Spatiotemporal Variability of Soil Temperature and Moisture across two Contrasting Timberline Ecotones in the Sergyemla Mountains, Southeast Tibet

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Abstract

Simultaneous measurements of soil temperature and moisture and related climate and vegetation variables at high altitudes are rare. Such knowledge is important to predict soil temperature and moisture across heterogeneous alpine landscapes and the impact of climate warming on alpine ecosystems. Based on the four-year observations in 12 plots across two contrasting timberline ecotones (north-facing *Abies georgei* var. *smithii* and south-facing *Juniperus saltuaria* timberlines of a valley) in the Sergyemla Mountains, we aimed to determine the role of altitude, aspect, climate, soil, and vegetation variables affecting the variability of soil temperature and moisture. The two timberlines had similar annual precipitation and seasonal mean air temperature, but the growing-season mean soil temperature differed by 0.8–1.0 K. The spring soil warming date was 20–30 days later on the north-facing slope than on the south-facing slope, which was associated with increased snow and vegetation covers on the north-facing slope. Slope aspect, canopy height, and leaf area index (LAI) rather than altitude were the major determining factors for spatial variability of seasonal mean soil temperatures across plots. A combination of aspect southness and canopy height/LAI explained 56–77% of the variations in the −20 cm mean soil temperatures for the year, growing season, and July across the 12 plots. In contrast, seasonal mean soil moistures did not correlate with altitude, aspect, and stand and soil variables. Furthermore, the −5 cm soil temperature amplitude in the growing season was much lower in the north-facing fir forest than in the south-facing juniper forest, suggesting an explanation for the distribution pattern of both species timberlines on opposite slopes of a valley in the Sergyemla Mountains.

Introduction

Soil temperature and moisture are two key factors directly determining many chemical and biological processes in the soil such as nutrient and water uptake by roots (Kozlowski and Pallardy, 1997; Weih and Karlsson, 2002), soil organic matter decomposition and mineralization rates (Van Cleve et al., 1981; Macdonald et al., 1995; Elberling and Brandt, 2003), and related plant growth processes (Domisch et al., 2002; Aphalo et al., 2006). Above all, soil temperature and moisture can control plant distribution and community composition at high altitudes (Tranquillini, 1979; Körner, 2003; Wieser and Tausz, 2007). Hence, the knowledge of spatial and temporal variability of soil temperature and moisture is crucial to understand the impact of climate change on alpine ecosystems. However, there is incomplete knowledge about spatial and temporal variability of soil temperature and moisture at high altitudes. While high-altitude air temperature can be easily interpolated from nearby low-altitude meteorological stations by using a lapse rate (Richardson et al., 2004; Gehrig-Fasel et al., 2008), there is not a general physical model that allows for interpolating soil temperature in the same way as that of air temperature (Green and Harding, 1980; Richardson et al., 2004; Wundram et al., 2010). Significant uncertainty can remain in predicting the impact of climate warming on alpine ecosystems based on air temperature (e.g. Dirnböck et al., 2003; Engler et al., 2009; Wilson and Nilsson, 2009; Rammig et al., 2010). One way to address this problem is to gain a better understanding of relative influences of altitude, aspect, climate, soil and vegetation variables on the spatial and temporal variability of soil temperature and moisture.

Soil temperature is controlled by a variety of factors that covary with topography (e.g. altitude and aspect), such as meteorological factors (e.g. radiation, air temperature, and snow cover), soil physical properties (e.g. texture and soil moisture), and vegetation cover (Balisky and Burton, 1995; Kang et al., 2000; Redding et al., 2003; Bond-Lamberty et al., 2005a, 2005b). It has been observed that the growing-season mean soil temperature decreases (Shanks, 1956; Siccama, 1974; Green and Harding, 1980) or increases (Karlsson and Weih, 2001; Richardson et al., 2004) with altitude, suggesting that the controls on the variability of soil temperature can vary geographically. At high altitudes, snow cover varies with season, wind, aspect, and vegetation cover (Hiemstra et al., 2006), which determines winter soil temperature and spring soil warming date (Mellander et al., 2005; Wieser and Tausz, 2007). Furthermore, soil moisture may affect soil temperature by changing soil heat capacity and thermal conductivity (Van Wijk, 1965), which generally results in a negative correlation between soil temperature and soil moisture (Balisky and Burton, 1995; Redding et al., 2003; Bond-Lamberty et al., 2005b; but see Morecroft et al., 1998). However, the simultaneous measurements of soil temperature and moisture and related climate and vegetation variables at high altitudes are rare (Körner, 2007).
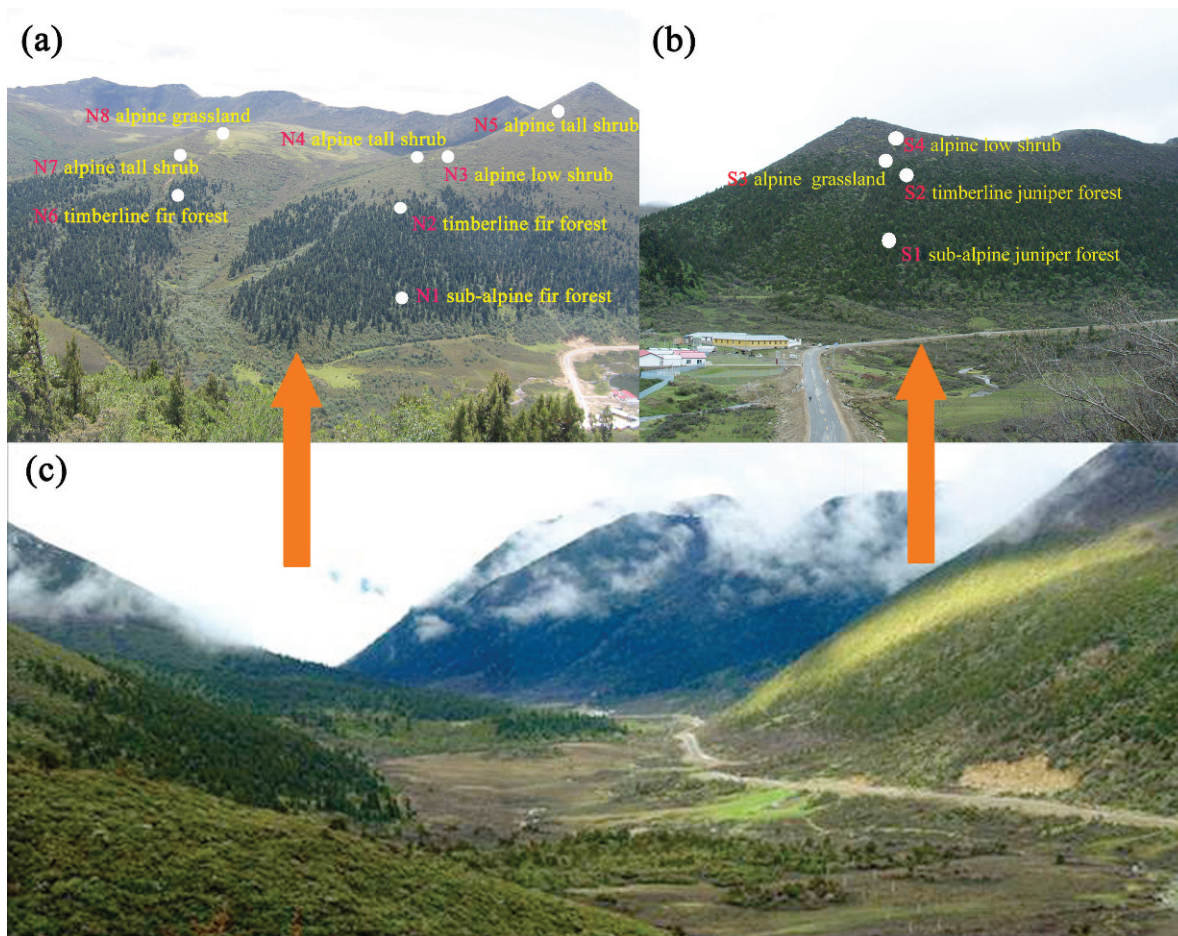
FIGURE 1. Location and vegetation type description of study sites across (a) north-facing fir and (b) south-facing juniper timberline ecotones of (c) a U-shaped valley in the Sergyema Mountains.

