MOSS COVERAGE IMPROVES THE MICROCLIMATES OF SUBALPINE FORESTS: IMPLICATIONS OF QINGHAI SPRUCE RECRUITMENT IN QILIAN MOUNTAINS, NORTHWEST CHINA

QINGTAO WANG1*, CHUANYAN ZHAO2†, YUNPU ZHENG2†, MUHAMMAD WASEEM ASHFAQ2, XIAOPING WANG2, SIMENG ZHOU1, YUHAO ZHAO3, HONG DANG1 and MING XU3†

1School of Landscape and Ecological Engineering, Hebei University of Engineering, Handan 056038, China
2State Key Laboratory of Grassland and Agro-Ecosystems, School of Life Sciences, Lanzhou University, Tianshui South Road 222, Lanzhou, China
3School of Water Conservancy and Hydropower; Hebei University of Engineering, Handan 056038, China
4School of Environmental Sciences, University of Guelph, 50 Stone Road East, Guelph, ON N1G2W1, Canada
5Institute of Arid Meteorological Lanzhou, Key laboratory of Arid Climate Change and Reducing Disaster of China Meteorological Administration, Donggang East Road 1234, Lanzhou, China
6Key Laboratory for Urban Habitat Environmental Science and Technology, Shenzhen Graduate School, Peking University, Shenzhen 518055, China
7Center for Remote Sensing and Spatial Analysis, Department of Ecology, Evolution and Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, NJ 08901, USA

*Corresponding author’s email: zhengyuppu_000@sina.com, mingxu@crssa.rutgers.edu
†Contributed equally to this work

Abstract

Understanding the mechanisms of moss affecting the understory microclimates may further shed lights on forest recruitment, which is closely associated with hydrological and ecological processes of forest ecosystems. We conducted a one-year field experiment to examine the effects of moss thickness on understory microclimates including ground surface temperature (GST), ground surface moisture (GSM), soil temperature (ST), and soil moisture (SM) in a Picea crassifolia forest of Qilian Mountains, northwest China. We found that moss coverage substantially reduced the fluctuation amplitudes of microclimates (p < 0.01), as evidenced by the slower diurnal changes in GST, GSM, ST, and SM of moss-covered soil than those of bare soil. Moreover, our results also showed that moss coverage obviously increased GST and ST in winter (December 2014), whereas significantly decreased GST and ST in summer (June 2015). Comparing with bare soil, thick-moss coverage decreased the average annual GST and ST by 0.55°C and 0.62°C, respectively. However, moss coverage significantly increased the annual GSM and SM (p < 0.01), especially the SM of thin-moss coverage was increased much higher than that of thick-moss coverage and bare soil. In addition, moss coverage may also prevent heat flux from air to soil surface because the light radiation was exponentially declined from the upper moss canopy to soil with the increase of moss depths. These results suggested that moss coverage may promote the microclimates of the forest understory with heat insulation and water holding, and thus facilitate the P. crassifolia germination and recruitment through changing the hydrological and ecological processes of subalpine forests.

Key words: Ground surface temperature; Soil temperature; Ground surface moisture; Soil moisture; Moss; Picea crassifolia.

Introduction

It is well demonstrated that mosses can affect soil thermal and hydrological regimes (Gornall et al., 2007; Stuiver et al., 2014; Kuglerová et al., 2016), and thus play a critical role in vegetation dynamics and succession in boreal ecosystems (Parker et al., 1997; Bruun et al., 2006; Startsev et al., 2007; Turetsky et al., 2010; Hayashi et al., 2016). Meanwhile, moss also features with the external capillary wicking either from the moist organic layers or air, resistant drought, and immediate reactivation of photosynthesis upon rewetting (Carleton & Dunham, 2003; Proctor et al., 2007) mainly due to its poikilohydric capacity on forming continued dense cushions on the ground (Proctor, 2000). The effects of moss on temperature and moisture regimes have recently drawn much more attention due to their importance in modifying microclimates in boreal ecosystems (Beringer et al., 2001; Turetsky et al., 2010; Nilsson & Wardle, 2005). For example, Gornall et al., (2011) compared both soil temperature (ST) and soil moisture (SM) under bare soil, shallow and deep moss layers, and found that the deep moss coverage reduced ST, while the shallow moss increased SM. Other studies also showed that the porous medium of moss (Price et al., 2009) reduced fluctuation ranges of ST and decreased the freeze-thaw frequency during the growing season (Gornall et al., 2007; Guglielmin et al., 2012; Soudzilovskaja et al., 2013).

To our knowledge, however, most of the available literatures concerning about the effects of moss on microclimates were from high-latitude or Antarctica regions (Gornall et al., 2007; Guglielmin et al., 2008; Gornall et al., 2011; Soudzilovskaja et al., 2013; Barve et al., 2014), and few studies were conducted in subalpine regions (Parker et al., 1997; Boudreault et al., 2000), having relatively more biodiversity (Chapin & Körner, 1994, 1995a) and more frequencies of freeze-thaw events (Chapin & Körner, 1995c; Edwards, 2007) than the high-latitudes areas. Moreover, the subalpine species are also sensitive to climate change (Sebastian, 2007) mainly due to the high altitudes reduced pressure, where CO2 is particularly limiting and could alter species interactions (Chapin & Körner, 1994). Additionally, the subalpine region is usually located in...
the vertical transition zones, and the species in these regions may not only saturate by low-elevation species (Chapin & Körner, 1995b), but also migrate upper mountains (Anthelme et al., 2014), and thus future climate change may have significant impacts on species migration (Cannone et al., 2007; Lenoir et al., 2008; Pauli et al., 2012), as well as subalpine ecosystem structure and function (Cornwell & Ackerly, 2009). Investigating the moss effects on microclimates and understanding the potential mechanisms that moss thickness affect hydrological and ecological processes in the subalpine region are critical to predicting the changes in species dynamics (Pauli et al., 2012), and community composition and structure (Cornwell & Ackerly, 2009) of subalpine ecosystems in response to future climate change (Sebastia, 2007).

