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Alpine Soil Temperature Variability at Multiple Scales

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Abstract

The functioning of ecosystems is strongly correlated to soil temperature dynamics. Because only a few studies so far have investigated the spatio-temporal variability of alpine soil temperatures, we proceeded to analyze soil temperatures in a heterogeneous alpine landscape by means of a multi-scale approach. We combined vertical soil temperature gradients from surface to 15 cm depth, microspatial variability within small catchments, and altitudinal changes of a continental mountain system. We analyzed differences at single sites and at multiple spatial scales. We found that microtopographic site conditions dominated thermal changes along altitudinal gradients. The adiabatic lapse rate did not show high correlations with local soil temperature gradients. We used isopleth diagrams of soil temperature gradients and corresponding scatterplots of soil temperature gradients between each pair of sites and low alpine–middle alpine mountain couples to quantify these overlying phenomena. This enabled us to quantify the significance of soil temperature gradients across vertical soil profiles, topography, and altitude in order to facilitate future microclimate extrapolation and modeling in high mountain (alpine) landscapes. Such procedures are crucial for describing expected responses of alpine ecosystems to global climatic change.

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Introduction

Within the discussion of the recent ongoing climatic change (Walther et al., 2002; IPCC, 2007), it has been suggested that sensitive mountain landscapes could act as indicators for the response of ecosystems to global warming (Ørebæk et al., 2004; Beniston, 2006; Becker et al., 2007; IPCC, 2007). Effects of rising temperatures have already left fingerprints on mountain vegetation: trees at the climatic treeline have never grown as fast as they do today (Körner, 2009). However, using treeline position as a climate change indicator remains difficult due to other factors (like land use) involved in its determination (e.g. Gehrig-Fasel et al., 2007; Moen et al., 2008). Focusing on the less disturbed alpine environments instead, empirical evidence of recent changes in the distribution of alpine and nival plant species (i.e. range shifts/reductions) attributable to climate warming is given by Walther et al. (2005), Pauli et al. (2007), and Lenoir et al. (2008), among others. Furthermore, a future increase of these changes is supported by a number of modeling studies (e.g. Dirnböck et al., 2003; Thuiller et al., 2005; Engler et al., 2009).

The general importance of temperature is one of the undisputed driving forces of these changes. Several investigations in arctic and alpine environments, however, emphasize the particular importance of soil temperature dynamics compared to atmospheric conditions: microbial activity and composition was found to be determined by soil temperatures (e.g. Björk and Molau, 2007; Monson et al., 2006) and consequently also the nutrient and carbon cycle (Starr et al., 2008; Saito et al., 2009). Furthermore, photosynthetic capacity and the related growth rates of plants (Weih and Karlsson, 2002; Starr et al., 2008; Bär et al., 2008) were found related to soil temperatures.

However, concerning the impact of future global warming on mountain ecosystems, most studies (e.g. Sætersdal and Birks, 1997; Dirnböck et al., 2003; Klanderud and Birks, 2003; Thuiller et al., 2005; Engler et al., 2009) considered general air temperature scenarios derived from global circulation models (GCMs) only. Their coarse spatial resolution has been found to be a serious limitation with respect to determining the impact of global change on ecosystems in general (O'Brien et al., 2004), leading to serious misinterpretations regarding, for instance, the rate of extinction for plant species as shown by Trivedi et al. (2008) and Randin et al. (2009). Furthermore, though downscaling of GCM results offers higher resolution (e.g. Engler et al., 2009), there is no guarantee that the results of these routines will be more reliable than those of the parent GCMs (Olesen et al., 2007). Hence, if we aim to identify and understand responses to global warming, temperature conditions of near-surface air and soil layers must be analyzed at different spatial scales (cf. ACIA, 2004).

As is well known, the alpine climate is differentiated most decisively by topography (Barry, 2008). Given that most official meteorological stations are located in valleys (Price and Barry, 1997), it is critical that common approaches to the interpolation of spatial data (Fleming et al., 2000) are used, due to the general lack of data from higher elevations. As a consequence of falls in altitudinal air pressure and associated thermodynamic processes, the air cools from about -0.98 (K/100 m) for dry air to about -0.4 (K/100 m) for saturated air and the cooling averages have a gradient of -0.65 (K/100 m) (Dodson and Marks, 1997). However, these values are approximations and are true primarily for the free atmosphere, not for near-surface air temperature conditions in complex terrain; hence, they are not suitable for temperature interpolation in mountain and alpine regions (Rolland, 2003; Lundquist and Cayan, 2007). Therefore, the utility of correlations between general meteorological trends and local climatic differentiations for the understanding of microspatial conditions is questionable (Lookingbill and Urban, 2003; Löffler