In southeast Tibet, alpine timberlines are frequently dominated by *Abies*, *Picea*, and *Juniperus* species with altitudes ranging from 4300 m to 4700 m a.s.l., which are among the highest timberlines in the world (Miehe et al., 2007). In the Sergyemla Mountains, there is a unique distribution pattern in timberlines of *Abies georgei* var. *smithii* and *Juniperus saltuaria*, which dominate at different altitudes on the opposite slopes of a valley (north-facing fir at 4300–4400 m vs. south-facing juniper at 4400–4500 m). The fir seedlings generally regenerate from seeds, while the juniper seedlings mainly regenerate via sprouting from the basal trunk (as the moss and litter build up) and root buds (Zhang et al., 2010). In southeast Tibet, the instrumental climatic data indicate a significant warming trend since the 1960s, which has been recorded in tree-ring chronologies of the timberline fir trees in the Sergyemla Mountains (Liang et al., 2009). Seed-based fir regeneration would be highly sensitive to the change of surface soil temperature caused by climate warming. However, there are few data on the causes for the distribution pattern of fir and juniper timberlines on opposite slopes of a valley in the Sergyemla Mountains. The knowledge of how soil temperature and moisture vary geographically can also be useful for understanding the sensitivity and response of both species' timberlines to past and future climate warming.

During 2005–2009, we conducted a transect investigation across the two contrasting timberline ecotones in the Sergyemla Mountains. We simultaneously monitored soil temperature and moisture and related meteorological factors (air temperature, relative humidity, rainfall, snow depth etc., with hourly records)

for 12 plots with altitudinal vegetation changes from forests to shrublands and grasslands. In each of the 12 plots, we further measured several vegetation and soil variables (leaf area index, canopy height, and soil bulk density). In this study, our objective was to determine the role of altitude, aspect, climate, soil, and vegetation variables affecting the spatial and temporal variability of soil temperature and moisture in the unique timberline ecotones. Our tasks were to: (1) examine the seasonal patterns in daily mean soil temperature and moisture associated with meteorological factors (air temperature, snow cover, rainfall, etc.) within a plot, and (2) quantify the relative contributions of altitude, aspect, soil and vegetation variables to the spatial variability of seasonal mean soil temperature and moisture across plots.

Materials and Methods

STUDY SITES

This study was conducted on the opposite slopes (north-facing and south-facing slopes) of a U-shaped valley at the peak of the Sergyemla Mountains (29°36′N, 94°36′E) in southeast Tibet, China. *Abies georgei* var. *smithii* and *Juniperus saltuaria* are the dominant tree species of timberlines on north-facing and south-facing slopes, respectively. The elevation of the juniper timberline is 100–200 m higher than that of the fir. Along three altitudinal transects (S1–S4 on the south-facing slope; N1–N5 and N6–N8 on the north-facing slope; Fig. 1), 12 long-term plots (50 × 50 m for forests, and 10 × 10 m for shrublands and

TABLE 1

Stand and soil variables in 12 plots along north-facing and south-facing slopes of a valley in the Sergyema Mountains, southeast Tibet of China.

Site no.	Altitude (m)	Aspect (°)	Soil bulk density (g cm^{-3})	Canopy height (m)	Leaf area index (m^2 m^{-2})	Dominant species*
N-slope						
N1	4210	291	1.00	14.69 ± 1.87	8.47 ± 2.53	AGS
N2	4320	320	1.04	11.16 ± 0.35	7.87 ± 2.01	AGS
N3	4390	334	1.08	0.32 ± 0.02	1.73 ± 0.12	RN
N4	4390	353	1.06	3.06 ± 0.12	3.39 ± 0.63	RAS
N5	4504	325	0.65	1.33 ± 0.10	2.96 ± 0.40	RAS
N6	4294	322	0.95	11.19 ± 0.87	7.97 ± 0.88	AGS
N7	4375	287	1.03	1.88 ± 0.21	2.07 ± 1.02	RAS
N8	4416	297	0.86	0.03 ± 0.00	0.80 ± 0.11	SL, PV, IX
S-slope						
S1	4291	157	1.08	7.86 ± 0.78	4.53 ± 1.20	JS
S2	4425	174	0.98	7.20 ± 1.19	4.13 ± 0.28	JS
S3	4441	168	1.10	0.09 ± 0.05	1.12 ± 0.21	KP, AF, AL
S4	4510	166	1.22	0.79 ± 0.05	1.41 ± 0.10	RN

* Abbreviations for dominant species: *Aster flaccidus* (AF), *Abies georgei* var. *smithii* (AGS), *Anaphalis lactea* (AL), *Illa xizangensis* (IX), *Juniperus saltuaria* (JS), *Polygonum viviparum* (PV), *Rhododendron aganniphum* var. *schizopeplum* (RAS), *Rhododendron nivale* (RN), *Salix lindleyana* (SL), *Kobresia pygmaea* (KP).

grasslands) were selected to represent altitudinal vegetation changes from subalpine and timberline forests (tree height >4 m and canopy density >40%) to alpine shrublands and grasslands (Table 1 and Fig. 1). In each of the 12 plots with different plant stature and coverage, the hourly recorded data logger and associated sensors (HOBO weather micro-station, Onset Inc., U.S.A.) were installed to measure soil temperature and moisture. Moreover, the simultaneous measurements of air temperature, relative humidity, rainfall, and snow depth, etc. were obtained from four automatic weather stations located at the sites for both upper limits of fir forest (N2) and juniper forest (S2) and their nearby shrubland (N3) and grassland (S3). The monitoring started in August 2005 for most sites (N1–N4 and S1–S4), and in June 2007 for other sites (N5–N8). In addition, we measured elevation, aspect, stand variables of canopy height and leaf area index (LAI), and soil bulk density for each of the 12 plots in August 2007 (Table 1).

MEASUREMENTS OF STAND AND SOIL VARIABLES

To quantify the effects of vegetation and soil variables on spatial variations in soil temperature and moisture, we measured two major stand variables of LAI and canopy height, as well as soil bulk density for each of the 12 plots. In each forest plot, tree height and diameter at breast height (DBH) were measured for all trees of over 3 cm in DBH. Leaf biomass of trees was calculated from measurements of DBH and tree height using species-specific allometric regressions that were developed in our previous work (Luo et al., 2002), while the undergrowth leaf biomass of shrubs and herbs were measured by harvesting three quadrats (4 × 4 m). For alpine shrublands and grasslands, species-specific leaf biomass of a plot was measured by harvesting three quadrats (4 × 4 m for tall shrubs, 2 × 2 m for low shrubs, and 0.5 × 0.5 m for grasses). We collected leaf samples in different leaf age classes of trees, shrubs and grasses, and measured the specific leaf area (SLA, the ratio of fresh leaf area to dry mass) for each leaf sample. The species-specific LAI was calculated as the product of species-mean SLA and leaf biomass. Forest LAI was the sum of the tree LAI and the undergrowth LAI. Mean canopy height of forests and tall shrublands was calculated from the average DBH (trees) or stem

basal diameter (tall shrubs) using the regression of individual tree height against DBH or stem basal diameter, while the canopy height of low shrublands and grasslands was directly measured by a tape. The soil bulk density (5–20 cm in depth) for each of the 12 plots was measured on soil samples extracted with a circular soil cutter (Table 1).

