to their association of the TWINSPAN small-scale groups. The soil temperature gradients as shown by PCA axes 1 and 2 fitted well with the floristic gradients represented in the TWINSPAN classification and the DCA ordination diagram (Fig. 2 and 6b).

Relationship between small-scale vegetation groups and soil temperatures

CVAs combined with Monte Carlo permutation tests were run to investigate which of the soil temperature variables were significant for the separation of the 20 small-scale vegetation groups (Table 4). The analysis of all small-scale vegetation groups showed that all variables were significant, except maximum temperature in summer and winter (Smax, Wmax), the time period between Julian day of snowmelt and the Julian day when the threshold of 6 °C in soil temperature was reached (dSM-TR6) and the Julian day when 1 °C was reached in autumn (dAUT). Minimum temperatures in April were most important to distinguish the small-scale vegetation groups (Table 4a: ER-LS-SB conditional effects). When each variable was analysed separately, all were significant (Table 4a: ER-LS-SB marginal effects).

To distinguish between small-scale vegetation groups when ERs were included, mainly winter temperatures (such as Amin, Smin, Wmea and Wmin) were significant. However, when only SBs and LSs were included, factors related to summer temperatures (such as dGSL, GSmea, Smea) were most important (Table 4b: LS-SB conditional effects). Also the marginal effects showed the same trend (Table 5 LS-SB marginal effects).

Specific soil temperature parameters of all small-scale vegetation groups are given in Table 5.

Discussion

Climate conditions during winter 2009/2010

Between December and February 2009/2010 air temperature and precipitation at Finse and Haukelisetter

| | Kruskal-Wallis test | Mann-Whitney test | | |
|---------|---------------------|-------------------|--------|--------|
| | | ER-LS | SB-LS | ER-SB |
| Amin | <0.001 | <0.001 | 0.353 | <0.001 |
| dGSL | <0.001 | 0.851 | <0.001 | <0.001 |
| Smin | <0.001 | <0.001 | 0.164 | 0.011 |
| dTR6 | <0.001 | 0.068 | <0.001 | <0.001 |
| Wmea | <0.001 | <0.001 | 0.937 | <0.001 |
| GSmea | <0.001 | <0.001 | 0.016 | 0.076 |
| Amea | <0.001 | <0.001 | 0.143 | 0.003 |
| Wmin | <0.001 | <0.001 | 0.382 | <0.001 |
| Smea | <0.001 | 0.029 | <0.001 | 0.011 |
| dSMELT | <0.001 | 0.002 | <0.001 | <0.001 |
| Smax | 0.089 | 0.039 | 0.208 | 0.503 |
| Wmax | <0.001 | <0.001 | 0.008 | 0.013 |
| dSM-TR6 | 0.002 | 0.065 | 0.019 | <0.001 |
| dAUT | <0.001 | 0.001 | <0.001 | 0.63 |

Table 3. Significance (p-values) for soil temperature parameter variation (abbreviations are explained in Table 1) between exposed ridges (ER), leesides (LS) and snowbeds (SB)

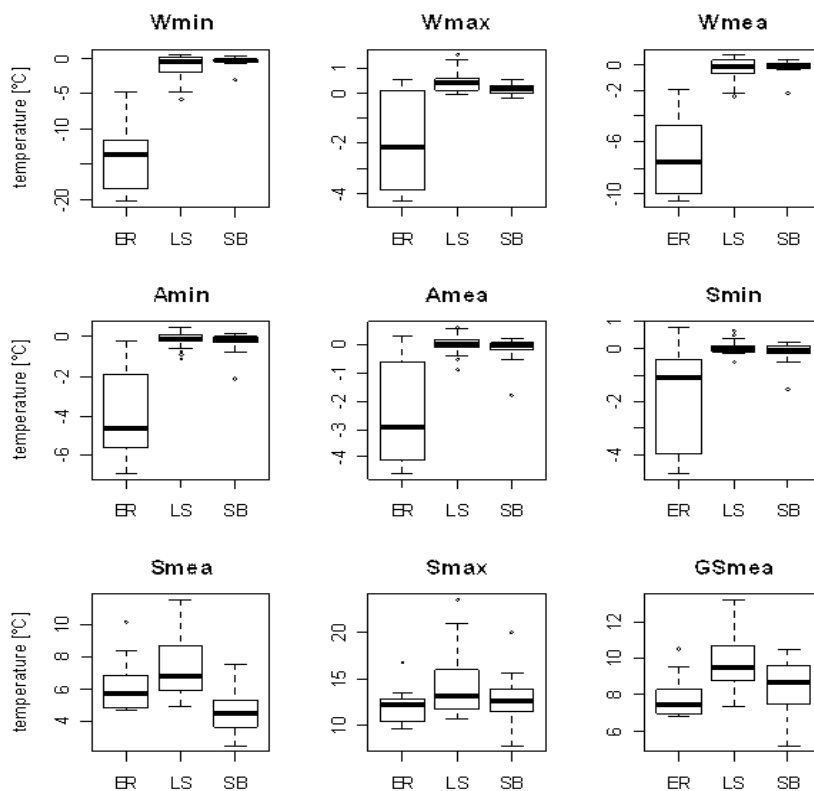


Fig. 4. Soil temperature parameters (abbreviation are explained in Table 1) with medians, 25th and 75th percentiles, maximum and minimum values, and outliers ordered by the main groups exposed ridges (ER), leesides (LS), and snowbeds (SB). The Kruskal-Wallis test showed that all soil temperature parameters except maximum soil temperature during summer (Smax) were significantly different between the three classification groups (Table 4).

