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 Correspondance 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. Gjærvoll 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 Haukeliseter (59° 49'N, 7° 12'E), in the south (Fig. 1). Both areas cover a west-east (oceanic-continental) 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 Haukeliseter 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 Haukeliseter (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 Haukeliseter) 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
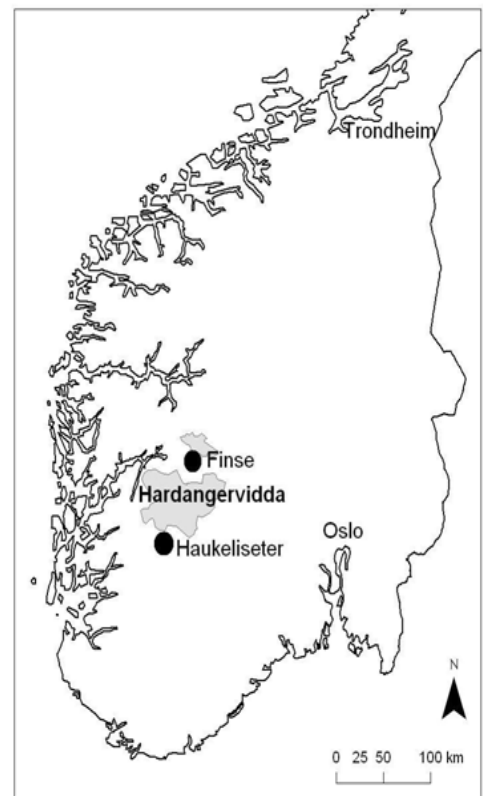

Fig. 1. Location of the study areas Finse and Haukeliseter in Southern Norway.

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, Gjærvoll 1956, Dierβen 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 *Deschampsia alpina*, *Eriophorum scheuzerii* snowbed	SB
B	1395 - 1410	Wet *Phippsia algida* snowbed	SB
C	1390 - 1415	Wet *Saxifraga rivularis*, *Ranunclus pygmaeus* snowbed	SB
G	1453 - 1505	Midalpine *Harimanella hypnoides* snowbed with *Silene acaulis* and *Salix herbacea*	SB
L	1042 - 1449	Early snowbed, graminoid dominated with *Salix herbacea*	SB
D	1542 - 1547	*Dryas octopetala ridge* with *Salix polaris*, and *Carex rupestris*	ER
E	1555 - 1556	*Dryas octopetala* ridge with *Oxytropis lapponum*	ER
F	1396 - 1472	*Dryas octopetala* ridge with *Kobresia myosuorides*, *Carex rupestris*, and *Festuca ovina*	ER
M	1046 - 1051	*Dryas octopetala* ridge with *Antenaria dioica* relatively poor in species	ER
H	1097 - 1168	Less exposed *Salix reticulata* ridge with *Dryas octopetala*	ER
I	1347 - 1477	Late herb meadow leeside with *Bistorta vivipara*, *Parnassia palustris*, and *Salix reticulata*	LS
J	1076 - 1449	*Alchmilla spp.* with *Astragalus alpinus* and *Geranium sylvaticum*	LS
K	1367 - 1392	*Salix reticulata*, *Silene acaulis*, *Saussurea alpina* meadow	LS
O	1068 - 1160	Willow shrub with *Geranium sylavaticum*, *Saussurea alpina* and graminoids	LS
P	1295 - 1325	Willow shrub with tall herbs, *Geranium sylvaticum*, *Cirsium heterophyllum* and *Angelica archangelica*	LS
Q	1024 - 1259	Willow shrub with *Geranium sylvaticum*, *Alchemilla spp.* and *Ranunculus acris*	LS
N	973 - 1017	*Dryas octopetala* with *Nardus stricta* with a sparse tree canopy	LS
R	870 - 946	Tall herb meadow with *Aconitum lycotonum* and *Filipendula ulmaria* under a sparse tree canopy	LS
S	779 - 806	Tall herb, dense birch forest with *Aconitum lycotonum* and *Cicerbita alpina*	LS
T	836	Tall herb meadow *Aconitum lycotonum* 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)
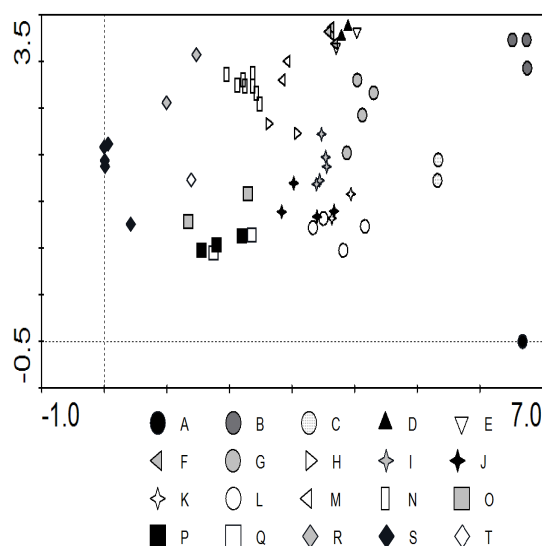