MEASUREMENTS OF SOIL TEMPERATURE AND MOISTURE

Within each plot, soil temperatures and volumetric moisture contents at soil depths of 5 cm (limited to sites N2–N3 and S2–S3), 20 cm, and 40 cm (or 60 cm at N2–N3 and S2–S3) were measured by using a single HOBO micro-station (Onset Inc., U.S.A.). The depth-specific smart sensors of soil temperature (S-TMB-M002, with accuracy ±0.2 °C) and soil moisture (S-SAM-M003, with accuracy ±3%) were connected to the HOBO logger by 2-meter cables. The logger recorded data at an interval of one hour. We downloaded the hourly recorded data from the logger to a computer at six-month intervals.

MEASUREMENTS OF AIR TEMPERATURE, RELATIVE HUMIDITY, RAINFALL, AND SNOW DEPTH

We further established four automatic weather stations at the sites for both upper limits of the north-facing fir forest (N2) and the south-facing juniper forest (S2) and their nearby low shrubland (N3) and grassland (S3) (Fig. 1). Air temperature and relative humidity at a height of 3 m above the ground were simultaneously measured across forested (N2, S2) and non-forested (N3, S3) sites, while the observation of rainfall and snow depth was limited to the two non-forested sites (N3, S3). The combined air temperature and relative humidity probe with vented radiation shield (MP101A, Rotronic Inc., U.S.A.) and the tipping-bucket rain gauge (7852M-AB, Wittich & Visser, Netherlands), as well as the ultrasonic snow depth sensor (260–700, NovaLynx Corp., U.S.A.) were connected to the data logger (HL20, Jauntering Inc., Taiwan). Also, the HL20 logger recorded data at an interval of one hour, and the hourly recorded data were downloaded to a computer at six-month intervals.

CALCULATIONS OF CLIMATIC PARAMETERS

Daily mean air and soil temperatures and soil moisture were the averages of hourly records within a day. Daily air and soil temperature amplitudes were the difference between the hourly records of maximum and minimum temperatures within a day. Hourly vapor pressure deficit was calculated from hourly air temperature and relative humidity (Sheng et al., 2003), and daily mean vapor pressure deficit was the average of the hourly vapor pressure deficits between 8:00 and 20:00 within a day. In this study, our analysis was based on the four-year (from 17 August 2005 to 10 September 2009 for sites N1–N4 and S1–S4) or two-year (from 22 June 2007 to 10 September 2009 for sites N5–N8) averages of daily measurements. Unfortunately, the entire winter and early growing season (2007–2009) data were lost at the grassland site on the north-facing slope (N8) because of power failure. Using the averaged data of daily mean air and soil temperatures, we calculated mean air temperatures for the year (ATa), growing season (ATg), January (AT$_1$), and July (AT$_7$), and mean soil temperatures for the year (STa), growing season (STg), January (ST$_1$), and July (ST$_7$), as well as the air (ATS) and soil (STS) temperature sums above 5 °C (the sum of daily values) and the growing season length (GSL, see definition below). The slope-specific annual precipitation (AP) was calculated as the average for the four-year sum of logger records, in which approximately 85% of annual precipitation was recorded during May and September. Additionally, we calculated mean soil moistures for the year (SMa), growing season (SMg), January (SM$_1$), and July (SM$_7$).

Thomson and Moncrieff (1982) indicated that an air temperature threshold of 2.8 °C was a good predictor of bud burst of Douglas fir in Canada. In this study, we adopted that air temperature threshold to define the growing season length (GSL) of shoot growth. The GSL equaled the growing period between both dates at which the daily mean air temperature first exceed 2.8 °C in spring and first dropped below 2.8 °C in autumn. There is evidence that bud burst and the start of new shoot elongation are mainly dependent on air temperature but not soil temperature (Domisch et al., 2002). According to our phenological observation, the bud burst of *Salix oritrepha* (a deciduous shrub) outside the forest stand occurred on 15–20 April on the south-facing slope but on 10–15 May on the north-facing slope, which were generally consistent with the predicted beginning dates of the growing season at two non-forested sites of S3 (15 April) and N3 (8 May). In the study area, the snow cover persisted from late November to late April on the south-facing plots but from late November to late May on the north-facing plots.

At high altitudes, the soil warming in spring lagged by over a week behind the increased air temperature because of seasonal snow cover and soil thawing (Gehrig-Fasel et al., 2008). Accordingly, the belowground root growth can start later than the aboveground shoot growth. In a previous worldwide study of high-altitude treeline soil temperature, Körner and Paulsen (2004) defined the belowground growing period by using a −10 cm soil temperature threshold of 3.2 °C. In this study, we did not measure the −10 cm soil temperature. At both species' timberlines, most of the fine roots of trees were distributed in the soils at the 10–30 cm depths. We assumed that the threshold of 3.2 °C could be used to calculate the growing season mean soil temperature based on the daily mean soil temperature at −20 cm. By using the threshold of 3.2 °C to define the beginning and ending of the belowground growing season, the estimated seasonal mean soil temperature at −20 cm was 0.2–1.0 °C lower than those at −5 cm across forested (0.3 °C for N2 and 0.5 °C for S2) and non-forested (1.0 °C for N3 and 0.2 °C for S3) sites. Given the non-linear decrease of soil temperature with depth in soil, the growing season mean soil temperature at −20 cm would be much closer to the −10 cm soil temperature than to the −5 cm soil temperature.

STATISTICAL ANALYSIS

The partial correlation coefficients of multiple linear regression were used for assessing the relative importance of altitude, aspect, soil, and vegetation variables to the spatial variability of soil temperature and moisture. The independent variables included elevation, aspect southness (because aspect is a circular variable, we transformed it to "southness" [cos(aspect − 180°)]), soil and vegetation variables (LAI, canopy height, and soil bulk density). The effect of soil moisture on soil temperature was also considered in the partial correlation analysis.

A simple linear model (y = a + bx) was used for examining the relationships of stand variables (canopy height and LAI) to the growing season and July mean soil temperatures (all variables were normalized by the natural logarithmic transformation). Based on observed data across the 12 plots, multiple linear regression models relating seasonal mean soil temperatures to selected significant independent variables were developed.

All statistical analysis was performed using SPSS 15.0 for Windows, and all significant differences were at $p < 0.05$.

Results

SEASONAL VARIABILITY OF DAILY MEAN SOIL TEMPERATURE AND MOISTURE AND DAILY TEMPERATURE AMPLITUDE

The difference of spring soil warming dates between north-facing (Figs. 2a–2b; N2–N3) and south-facing (Figs. 2c–2d; S2–S3) slopes was up to 20–30 days, which was associated with the much deeper snow depth on the north-facing slope (Figs. 2b, 2d). During snow cover period, daily mean soil temperature across depths and sites was much higher than the mean air temperature (Fig. 2).

In summer, the −5 cm soil temperature amplitude at the north-facing fir timberline (N2, <1 °C; Fig. 3a) was much lower than that at the north-facing low shrubland (N3, 2–5 °C; Fig. 3b) and the south-facing juniper timberline and grassland (S2–S3, 2–6 °C; Figs. 3c–3d). In contrast, similar air temperature amplitudes were found at both timberlines (Figs. 3a, 3c). During snow cover period, the −5 cm soil temperature amplitude was generally close to 0 °C (Figs. 3a–3c) except for that of the south-facing grassland where the higher −5 cm soil temperature amplitude (1–6 °C) did not have a seasonal trend (S3; Fig. 3d).