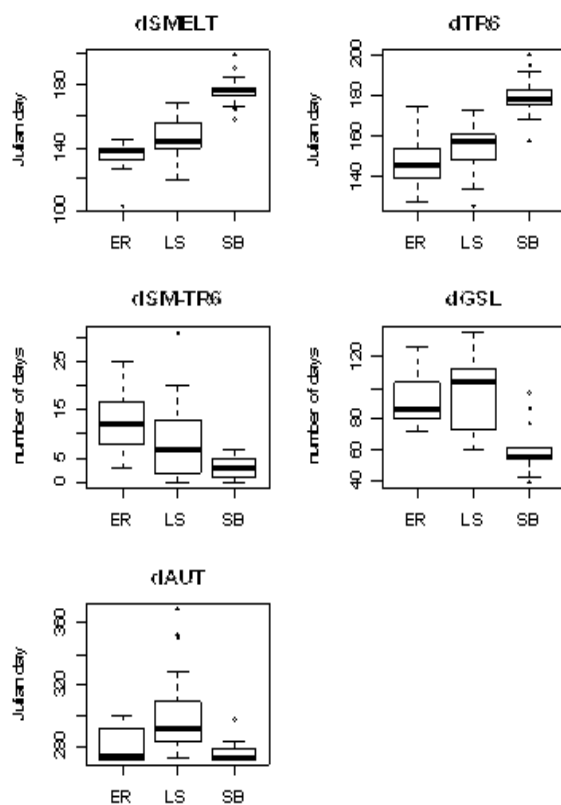


Fig. 5. Soil temperature parameters (abbreviation are explained in Table 1) with medians, 25th and 75th percentiles, maximum and minimum values, and outliers, ordered by the main groups exposed ridges (ER), leesides (LS), and snowbeds (SB). The Kruskal-Wallis test showed that all parameters were significantly different between the three classification groups (Table 4).

were lower than normal (1961-1990, data provided by the Norwegian Meteorological Institute). Less snow cover than normal implied less protection of the ground from lower air temperatures. This was particularly obvious in soil temperatures at LSs. At wind exposed sites, less snowfall than normal was expected to have little effect because of snowdrift. The snow, regardless of depth, was expected to be blown away anyway. In 2009/2010 soil temperature at ERs dropped below -20°C at its most extreme. In the previous year minimum soil temperatures at ERs were about $6-7^{\circ}\text{C}$ higher (Reinhardt, unpublished). At LSs, soil temperatures could drop to almost -5°C in 2009/2010, compared to the year before when all remained close to 0°C (Reinhardt, unpublished). In years with cold winters and/ or less snowfall, the variation in soil temperatures between different vegetation groups within LS vegetation becomes more pronounced than in milder winters. The Julian day of snowmelt in the study plots did not show significant variations between winter 2009/2010 and the previous winter (Reinhardt, unpublished).

Soil temperature variation between ER, LS, and SB

Our results, showing winter soil temperatures in SBs remaining at ca. 0°C whereas soil temperatures at ERs dropped far below the freezing point, are supported by previous studies (e.g. May *et al.* 1982, Körner *et al.* 2003, Björk and Molau 2007, Wundram *et al.* 2010). On snow covered sites a snowpack of 0.5 to 0.8 m insulates the ground from low air temperatures and causes stable soil temperatures at ca. 0°C (Dahl 1956, Salisbury 1985). Körner *et al.* (2003), who could not find a latitudinal trend through Europe in minimum soil temperatures, concluded that the differences in soil winter temperatures were associated with variable snow cover.