With regarding to moss modifying microclimates, previous studies mainly investigated moss layer effects on the soil regimes of subalpine ecosystems (Liu et al., 2010; Souzdilovskaya et al., 2013), and few studies focused on the impacts of moss coverage on the ground surface microclimate such as temperature and moisture (Startsev et al., 2007). Gornall et al., (2007) reported that the SM at the depth of 6 cm was reduced by the deep moss layer. Souzdilovskaya et al., (2013) found that moss coverage decreased the amplitudes of the 1.5-cm depth soil temperature (ST) fluctuations and the freeze-thaw frequency during the growing season, in turn, affected on soil carbon and nutrient dynamics. Liu et al., (2010) investigated moss effect on soil moisture (SM) in Qilian Mountains, northwest of China, and found that the SM in the depth of 5 cm with moss coverage in the understory of Qinghai spruce (Picea crassifolia) forests had higher values and less variation than those values of SM without moss coverage. Therefore, the ground surface temperature and moisture may be critical for seed germination and seedling establishment of Qinghai spruce (Picea crassifolia), because the moss layer on the ground surface can modify the microclimates through changing the hydrological processes of Qinghai spruce forests. Compared with the soil temperature and moisture, the ground surface temperature and moisture may be more closely related to the recruitment of Qinghai spruce forests. Furthermore, it is speculated that the ground surface and soil characterize different microclimates such as temperature and moisture, because the ground surface microclimate features higher spatial and temporal variations than that of soil during the freeze-thaw process (Guglielmin et al., 2008; Cannone et al., 2009; Wang et al., 2017). In fact, several studies have found that the ground moss layer substantially improved the ground surface microclimates and thus benefited the seed germination and seedling establishment of Qinghai spruce forests (Wang et al., 2016; Wang et al., 2017). In addition, several studies also examined the effect of moss coverage on microclimates for short-term durations of growing season (Gornall et al., 2011; Souzdilovskaya et al., 2013), which might be insufficient for well understanding the mechanisms of moss coverage affecting microclimates through changing the hydrological and ecological processes of forests. Hence, long-term experiments (a complete year) with freeze-thaw cycles might further shed light on microclimate modification with moss coverage through modifying ecological processes of subalpine forests.

Qinghai spruce (Picea crassifolia), the keystone tree species in the north-facing subalpine ecosystem, is crucial for maintaining water conservation and carbon (C) sequestration of Qilian Mountains, northwest of China (Peng et al., 2014a, 2014b). The understory of P. crassifolia is usually covered by extensive moss with an average coverage rate of more than 80% with the thickness of approximately 15 cm (Wang et al., 2017). Meanwhile, in a recent study it was observed that P. crassifolia seedling grew well with moss plants (Wang et al., 2017), which implied that moss plants might provide conducive environments for the germination and recruitment of P. crassifolia through modifying the local microclimates and regulating the hydrological processes such as rainfall storage (Carleton & Dunham, 2003) and evapotranspiration (McCarter & Price, 2014). So far, however, the underlining mechanism of moss plants on the microclimates of subalpine forests is still unknown, especially the moss effects on the germination and recruitment of P. crassifolia through changing ecological and hydrological processes in subalpine forests. Understanding the effects of moss coverage on the microclimate is critical in identifying the mechanisms and processes controlling the succession of Qinghai spruce forests and projecting the dynamics and species composition of the forest landscape in Qilian Mountains of northwestern China, as it was predicted to be sensitive to future climate change (Pfaff, 1999; Geist & Lambin, 2002; Xu et al., 2012; Bie et al., 2013). The objectives of the current studies are to examine the effects of moss thickness on ground surface temperature (GST) and moisture (GSM) as well as the soil temperature (ST) and moisture (SM) in the 5-cm depth with a completed one-year field measurement from June 15th, 2014 to June 15th, 2015 in the understory of subalpine forests in Qilian Mountains, northwest of China.

Study area and field site selection: The Qilian Mountain is located at the northeastern edge of the Tibet Plateau, where features typically alpine semi-arid climates (Peng et al., 2014a). The climate of Qilian Mountain has an annual precipitation of 437 mm with 85% of the precipitation falling between June and September and annual potential evaporation of 1,052 mm; the mean temperature ranges from -16.86°C (January) to 9.47°C (June), and the annual sunshine hours is 1,893 hours.