The daily mean soil moisture varied greatly with seasons, aspects, and vegetation types, compared to the relatively unchanged vapor pressure deficit (Fig. 4). At 20 cm depth where most of fine roots of trees were distributed, the daily mean soil moisture was typically >20% during the growing season (Fig. 4).

SPATIAL VARIABILITY OF SEASONAL MEAN SOIL TEMPERATURE AND MOISTURE

The north-facing and south-facing slopes had similar annual precipitation (Table 2). On non-forested sites, mean air temperatures for the year, growing season, January, and July were 1.0–1.9 K higher at the south-facing grassland (S3 at 4441 m) than at the north-facing low shrubland (N3 at 4390 m) (Table 2). The growing season length and the air temperature sum above 5 °C were 25 days longer and 361 degree-days higher at the south-facing
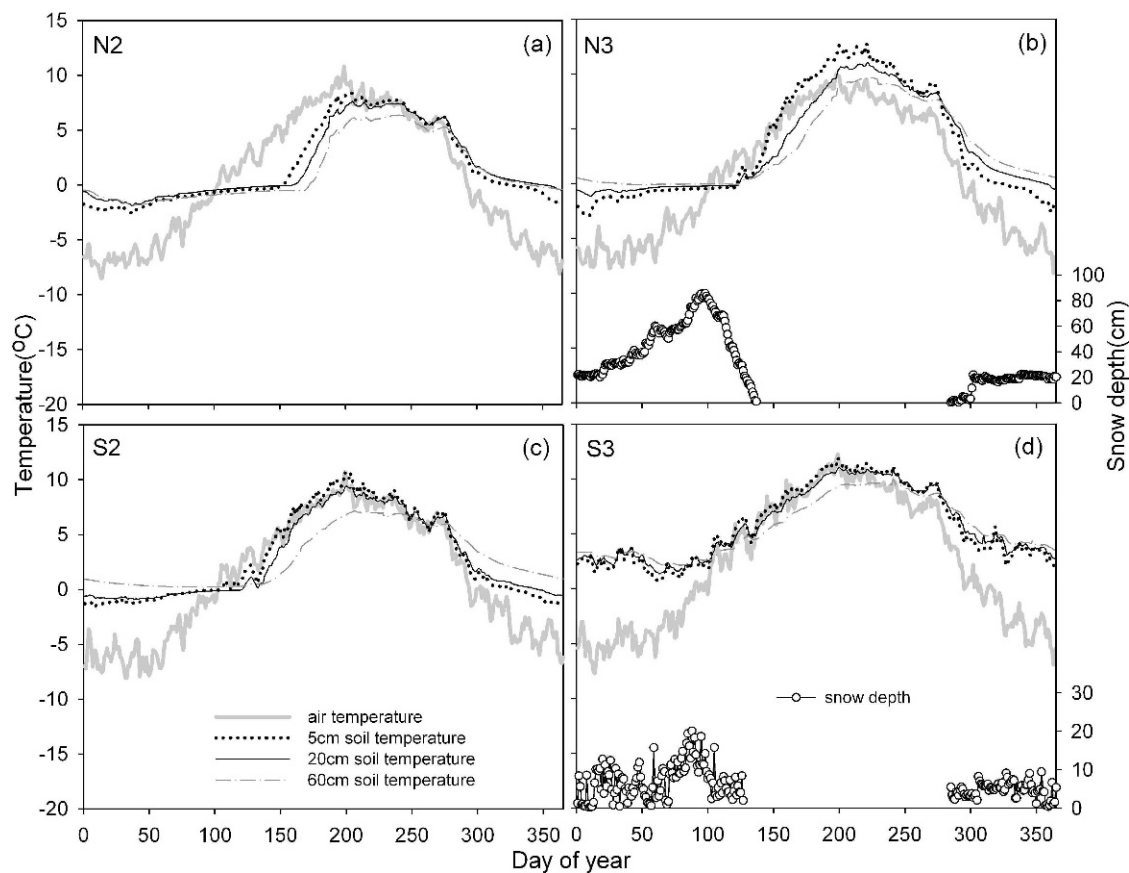
FIGURE 2. The annual course of daily mean air and soil temperatures and snow depth across the north-facing (a, N2) fir timberline and (b, N3) low shrubland; and the south-facing (c, S2) juniper timberline and (d, S3) grassland. Snow depth was recorded only at sites N3 and S3.

grassland than at the north-facing low shrubland. In contrast, the mean air temperatures of both timberline sites (N2 at 4320 m and S2 at 4425 m) differed little (0–0.8 K; Table 2).

On average, seasonal mean soil temperatures at −20 cm across altitudinal vegetation types were generally 1.1–2.2 K higher on the south-facing slope than on the north-facing slope (Table 3). Accordingly, the average soil temperature sum above 5 °C was 531 degree-days higher at the south-facing sites (1241 ± 257 degree-days) than at the north-facing sites (710 ± 202 degree-days). Between both timberline sites (S2 vs. N2 and N6), the differences of the −20 cm mean soil temperatures were 1.0–1.1 K for the year, 0.8–1.0 K for growing season, 2.0–2.2 K for July, and 0.6–1.0 K for January. The −20 cm mean soil temperatures for shrublands and grasslands above both timberlines were generally 0.5–1.8 K higher than those of forest sites (at lower altitudes) (Table 3).

Partial correlation analysis of the pooled data from all 12 plots indicated that canopy height, LAI, and aspect southness were the main factors affecting the spatial variability of seasonal mean soil temperatures (Table 4). Canopy height and LAI, which were higher on the north-facing slope and decreased with altitude ($p < 0.01$; from Table 1), were negatively correlated with the growing season and July mean soil temperatures (Fig. 5) even though the mean soil temperatures varied little with altitude ($p > 0.10$; from Table 3). A combination of aspect southness and canopy height/LAI explained 56–77% of the variations in the −20 cm mean soil temperatures for the year, growing season, and July across the 12 plots (Table 5).

In contrast, seasonal mean soil moistures for the year, growing season, July, and January did not correlate with altitude,

aspect, or stand and soil variables (canopy height, LAI, soil bulk density) across the 12 plots ($p > 0.10$, data not shown).

Discussion

CONTROLS OF SNOW AND PLANT COVER ON TEMPORAL VARIABILITY OF ALPINE SOIL TEMPERATURE

In winter, daily mean soil temperatures across depths and sites were generally stable (Fig. 2). In spring, the soil warming date was 20–30 days later on the north-facing slope than on the south-facing slope (Fig. 2). At high altitudes or latitudes, snow cover generally plays a key role in determining winter soil temperature and spring soil warming date (Mellander et al., 2005; Wieser and Tausz, 2007). The insulating effect of snow cover prevents the ground from cooling, and the soils under thick snow cover are typically characterized by an even soil temperature regime (Wundram et al., 2010). In boreal forests, deep snow cover needs substantial energy to melt and generally results in a delayed soil warming date in spring (Mellander et al., 2005; Sutinen et al., 2009). Hence, soil temperature is decoupled from air temperature when the ground is covered with insulating snow.