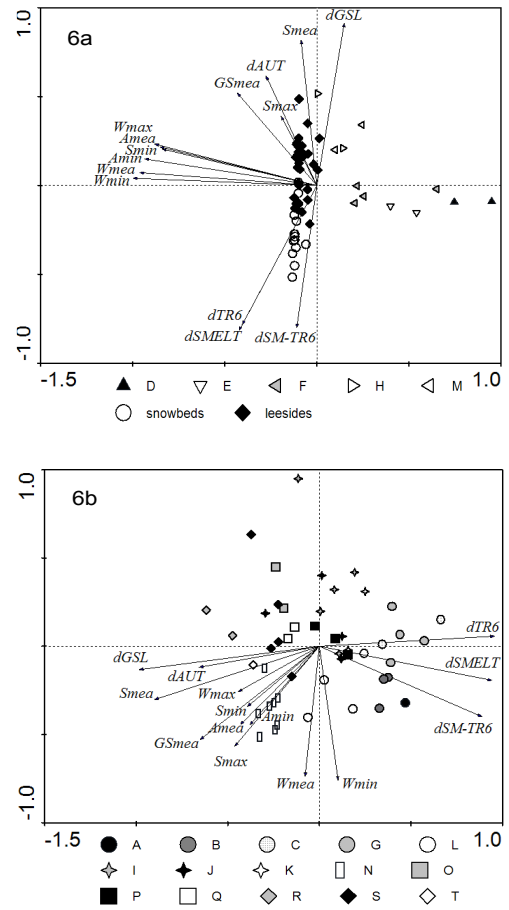


Fig. 6a and b. PCA axes 1 and 2 showing the relation of soil temperature parameters (abbreviations are explained in Table 1) to each other, and the vegetation groups (snowbeds (SB) = circles, leesides (LS) = rectangles/ stars, exposed ridges (ER) = triangles). The different small-scale vegetation groups A-T are described in Table 2 and 3. In Fig. 6b ER were omitted.

| | a: ER – LS - SB | | | | | | b: LS - SB | | | | | |
|-------------------|---------------------|--------|------|------------------|--------|------|---------------------|--------|------|------------------|--------|------|
| | Conditional effects | | | Marginal effects | | | Conditional effects | | | Marginal effects | | |
| | LaA | P | F | La1 | P | F | LaA | P | F | La1 | P | F |
| A _{min} | 0.98 | <0.001 | 3.15 | 0.98 | <0.001 | 3.15 | 0.37 | 0.113 | 1.57 | 0.58 | 0.042 | 1.99 |
| dGSL | 0.89 | <0.001 | 2.98 | 0.90 | <0.001 | 2.87 | 0.68 | <0.001 | 2.63 | 0.91 | <0.001 | 3.19 |
| S _{min} | 0.89 | <0.001 | 3.05 | 0.97 | <0.001 | 3.11 | 0.22 | 0.496 | 0.96 | 0.52 | 0.059 | 1.77 |
| dTR6 | 0.75 | <0.001 | 2.69 | 0.86 | <0.001 | 2.73 | 0.48 | 0.021 | 1.92 | 0.90 | <0.001 | 3.16 |
| W _{mea} | 0.74 | <0.001 | 2.69 | 0.97 | <0.001 | 3.13 | 0.11 | 0.924 | 0.48 | 0.56 | <0.011 | 1.92 |
| GS _{mea} | 0.63 | <0.001 | 2.37 | 0.85 | <0.001 | 2.71 | 0.63 | 0.002 | 2.40 | 0.81 | <0.001 | 2.82 |
| A _{mea} | 0.60 | 0.005 | 2.31 | 0.96 | <0.001 | 3.09 | 0.44 | 0.024 | 1.89 | 0.59 | 0.032 | 2.03 |
| W _{min} | 0.60 | 0.004 | 2.38 | 0.92 | <0.001 | 2.96 | 0.40 | 0.058 | 1.64 | 0.55 | 0.023 | 1.88 |
| S _{mea} | 0.55 | 0.011 | 2.20 | 0.90 | <0.001 | 2.87 | 0.91 | <0.001 | 3.19 | 0.91 | <0.001 | 3.19 |
| dSMELT | 0.45 | 0.021 | 1.84 | 0.88 | <0.001 | 2.83 | 0.77 | <0.001 | 2.81 | 0.89 | <0.001 | 3.13 |
| S _{max} | 0.34 | 0.148 | 1.40 | 0.72 | <0.001 | 2.28 | 0.42 | 0.069 | 1.71 | 0.72 | <0.001 | 2.50 |
| W _{max} | 0.31 | 0.190 | 1.33 | 0.94 | <0.001 | 3.02 | 0.34 | 0.157 | 1.43 | 0.62 | 0.003 | 2.14 |
| dSM-TR6 | 0.29 | 0.256 | 1.19 | 0.70 | 0.011 | 2.23 | 0.28 | 0.267 | 1.22 | 0.81 | <0.001 | 2.81 |
| dAUT | 0.24 | 0.409 | 1.03 | 0.63 | 0.002 | 1.99 | 0.18 | 0.709 | 0.77 | 0.58 | 0.006 | 1.99 |

Table 4. Results of the CVA: significance (p-values) for soil temperature parameter variation (abbreviations are explained in Table 1) between small-scale vegetation groups (a = all groups included, b = only LS and SB groups included; ER = exposed ridges, LS = leesides, SB = snowbeds)