Fig. 2. Relative position of the studied plots (circles = snowbeds, triangles = exposed ridges, others = leesides), classified into 20 TWINSPAN groups (small-scale groups: A-T), in relation to DCA axes 1 and 2. See Table 2 and Appendix for descriptions of the small-scale groups and for an overview of 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 Haukeliseter (one exception: January 8 in the plot that reached lowest soil temperature at Haukeliseter, which was also the plot that melted out earliest and had the thinnest snow cover at Haukeliseter). 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).
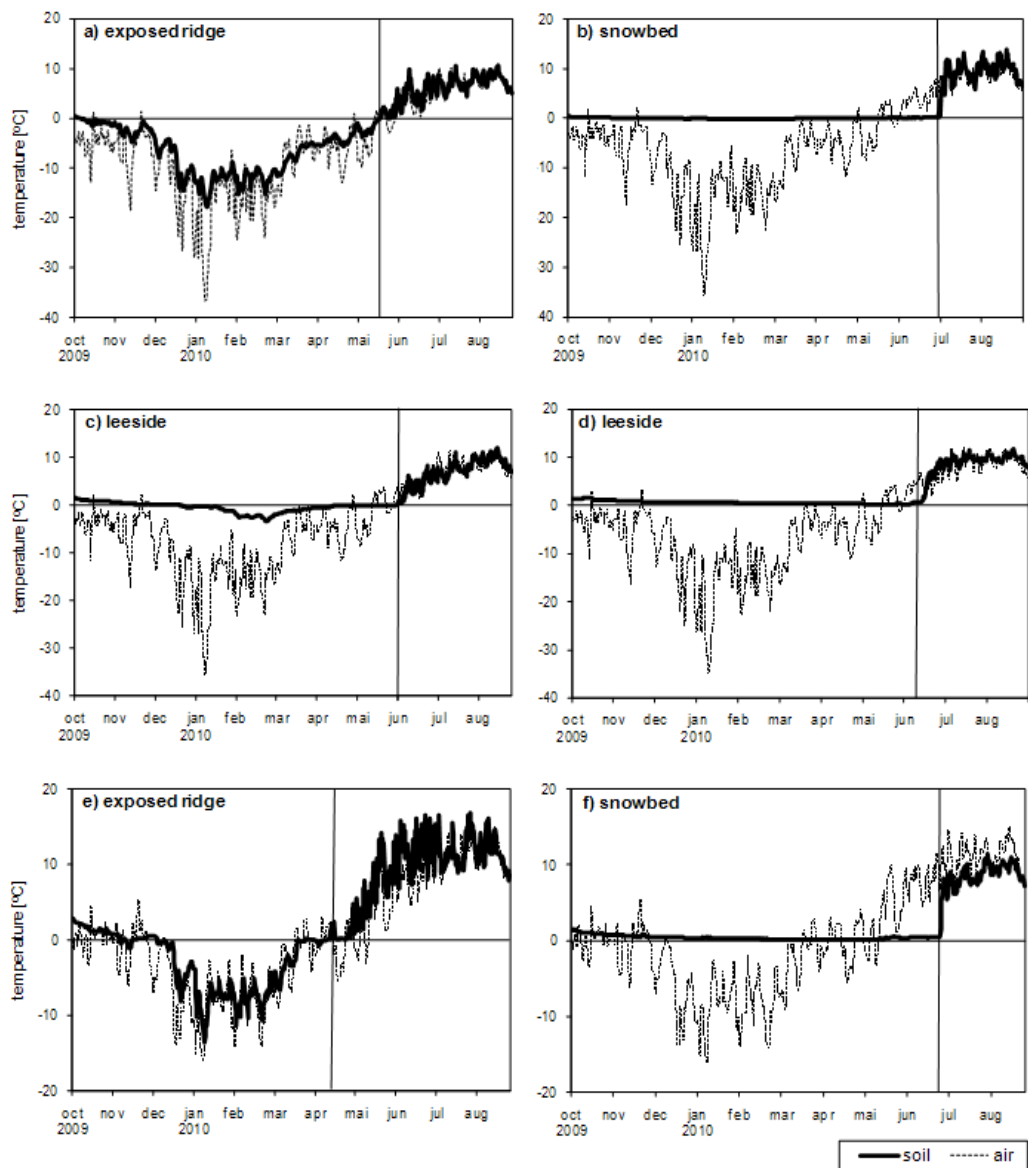
Fig. 3. Seasonal courses of soil temperatures (continuous line) and corresponding air temperatures (dashed line), using typical plots as examples to represent exposed ridges, leesides, and snowbeds at Finse (a-d) and at Haukeliseter (e-f). The vertical line marks the Julian day of snowmelt. Soil temperatures 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.