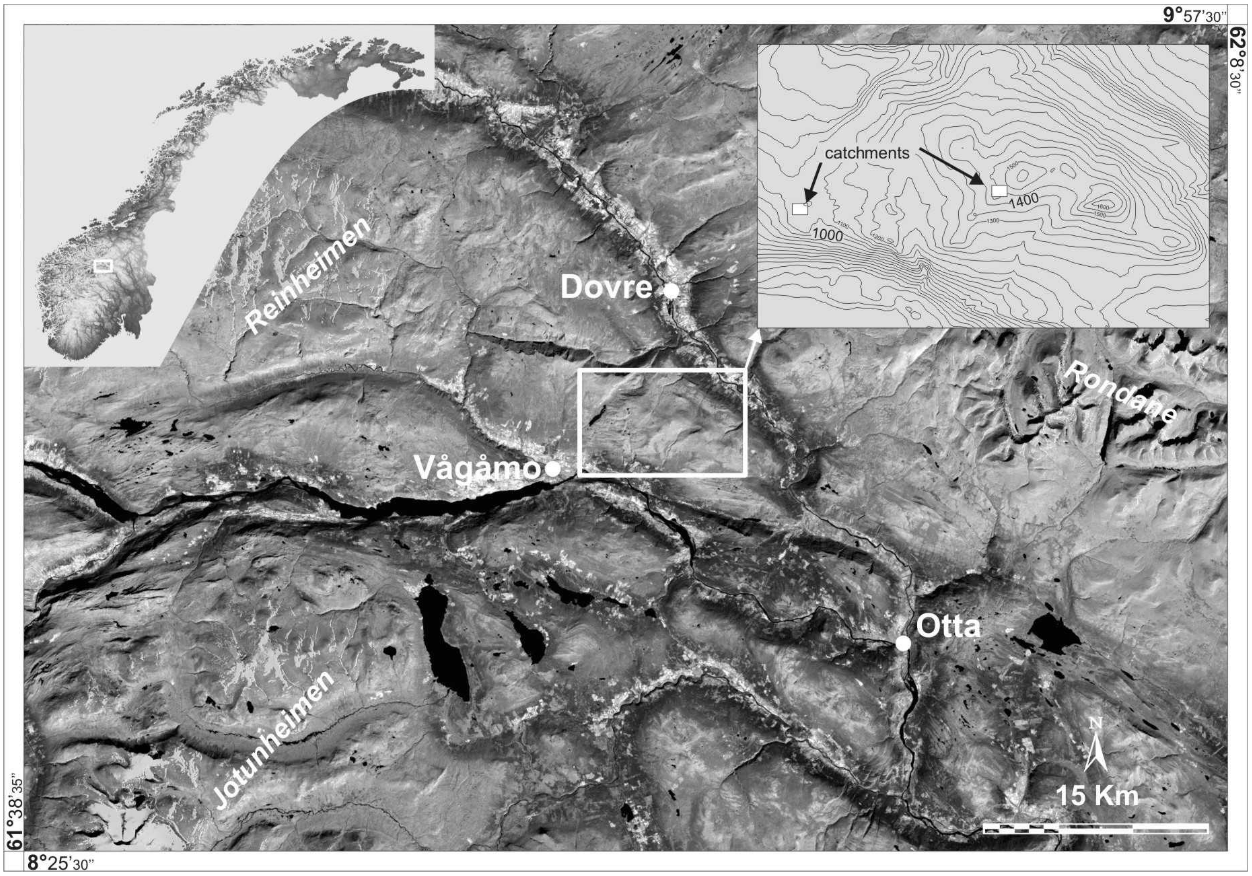

FIGURE 1. Location of the study area in central Norway. Contour interval = 50 m.

and Pape, 2004; Löffler and Finch, 2005; Pape et al., 2009). That being so, taking nonlinearities of climate systems into consideration was found to be of greater importance when assessing the impact of global climatic change on mountain ecosystems (Peterson, 2000; Diaz et al., 2003; Rial et al., 2004).

In consideration of these facts, it seems surprising that at the time of writing, only a few studies have investigated the spatio-temporal variability of mountain or alpine soil temperatures (Green and Harding, 1980; Takahashi, 2005). As a response to this lack of data, the study herein addressed the temporal variability of alpine soil temperatures along different spatial gradients. The aim of the study was to identify the principles that determine soil temperature gradients at multiple spatial scales, such as vertical soil temperature gradients, microtopographical differences, and altitudinal gradients across the alpine belts. Our hypotheses were as follows:

> (H1): Alpine soil temperatures are determined primarily by local topography.
> (H2): Soil temperatures in alpine environments that do not follow linear adiabatic lapse rates of air temperatures are thus decoupled from general linear altitudinal gradients.

Study Areas

Central Norway shows a clearly defined oceanic-continental gradient, which is represented by the western and eastern slopes of the mountain chain. The most continental climate is found only 150 km east of the coast in the Vågå/Oppland region (61°53′N; 9°15′E). The study area situated within this climatic region is characterized by low annual precipitation of about 300–400 mm yr^{-1} (in the valleys), which is the highest aridity found in Norway (Moen, 1999). The alpine altitudinal zonation is differentiated into a low alpine belt, which is dominated by shrub and heather communities, and a middle alpine belt, which is dominated by patchy grassy vegetation (Dahl, 1986) that reaches from the treeline at 1000–1050 m a.s.l., to the highest peak, i.e. the Blåhø (1618 m a.s.l.). The transition zone between low and middle alpine belts is found at around 1350 m a.s.l. Two investigation areas were chosen as representative alpine catchments in each altitudinal belt for (a) fine-scale analyses of topographical gradients and (b) analysis of the broad scaled determination of soil temperature according to altitude (Fig. 1).

Materials and Methods

Near-surface microclimatologic investigations were made into key topographical positions of the two chosen alpine catchments: ridges (R), depressions (D), and north- and south-facing mid-slopes (NFS and SFS). Two meteorological stations, at ridge positions (R) at 1100 m (equipped with DL2e® logger, Delta-T devices) and 1465 m a.s.l. (DL15® logger, Thies Clima) registered air (+100/+15 cm) and soil (−1/−15/−30 cm) temperatures, precipitation, solar radiation, air humidity, barometric pressure, wind direction, and wind speed throughout the year as hourly means and sums. Temperature data from depressions (D), and south- (SFS) and north-facing slopes (NFS) were acquired by data loggers (Tempdan®, ESYS GmbH) at +15, −1, and −15 cm, providing the same temporal resolution. All temperature measurements were made with Pt100-sensors at an accuracy of ±0.1 K,