The study area is located at the Tianlaochi catchment in the medial of Qilian Mountains (38°23′56″-38°26′47″N, 99°53′57″-99°57′10″E, Elevation 2,700-4,440 m, Fig. 1). The growing season is generally from the end of April to the middle of September. The progression of vegetation types from low to high altitudes of the Qilian Mountains is beginning with subalpine meadow, which is mainly
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composed of Carex tristachya, Polygonum viviparum, and Plantago depressa, and the sub-alpine shrubby meadows are dominated by Potentilla fruticosa, Salix gilashanica, Caragana jubata, and Spiraea alpine (Wang et al., 2013). The forest soil is composed of mountain grey cinnamon soil characterizing by high-permeability and high-fertility with a soil depth of 30-50 cm. Qinghai spruce (P. crassifolia), the predominant tree species of the subalpine forests, features marginally cold tolerance and is distributed along the north-facing slopes at altitude from 2,700 to 3,350 m. Qinghai spruce forests dominate the vegetations in the study region, where the understory vegetation consists of low herbs and mosses. Given that the herbaceous understory of the study site is very sparse, the influence of herbaceous species on the regeneration of P. crassifolia can be neglected compared with the effects of moss plants, which account for > 80% of the total understory cover of Qinghai spruce forests.

We established a 15 m × 20 m plot with different moss thickness of 7.25 ± 0.35 cm (thick moss) and 3.11 ± 0.17 cm (thin moss) on March 15th, 2014 in the study site (38.26°19.67′N, 99.55°5.68′E; 2,833 m a.s.l.; the slope of 8 and the aspect of 7; (Fig. 1). In order to avoid the influence of the different moss growth conditions on the hydrological properties, we manipulated the thickness of moss layer with a scissor before setting temperature and moisture sensors in the established plots. Two circular plots of radius 2.5 m (plot A and plot B) at 8 m apart were laid within the study site to collect data of the selected microclimatic variables (Fig. 2).

**Gap light index and photosynthetic photon quanta flux density measurements:** We took hemispherical photographs of the canopy using a digital camera (Nikon, Coolpix 995) from a height of 90 cm above the ground at five sites within each plot. Photos were taken in the morning before sunrise or in the evening after sunset to reduce the effects of scattering and diffusion of sunlight on the observations (Jennings et al., 1999). These photos were used to compute a GLI using the software Gap Light Analyzer (version 2.0) (Canham, 1988; Webb & Peart, 2000; Jonckheere et al., 2004). In addition, we also randomly selected five locations (outside the circles, Fig. 2 – locations marked by △) within the study site for measuring the photosynthetic photon flux density (PPFD). To examine the effect of moss depth on PPFD, we took moss layer up to the 6-cm depth with 1-cm interval at each location PPFD measurements with an ACCUPAR LP-80 sensor (Decagon, USA).

Three square quadrats (50 cm × 50 cm) were laid representing thick moss, thin moss and bare soil for monitoring the variation of microclimates in each circular plot (Fig. 2). The mean moss depth in each quadrat was measured with randomly selected five locations using the point-hit method (Belnap, 2006). As moss thickness changed with the water contents, we took measurements not only on sunny days but also on three days after rainfall to get stable thickness measurements.

![Fig. 1. Location of the field study site in the Qilian Mountain.](image-url)
Fig. 2. Distribution of sampling plots in the study site. Note: Two suits of USB data logger sensors (Plot A and Plot B) for monitoring ground surface temperature (GST) and ground surface moisture (GSM) and two suits of 5TE sensors (Plot A and Plot B) for monitoring soil temperature (ST) and soil moisture (SM). Note: ■, represents thick moss; □, represents thin moss; □, represents bare soil; ×, represents the locations of gap light index (GLI) measurement; △, represents the locations of photosynthetic photon flux density (PPFD) measurement.

Ground surface temperature and moisture measurements: The ground surface temperature (GST) and ground surface moisture (GSM) was measured at two levels of moss thickness (thick moss and thin moss) and bare soil in both the plot A and plot B as two replicates (Fig. 2). We carefully removed the covered thin or thick moss, plant species and litter within the quadrats, and then employed a HUATU USB data logger (HE172 USB Temperature Data Logger, Shenzhen Huatu Co., Ltd. China) for long-term monitoring the GST and GSM with setting sensors at 3 cm above the bare soil (control) or within the moss layer in the plots (Fig. 3). The data logger continuously recorded data at 1-hour interval from 15th July 2014 to 15th July 2015. In addition, we also collected data at 20 minutes interval during winter (December 2014) and summer (June 2015) to observe variations in shorter intervals (Gornall et al., 2007; Yang et al., 2010).

Soil temperature and moisture measurements: The soil temperature (ST) and soil moisture (SM) at each plot were also continuously monitored with 5TE sensors (5TE, ECH2O-TE sensor, Decagon Devices Co., Ltd. USA), which were placed into the soil at a depth of 5 cm in the bare soil plots or installed beneath the litter with a 5-cm depth in the moss coverage plots (Fig. 3b). To minimize the spatial variation in the thickness and density of moss layers and soil composition. A study site was selected characterizing with relatively uniform moss layers to install USB data loggers and 5TE sensors for microclimate variables measurements. In addition, we also installed two suits of USB data loggers and 5TE sensors as two replicates (one suit for each treatment in each of the two plots).