| | N | Amin [° C] | dGSL [days] | Smin [° C] | dTR6 [Julian day] | Wmea [° C] | GSmea [° C] | Smea [° C] | dSMELT [Julian day] | Wmin [° C] | Smax [° C] |
|-----|----|---------------|----------------|---------------|-------------------------|---------------|----------------|---------------|---------------------------|---------------|---------------|
| All | 60 | -0.9 ±1.9 | 87 ±24 | -0.4 ±1.1 | 159 ±16 | -1.7 ±3.2 | 9.2 ±1.9 | 6.5 ±2.1 | 151 ±19 | -3.6 ±5.9 | 13.4 ±2.9 |
| SB | 14 | -0.3 ±0.6 | 60 ±16 | -0.2 ±0.4 | 180 ±11 | -0.2 ±0.6 | 8.6 ±1.5 | 4.6 ±1.3 | 177 ±10 | 0.4 ±0.8 | 12.8 ±2.8 |
| A | 1 | 0.1 | 55 | 0.1 | 200 | 0.1 | 8.4 | 3.6 | 199 | 0.1 | 12.1 |
| B | 3 | 0.0 ±0.1 | 56 ±2 | 0.0 ±0.1 | 178 ±2 | -0.1 ±0.1 | 9.8 ±0.2 | 5.1 ±0.3 | 175 ±2 | 0.2 ±0.0 | 16.0 ±3.4 |
| C | 2 | 0.1 ±0.1 | 48 ±12 | 0.1 ±0.1 | 187 ±12 | 0.2 ±0.0 | 6.3 ±1.5 | 3.2 ±1.1 | 183 ±11 | 0.0 ±0.0 | 9.2 ±1.9 |
| G | 4 | -0.9 ±0.8 | 50 ±6 | -0.6 ±0.6 | 183 ±6 | -0.7 ±1.0 | 8.0 ±0.7 | 3.7 ±0.3 | 179 ±4 | -0.1 ±1.5 | 11.8 ±0.9 |
| L | 4 | -0.1 ±0.2 | 81 ±15 | -0.1 ±0.2 | 169 ±7 | -0.1 ±0.3 | 9.3 ±0.9 | 5.9 ±1.2 | 167 ±8 | -0.3 ±0.3 | 13.3 ±1.7 |
| ER | 12 | -4.0 ±2.3 | 92 ±18 | -1.8 ±2.0 | 148 ±13 | -7.4 ±3.0 | 7.9 ±1.2 | 6.2 ±1.7 | 134 ±11 | -141 ±46 | 12.1 ±1.9 |
| D | 2 | -6.8 ±0.2 | 92 ±1 | -4.7 ±0.1 | 140 ±1 | -10.6 ±0.0 | 6.9 ±0.1 | 5.5 ±0.0 | 136 ±3 | -19.8 ±0.6 | 12.3 ±0.2 |
| E | 2 | -5.6 ±0.1 | 78 ±4 | -4.0 ±0.1 | 154 ±4 | -10.1 ±0.3 | 6.9 ±0.1 | 4.8 ±0.2 | 140 ±0 | -17.0 ±1.3 | 11.4 ±1.2 |
| F | 4 | -4.5 ±0.7 | 83 ±9 | -1.0 ±0.3 | 151 ±9 | -8.0 ±1.2 | 7.8 ±0.6 | 5.9 ±0.8 | 140 ±4 | -14.3 ±3.1 | 11.7 ±1.2 |
| M | 2 | -0.5 ±0.4 | 121 ±9 | 0.4 ±0.6 | 134 ±9 | -4.7 ±0.6 | 10.0 ±0.7 | 9.3 ±1.3 | 116 ±18 | -11.5 ±3.0 | 15.0 ±2.6 |
| H | 2 | -1.9 ±0.1 | 97 ±24 | -0.5 ±0.6 | 157 ±26 | -3.1 ±1.7 | 7.7 ±0.6 | 5.9 ±1.6 | 136 ±13 | -7.7 ±4.2 | 11.7 ±2.8 |
| LS | 34 | -0.1 ±0.3 | 96 ±22 | 0.0 ±0.2 | 155 ±11 | -0.4 ±0.8 | 9.7 ±1.5 | 7.5 ±1.9 | 146 ±11 | -1.2 ±1.8 | 14.1 ±3.1 |
| I | 5 | -0.4 ±0.2 | 73 ±8 | -0.1 ±0.1 | 162 ±7 | -1.2 ±0.8 | 8.1 ±0.6 | 5.5 ±0.4 | 154 ±5 | -3.0 ±1.9 | 12.6 ±1.9 |
| J | 4 | -0.1 ±0.1 | 80 ±18 | -0.1 ±0.1 | 161 ±9 | -0.2 ±0.2 | 9.6 ±0.5 | 6.6 ±1.1 | 154 ±9 | -0.6 ±0.4 | 12.6 ±1.1 |
| K | 2 | -0.5 ±0.6 | 65 ±4 | -0.3 ±0.3 | 171 ±4 | 0.8 ±0.9 | 9.3 ±0.2 | 5.4 ±0.6 | 159 ±1 | -2.4 ±2.8 | 12.0 ±0.2 |
| O | 2 | -0.2 ±0.1 | 100 ±1 | -0.1 ±0.1 | 149 ±8 | -1.2 ±0.5 | 9.5 | 7.5 ±0.5 | 137 ±4 | -3.9 ±1.1 | 12.6 ±1.1 |
| P | 3 | 0.2 ±0.2 | 73 ±7 | 0.1 ±0.1 | 165 ±7 | 0.2 ±0.3 | 9.6 ±0.6 | 6.2 ±0.3 | 161 ±9 | 0.1 ±0.5 | 12.5 ±0.9 |
| Q | 2 | 0.0 ±0.1 | 95 ±3 | 0.0 ±0.1 | 159 ±0 | 0.1 ±0.2 | 9.1 ±1.3 | 6.7 ±1.3 | 147 ±11 | -0.2 ±0.1 | 12.1 ±1.8 |
| N | 8 | 0.1 ±0.2 | 112 ±4 | 0.2 ±0.3 | 146 ±4 | 0.5 ±0.2 | 11.6 ±1.0 | 9.6 ±1.0 | 143 ±3 | 0.3 ±0.2 | 18.2 ±3.0 |
| R | 2 | 0.3 ±0.3 | 132 ±6 | 0.3 ±0.3 | 130 ±6 | 0.0 ±1.0 | 11.9 ±0.7 | 11.4 ±0.3 | 126 ±2 | -1.1 ±2.1 | 17.2 ±1.7 |
| S | 5 | 0.0 ±0.1 | 110 ±5 | 0.0 ±0.1 | 155 ±11 | -0.8 ±0.8 | 9.1 ±0.7 | 6.7 ±0.6 | 146 ±11 | -1.9 ±2.2 | 14.1 ±3.1 |
| T | 1 | 0.0 | 123 | 0.0 | 140 | 0.5 | 9.9 ±0.6 | 8.6 | 140 | 0.2 | 13.2 |