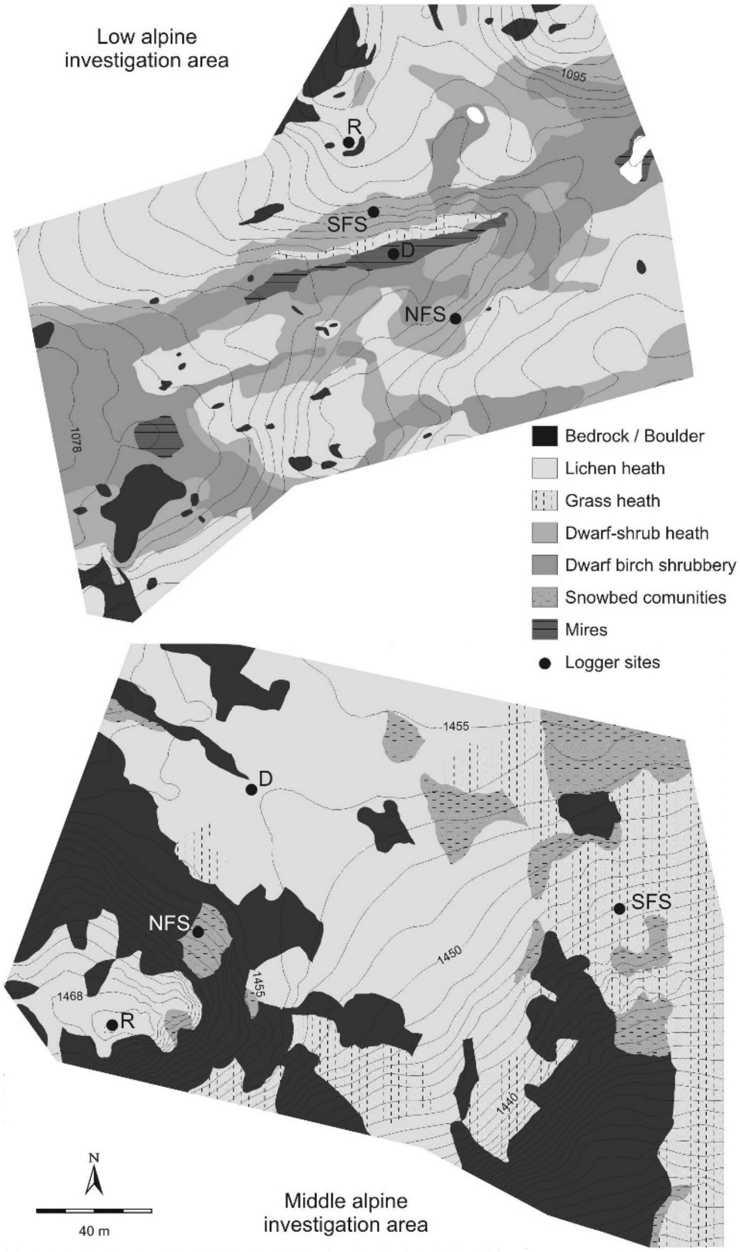

FIGURE 2. Spatial patterns of the catchment areas. Contour intervals = 1 m.

in case of air temperature measurements equipped with a passively ventilated radiation shield. Spatial patterns of the catchment areas are shown in Figure 2, and some key site parameters are listed in Table 1. Data on thickness and duration of snow cover given therein are based on soundings and monitoring.

The analysis presented in this paper is based on soil temperatures at −1 cm depth (hereafter referred to as T1) and −15 cm depth (hereafter referred to as T15) at the eight above-mentioned sites. Measurements started in 1994 and have continued to the present, but the analysis was based on data

TABLE 1

Key site parameters of the logger locations (R denotes ridge position; D, depression; SFS and NFS, south- and north-facing slopes, respectively).

	Low alpine belt				Middle alpine belt			
	R	D	SFS	NFS	R	D	SFS	NFS
Altitude [m]	1092	1084	1087	1088	1469	1454	1442	1462
Aspect [°]	—	—	175	340	—	—	163	20
Slope [°]	0–2	0–2	22	17	0–2	0–2	18	19
Substrate thickness [cm]	25	>70	>50	>50	15–30	>50	>50	>50
Vegetation type	Lichen heath	Mire	Dwarf-shrub heath	Dwarf-shrub heath	Lichen heath	Lichen heath	Grass heath	Snowbed
Max. snow cover [cm]	10	400	200	120	15	80	250	200
Snow cover duration [weeks]	12	34	31	32	20	35	34	37

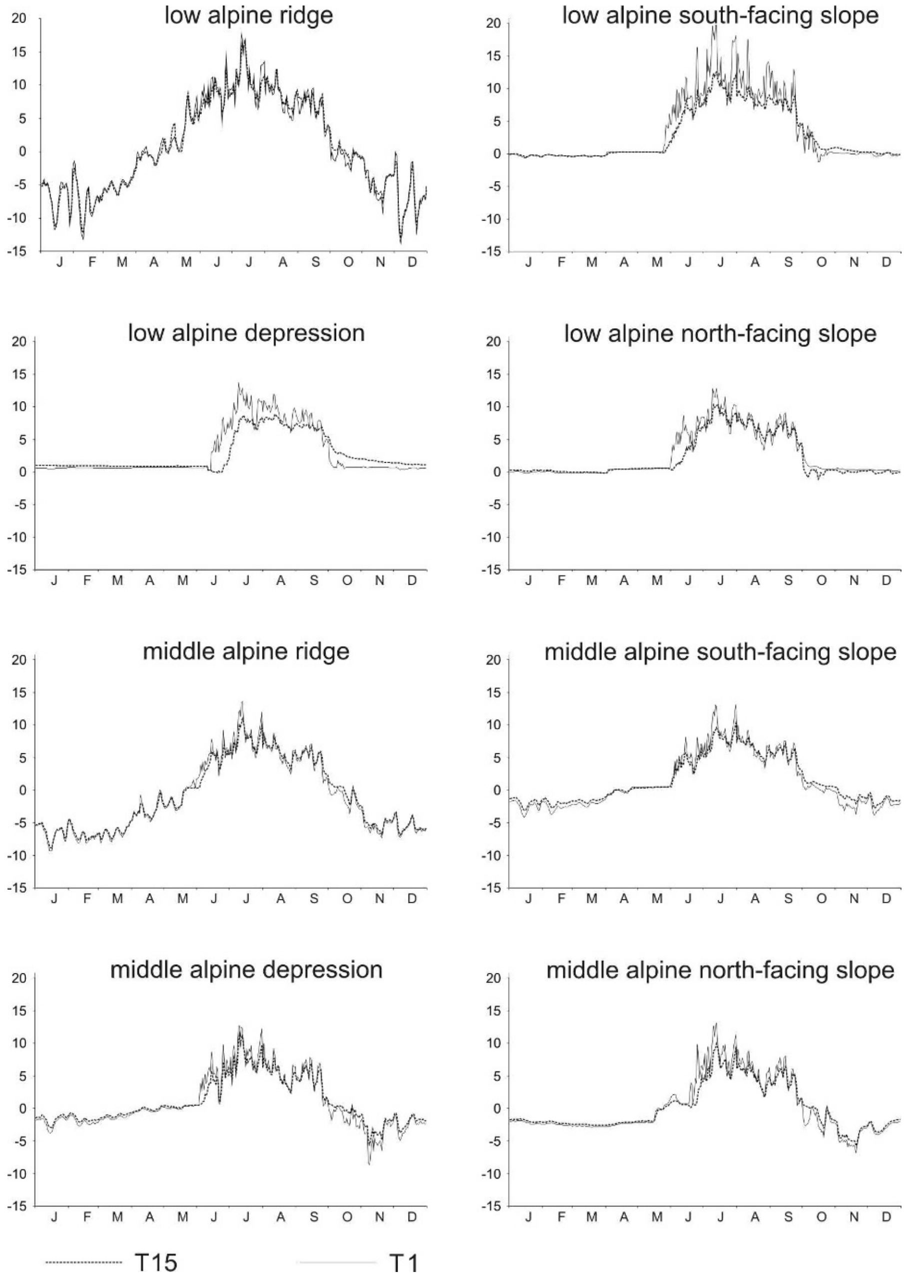

FIGURE 3. Mean daily soil temperatures T1 and T15 at different sites during 1999.

from 1998 to 1999, which is a period without data gaps. To address multiple spatial scales of variations in alpine soil temperature (ACIA, 2004) and to test our hypotheses H1 and H2, we analyzed the data in various ways, using (a) vertical gradients at local sites (H1, H2), (b) microtopographic gradients among different sites (H1), and (c) altitudinal gradients between the low alpine and middle alpine belt (H2). Hourly means of soil temperature data were used to create thermoisopleth diagrams. By using GIS-overlay operations (Idrisi, 1999), distinctions (expressed as ΔT) between sites at different scales were analyzed:

Vertical soil temperature gradients between T1 and T15 were calculated by determining the absolute values of vertical temperature differences: $\Delta T = |T1–T15|$. Relationships between T1 and T15 were evaluated by linear regression analysis including residual analysis.