	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)

Discussion

Climate conditions during winter 2009/2010

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

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).
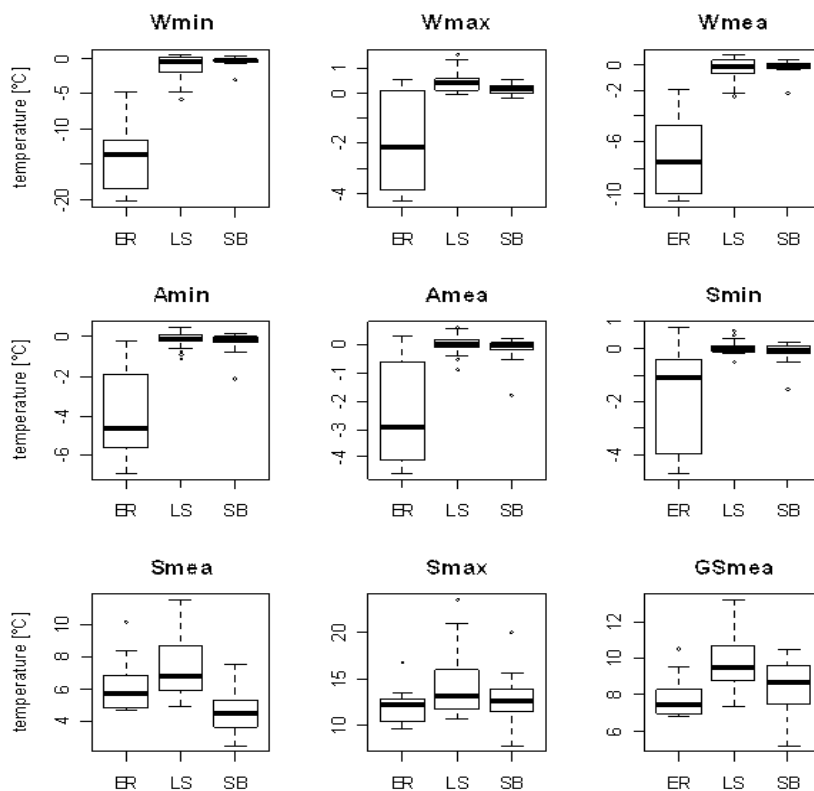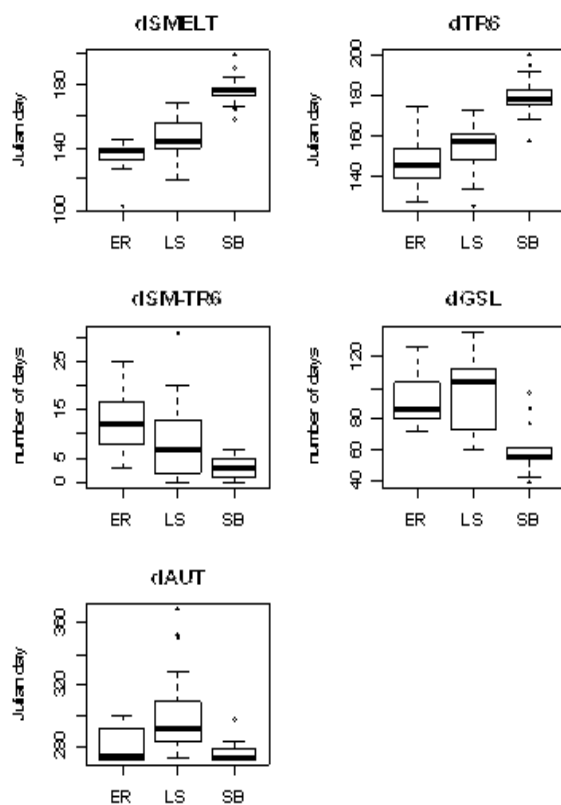