Table 5. Soil temperature parameters (mean and standard deviation) that showed a significant variation between small-scale vegetation groups, and minimum and maximum temperatures in the small-scale groups (abbreviations of the soil temperature parameters are explained in Table 1). The small-scale vegetation groups (A-T, described in Table 2 and 3) were arranged as snowbeds (SB), exposed ridges (ER), and leesides (LS)

In LSs the lowest soil temperatures were measured in the middle of February both at Finse and Haukelisetter, whereas in extremely ERs lowest soil temperatures were measured in the beginning of January (compare Fig. 3a extreme ER with Fig. 3c LS, both at Finse). The time lag between air- and soil temperatures in LSs and less ERs indicates that a snow layer was protecting these sites, although this snow layer was a relatively thin layer compared to those sites where soil temperature remained close to 0 °C during the whole winter.

In April the differences between ERs and SBs were less pronounced than during winter because temperatures in ridges had already started to rise towards 0 °C due to warmer air temperatures. The Julian day when the threshold of 6 °C soil temperature was reached was correlated with the Julian day of snowmelt, which was earliest in ERs, but also relatively early in LSs. But the time span between the date of snowmelt and the date when soil temperature exceeded the threshold was significantly longer in ERs (13 days ±7.2) than in SBs (3 days ±2). LS soils needed 9 days (±8) to reach the threshold. Odland and Munkejord (2008) found that the soil in some ERs needed more than 60 days to

reach the 6 °C threshold after snowmelt. These sites were comparable to the sites at ERs in the present study, but our plots had a thinner humus layer and accordingly less water content, inhibiting deep freezing. It has been shown by Bonan (1992) that freezing depth strongly regulates the time period needed to thaw the soil. Odland and Munkejord (2008) found a time span of 4 to 8 days (mean values) to reach the 6 °C threshold after snowmelt in SBs and 6 to 18 days (mean values) in LSs. The short time span in SBs is a response to high air temperatures, since SBs are melting out relatively late in the year. Soil temperatures remaining below 6 °C for a longer period after snowmelt, as in ERs, prevent plants from becoming biologically active until late spring and thereby protect them from severe freezing damage. Freeze-thaw related damage of fine roots may affect plant performance (Rixen *et al.* 2008). Earlier studies in northern and alpine areas have shown that net growth and/or nutrient uptake was very low at soil temperatures below 5-7 °C (e.g. Kaspar and Bland 1992, Karlsson and Nordell 1996, Rabenhorst 2005, Alvarez-Uria and Kömer 2007). The Julian day when the threshold of 6 °C soil temperature was reached was used

to determine the theoretical beginning of growing season in our study. However the temperature when plants become photosynthetically active may differ between species. Some vascular plant species are able to carry out photosynthesis at colder temperatures and under snow, as long as they are not frozen and the snow allows light transmission (Marchand 1987).

Comparisons of growing season lengths are difficult because different definitions might have been used in different studies. Odland (2011) showed that variation in growing season length is highly variable primarily because start and end of the growing season have been defined differently. He demonstrated that the variation in growing season length based on three estimation methods was higher than its variation between different vegetation types. The growing season length we estimated ranged from 39 to 136 days, and the mean soil temperature during the growing season in all studied plots was 9.2 °C. Körner *et al.* (2003) found an average of about 120 days for the growing season length in alpine Europe, and mean soil temperatures during the growing season ranged between 5.7 °C and 11.6 °C. They maintained that shorter seasons could be found in the Scandes. In the Southern Rocky Mountains, May and Webber (1982) found a growing season length of 50 to 110 days for alpine vegetation. Due to the growing season definition that we used in the present study, Odland (2011) estimated a growing season length of 69 days in a late SB vegetation type and 114 days in LS vegetation, ERs showed growing season lengths between 93 and 112 days.