To test whether alpine soil temperatures are determined primarily by local topography (H1), microscale differences of the vertical soil temperature gradients among R, D, NFS, and SFS within each catchment were estimated by subtracting the absolute values of the vertical soil temperature gradient of different sites (e.g. ΔT of the low alpine ridge versus ΔT of the low alpine depression).

To test whether alpine soil temperatures are decoupled from general linear altitudinal gradients (H2), two approaches were used: First, differences in soil temperature according to altitude were calculated by subtracting the temperature values of corresponding sites at different altitudes (e.g. T15 at the low alpine ridge versus T15 at the middle alpine ridge). Linearity of the altitudinal lapse rate between adequate time series of temperature data was estimated by means of linear regression analysis and analysis of its residuals. Second, differences among the soil temperature gradients among corresponding sites in different altitudinal belts were estimated by subtracting the absolute values of the vertical soil temperature gradient (e.g. ΔT of the low alpine ridge versus ΔT of the middle alpine ridge).

General results of this stepwise analysis of mountain soil temperatures were illustrated by time-variation curves of daily average temperatures and thermoisopleth diagrams of hourly means. Accordingly, diurnal and seasonal soil temperature

TABLE 2

Soil temperature variables.

	Low alpine ridge	Low alpine south-facing slope	Low alpine depression	Low alpine north-facing slope	Middle alpine ridge	Middle alpine south-facing slope	Middle alpine depression	Middle alpine north-facing slope
Mean T1 (°C)	0.6	3.1	2.5	2.2	−1.4	0.9	0.5	−0.2
Maximum T1(°C)	29.1	45.6	21.3	19.3	20.6	21.6	20.8	18.0
Minimum T1 (°C)	−15.1	−3.6	−0.4	−0.5	−9.9	−4.5	−10.2	−7.2
Mean T15 (°C)	0.6	2.4	2.3	1.8	−1.3	1.0	0.6	−0.3
Maximum T15 (°C)	20.9	14.4	8.7	10.7	11.3	10.9	14.2	10.3
Minimum T15 (°C)	−13.4	−0.8	−0.9	−1.9	−9.3	−3.4	−6.1	−6.1
r^2 of T1 and T15 (Pearson)	0.93**	0.63**	0.83**	0.66**	0.95**	0.90**	0.89**	0.87**
Mean ΔT (K)	1.2	1.7	0.8	1.3	0.7	0.9	1.0	0.9
Maximum ΔT (K)	16.3	34.8	10.0	18.3	10.0	12.2	12.0	13.3

** Significant at the 0.01 level.

variability was considered. Moreover, thermal differences and temperature gradients were reclassified and visualized by three-stage (warmer, cooler, equal) isopleth diagrams. These were used to accentuate and generalize complex variations in soil temperature according to spatial differences.

Results

Near-surface differences in vertical soil temperature as a function of spatial variation of local site conditions behaved in generally the same way at all sites. As indicated by daily mean soil temperatures, differences were, not surprisingly, more pronounced during the summer months at all sites (Fig. 3). The general temperature level, indicated by the mean values of T1 and T15, was found to be lower in the middle alpine belt (Table 2).

TOPOGRAPHIC CONTROL

Compared to the other sites, pronounced temperature amplitudes during winter were restricted to the ridges in both altitudinal belts. In contrast, the slopes and depressions were characterized by more or less isothermal conditions for more than half the year (Fig. 4).

Maximum T1 (45.6 °C) occurred at the low alpine SFS. The highest T15 (20.9 °C), lowest T15 (−13.4 °C), and lowest T1 (−15.1 °C) were observed at the ridge site in the low alpine belt (Table 2).

As illustrated in Table 2, maximum differences between T1 and T15 were found at the SFS in the low alpine belt. Values there increased up to about 35 K. In the low alpine depression and at the middle alpine ridge, the values just reached 10 K. Comparing the T1 and T15 curves by means of correlation coefficients indicates higher correlations at the low alpine ridge ($r^2 = 0.93$) and generally at all middle alpine sites ($r^2 = 0.87$–0.95). In contrast, correlations were least developed at the low alpine SFS ($r^2 = 0.63$) and the low alpine depression ($r^2 = 0.66$), indicating a divergence of T1 and T15 at these sites which was found to be independent from the absolute differences between T1 and T15 (SFS—large, D—small). Furthermore, analyses of the residuals revealed linear approaches in general to be inappropriate to model the relationship between T1 and T15.

Focusing on these vertical soil temperature gradients, isopleth diagrams offer a detailed analysis of diurnal and seasonal variability (Fig. 5). At the end of the already-mentioned isothermal winter period, the temperature gradients suddenly turned to the summer state of pronounced daily variations characterized by higher daily T1 and higher nocturnal T15. The transition from autumn to winter was characterized by short events or longer periods of higher T15. The described patterns of temperature-gradient dynamics are similar at all sites; differences between sites were found to be distinguished by (a) beginning, duration, and daily patterns of the summer period, and (b) patterns and duration of the autumn transition period.

These differences are obvious from direct comparison of site-specific vertical temperature gradients (Fig. 6). In the low alpine, the vertical temperature gradient became more pronounced at the ridge early in May. Compared to the depression site, this pattern persisted until the middle of June, when the ratio of the gradients became inverted and vertical soil temperature differences became more pronounced at the depression site until early autumn. At the south-facing slope, the ratio had already become inverted at the end of May. Furthermore, at both sites a diurnal change in soil temperature gradients compared to the ridge was observed. During the day, gradients were most pronounced at the south-facing slope and depression, while during the night they were most pronounced at the ridge site. Compared to ridge and south-facing slope, the north-facing slope showed the smallest gradients. In contrast, site-to-site differences of vertical temperature gradients in the middle alpine belt were less pronounced. During spring, only a short period of larger soil temperature gradients at the ridge compared to the other sites was observed. Gradients at the south-facing slope were no more clearly pronounced during the summer period than at the other sites. However, the middle alpine north-facing slope showed the most distinct soil temperature gradients during the summer.

