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Belowground carbon responses to experimental warming regulated by soil moisture change in an alpine ecosystem of the Qinghai–Tibet Plateau

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Keywords

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Abstract

Recent studies found that the largest uncertainties in the response of the terrestrial carbon cycle to climate change might come from changes in soil moisture under the elevation of temperature. Warming-induced change in soil moisture and its level of influence on terrestrial ecosystems are mostly determined by climate, soil, and vegetation type and their sensitivity to temperature and moisture. Here, we present the results from a warming experiment of an alpine ecosystem conducted in the permafrost region of the Qinghai–Tibet Plateau using infrared heaters. Our results show that 3 years of warming treatments significantly elevated soil temperature at 0–100 cm depth, decreased soil moisture at 10 cm depth, and increased soil moisture at 40–100 cm depth. In contrast to the findings of previous research, experimental warming did not significantly affect NH_4^+-N, NO_3^--N, and heterotrophic respiration, but stimulated the growth of plants and significantly increased root biomass at 30–50 cm depth. This led to increased soil organic carbon, total nitrogen, and liable carbon at 30–50 cm depth, and increased autotrophic respiration of plants. Analysis shows that experimental warming influenced deeper root production via redistributed soil moisture, which favors the accumulation of belowground carbon, but did not significantly affected the decomposition of soil organic carbon. Our findings suggest that future climate change studies need to take greater consideration of changes in the hydrological cycle and the local ecosystem characteristics. The results of our study will aid in understanding the response of terrestrial ecosystems to climate change and provide the regional case for global ecosystem models.

Introduction

Soil moisture plays a key role in terrestrial ecosystems by regulating energy and nutrient exchange processes among soil, vegetation, and atmosphere (Illeris et al. 2004; Karsten et al., 2006; Seneviratne et al. 2010; Tiemann and Billings 2011). For example, soil moisture can affect NPP (net primary productivity) by controlling plant transpiration and photosynthesis (Lindroth et al. 1998; Melillo et al. 2002). It can also affect soil carbon (C) and nitrogen (N) cycling by controlling microbial community activities (Davidson et al. 1998, 2000; Risch and Frank 2007; Liu et al. 2009; Falloon et al. 2011 Suseela et al. 2012; Fujita et al. 2013; Luo et al. 2013). The response of terrestrial ecosystems to elevated temperature has been the subject of a considerable amount of research due to the preponderant evidence of warming at the global level (Orchard and Cook 1983; Xu et al. 2004; Yuste et al. 2007; Liu et al. 2009; Sjögersten et al. 2012). However, research based on field experiments and model simulations shows uncertainty in ecosystem response to elevated temperature. Studies report that warming might cause increased, decreased, or unchanged soil respiration and that soils might act as carbon sources or sinks in different ecosystems (Rustad et al. 2001; Lu et al. 2013). These inconsistent responses could be due to water limitations offsetting or even reversing the effect of simulated elevated temperature, which changed the decomposition and production processes (Weltzin et al. 2003; Davidson and

Janssens 2006; Falloon et al. 2011; Poll et al. 2013). Therefore, there is an urgent need for additional study of soil moisture change and its effects on terrestrial ecosystems.

Soil moisture is an important component of the hydrological cycle that is primarily controlled by climate factors but also depends on the interplay of infiltration, drainage, capillary rise, evapotranspiration, and lateral subsurface flows (Chapin et al. 2002; Daly and Porporato 2005). Climate change is expected to have a profound influence on soil moisture. The influence mainly comes from changes in the number, frequency, and size of precipitation events (Knapp et al. 2002; Karl and Trenberth 2003) as average surface temperatures increase (Solomon et al. 2007). Although there is no decline in precipitation at the global scale, drought has still been found in some regions due to altered precipitation regimes (Easterling et al. 2000; Knapp et al. 2008) as well as increasing evaporation and infiltration from an elevated temperature, which leads to a decrease in soil moisture (Gregory et al. 1997; Naden and Watts 2001; Jasper et al. 2006; Gerten et al. 2007; Holsten et al. 2009).