During the snow-free period, vegetation cover exerts a great influence on soil temperature by changing its relationship with air temperature. Gehrig-Fasel et al. (2008) indicated that daily mean air temperature of previous 1 and 2 days can predict well the daily mean soil temperature during the growing season at treelines in Switzerland. However, our observations demonstrated that the
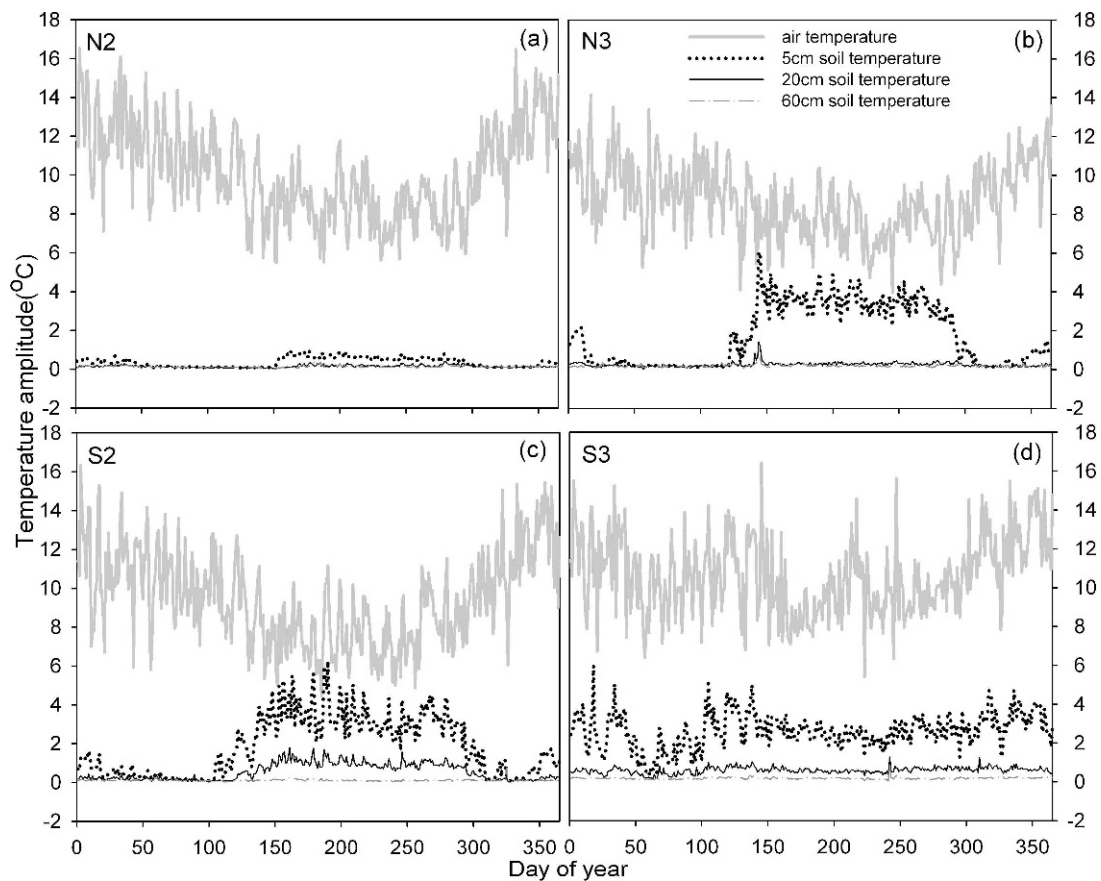
FIGURE 3. The annual course of daily air and soil temperature amplitudes across the north-facing (a, N2) fir timberline and (b, N3) low shrubland; and the south-facing (c, S2) juniper timberline and (d, S3) grassland.

air-soil temperature hysteresis during the growing season (June–September) varied significantly with vegetation types (Fig. 2). The −5 cm soil temperature had the highest correlation with the air temperature of the previous 10–21 days at the north-facing sites (N2 and N3) but of the current day or previous day at the south-facing sites (S2 and S3) (from Fig. 2, data not shown). High LAI and large moss/litter accumulation insulate the soils, resulting in the air-soil temperature decoupling during the growing season (Balisky and Burton, 1995; Bond-Lamberty et al., 2005a).

RELATIVE IMPORTANCE OF ALTITUDE, ASPECT, VEGETATION, AND SOIL VARIABLES TO THE SPATIAL VARIABILITY OF SEASONAL MEAN SOIL TEMPERATURE AND MOISTURE

Under timberline canopies on the opposite slopes of a valley, the exponential decrease in sunlight penetration through the closed canopy can create a similar microclimate, especially seasonal mean air temperature (Table 2). The growing season mean soil temperatures at −20 cm for both timberlines (6.0–7.0 °C) fall within the −10 cm threshold temperature of 6.7 ± 0.8 °C found in global climatic treelines (Körner and Paulsen, 2004). However, the growing-season mean soil temperature was 0.8–1.0 K higher at the south-facing juniper timberline than at the north-facing fir timberline (Table 3), which was directly attributed to the contrasting snow depths and/or LAIs between north-facing and south-facing slopes (Figs. 2b, 2d; Table 1). This is in contrast to the previous reports in European treelines where there is a weak effect of aspect on seasonal mean soil temperature (Körner and Paulsen, 2004; Treml and Banaš, 2008). At high altitudes, slope

aspect can affect the amount and daily cycle of solar radiation received at different times of the year, and then local microclimatic differences in snow cover duration and soil temperature and moisture become important factors (Rosenberg et al., 1983; Wieser and Tausz, 2007). In general, snow depth and soil thawing significantly influence seasonal mean soil temperature and soil warming date in boreal forests (Mellander et al., 2005).

Our data further indicated that aspect southness and vegetation variables (canopy height and LAI) rather than altitude were the main factors affecting the spatial variability of seasonal mean soil temperatures across both timberline ecotones (Table 4 and Fig. 5). It has been suggested that there is a remarkable influence of plant stature and canopy on seasonal mean soil temperature at high altitudes (Ballard, 1972; Munn et al., 1978; Körner and Paulsen, 2004; Bader et al., 2007). While global radiation may not change significantly with altitude due to the frequency of cloud cover at high altitudes (Körner, 2003), the significant decrease of LAI and canopy height with increasing altitude at the timberline ecotones enhances solar radiation reaching the ground surface (Balisky and Burton, 1995; Redding et al., 2003; Bond-Lamberty et al., 2005a). Additionally, in contrast to upright tall trees, dwarf plants above alpine timberlines can increase soil temperature by enhancing aerodynamic resistance (Green et al., 1984). LAI and canopy height were negatively correlated with seasonal mean soil temperatures across altitudinal vegetation types even though the mean soil temperatures varied little with altitude.