Fig. 3. Sensor settlements in each sampling plot of the study site. Note: (a) photographic view of the study site, (b) USB logger sensor above bare soil (3 cm) for monitoring the ground surface temperature (GST) and ground surface moisture (GSM), (c) USB logger sensor in thin moss for monitoring the GST and GSM, and (d) USB logger sensor in thick moss for monitoring the GST and GSM. For the three treatments (bare soil, thin moss and thick moss), 5TE sensors were installed at a soil depth of 5 cm below the bare ground (bare soil) or beneath the litter (thin and thick moss) for monitoring soil temperature (ST) and soil moisture (SM) from June 15, 2014 to June 15, 2015.
In winter, GST was obviously over bare soil peaked (18.7°C) around 00:00 h (Fig. 7c).GST showed similar pattern in summer (Fig. 7). In the case of GSM, the min value of GSM occurred at about 09:40 h, which in thick moss was decreased and the minimum value occurred approximately around 13:40 h (15.5°C) and 14:00 h (14.5°C), respectively. The minimal GST occurred at night with the range from 3.3-4.2°C among three treatments (Fig. 5a). In winter, GST was obviously separated by magnitude value due to the different treatments (Fig. 5b). GST among three treatments peaked around 16:40 h, however, on bare soil it reached the lowest value (-23.5°C) at about 09:40 h, which in thick and thick moss was the lowest around 10:00 h (-15.4°C) and 10:40 h (-9.0°C), respectively. By contrast, the minimum value of GST in summer occurred at night (around 02:00 h) whilst in winter it occurred in the morning (around 10:00 h). Time is delayed approximately by one hour (Fig. 5b) in winter and 40 minutes in summer (Fig. 5a) comparing with bare soil, respectively.

**Results**

**Effect of moss on photosynthetic photon flux density:** The amount of light in moss layers in *P. crassifolia* understory was strongly and negatively related to the moss thickness (Fig. 4). On June 28th, 2014 at 12:00 h, with cloudless, the mean PPFD in the depth of 1 cm under moss layer was approximately 19.67 μmol·s⁻¹·m⁻²; however, with the increasing depth of moss, the PPFD values were decreased exponentially. The PPFD in 5 cm moss depth was 1.12 μmol·s⁻¹·m⁻² whereas, the PPFD in 6 cm moss depth was 0 μmol·s⁻¹·m⁻². The patterns of temperature and moisture both in ground surface and soil were drawn by using the averaged data of microclimate variables in the two plots, i.e. there were two replicates for each treatment, located in plot A and plot B, respectively. Therefore, we used different time series as the replicates for testing the effect of moss cover. We analyzed the averaged data from the two plots for characterizing the diurnal dynamics of microclimate variables and averaged the data from the same treatment (plot A and plot B) for exploring their seasonal and annual dynamics. The fluctuation amplitudes of GST, GSM, ST and SM were obtained by calculating the max values minus the min of a day throughout a year. We tested the differences in the annual and seasonal variations as well as the fluctuation amplitudes of GST, GSM, ST and SM among the three treatments (bare soil, thin moss and thick moss) with paired t-test.

ST in summer was the highest in bare soil, followed by under thin and thick moss (Fig. 5c). In summer, ST in the absence of moss was increased at about 08:40 h, while ST under thin and thick moss was increased at about 09:40 h and 09:20 h, respectively, and which peaked around 18:00 h (Fig. 5c). In winter, however, ST under thin moss was the highest followed by thick moss and bare soil. Difference between the latter two was minor (Fig. 5d). In general, the increase in GST and ST under moss layer was a little delayed than the bare soil.

Results of diurnal variation of GSM and SM in summer and winter are shown in Fig. 6. GSM above bare soil was decreased around 08:40 h in the morning in summer (Fig. 6a), whilst it decreased around 10:20 h in thin moss, GSM dropped to the minimum around 15:20 h (moisture: 53%) and 16:20 h (moisture: 93%) in bare soil and in thin moss respectively (Fig. 6a). The presence of moss enhanced GSM, especially in thick moss and which continued a state of saturated moisture (99.9%) over the day. In winter, the thick snowpack covered ground surface, GSM above bare soil ranged from 75.8% to 87.5% over the day (Fig. 6b), whilst GSM both in thin and thick moss remained in saturated (99.9%) condition (Fig. 6b). SM among three treatments showed similar pattern in summer (Fig. 7). In the case of bare soil (Fig. 7a), SM firstly peaked around 05:20 h, and then followed by thick (around 06:00 h) (Fig. 7c) and thin moss (around 08:00 h) (Fig. 7b). Subsequently, the SM was decreased, and the minimum value occurred at about 19:00 h in the evening among three treatments (Fig. 7). In winter, SM did not show any clear trend due to continuous cold weather (Fig. 8). SM was the lowest during the period from 09:20-13:00 h, and the highest SM appeared under thin moss over a day whether it was in summer (Fig. 7) or in winter (Fig. 8).
Fig. 5. Diurnal variation profiles of ground surface temperature (GST) and soil temperature (ST) in bare soil (red), thin moss (green) and thick moss (blue). Data were collected for winter and summer on cloudless days of December 12, 2014 and June 22, 2015, respectively. (a) Diurnal variation for GST in summer, (b) diurnal variation for GST in winter, (c) diurnal variation for ST in summer, and (d) diurnal variation for ST in winter under different treatments in the field site.

Fig. 6. Diurnal variation profiles of ground surface moisture (GSM) in bare soil (red), thin moss (green) and thick moss (blue). Data from winter and summer on cloudless days of December 12, 2014 and June 22, 2015, respectively. (a) Diurnal variation for GSM in summer, and (b) diurnal variation for GSM in winter under different treatments in the field study site.
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Fig. 7. Diurnal variation profiles of soil moisture (SM) in bare soil (a), thin moss (b), and thick moss (c). Data from summer on a cloudless day June 22, 2015.