During summer it could be expected that the relationship between vegetation and soil temperatures are interactive. Soil temperature conditions affect vegetation composition and on the other hand vegetation cover affects soil temperatures. This might explain why there were only small differences in summer soil temperatures between LS vegetation groups, which tended to be located at low altitudes, and ERs, respectively SBs, mainly located at higher altitudes with lower air temperatures. The shading plant canopy in the LSs might even out warmer air temperatures at lower altitudes. Ballard (1972) found that temperature amplitude differences between sites of bare ground, evergreen shrub, herbaceous meadow, single tree, and tree clump in a subalpine area of British Columbia strongly reflected differences in plant cover. Soil temperatures measured 5 cm below ground showed highest diurnal amplitudes on bare ground and lowest diurnal amplitudes under the tree clump. The seasonal development of the herbaceous meadow with a considerable decline in diurnal soil temperature amplitude, followed by a slight rise in amplitude in the fall when vegetation died back strengthen the assumption that vegetation cover affects soil temperatures. Anyway there are discussions about to what degree vegetation cover influences soil temperatures. Karlsson and Weih (2001) found that summer soil temperatures were slightly but not significantly higher in heathlands than under birch trees. And Scherrer and Körner (2010) only found a weak influence of vegetation on soil temperature, and soil temperatures were mainly affected during

the nights. Sites with more bare ground had low soil temperatures because of radiative cooling under clear sky conditions which is reduced under a closed plant cover.

Seepage water may play an important role for soil temperatures during spring and summer, particularly in SBs, but also in LSs. Since exposed sites are often located on ridges, seepage water is of little importance there. Walker *et al.* (1994) found soil moisture to be important for determining plant species distribution and the composition of different plant communities in the alpine.

Soil temperature variation between small-scale vegetation groups

The results of this study indicate that soil temperature and floristic gradients of the small-scale vegetation groups are well correlated. Soil temperatures are quite similar in study plots belonging to the same vegetation groups. Also Scherrer and Körner (2011) showed from a study in the Swiss central Alps that similar soil temperatures occur at similar vegetation units.

Since vegetation composition seems to be correlated with soil temperatures, the question arises which soil temperature factors are most important to distinguish between different vegetation groups. The conditional effects showed that minimum temperature in April was best to explain differences between the vegetation groups when all study plots were included. Only considering LSs and SBs, the date of snowmelt (when soil temperature reached the 1 °C threshold) was most important. Thus spring soil temperatures, or the soil temperatures in the snowmelt period were most relevant to distinguish between the small-scale vegetation groups and autumn temperatures were of no importance. May and Webber (1982), who studied six different alpine vegetation groups in the Southern Rocky Mountains, found that only during late summer to autumn period (August-October) the soil temperatures were similar in all studied vegetation groups.

Our study shows that winter soil temperatures are of importance for the vegetation composition. Weih and Karlsson (2002) found that low winter soil temperatures affected the nutrient uptake and growth rate of mountain birch seedlings. But why are winter temperatures important when vegetation is dormant anyway (Körner and Paulsen 2004)? An explanation might be that the crucial soil temperature conditions in the spring and early summer are associated with the winter soil temperatures.

Previous studies have shown that soil temperatures remained around the freezing point in SBs. The present study confirms these findings, and reveals in addition that there are differences in soil winter temperatures in SBs anyway, since in some study plots soil temperatures dropped below the freezing point and in others they remained above. Soil temperature in SBs that already dropped below 0 °C in early winter evened out at a temperature just below 0 °C. Whereas those SBs in which soil temperatures did not drop below 0 °C earlier also made it through the whole winter without freezing. Björk and Molau (2007) pointed out that air and soil temperatures during the days before a site is covered with snow might be important for the soil temperature conditions for the whole winter period.

The Julian day of snowmelt within SBs varied

approximately one month and fits well with dates summarized by Björk and Molau (2007) who found that the Julian day of snowmelt occurred between Mid-June in light snowpack zones and Mid-July in very snow rich SBs.

The mean growing season length in SB small-scale vegetation groups showed large variation (48 and 81 days) and one group had a longer growing season than estimated in some of the LS and ERs vegetation groups. Based on the same estimations for start and end of growing season, Odland (2011) found a growing season length between 69 and 86 days in late snowbeds and 78 to 95 days in early snowbeds, in a year with warmer spring temperatures than normal. Galen and Stanton (1995) estimated a growing season length variation in SBs between ca. 50 days on early melting sites and 35 days on late melting sites. As discussed above, differences in length of the growing seasons are difficult to compare because of different estimation methods (Odland 2011).

The very low summer maximum soil temperature and growing season mean temperature in vegetation group C was probably a result of cold seepage water from upper snow patches. In SB vegetation group G lower soil temperatures were measured in April than during the winter period. In Walker et al. (2001) found similar observations, plant temperatures were lower after the melt had begun than during the time when the sites were still covered with snow.