ALTITUDINAL GRADIENTS

Coming back to the general decrease of daily mean soil temperatures by altitude at all sites, as already indicated by Figure 3, the average lapse rate varied from 0.4 to 0.6 K/100 m (Table 3). However, we found an absolute minimum of −3.7 K/100 m and maximum of 9.4 K/100 m. This pronounced variability is also indicated by standard deviations from 0.3 up to 1.0 K. Thus, the correlation patterns of T1 and T15 were neither similar nor, as indicated by residual analysis, linear at all sites. The strongest correlations were found between soil temperatures at the ridges of the low alpine and middle alpine belts. In contrast, T1 (SFSs and depressions) and T15 (depressions) were irregular (Table 3).

Changes in soil temperature according to altitude varied from site to site (Fig. 7). During winter, we found an irregular alteration of warmer and colder conditions at the middle alpine ridge,

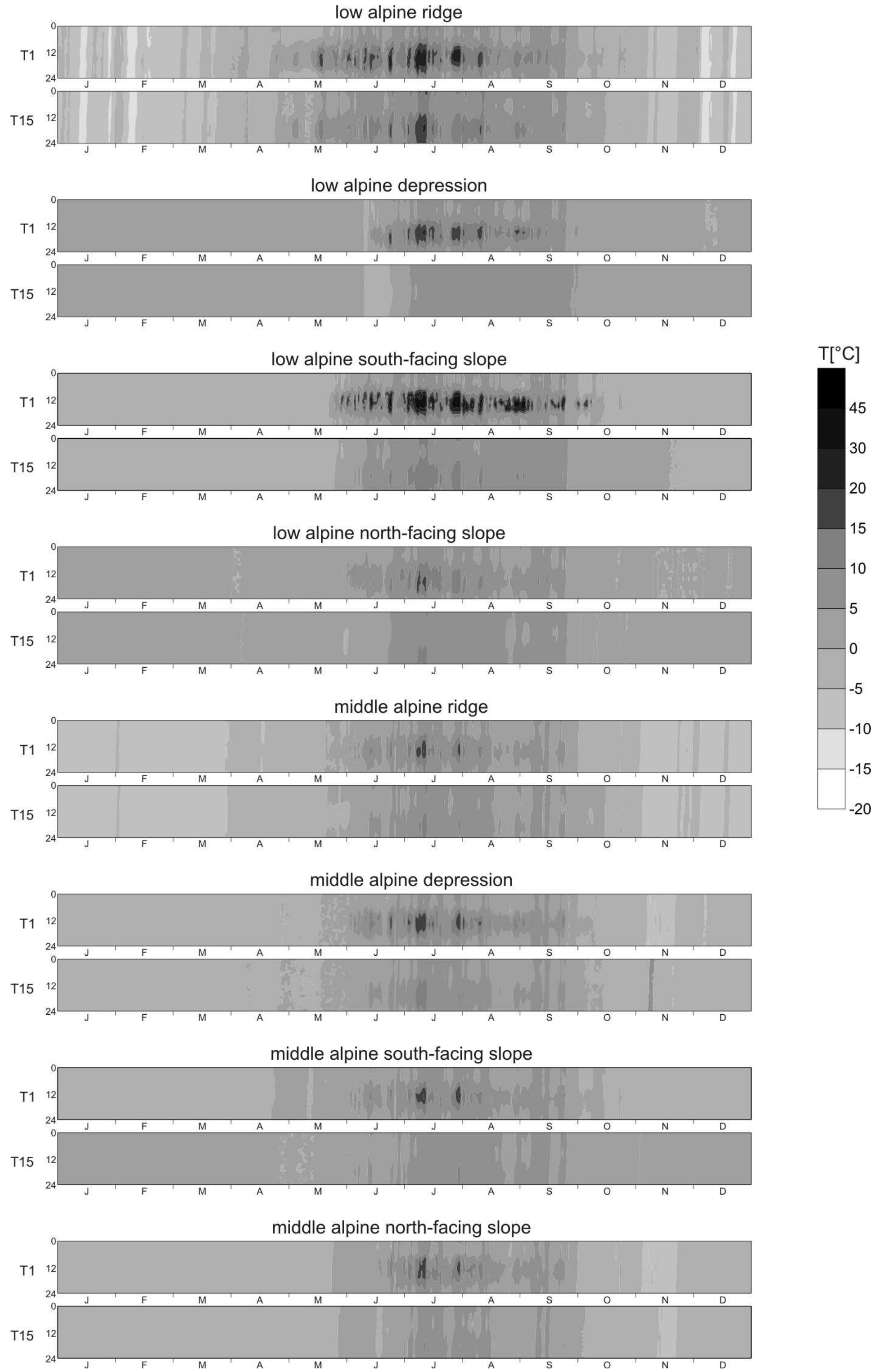

FIGURE 4. Diurnal and seasonal soil temperature variability (T1 and T15) during 1999.

whereas middle alpine slopes and depression were permanently colder than in the low alpine. During the snow-free season, the ratio between ridge and the other positions changed: Conditions at the middle alpine ridge were nearly permanently colder than at the low alpine, whereas altitudinal gradients between slopes and depressions were subject to diurnal or intraseasonal alterations: Uniform warmer temperatures in the low alpine depression during winter faded to isotherm conditions during spring. Early summer was marked by the beginning of diurnal alterations, with higher daytime soil temperatures in the middle alpine belt. During the summer, these conditions attenuated and the ratio turned again to predominantly higher soil temperatures at the low alpine depression throughout the day. The south-facing slopes showed similar patterns until early summer, but T1 was regularly higher during the day and lower at night in the low alpine belt over the following months. For most of the year, the patterns of the north-facing slopes were similar, but the T1 ratio was reversed during the summer months.