Fig. 8. Diurnal variation profiles of soil moisture (SM) in bare soil (a), thick moss (b), and thin moss (c). Data from winter on a cloudless day of December 12, 2014.
Temperature and moisture fluctuations: Our results (Fig. 9) showed that the presence of moss reduced the fluctuation amplitude both in temperature and moisture. During the study period of one year the average GST fluctuation amplitude of bare soil, thin moss and thick moss were 15.12°C ± 4.62, 11.46°C ± 3.11 and 4.42°C ± 2.05 respectively (Fig. 9a; Fig. 10a). The GST fluctuation amplitude in moss was significantly lower than that of bare soil ($p<0.01$) (Fig. 10a). Although the ST fluctuation amplitude both in thin moss (2.17°C ± 0.82) and thick moss (1.93°C ± 0.18) were significantly lower ($p<0.01$) than the bare soil (3.16°C ± 0.23) (Fig. 9b; Fig. 10b), the differences between thin and thick moss were not significant ($p=0.18$). Similar results were observed for GSM and SM. The GSM fluctuation amplitude in thin moss (6.74 ± 2.41) and thick moss (1.92 ± 0.57) were significantly lower ($p<0.01$) than above bare soil (29.13 ± 8.61) (Fig. 9c; Fig. 10c); the SM fluctuation amplitude under thin and thick moss (0.21± 0.02 and 0.14 ± 0.01) were significantly lower ($p<0.01$) than that in bare soil (0.34 ± 0.03) (Fig. 9d; Fig. 10d).

Annual temperature and moisture variation: There appeared an annual cycle both in GST and ST under three treatments throughout a year (Fig. 11). When the GST was above 0°C (from late March to early October), both
the GST and ST in moss decreased significantly ($p<0.01$; paired t-test) with the increase of moss thickness, and the mean GST during the same period in the three treatments (bare soil, thin moss and thick moss) was 9.68°C, 6.51°C and 5.21°C, respectively. Conversely, when GST was below 0°C (from early October to mid-March), GST in moss was significantly enhanced ($p<0.01$; paired t-test), and the mean GST during the period in the three treatments (bare soil, thin moss and thick moss) was -6.46°C, -5.06°C and -4.18°C, respectively (Fig. 11a). The freezing period of a year was from later October to the middle of March, and the rest time was the thaw period (Fig. 11b). However, the presence of moss layers reduced the mean GST (Fig. 12a), the annual mean GST in the three treatments was 0.31°C, -0.21°C and -0.24°C ($p=0.053$; paired t-test) (Fig. 12a), respectively; in the case of thick moss, the annual mean GST was reduced by 0.55°C (Fig. 12a). The annual mean ST under thick moss (1.67°C) was also decreased significantly ($p<0.05$; paired t-test) than that under bare soil (1.05°C), 37% lower than above bare soil (Fig. 12b).

The presence of moss has a great influence both on GSM and SM (Fig. 13), especially the GSM which increased significantly ($p<0.01$) (Fig. 14a). GSM in thick moss was approximate saturation across a year (Fig. 13a), however, which above bare soil was lower ($p<0.01$) and has large fluctuations, notably from March to April (Fig. 13a), GSM was the lowest in the year. The mean annual GSM was significantly improved ($p<0.01$) in moss compared to bare soil (Fig. 14a).

The presence of moss also affected SM (Fig. 13b), SM increased significantly under thin moss ($p<0.01$) and decreased significantly ($p<0.01$) under thick moss (Fig. 13b; Fig. 14b) compared with that above bare soil. SM was consistent in low level (the mean SM under thin moss, bare soil and thick moss was approximately 7.62%, 2.57% and 2.71%, respectively) during non-growing season (from late October in 2014 to early April in 2015) (Fig. 13b). However, from the late March to early April, before growing season precipitation, SM under three treatments increased abruptly (Fig. 13b); the it SM was high during the seven months (from April to mid-October), in mid-October SM suddenly dropped in the case of high soil water content, and then soil moisture reverted to the lower level until the next growing season (Fig. 13b). From the annual mean SM, which under thick moss was the lowest (the annual mean SM was approximate 9.71%) ($p<0.01$) among the three treatments (Fig. 14b), SM under thin moss was the highest (the annual mean SM was approximate 20.70%) ($p<0.01$), and which in bare soil was the intermediate (the annual mean SM was approximate 12.66%) (Fig. 14b).

![Fig. 10. Annual mean fluctuation range of (a) ground surface temperature (GST), (b) soil temperature (ST), (c) ground surface moisture (GSM %), and (d) soil moisture (SM %) under different treatments throughout a year. Error bars indicate standard deviations, different letters on error bars show the differences between treatments are significant at $p<0.01$ (capital letters), by paired t-test.](image-url)
Fig. 11. Annual variation profiles of (a) ground surface temperature (GST) and (b) soil temperature (ST) in bare soil (red), thin moss (green) and thick moss (blue). Data were collected from June 15, 2014 to June 15, 2015 in the field site.