In contrast to the seasonal mean soil temperature, the seasonal mean soil moisture varied insignificantly with altitude, aspect, and stand and soil variables. The daily mean soil moisture
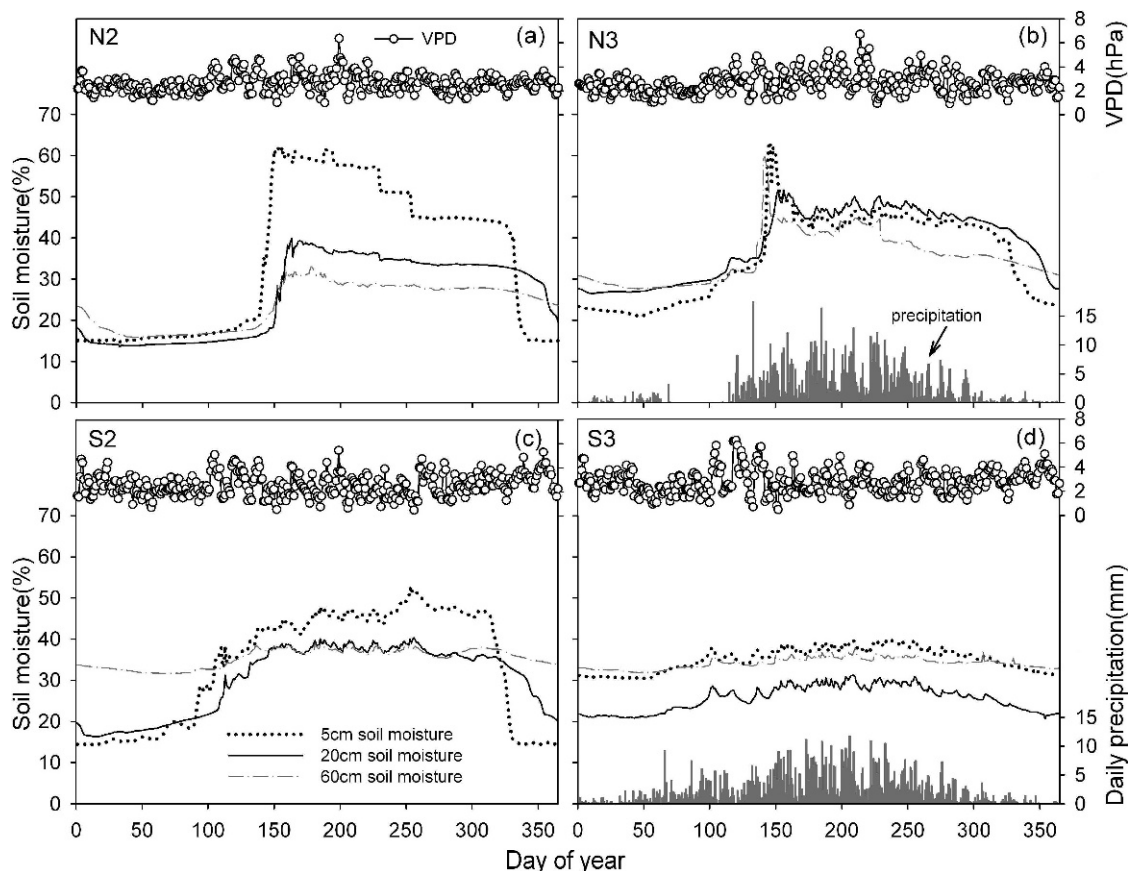
FIGURE 4. The annual course of daily mean soil moisture, daily precipitation and daily mean daytime vapor pressure deficit (VPD) across the north-facing (a, N2) fir timberline and (b, N3) low shrubland; and the south-facing (c, S2) juniper timberline and (d, S3) grassland. Precipitation was only recorded at sites N3 and S3.

across vegetation types was generally more than 20% during the growing season (Fig. 4). Within a plot, daily mean soil moisture was poorly correlated with daily mean soil temperature (negative or positive). It has been suggested that soil moisture has no significant effect on soil temperature in temperate and boreal forests. This is partly because of the lesser sensitivity of thermal diffusivity to soil moisture in a small soil heat flux (Morecroft et al., 1998) and/or the buffer effect of high LAI on soil temperature variability (Bond-Lamberty et al., 2005b).

TABLE 2

Seasonal mean air temperature and annual precipitation across the north-facing fir timberline (N2, 4320 m) and low shrubland (N3, 4390 m), and the south-facing juniper timberline (S2, 4425 m) and grassland (S3, 4441 m) of a valley in the Sergyema Mountains during 2005–2009. The climatic variables were calculated for mean air temperatures for the year (ATa), growing season (ATg), July (AT_7) and January (AT_1), the growing season length (GSL), the air temperature sum above 5 °C (ATS), and annual precipitation (AP).

Sites	ATa (°C)	ATg (°C)	AT_7 (°C)	AT_1 (°C)	GSL (d)	ATS (°C d)	AP (mm)
N-slope							
N2	0.6	6.5	8.7	−6.9	155	884.0	
N3	0.9	6.6	8.7	−6.4	161	941.2	847.8
S-slope							
S2	1.1	6.6	8.7	−6.1	160	937.8	
S3	2.5	7.7	10.6	−5.4	186	1302.0	940.2

EFFECTS OF SOIL TEMPERATURE AND MOISTURE ON LOCAL TIMBERLINE DISTRIBUTION PATTERNS

In the Sergyemla Mountains, there is a lack of explanation for the unique distribution pattern of fir and juniper timberlines that dominate at different altitudes on the opposite slopes of a valley.

TABLE 3

Seasonal mean soil temperature at −20 cm for 12 study sites across north-facing and south-facing timberline ecotones of a valley in the Sergyema Mountains during 2005–2009. The soil temperature variables were calculated for mean soil temperatures for the year (STa), growing season (STg), July (ST_7) and January (ST_1), and the soil temperature sum above 5 °C (STS).

Sites	STa (°C)	STg (°C)	ST_7 (°C)	ST_1 (°C)	STS (°C d)
N-slope					
N1 (4210 m)	2.0	5.9	5.3	−0.4	564.9
N2 (4320 m)	1.8	6.2	6.5	−1.3	635.7
N3 (4390 m)	3.3	8.2	9.5	−0.8	1092.4
N4 (4390 m)	1.7	5.6	5.7	−0.7	554.0
N5 (4504 m)	1.9	6.1	6.7	−1.3	607.8
N6 (4294 m)	1.7	6.0	6.7	−1.7	630.3
N7 (4375 m)	2.4	7.0	8.1	−2.0	888.2
N8 (4416 m)			11.0		
S-slope					
S1 (4291 m)	4.1	7.4	9.1	0.7	1171.9
S2 (4425 m)	2.8	7.0	8.7	−0.7	918.7
S3 (4441 m)	5.8	7.7	10.4	2.6	1515.7
S4 (4510 m)	4.6	7.7	10.1	0.3	1357.9

X. Liu and T. Luo / 235

TABLE 4

Coefficients of partial correlations for linear relationships of -20 cm mean soil temperatures for the year (STa, °C), growing season (STg, °C), January (ST$_1$, °C) and July (ST$_7$, °C) to stand variables (canopy height, m; LAI, m^{2}m^{-2}) and environmental variables (altitude, m; southness, calculated as cos(aspect $-$ 180°); soil moisture, %) across 12 plots with altitudinal vegetation changes from forests to shrublands and grasslands in the Sergyema Mountains. Because canopy height and leaf area index (LAI) were highly correlated, their correlations with soil temperature were separately analyzed.

Independent variables	STa	STg	ST$_1$	ST$_7$
Canopy height and environmental variables				
Canopy height	−0.693*	−0.731**	−0.320	−0.699**
Altitude	−0.483	−0.463	−0.265	−0.330
Southness	0.882***	0.820**	0.699*	0.742**
Soil moisture	0.256	0.707*	0.339	0.351
LAI and environmental variables				
LAI	−0.582	−0.703*	−0.222	−0.718**
Altitude	−0.286	−0.338	−0.163	−0.227
Southness	0.801**	0.695*	0.647*	0.628*
Soil moisture	0.250	0.688*	0.367	0.379

  *r marginally significant at $p < 0.10$; **r significant at $p < 0.05$; ***r significant at $p < 0.01$.

Shi et al. (2008) indicated that the winter air-temperature extreme is pronounced at the valley bottom juniper site where fir is absent. However, we found that the daily air temperature amplitude was identical between fir and juniper timberlines (Figs. 3a, 3c). Our data further indicated that the -5 cm soil temperature amplitude in the growing season was much lower and stable at the north-facing fir timberline (Fig. 3a), compared to the south-facing juniper timberline (Fig. 3c) and the two nearby non-forested sites (Figs. 3b, 3d). The seed-regenerated fir species (including seedlings, saplings, and trees) was excluded from the south-facing

FIGURE 5. Relationships of mean soil temperatures for growing season (ST$_g$) and July (ST$_7$) to (a, c) canopy height and (b, d) LAI across 12 plots with altitudinal vegetation changes from forests to shrublands and grasslands in the Sergyemla Mountains. All variables were in natural logarithmic transformation (original data found in Tables 1 and 3). The trend lines were for the data pooled from the 12 plots.