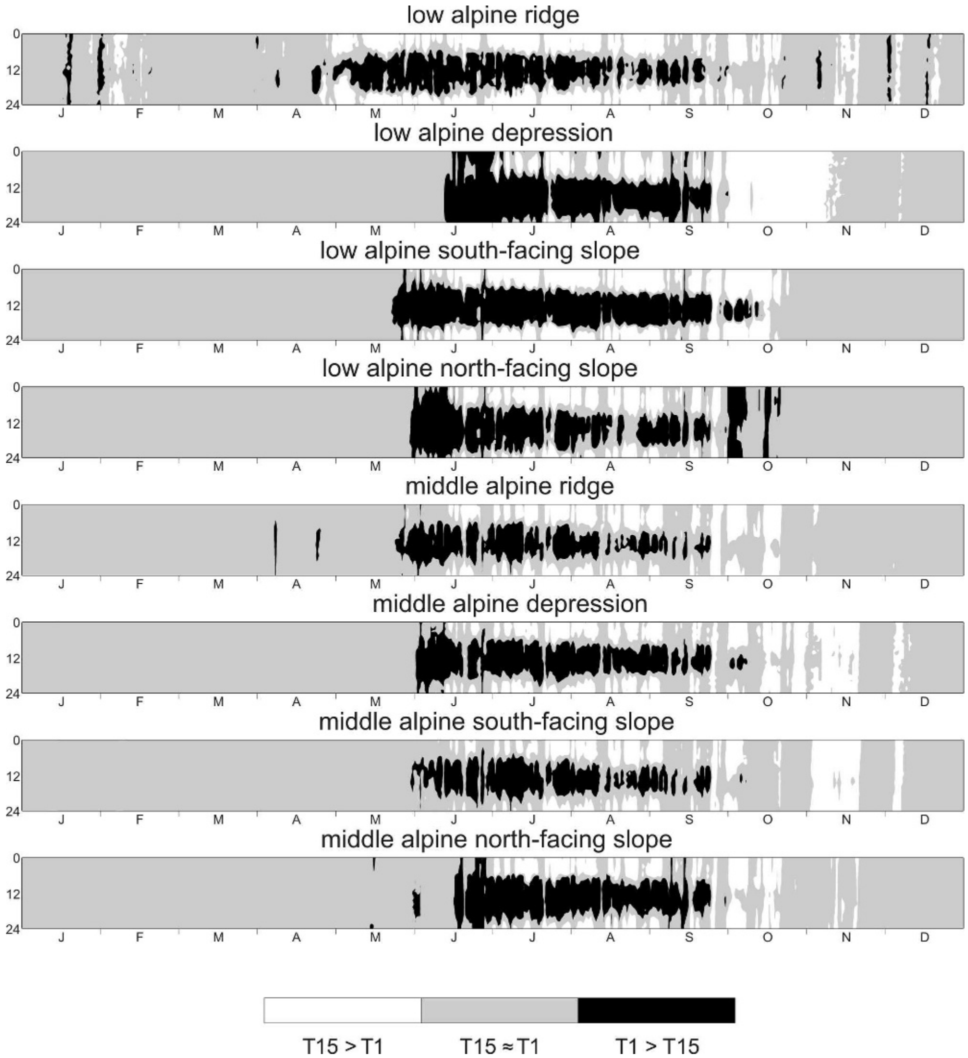

FIGURE 5. Diurnal and seasonal variability of vertical soil temperatures during 1999.

Soil temperature gradients between the same lateral positions for different altitudes were found to exhibit pronounced contrasts (Fig. 8). While soil temperature gradients during winter were similar between sites of the same topographical position, the patterns during summer were less consistent. The ratio between the ridge sites altered irregularly but showed slightly pronounced gradients at night in the low alpine belt. Regarding the depressions, gradients in the middle alpine were more distinct at the beginning of June and during summer after sunrise, but the situation reversed during the afternoon. Conditions at south-facing slopes were regularly as follows: pronounced gradients at the low alpine site during most of the day, alternating with short periods of similar conditions in the morning and evening. In contrast, the difference between the north-facing slopes was characterized by pronounced daily soil temperature gradients in the middle alpine belt throughout the summer. The only exception was observed in early summer, when the low alpine north-facing slope was characterized by a pronounced gradient throughout the day.

Discussion and Conclusions

Our analyses of alpine soil temperatures revealed different sites characterized by pronounced and unique soil temperature regimes. These different regimes emerge from site-specific interactions of environmental factors characterized by differentiated patterns on different scales of observation. In a seasonal perspective, snow cover accounts for the winterly isothermal conditions observed at all of our sites but the ridges (Jones, 1999). The presence, thickness, and duration of the snow cover is in turn controlled by topography (Löffler, 2005, Trujillo et al., 2007). While the wind-blown ridges remain snow-free during winter, most snow accumulates at the leeward south-facing slopes. Hence, one important differentiating factor between the sites, the onset of the summer period (which depends on the date of snowmelt) can be attributed to topography. Focusing on the summer period and its internal differentiation, the slopes showed a pronounced differentiation due to the different input of solar radiation (Barry, 2008): highest subsurface temperatures (T1) were found at the south-facing slopes, lowest at north-facing slopes—a direct effect of topography on temperature conditions. The observed differences in vertical temperature gradients can be attributed to varying substrate conditions. The highest subsurface temperature (T1) at the low alpine south-facing slope does not find its equivalent in highest T15 at the same site; it is found at the ridge instead. A thick dark humus layer is effectively heated by solar radiation but also isolates the deeper soil at the slope, while at the ridge the shallow, lichen-covered soil is warmed from underneath by adjacent massive bedrock covering the surface. The depression is characterized by a water saturated organogenic soil, resulting in a completely different thermal regime compared to the neighboring minerogenous soils, explaining the second largest vertical temperature gradient of the investigated sites in the low alpine belt.