Fig. 12. Annual average ground surface temperature (a) and average soil temperature (b) in bare soil, thin moss and thick moss. Error bars indicate standard deviations, different letters on error bars show the differences between treatments are significant at $p < 0.05$ (lowercase letters), NS indicates non-significant (paired t-test).
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Fig. 13. The annual variation profiles of ground surface moisture (a) and soil moisture (b) in bare soil (red), thin moss (green) and thick moss (blue). The dark gray bar indicates the diurnal precipitation. Data were collected from June 15, 2014 to June 15, 2015 in the field site.

Fig. 14. The average annual ground surface moisture (a) and soil moisture (b) in bare soil, thin moss, and thick moss. Error bars indicate standard deviations, different letters on error bars show the differences between treatments are significant at $p < 0.01$ (capital letters, paired t-test).
Discussion

The microclimate is strongly governed by the presence of moss cover (O’Donnell et al., 2009; Soudzilovskaia et al., 2013). These effects not only control hydrological and ecological process (O’Donnell et al., 2009; Wallenstein et al., 2009) but also influence new recruitment and community structure (Gornall et al., 2011; Sand-Jensen & Hammer, 2012; Zheng et al., 2014). Although the impact of moss layer on soil thermal regimes has been assessed (Bonan & Shugart, 1989; Gornall et al., 2007; Gornall et al., 2011) in high latitudes, our study is the important document to demonstrate the complete spectrum of these effects (light, GST, GSM, ST and SM) on the microclimate for the various thickness of moss layers in the understory of subalpine areas throughout a complete year.

Moss effect on photosynthetic photon flux density: In the study, the Photosynthetic Photon Flux Density (PPFD) within the moss decreased sharply with the increased moss depth (Fig. 4). In line with other studies, which found an exponential decline of light density with an increasing number of bryophytes or litter cover, the thickest cover lead to almost complete darkness (<0.5% of ambient Photosynthetically active radiation (PAR)) (Eckstein & Donath, 2005; Donath & Eckstein, 2010). Our results suggested that a decrease in light intensity within the moss layer might cause both a decline in temperature and evapotranspiration within moss, in turn, potentially influenced the interaction between species (Gornall et al., 2011) and plants recruitment (Wang et al., 2017).

Delay effect of moss on microclimate: In this study, we observed lag effect both on GST and ST in the presence of moss; especially for the GST under thick moss. Our result was in line with Cannone & Guglielmin (2009), who reported the delayed response of a daily scale warmest peak in the cryptogamic tundra than that on bare ground. Studies suggested that the delayed effect should contribute to the insulating properties of moss layer, and these properties have been highlighted also on ST in several studies (Sharratt, 1997; Beringer et al., 2001; Van der Wal & Brooker, 2004). For example, researchers showed that deeper moss layers delayed the onset of soil thaw for several weeks in high arctic regions (Gornall et al., 2007), resulting in altering the reproductive phenologies of neighbor plants in the region (Legault & Cusa, 2015). We suggested that these insulating properties can be explained by the following three factors (1) the moss layers act as a barrier to incoming radiant energy (Fig. 4 shows exponential decay in PPFD with increasing moss thickness); (2) live shoots of moss absorb energy for photosynthesis, thereby preventing it reaching the inner of moss or the soil under it (Miller et al., 1980); and (3) moss has four times lower thermal conductivity (Hinzman et al., 1991) than bare soil due to the presence of large airspaces, as opposed to water-filled spaces, inside the moss mat (Beringer et al., 2001). The insulating properties of moss leading to the energy transfer were lower than that in air, causing the delayed effects on GST and ST in the presence of moss. In winter (non-growing season), particularly, when snow covered the ground, a large amount of solar radiation was reflected, resulting in less sensible heat flux reaching to the ground under snow (Goodrich, 1982; Zhang, 2005), more delayed the energy transformation. However, others suggested that the presence of ground vegetation cooled the GST due to the increase in thermal conductivity of the frozen vegetation or litter when compared to bare ground (Williams & Smith, 1989; Fukui et al., 2008).

The onset of decreased GSM was delayed in thin moss in summer (Fig. 6a). The possible reason was the great capacity of water-holding of moss layers (Zotz et al., 2000; O’Donnell et al., 2009), these may be related to the morphological characteristics of moss layer. Commonly, most of mosses have the interconnected forming loose to fairly dense turfs of erect (Steijlen et al., 1995), therefore, developing a boundary layer of reduced wind speed immediately above its surface, and to have stagnant air of higher humidity among the shoots, as a result, reducing the evapotranspiration; and second, since the most mosses are poikilohydric plants, they can efficiently absorb dewfall from air directly through gametophyte (Parker et al., 1997; Sand-Jensen & Hammer, 2012) during the night, resulting in a higher moisture conditions in it. Additionally, the retention of dust and soil particles is within moss layers, in turn, also increased the supply of water (Sand-Jensen & Hammer, 2012). In winter, GSM above bare soil was consistent a stable condition in winter (Fig. 6b). It may be a consequence of the GST in moss layer in winter (Fig. 5b) compared to lower GST above bare soil; the higher GST in moss improved the snow melt, leading to the higher GSM. On the one hand, GSM in moss was higher than that above bare soil resulted from the water retention properties of moss (Parker et al., 1997; Sand-Jensen & Hammer, 2012); A considerable variation appeared between summer (Fig. 7) and winter (Fig. 8) in terms of SM. This may be due to moss layer absorbing dew during the night (GSM in P. crassifolia forest was often more than 90% in night in summer according to our observation (Fig. 6a), and then the sufficient water may migrate down to soil by moss gametophyte, resulting in the highest SM occurred early in the morning. In addition, the relatively low evapotranspiration in the night may be another reason that caused the high SM in the early morning. Conversely, when undergoing a strong evapotranspiration during the daytime, SM was the lowest from afternoon to the evening (Fig. 7). Interestingly, among the three treatments (bare soil, thin and thick moss), SM under thin moss was the highest (Fig. 7b) rather than under thick moss (Fig. 7c); this might result from the thin moss not only can reduce the evapotranspiration due to retained the moisture in soil (Gornall et al., 2007) but also can transform the over-saturated throughfall into soil after precipitation. Although the thick moss also can inhibit the evapotranspiration, comparing with forming a thickness bar that prevented both the air moisture and precipitation to soil, the positive effect of which inhibiting evaporation was seemingly insignificant, because which intercepted almost all of the throughfall from the canopy of P. crassifolia, another important reason may that, in most of cases, litter under thick moss was commonly thicker (Fig. 3d) than that under thin moss, subsequently, occurring the
second intercept by the thicker litter, leading to hardly water into the soil under thick moss. In winter, the trend of SM was not clear, it may be due to that soil liquid water changed into solid water due to freezing: only little liquid water in soil was measured by 5TE sensors thus, SM has a little change in winter (Fig. 8), and this measuring characteristics by 5TE sensors also can account for why the SM abruptly reduced in the early November when the soil water content was high; and which abruptly climbed in the early April in the cast of the soil water content was low (Fig. 13b).