Fig. 5. Soil temperature parameters (abbreviation are explained in Table 1) with medians, 25th and 75th percentiles, maximum and minimum values, and outliers, ordered by the main groups exposed ridges (ER), leesides (LS), and snowbeds (SB). The Kruskal-Wallis test showed that all parameters were significantly 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 ˚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.
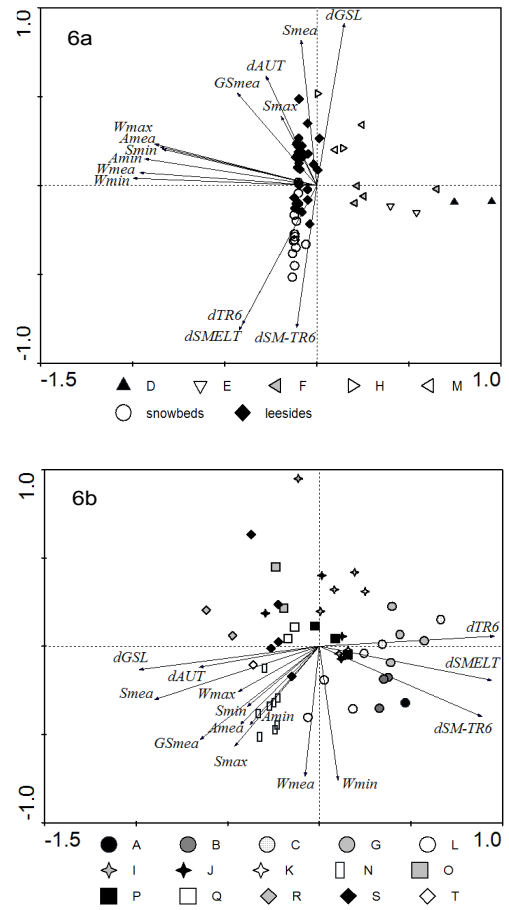
Fig. 6a and b. PCA axes 1 and 2 showing the relation of soil temperature parameters (abbreviations are explained in Table 1) to each other, and the vegetation groups (snowbeds (SB) = circles, leesides (LS) = rectangles/ stars, exposed ridges (ER) = triangles). The different small-scale vegetation groups 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	-14.1 ±4.6	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 Haukeliseter, 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 Körner 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 alpines.