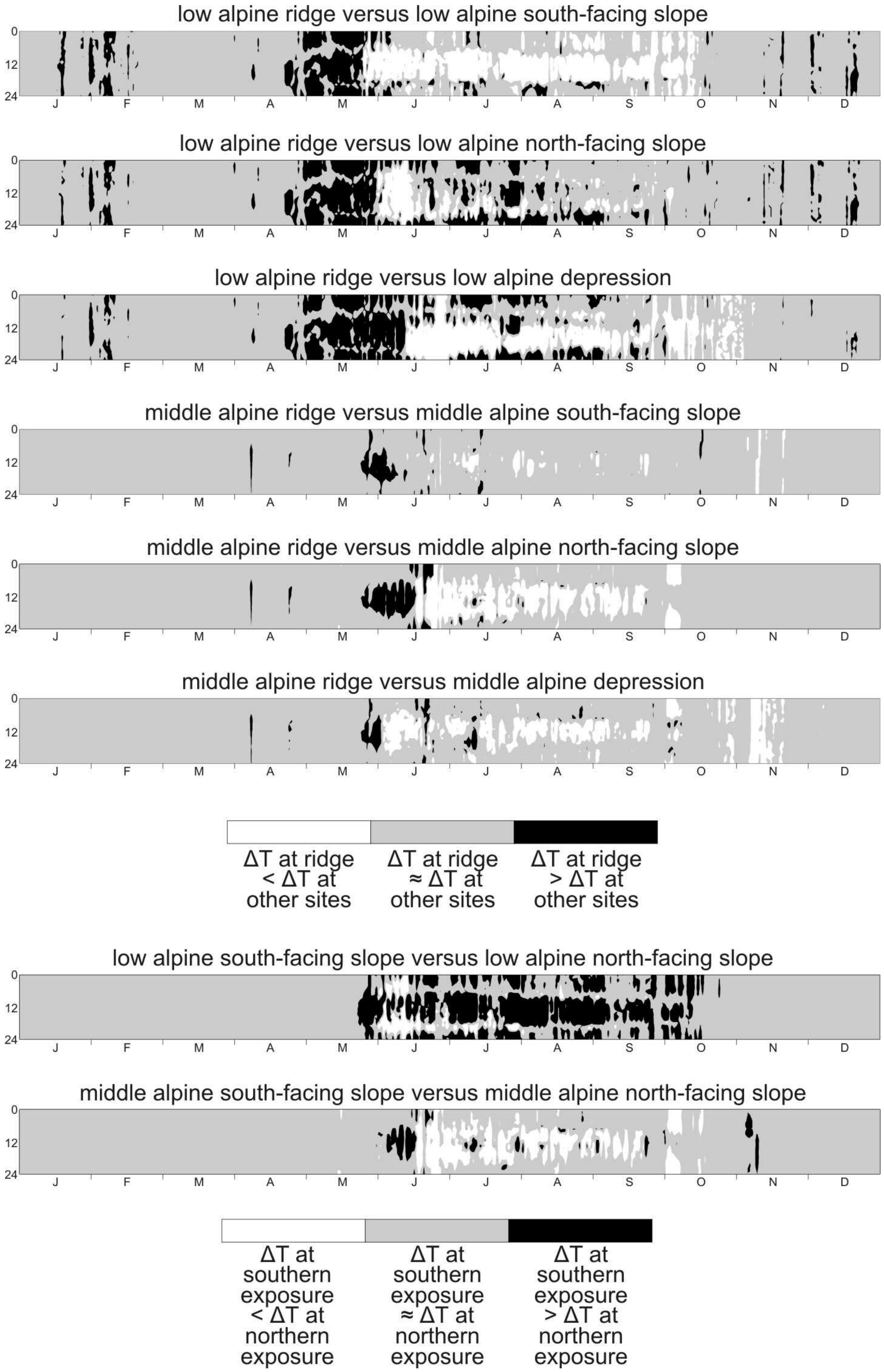

FIGURE 6. Microtopographical comparison of vertical soil temperature gradients during 1999.

Compared to the low alpine belt, site-specific vertical temperatures gradients in the middle alpine belt are less pronounced, what might be attributed to a combination of less vegetation cover and higher contents of soil skeleton, resulting in a better heat conduction within the soils. To summarize, extreme diurnal and seasonal temperature amplitudes and gradients were observed at sites with shallow snow cover and/or with shallow soils combined with high thermal conductivity of the near-surface massive bedrock. In contrast, sites with thick snow cover during winter and high soil moisture during summer were characterized by much more even soil temperature regimes. These findings accord with previous investigations (Takahashi, 2005), but our detailed examinations of diurnal and seasonal temperatures highlight differentiated patterns on different scales of observation. Detected temperature amplitudes of up to 35–45 K, as well as microscale site-specific temperature variability of more than 15 K, are well-known climatic phenomena of alpine environments (Barry, 2008), but are, as shown, not common to all sites. Concluding, our starting hypothesis of alpine soil temperatures to be primarily controlled by topography is strongly supported by our findings.

Focusing on the altitudinal gradients of alpine soil temperatures, observed mean values of the altitudinal lapse rates (0.4–

TABLE 3

Variables of altitudinal soil temperature differences.

	Ridges		Depressions		South-facing slopes		North-facing slopes	
	T15	T1	T15	T1	T15	T1	T15	T1
r^2 of temperatures in different altitudinal belts (Pearson)	0.9**	0.9**	0.6**	0.7**	0.9**	0.8**	0.9**	0.9**
Mean altitudinal lapse rate (K/100 m)	0.5	0.5	0.5	0.6	0.4	0.6	0.6	0.6
Minimum altitudinal lapse rate (K/100 m)	−1.8	−2.0	−3.1	−3.7	−0.6	−0.9	−0.4	−2.1
Maximum altitudinal lapse rate (K/100 m)	3.7	5.0	2.1	2.9	1.7	9.4	1.6	3.2
Standard deviation of altitudinal lapse rate (K/100 m)	0.7	0.8	0.6	0.6	0.3	1.0	0.3	0.5