It should be noted that biological processes of moss like respiration, decomposition and photosynthesis also influence GSM and SM, however, the impact is considerable weak, and hence, it can be negligible (Soudzilovskaia et al., 2013). Furthermore, bryophyte thermal conductivity and volumetric heat capacity were independent of mat density, and depended linearly on mat moisture content, but the dependencies were not species-specific, therefore, even several moss species were growing mixed in the dominated A. abietina moss, other moss species could not affect both the insulation and transmission properties (Soudzilovskaia et al., 2013). In addition, the albedo on moss layer surface was assumed the same due to the most moss was consisting of A. abietina.

Furthermore, we acknowledge that for some locations we overestimated or underestimated GST, GSM, ST and SM by assuming spatial homogeneity. However, we expect that the overall variability in monitoring microclimates would not change significantly. This is because the biggest determinant of variability in peak value in GST, GSM, ST and SM is their fluctuation amplitude which will be most strongly influenced by the presence or absence of moss layers. Finally, other influence factors, such as root water uptake of plants, uneven distribution of radiation in understory due to the canopy shelter and solar elevation angle and azimuth variational constantly, also may affect the moisture and temperature, but these effects are implicit in the temperature and moisture fluctuation amplitude (Bense et al., 2016).

Effect of moss on temperature and moisture fluctuations: Our experiments demonstrated that the presence of moss could significantly decrease the fluctuation range of microclimate both above and below ground, particularly in GST and GSM; this was likely due to insulating property of moss (Van Cleve et al., 1983; Kleier & Rundel, 2009; Donath & Eckstein, 2010; Soudzilovskaia et al., 2011), since it was more porous and therefore less thermal conductivity compared to soil (Beringer et al., 2001; Soudzilovskaia et al., 2011). The insulating property plays critical roles not only in delaying the temperature or moisture regime (Figs. 5-8) but also in contracting the fluctuations of temperature/moisture in the field experiments (Fig. 9). Thus, we suggest that moss as a porous dielectric layer can effectively mitigate the energy and water transfer between land and atmosphere, resulting in the lower fluctuation range of GST and GSM in moss.

In terms of ST, Soudzilovskaia et al. (2011) suggested that the effect of moss on ST seemed to be site dependent, whereas other studies reported that the reduction of ST fluctuation only occurred during growing season, but not in winter (Gornall et al., 2007; Guglielmim et al., 2012). Our results showed that, however, ST fluctuation under thick moss was significantly lower than that under bare soil throughout the year. The above studies were conducted either in high latitudes or in Antarctic regions, where the permafrost was continued longer than that in our study areas (permafrost in our study area only occurred during the non-growing season), leading to the less fluctuation amplitude than ours. In addition, the difference in depth of snow cover in different study areas may also induce the different extent of fluctuation amplitude of ST (Kade et al., 2006).

Several studies have found that moss affected the composition of vascular plants or the recruitment of neighbor plants via, among insulating properties, control over ground and soil microclimate (Gornall et al., 2011; Soudzilovskaia et al., 2011; Wang et al., 2017). In this study, although the enhanced GSM and SM in thin moss (Fig. 13; Fig. 14) and the declined fluctuation amplitudes at the onset of the growing season (April and May) (Fig. 12a) might facilitate the germination and seedling establishment of neighbor plants before the summer precipitation. The reduction in ST fluctuation amplitudes could appear the effective suppressors of plant germination (Soudzilovskaia et al., 2011). In addition, the lower temperature fluctuation amplitudes below certain thresholds may constrain to the seed germination in mosses (Thompson, 1977; Thompson & Grime, 1983).