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 $^{\circ}$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 $^{\circ}$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 $^{\circ}$C in snowbeds. Winter soil temperatures in leesides remained either around 0 $^{\circ}$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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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 Haukeliseter = 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 Haukeliseter	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
Deschampsia alpina	33	33	33				4		7	13	25									
Cerastium cerastoides	17	39	17				4					8								
Ranunculus pygmaeus		11	8									4								
Carex lachenalii	33	22	17								8	4								
Eriophorum scheuzerii	33																			
Juncus biglumis		22	25				4					8								
Phippsia algida		28																		
Saxifraga rivularis		11	8																	
Saxifraga stellaris	17	44	25									4								
Dryas octopetala				33	33	54	8	33						67	60					
Antenaria dioica				8		4	4	17	10	8				25	29					
Molinia caerulea														35						
Salix polaris			17	42	17		8				17									
Carex rupestris				50	17	38														
Festuca ovina					8	38	25		13	4	8			8						
Harrimanella hypnoides							54													
Kobresia myosuroides						29														
Oxytropis lapponum				17	25	4			10											
Cerastium alpinum				33	17	8	13	8	7	8		4								
Silene acaulis				42	50	42	42	25	37	29	50			17						
Salix reticulata				25	42	33	38	42	40	33	50						6			
Juncus trifidus						4	8	25	17			4		17	2					
Salix herbacea			8	17	33		58	25	20	21	8	63		2		6	8			
Thalictrum alpinum			8	33	25	21	29		43	42	50	4		25	6					
Sibaldia procumbens			8				8		10	4	8	29								
Festuca vivipara				33	42		4	17	3					17		8		8		
Parnassia palustris						13		8	47	33	17			8		6				
Potentilla crantzii				17	25	8	17	17	27	8		4		2	8			8		
Leontodon autumnalis		6	8				4		27	29	25	25			8		17			
Bistorta vivipara			8	42	50	33	42	17	57	42	42	29	17	17	8	6	17			17
Euphrasia wettsteinii				17		8	17	8	23	25	17	4	17	4		11	8	8		
Poa alpina	17	6	17				13	8	33	21	17	25		8		11				
Carex bigelowii				8	8	25	13	17	23	13	33	8	17	2			17			
Oxyria dygina			8								25									
Bartsia alpina				17	25	17	25	17	30	17	8	8	8	21	17	6	8			
Nardus stricta									3	38	8	13		56	17		8			
Astragalus alpina				17	8	8	8	8	30	50	25			8	33	33				
Viola biflora			8						10	4	8	4		17						

Species																		
Anthoxanthum nipponicum	8			4	4	33	27	25	17	25	17	35	17	33	25	17	3	33
Campanula rotundifolia			8			8	13	4		4	17	17	8	11	8	17		
Lotus corniculatus											25	21	25			8		
Saussurea alpina		25	17	17	25	8	43	33	42	25	8	17	33	22	33			
Ranunculus acris	17					8	30	25	17	13		2	8	33	42		13	
Alchemilla spp	17					42	10	63	50	21			33	44	42	8	10	67
Solidago virgaurea						17				4	17	23		33	8	8	13	
Avenella flexuosa						8	10	8		33	8	10	33	17	8	8	3	50
Deschampsia cespitosa						17		4	8	4	17	4	42		33	17		
Salix glauca						8		4				13	33	28	33			
Viola palustris										8		2			33			17
Geum rivale								21					17	6	8	25		50
Salix lanata						17		4					58	61	8		3	
Cirsium heterophyllum														33		8		
Filipendula ulmaria																58	7	17
Alchimilla alpina						8						2				33		17
Hypericum maculatum																50		34
Salix lapponum										4			6	28	58		7	17
Angelica archangelica														28	25	13		
Geranium sylvaticum						17		33		8		10	33	67	67	17	33	
Aconitum lycotonum																50	77	100
Cicerbita alpina																73		
Oxalis acetosella																30		
Stellaria nemorum																40		17