** Significant at the 0.01 level.

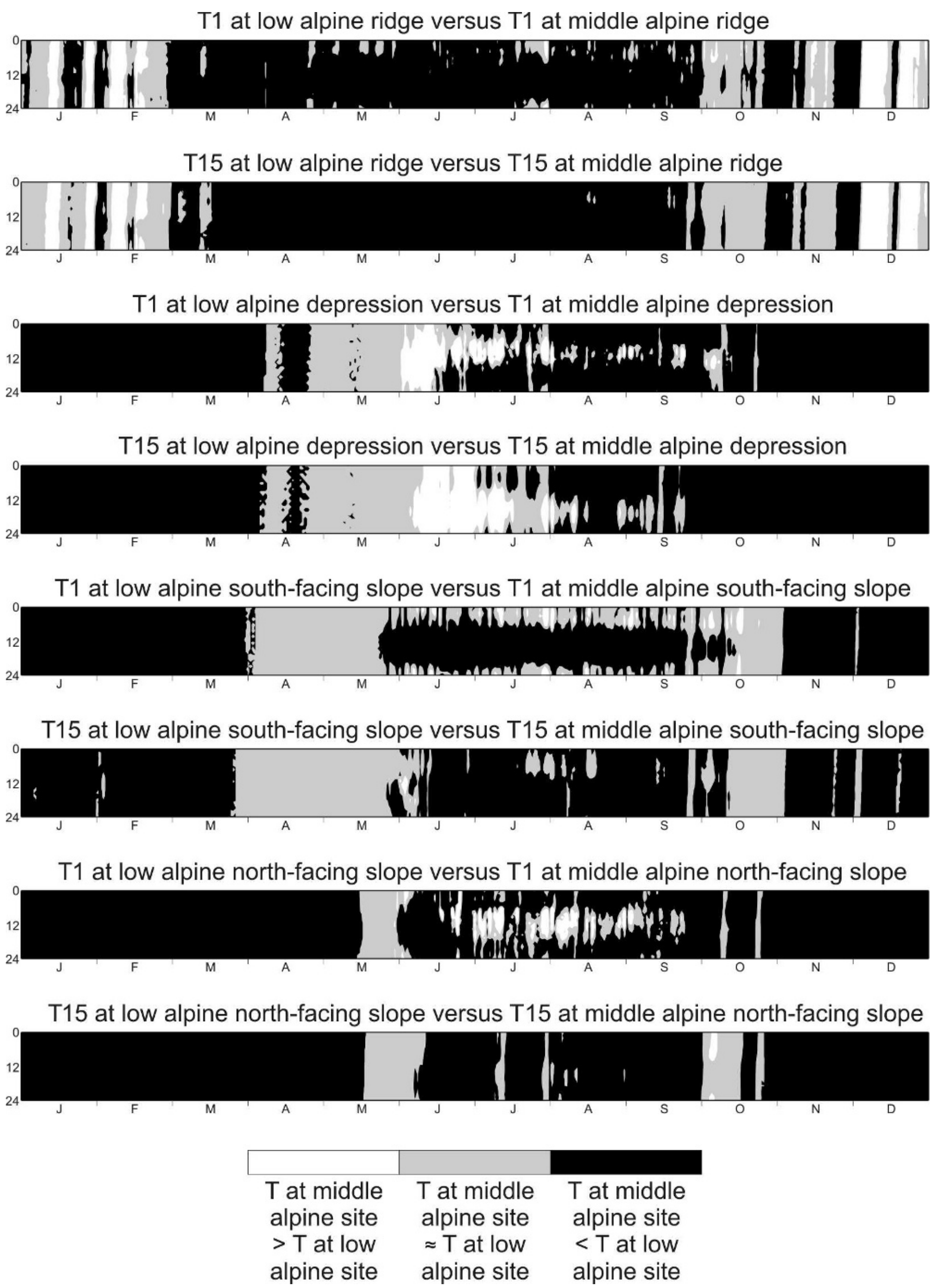

FIGURE 7. Diurnal and seasonal variability of altitudinal soil temperature differences during 1999.

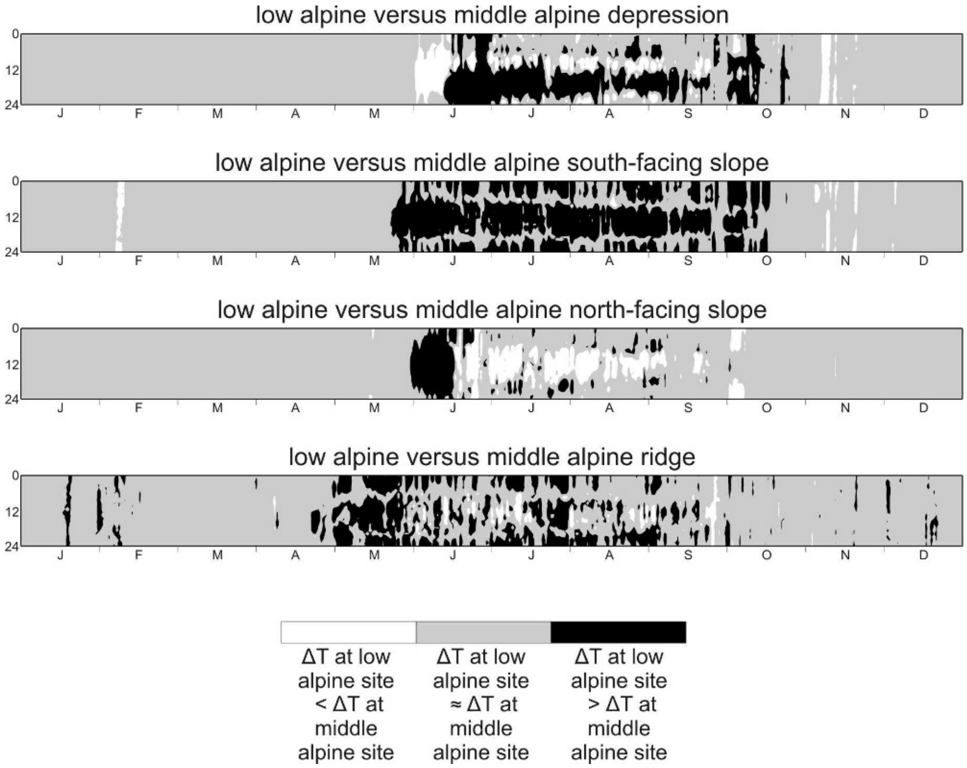

FIGURE 8. Altitudinal changes of vertical soil temperature gradients at different sites during 1999.

0.8 K/100 m) conform to well-known altitudinal trends of air temperature (Whiteway et al., 1995), seemingly contradicting our hypothesis that alpine soil temperatures are decoupled from linear trends. However, this finding evolved to be a matter of scale: Standard deviations within a range of 0.3–1.0 K, as well as the maximum absolute lapse rates (−3.7 to 9.4 K/100 m), indicate less linear conditions for specific occasions than the mean values suggest (Lundquist and Cayan, 2007; Pepin and Norris, 2005; Rolland, 2003). Our soil temperatures varied greatly with respect to diurnal and seasonal amplitudes and were subject to fine-scale microtopographical site conditions. Therefore, it is difficult to predict them without knowledge of the variability of spatial patterns (Richardson et al., 2004). Again, in a seasonal perspective, spatial patterns of snow cover are the most important factor: The winterly irregular gradients found between the ridges are determined by the presence or absence of a shallow snow cover before redistribution by stronger winds, whereas the evolution of a long-lasting snow cover at the other sites in the middle alpine belt preserves the cooler conditions there from autumn throughout the winter. Furthermore, differences during spring can be attributed to differences in the date of snowmelt, as observed for the north-facing slopes (low alpine snow-free first) and depressions (middle alpine snow-free first). During the snow-free season, the similar substrate and vegetation cover of the ridges resulted in the observed uniform altitudinal temperature gradients, whereas the differences in substrate and vegetation cover, no longer masked by the snow cover, result in the observed variation of the altitudinal temperature gradients at the other sites. As a consequence, these primarily topographically induced small-scale soil temperature gradients outbalance the general (mean) altitudinal gradient during specific diurnal and seasonal periods and finally lead to the hypothesized decoupling of alpine soil temperatures from mesoscale air temperature conditions.

Recent studies on modeling climatic change have usually been restricted to low-resolution topography data (Guisan and Theurillat, 2000; Dirnböck et al., 2003). However, we conclude, on the basis of our observations, that mountain soil temperatures vary on multiple spatial scales, and we reason that any approach to modeling, and predicting changes in, mountain soil temperature depends on input data of appropriate spatial and temporal resolution (Wundram and Löffler, 2008; Pape et al., 2009).

Against the background of these findings, the downscaling of global warming trends to regional and local scales is critical (Peterson, 2000; Diaz et al., 2003; Rial et al., 2004; Trivedi et al., 2008). Furthermore, we argue that mean temperature values are unsuitable for representing the altitudinal changes of high mountain climate. As to the observed enormous spatial temperature variability at multiple scales, we question the use of mean temperature values as well as mean lapse rates in modeling the ecological response to possible climate change (Gottfried et al., 1999; Guisan and Theurillat, 2000; Dirnböck et al., 2003; Löffler et al., 2006).

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