Some of the LS vegetation groups were located below the climatic forest limit, but with sparse tree canopy and variable understory (groups N, O, and T). Mean soil temperature during the growing season varied between 9.5 and 11.6 °C. Lower growing season soil temperatures occurred in very dense tall herb vegetation of *Aconitum lycotonum*. Higher growing season soil temperatures were reached in very open vegetation and also there the highest maximum summer soil temperatures were found (Table 5). The understory vegetation cover, besides tree cover, seemed to be very important for soil temperature conditions. Körner and Paulsen (2004) conducted a study of high altitude treeline temperatures, with temperature loggers located in the deep shade of the trees, unlike our study, and found a seasonal mean soil temperature of 6.7 °C worldwide, and a bit lower in subarctic and the boreal zone. Other studies have given similar results (Mook and Vorren 1996, Gehrig-Fasel et al. 2008).

Soil temperatures and climate change

Warmer air temperatures and more precipitation are expected in Norway in the future (IPCC 2007, Hansen-Bauer et al. 2009). For Norwegian mountain areas in particular this may imply a thicker maximum snow cover during winter, but an earlier snowmelt and a longer growing season (Hansen-Bauer et al. 2009). Hence most effects of climate changes are predicted for the periods of the year when soil temperatures differ most significantly in relation to vegetation, as found in this study. Previous studies found that climate warming will implicate an altitudinal upward shift of plant species (e.g. Walther 2003, Kullman 2010) and endanger low competitive mountain plant species because they do not have

the possibility to climb higher than on the highest mountain summits (Sætersdal et al. 1998). In the present study it was found that soil temperatures may be highly different within the same altitudinal levels. This supports the hypothesis of Scherrer and Körner (2011) who maintained that due to the topographic and consequential micro thermal variability in mountain areas, mountains could be safer places for many species than lowland terrain in a warmer world. Plant species will find thermally suitable niches within short distances that fit to their temperature demand.

Conclusions

1. The presented results confirm that annual soil temperature patterns differ between exposed ridges, leesides and snowbeds. In exposed ridges, winter soil temperatures varied, whereas they remained around 0 °C in snowbeds. Winter soil temperatures in leesides remained either around 0 °C or dropped clearly below, but not as low as in exposed ridges. Growing season mean soil temperature was highest in leesides, and lowest in exposed ridges at high altitudes. Snowbeds were melted out latest but the soils warmed up faster than in leesides and exposed ridges. The growing season length was shorter in snowbeds than in leesides and exposed ridges.
2. There were significant differences in soil temperatures between the 20 small-scale vegetation groups, separated within exposed ridges, leesides, and snowbeds. Plant species composition was highly correlated with soil temperatures, confirming that soil temperatures in relation to the amount of snow and topography, are important factors for the composition of mountain vegetation.
3. Soil temperature conditions during the snowmelt period, followed by growing season and winter conditions were most important to distinguish between small-scale vegetation groups. Soil temperatures during autumn were not important. Spring, summer and winter are the periods of the year that are predicted to be most affected by climate warming in Norwegian mountains, thus changes in mountain vegetation on local scales can be expected in the future.

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APPENDIX

Classified TWINSPAN groups (small-scale vegetation groups: A-T) with corresponding taxa (381 in total, only 62 vasculars shown in this table). Relative species occurrence and abundance of each species within the different groups are given as percentage of their maximum possible value (SOA). Species above the highest possible cut-level (6 which is 60 %) in all plots in a particular group would get a SOA value of 100. N samples = number of plots belonging to each group; n Finse respectively Haukelisetser = number of samples in the particular study area. A main classification into ER=exposed ridges, LS = leesides, and SB = snowbeds is given due to floristical composition.