TABLE 5

Multiple linear regression models relating seasonal mean soil temperatures at -20 cm (for the year, STa; growing season, STg; July, ST$_7$) to aspect southness (calculated as cos(aspect $-$ 180°)) and canopy height (H, m) or leaf area index (LAI, m^{2}m^{-2}) across 12 plots with altitudinal vegetation changes from forests to shrublands and grasslands in the Sergyema Mountains.

Independent variables	Regression equation	r^2	p
H and Southness			
	STa = 1.162Southness − 0.102H + 3.583	0.77	0.003
	STg = 0.508Southness − 0.082H + 7.293	0.56	0.038
	ST$_7$ = 1.176Southness − 0.223H + 9.406	0.68	0.006
LAI and Southness			
	STa = 1.039Southness − 0.195LAI + 3.828	0.75	0.004
	STg = 0.395Southness − 0.170LAI + 7.545	0.58	0.032
	ST$_7$ = 0.905Southness − 0.446LAI + 9.989	0.71	0.004

juniper timberline and nearby non-forested sites. More interestingly, some root-sprouting seedlings and adult trees of juniper have been observed at the edge of the north-facing fir timberline. Compared to the relatively widespread root-sprouting juniper seedlings, the seed-based fir seedlings (rooting depth <10 cm) were limited to a stable soil temperature environment during the growing season. Since seedling establishment is important to the position of alpine treeline (Smith et al., 2003; Holtmeier and Broll, 2005), such a biological difference in forest regeneration adapted to the growing-season soil temperature extreme suggests an explanation for the distribution pattern of fir and juniper timberlines on opposite slopes of a valley in the Sergyemla Mountains. In response to future climate warming, the position of the fir timberline could remain steady because of the difficulty in seedling establishment, while the juniper timberline might advance and even extend to the north-facing slope consistent with the present observation that some seedlings and adult trees of juniper did scatter at the edge of the north-facing fir timberline.

It has been suggested that adaptations of plants to local climate lead to a LAI that is closely coupled with soil water and nitrogen availability (Woodward et al., 1995; Hirose et al., 1997). Given the similar plant stature and canopy cover such as the two non-forested sites nearby both timberlines (N3 vs. S3, Table 1), daily mean soil moisture at -20 cm during the growing season on the north-facing slope was almost double that on the south-facing slope (Figs. 4b, 4d). Between the fir and juniper timberlines, there were large differences in mean tree height and LAI (10–12 m and 6–8 m^2 m^{-2} for the fir trees, 6–8 m and 4–5 m^2 m^{-2} for juniper trees; Table 1), leading to the similar soil moisture contents at -20 cm (Figs. 4a, 4c). Across ecosystems, stand LAI and productivity are negatively correlated with foliar carbon isotope ratio (δ^{13}C) that is mainly determined by soil water availability (Luo et al., 2009). The carbon isotope data by Li (2007) indicate that foliar δ^{13}C is >3‰ higher in the south-facing juniper trees (-24.80 ± 1.05‰, $n = 48$) than in the north-facing fir trees (-27.91 ± 1.08‰, $n = 130$). This implies that the juniper is a relatively drought-resistant and low productivity species, and the north-facing fir forests with high LAI and productivity might not maintain the long-term soil water balance on the south-facing slope.

Conclusions

This study is a step forward in attempts to quantitatively determine relative influences of altitude, aspect, climate, soil, and
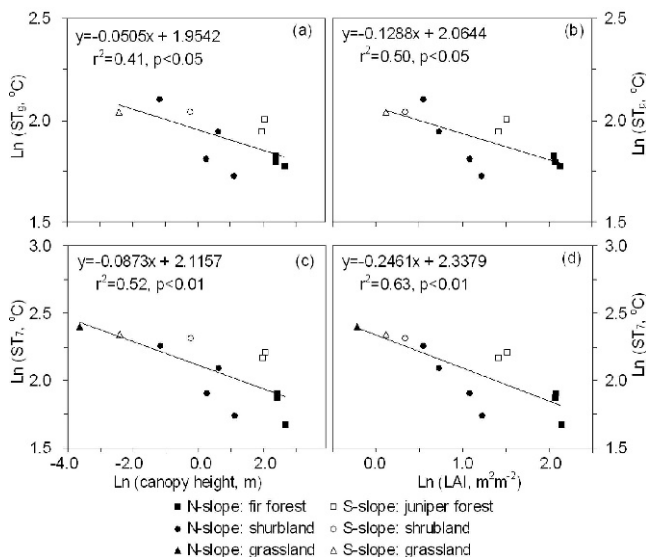
vegetation variables on the spatial and temporal variability of soil temperature and moisture across two contrasting timberline ecotones in the Sergyemla Mountains. The north-facing fir and south-facing juniper timberlines had similar annual precipitation and seasonal mean air temperature, but the seasonal mean soil temperature differed by 0.8–1.0 K. The larger air-soil temperature hysteresis on the north-facing slope was associated with increased snow and vegetation covers. Slope aspect and vegetation variables rather than altitude were the major determining factors for spatial variability of seasonal mean soil temperatures. Across both timberline ecotones, a combination of aspect southness and canopy height/LAI predicted well the altitudinal patterns in the −20 cm mean soil temperatures for the year, growing season, and July. The daily −5 cm soil temperature amplitude differed greatly between north-facing fir and south-facing juniper forests, suggesting an explanation for the distribution pattern of both species' timberlines on opposite slopes of a valley in the Sergyemla Mountains.

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References Cited

Aphalo, P. J., Lahti, M., Lehto, T., Repo, T., Rummukainen, A., Mannerkoski, H., and Finer, L., 2006: Responses of silver birch saplings to low soil temperature. *Silva Fennica*, 40: 429–442.

Bader, M. Y., Rietkerk, M., and Bregt, A. K., 2007: Vegetation structure and temperature regimes of tropical alpine treelines. *Arctic, Antarctic, and Alpine Research*, 39: 353–364.

Balisky, A. C., and Burton, P. J., 1995: Root-zone soil temperature variation associated with microsite characteristics in high-elevation forest openings in the interior of British Columbia. *Agricultural and Forest Meteorology*, 77: 31–54.

Ballard, T. M., 1972: Subalpine soil temperature regimes in southwestern British Columbia. *Arctic and Alpine Research*, 4: 139–146.

Bond-Lamberty, B., Wang, C., and Gower, S. T., 2005a: Spatiotemporal measurement and modeling of boreal forest soil temperatures. *Agricultural and Forest Meteorology*, 131: 27–40.

Bond-Lamberty, B., Brown, K. M., Goranson, C., and Gower, S. T., 2005b: Spatial dynamics of soil moisture and temperature in a black spruce boreal chronosequence. *Canadian Journal of Forest Research*, 36: 2794–2802.

Dirnböck, T., Dullinger, S., and Grabherr, G., 2003: A regional impact assessment of climate and land-use change on alpine vegetation. *Journal of Biogeography*, 30: 410–417.

Domisch, T., Finer, L., and Lehto, T., 2002: Growth, carbohydrate and nutrient allocation of Scots pine seedlings after exposure to simulated low soil temperature in spring. *Plant and Soil*, 246: 75–86.