Roles of moss in ecological and hydrological processes: Exploring the effects of moss on microclimate in the understory of boreal conifer forest can help us in understanding the role of moss in ecological and hydrological process as well as the interactions with P. crassifolia. Over a complete year observations, we found that the growing season was shortened in the presence of moss comparing bare soil in P. crassifolia forest, as a result, impact on the survival of which, especially for seedlings and samplings (Giménez-Benavides et al., 2007; Wang et al., 2017). Conversely, the mean GST in moss was higher than that above bare soil when it was below 0°C suggesting the presence of moss could positively protect plant roots from very low temperature in winter (Jeschke & Kiehl, 2008), might facilitate seedling-sapling’s survival of P. crassifolia. In addition, exploring the effect of moss on microclimates also can help us more deeply understand how moss influences both the biodiversity and carbon exchange in the context of climate change. Over the past century, global warming has been widely confirmed by ecologist (Malcolm et al., 2006; Botkin et al., 2007; Benton & Newell, 2014) and which might affect the stability of community structure (Dieleman et al., 2015), particularly in subalpine species that are sensitive to climate change due to some species are the dependence of temperature and water utilization (Sebastia, 2007), which may result in upward-migration of alpine communities (Anthemle et al., 2014) or face the risk of biodiversity loss (Dullinger et al., 2003; Thomas et al., 2004; Keith et al., 2008). Furthermore, our experiments demonstrated that both the annual mean GST and ST was decreased by the presence of moss, implying
a reduction in ST was associated with soil CO$_2$ flux (Monson et al., 2006; Zheng et al., 2014). Previous studies showed that the decreased ST inhibited soil microbial activity and roots respiration (O’Neill et al., 2002; Monson et al., 2006; Curiel et al., 2007), implicating reduced soil CO$_2$ emissions to the atmosphere (Maier & Kress, 2000; Coxson & Wilson, 2004; Zheng et al., 2014), resulting in positive resistant the global warming because of the greenhouse effect.

The presence of moss also strongly affects the GSM and SM through influencing the precipitation interception (Pypker et al., 2006) and evapotranspiration (Nichols & Brown, 1980; McCarter & Price, 2014). In our study, GSM in moss was consistently higher than that above bare soil (Fig. 13a) both during thawing and freezing, contributing to the considerable water-holding capacity of moss. Moul & Buell (1955) reported that mats of Cladonia rangiferina may absorb water as much as 4.5 times than their weight before allowing moisture to pass to the soil beneath. In addition, others showed that evaporation was negatively correlated with temperature in the moss (e.g. Nichols & Brown, 1980), indicating that the decreased temperature in moss (Fig. 12a) could inhibit evapotranspiration, in turn, improving moisture conditions (Fig. 14a), therefore, the increased GSM by moss could benefit the seed germination and seedling emergence during the early period of recruitment of P. crassifolia. In P. crassifolia forest, precipitation was firstly intercepted by the upper canopy, subsequently, and throughfall was intercepted by moss layer; in the thin moss, the precipitation might more easily enter soil across the thin moss and litter layer. In the thick moss (when the moss thickness exceeds 7 cm), however, we concluded that the strong ability for absorbing water of moss may hold the most of throughfall, as well as the thicker litter, as a result, SM under thick moss was the lowest in the three treatments (Fig. 13b; Fig. 14b).

The variation of GSM and SM by the presence of moss influences the survival and recruitment of P. crassifolia (Wang et al., 2017) as well as other plants (Parker et al., 1997; Jeschke & Kiehl, 2008; Donath & Eckstein, 2010; Soudzilovskaia et al., 2011). During freeze-thaw period (late March to May in the study area), GSM above bare soil was the lowest, and this period was just the time for germination and to growth period of plants, notably by the dominated tree species P. crassifolia. The lower moisture on bare soil might limit the germination of P. crassifolia, whilst when the seeds fall into the moss, the higher moisture provide a favorable and safe habitat (van Torne, 1990), such as protection against predation (Jeschke & Kiehl, 2008). Buffer soil temperatures (Gornall et al., 2011) for the germination, would be beneficial to the recruitment (Parker et al., 1997; Wang et al., 2017). However, in case of thick moss, the lower SM under thick moss may inhibit seedling recruitment and survival due to competing for water availability (Zamfir, 2000), on the other hand, with increasing thickness, moss cover may interfere with the ability of the radicle to establish soil contact to absorb water and uptake nutrient from soil (Zamfir, 2000; Donath & Eckstein, 2010), consequently, negative interactions between species. Briefly, with regard to the effect of moss on neighboring plants as well as the role in the hydrological and ecological process in the forest ecosystems, more detailed investigations should be carried out to assess the impacts, so as to better respond to the risk of climate change.

Conclusion

This study demonstrates that in the understory of subalpine conifer forest, moss strongly prevents the light radiation, influencing the heat transfer. Both the changes of temperature and moisture and the reduction of the fluctuation amplitude might influence the phenology and germination of plants. Moreover, the decrease in mean annual GST and mean annual ST in the presence of moss implies a shorter growing season as well as inhibit activity of soil microbe and roots respiration, that in turn decreases soil CO$_2$ release to the atmosphere. In addition, the increased GSM by moss could facilitate the recruitment of P. crassifolia, however, thick moss significantly reduced SM, restricted the water availability for plant roots. In the understory of subalpine P. crassifolia forest, which are characterized by the independence of climate, hence little changes in temperature and moisture may influence the recruitment and species composition, in turn, impact the community assemble in this region. Therefore, more knowledge with reference to the effect of moss on the microclimates may help us better to predict the risk of ecosystem stability in the context of climate change.

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Picea glauca


Review
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