| TWINSPAN group | A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T |
|-------------------------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|
| n samples | 1 | 3 | 2 | 2 | 2 | 4 | 4 | 2 | 5 | 4 | 2 | 4 | 2 | 8 | 2 | 3 | 2 | 2 | 5 | 1 |
| n Finse | | 3 | 2 | 2 | 2 | 4 | 4 | | 5 | 3 | 2 | 1 | | | 3 | 1 | | 5 | | |
| n Haukelisetser | 1 | | | | | | | 2 | | 1 | | 3 | 2 | 8 | 2 | | 1 | 2 | | 1 |
| classification | SB | SB | SB | ER | ER | ER | SB | ER | LS | LS | LS | SB | ER | LS | LS | LS | LS | LS | LS | LS |
| <i>Deschampsia alpina</i> | 33 | 33 | 33 | | | | 4 | 7 | 13 | 25 | | | | | | | | | | |
| <i>Cerastium cerastoides</i> | 17 | 39 | 17 | | | | 4 | | | | | 8 | | | | | | | | |
| <i>Ranunculus pygmaeus</i> | | 11 | 8 | | | | | | | | | 4 | | | | | | | | |
| <i>Carex lachenalii</i> | 33 | 22 | 17 | | | | | | | 8 | 4 | | | | | | | | | |
| <i>Eriophorum scheuzerii</i> | 33 | | | | | | | | | | | | | | | | | | | |
| <i>Juncus biglumis</i> | | 22 | 25 | | | | 4 | | | | 8 | | | | | | | | | |
| <i>Phippsia algida</i> | | 28 | | | | | | | | | | | | | | | | | | |
| <i>Saxifraga rivularis</i> | | 11 | 8 | | | | | | | | | | | | | | | | | |
| <i>Saxifraga stellaris</i> | 17 | 44 | 25 | | | | | | | | | 4 | | | | | | | | |
| <i>Dryas octopetala</i> | | | | 33 | 33 | 54 | 8 | 33 | | | | | 67 | 60 | | | | | | |
| <i>Antenaria dioica</i> | | | | 8 | | 4 | 4 | 17 | 10 | 8 | | | 25 | 29 | | | | | | |
| <i>Molinia caerulea</i> | | | | | | | | | | | | | | 35 | | | | | | |
| <i>Salix polaris</i> | | | 17 | 42 | 17 | | 8 | | | | 17 | | | | | | | | | |
| <i>Carex rupestris</i> | | | | 50 | 17 | 38 | | | | | | | | | | | | | | |
| <i>Festuca ovina</i> | | | | | 8 | 38 | 25 | | 13 | 4 | 8 | | 8 | | | | | | | |
| <i>Harrimanella hypnoides</i> | | | | | | | 54 | | | | | | | | | | | | | |
| <i>Kobresia myosuroides</i> | | | | | | 29 | | | | | | | | | | | | | | |
| <i>Oxytropis lapponum</i> | | | | 17 | 25 | 4 | | | 10 | | | | | | | | | | | |
| <i>Cerastium alpinum</i> | | | | 33 | 17 | 8 | 13 | 8 | 7 | 8 | | 4 | | | | | | | | |
| <i>Silene acaulis</i> | | | | 42 | 50 | 42 | 42 | 25 | 37 | 29 | 50 | | 17 | | | | | | | |
| <i>Salix reticulata</i> | | | | 25 | 42 | 33 | 38 | 42 | 40 | 33 | 50 | | | | | 6 | | | | |
| <i>Juncus trifidus</i> | | | | | | 4 | 8 | 25 | 17 | | | 4 | 17 | 2 | | | | | | |
| <i>Salix herbacea</i> | | | 8 | 17 | 33 | | 58 | 25 | 20 | 21 | 8 | 63 | | 2 | | 6 | 8 | | | |
| <i>Thalictum alpinum</i> | | | 8 | 33 | 25 | 21 | 29 | | 43 | 42 | 50 | 4 | 25 | 6 | | | | | | |
| <i>Sibaldia procumbens</i> | | | 8 | | | | 8 | | 10 | 4 | 8 | 29 | | | | | | | | |
| <i>Festuca vivipara</i> | | | | 33 | 42 | | 4 | 17 | 3 | | | | 17 | | 8 | | | 8 | | |
| <i>Parnassia palustris</i> | | | | | | 13 | | 8 | 47 | 33 | 17 | | | | 8 | 6 | | | | |
| <i>Potentilla crantzii</i> | | | | 17 | 25 | 8 | 17 | 17 | 27 | 8 | | 4 | | 2 | 8 | | | 8 | | |
| <i>Leontodon autumnalis</i> | | 6 | 8 | | | | 4 | | 27 | 29 | 25 | 25 | | 8 | | 17 | | | | |
| <i>Bistorta vivipara</i> | | | 8 | 42 | 50 | 33 | 42 | 17 | 57 | 42 | 42 | 29 | 17 | 17 | 8 | 6 | 17 | | | 17 |
| <i>Euphrasia wettsteinii</i> | | | | 17 | | 8 | 17 | 8 | 23 | 25 | 17 | 4 | 17 | 4 | | 11 | 8 | 8 | | |
| <i>Poa alpina</i> | 17 | 6 | 17 | | | | 13 | 8 | 33 | 21 | 17 | 25 | | 8 | | 11 | | | | |
| <i>Carex bigelowii</i> | | | | 8 | 8 | 25 | 13 | 17 | 23 | 13 | 33 | 8 | 17 | 2 | | | 17 | | | |
| <i>Oxyria dygina</i> | | | 8 | | | | | | | | | 25 | | | | | | | | |
| <i>Bartsia alpina</i> | | | | 17 | 25 | 17 | 25 | 17 | 30 | 17 | 8 | 8 | 8 | 21 | 17 | 6 | 8 | | | |
| <i>Nardus stricta</i> | | | | | | | | | 3 | 38 | 8 | 13 | | 56 | 17 | | 8 | | | |
| <i>Astragalus alpina</i> | | | | 17 | 8 | 8 | 8 | 8 | 30 | 50 | 25 | | | 8 | 33 | 33 | | | | |
| <i>Viola biflora</i> | | | | 8 | | | | | 10 | 4 | 8 | 4 | | | 17 | | | | | |

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