Elberling, B., and Brandt, K. K., 2003: Uncoupling of microbial CO_2 production and release in frozen soil and its implications for field studies of arctic C cycling. *Soil Biology and Biochemistry*, 35: 263–272.

Engler, R., Randin, C. F., Vittoz, P., Czáka, T., Beniston, M., Zimmermann, N. E., and Guisan, A., 2009: Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? *Ecography*, 32: 34–45.

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

Green, F. H. W., and Harding, R. J., 1980: Altitudinal gradients of soil temperatures in Europe. *Transactions of the Institute of British Geographers*, 5: 243–254.

Green, F. H. W., Harding, R. J., and Oliver, H. R., 1984: The relationship of soil temperature to vegetation height. *Journal of Climatology*, 4: 229–240.

Hiemstra, C. A., Liston, G. E., and Reiners, W. A., 2006: Observing, modelling, and validating snow redistribution by wind in a Wyoming upper treeline landscape. *Ecological Modelling*, 197: 35–51.

Hirose, T., Ackerly, D. D., Traw, M. B., Ramseier, D., and Bazzaz, F. A., 1997: CO_2 elevation, canopy photosynthesis, and optimal leaf area index. *Ecology*, 78: 2339–2350.

Holtmeier, F. K., and Broll, G., 2005: Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography*, 14: 395–410.

Kang, S., Kim, S., Oh, S., and Lee, D., 2000: Predicting spatial and temporal patterns of soil temperature based on topography, surface cover and air temperature. *Forest Ecology and Management*, 136: 173–184.

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

Körner, C., 2003: *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems.* 2nd edition. Berlin, Heidelberg: Springer.

Körner, C., 2007: The use of 'altitude' in ecological research. *Trends in Ecology and Evolution*, 22: 569–574.

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

Kozlowski, T. T., and Pallardy, S. G., 1997: *Physiology of Woody Plants.* San Diego: Academic Press.

Li, M. C., 2007: *Leaf $\delta^{13}C$ and related physio-ecological characteristics across different plant life forms at alpine timberline, southeastern Tibetan Plateau.* Ph.D. dissertation. Graduate University of Chinese Academy of Sciences, Beijing, China.

Liang, E. Y., Shao, X. M., and Xu, Y., 2009: Tree-ring evidence of recent abnormal warming on the Tibetan Plateau. *Theoretical and Applied Climatology*, 98: 9–18.

Luo, T. X., Shi, P. L., Luo, J., and Ouyang, H., 2002: Distribution patterns of aboveground biomass in Tibetan alpine vegetation transects. *Acta Phytoecologica Sinica*, 26: 668–676.

Luo, T. X., Zhang, L., Zhu, H., Daly, C., Li, M. C., and Luo, J., 2009: Correlations between net primary productivity and foliar carbon isotope ratio across a Tibetan ecosystem transect. *Ecography*, 32: 526–538.

Macdonald, N. W., Zak, D. R., and Prenitzer, K. S., 1995: Temperature effects on kinetics of microbial respiration and net nitrogen and sulfur mineralization. *Soil Science Society of America Journal*, 59: 233–240.

Mellander, P. E., Laudon, H., and Bishop, K., 2005: Modeling variability of snow depths and soil temperatures in Scots pine stands. *Agricultural and Forest Meteorology*, 133: 109–118.

Miehe, G., Miehe, S., Vogel, J., Co, S., and Duo, L., 2007: Highest treeline in the northern hemisphere found in southern Tibet. *Mountain Research and Development*, 27: 169–173.

Morecroft, M. D., Taylor, M. E., and Oliver, H. R., 1998: Air and soil microclimates of deciduous woodland compared to an open site. *Agricultural and Forest Meteorology*, 90: 141–156.

Munn, L. C., Buchanan, B. A., and Nielsen, G. A., 1978: Soil temperatures in adjacent high elevation forests and meadows of Montana. *Soil Science Society of America Journal*, 42: 982–983.

Rammig, A., Jonas, T., Zimmermann, N. E., and Rixen, C., 2010: Changes in alpine plant growth under future climate conditions. *Biogeosciencces*, 7: 2013–2024.

Redding, T. E., Hope, G. D., Fortin, M.-J., Schmidt, M. G., and Bailey, W. G., 2003: Spatial patterns of soil temperature and

moisture across subalpine forest-clearcut edges in the southern interior of British Columbia. *Canadian Journal of Soil Science*, 83: 121–130.

Richardson, A. D., Lee, X., and Friedland, A. J., 2004: Microclimatology of treeline spruce-fir forests in mountains of the northeastern United States. *Agricultural and Forest Meteorology*, 125: 53–66.

Rosenberg, N. J., Blad, B. L., and Verma, S. B., 1983: *Microclimate: the Biological Environment*. New York: Wiley.

Shanks, R. E., 1956: Altitudinal and microclimatic relationships of soil temperature under natural vegetation. *Ecology*, 37: 1–7.

Sheng, P. X., Mao, J. T., Li, J. G., Zhang, A. S., Sang, J. G., and Pan, N. X. (eds.), 2003: *Atmospheric Physics*. Beijing: Peking University Press, 18–25.

Shi, P., Körner, C., and Hoch, G., 2008: A test of the growth-limitation theory for alpine tree line formation in evergreen and deciduous taxa of the eastern Himalayas. *Functional Ecology*, 22: 213–220.

Siccama, T. G., 1974: Vegetation, soil, and climate on the Green Mountains of Vermont. *Ecological Monographs*, 44: 325–349.

Smith, W. K., Germino, M. J., Hancock, T. E., and Johnson, D. M., 2003: Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology*, 23: 1101–1112.

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

Thomson, A. J., and Moncrieff, S. M., 1982: Prediction of bud burst in Douglas-fir by degree-day accumulation. *Canadian Journal of Forest Research*, 12: 448–452.

Tranquillini, W., 1979: *Physiological Ecology of the Alpine Tree Line*. Berlin: Springer.

Treml, V., and Banaš, M., 2008: The effect of exposure on alpine treeline position: a case study from the High Sudetes, Czech Republic. *Arctic, Antarctic, and Alpine Research*, 40: 751–760.

Van Cleve, K., Barney, R. J., and Schlentner, R. E., 1981: Evidence of temperature control of production and nutrient cycling in two interior Alaska black spruce ecosystems. *Canadian Journal of Forest Research*, 11: 258–273.

Van Wijk, W. R., 1965: Soil microclimate, its creation, observation and modification. *Meteorological Monographs*, 6: 59–73.

Weih, M., and Karlsson, P. S., 2002: Low winter soil temperature affects summertime nutrient uptake capacity and growth rate of mountain birch seedlings in the subarctic Swedish Lapland. *Arctic, Antarctic, and Alpine Research*, 34: 434–439.

Wieser, G., and Tausz, M., 2007: *Trees at Their Upper Limit: Treelife Limitation at the Alpine Timberline*. Dordrecht, Netherlands: Springer.

Wilson, S. D., and Nilsson, C., 2009: Arctic alpine vegetation change over 20 years. *Global Change Biology*, 15: 1676–1684.

Woodward, F. I., Smith, T. M., and Emanuel, W. R., 1995: A global land primary productivity and phytogeography model. *Global Biogeochemical Cycles*, 9: 471–490.

Wundram, D., Pape, R., and Löffler, J., 2010: Alpine soil temperature variability at multiple scales. *Arctic, Antarctic, and Alpine Research*, 42: 117–128.

Zhang, L., Luo, T. X., Liu, X. S., and Kong, G. Q., 2010: Altitudinal variations in seedling and sapling density and age structure of timberline tree species in the Sergyemla Mountains, southeast Tibet. *Acta Ecologica Sinica*, 30: 76–80.