In tundra regions located in high latitudes and altitudes, climate-induced decreases in soil moisture are more evident due to permafrost thaw and active layer thickening, which greatly alter soil thermal and hydrological conditions (Jorgenson et al. 2001; Romanovsky et al. 2010). Tundra regions cover a large area of the world and altogether contain approximately 1700 Pg of C, accounting for nearly 50% of the global belowground OC (organic carbon) pool (Tarnocai et al. 2009). Understanding the carbon cycle and its feedback mechanisms related to regional climate is very important for forecasting future climate change. Warming can influence C loss by increasing decomposition rates (Nelson et al. 2002; Schuur et al. 2008, 2009; Schuur and Benjamin 2011). However, warming-caused soil moisture loss can strongly constrain soil heterotrophic respiration, belowground biomass, nitrogen mineralization rate, and microbial activity. These effects can significantly reduce the temperature sensitivity of the tundra ecosystem (Knapp et al. 2002; Smith et al. 2005; Craine and Gelderman 2011). Therefore, a better understanding of soil moisture effects on the tundra belowground ecosystem is needed in order to reduce this uncertainty and improve our confidence in climate change predictions.

The QTP (Qinghai–Tibet Plateau) is the highest and largest plateau on the planet with a mean elevation of 4000 m ASL and an area of 2.0×10^6 km^2 (Li and Zhou 1998; Yang et al. 2008). In the QTP, 12.3 Pg of carbon (C) is stored in the shallow active layer of the permafrost region, which has an area of 1.5×10^6 km^2 (Wang et al. 2002). The surface temperature of the QTP is currently rising at the rate of 0.01–0.03°C per year (Wei et al. 2003). The increase greatly affects the moisture and temperature patterns in the shallow active layer of the permafrost regions (Cheng et al. 1993; Wu and Liu 2004; Zhao et al. 2004; Pang et al. 2009; Yang et al. 2010). The QTP is predicted to see "much greater than average" increases in surface temperature in the future (Giorgi et al. 2001; Klein et al. 2005), which could result in drought or even alpine ecosystem degradation via positive feedbacks. However, the response of alpine ecosystem in the QTP to warming-induced shifts in soil moisture has been less studied (Luo et al. 2010; Wang and Wu 2013), although the QTP is a very special and important ecosystem and urgently needs research on soil moisture-mediated ecosystem processes. Therefore, we conducted a warming experiment in a typical permafrost region of the QTP in order to understand the influence of warming on soil moisture and moisture sensitivity in an alpine ecosystem. The specific objectives of this study were to (1) investigate the response of soil moisture to manipulated warming and natural precipitation in a typical permafrost region, (2) identify the influence of changes in soil moisture on the belowground production and decomposition processes of an alpine meadow ecosystem in a permafrost region, and (3) try to understand the direct and indirect influence of elevated ground temperature as well as changed soil moisture on the belowground carbon process in the alpine meadow ecosystem via multiple regression, partial correlation, and path analysis methods. This study will aid understanding of warming-induced soil moisture change and ecosystem response mechanisms to drought as well as provide a reference for predicting the development of alpine ecosystem in permafrost regions.

Materials and Methods

Experimental site

The experimental site is near the source of the Yangtze River on the QTP at 92°55′ E, 34°49′ N with an elevation of 4635 m above sea level. The site belongs to an alpine climate region. Based on 10 years (2002–2011) of meteorological data from the local weather station, the mean annual, mean annual maximum, and mean annual minimum air temperatures are –3.8°C, 19.2°C, and –27.9°C, respectively. The mean annual precipitation is 290.9 mm with over 95% falling during the warm season from April to October, the mean annual evaporation is 1316.9 mm, the mean annual relative humidity is 57%, and the mean annual wind velocity is 4.1 m sec^{-1}.

Soil development is weak because of the high elevation and cold climate, and soils are classified as Mattic Cryic Cambisols (alpine meadow soil, as Cambisols in FAO/UNESCO taxonomy). Dense, compact, and flexible roots are abundant in the 0–10 cm layer of soil and can protect soil and organic matter from wind and water erosion. There is an organic-rich layer at the 20–30 cm depth. In the soil profile, sand content gradually decreases from 96.87% at the 0–10 cm depth to 78.95% at the 70–100 cm depth. Silt content increases from 3.13% at the 0–10 cm depth to 20.12% at the 70–100 cm depth. Coarse particles make up the largest percentage of soil, which results in rapid water conductivity and weak water-holding capacity. Soil bulk density gradually increases from 1.05 ± 0.18 g cm^{-3} at the 0–10 cm depth to 1.45 ± 0.06 g cm^{-3} at the 70–100 cm depth (Xue et al. 2014). Soil field moisture capacity and wilting point are 22% and 5–7%, respectively.

The research site is dominated by alpine meadow vegetation such as *Kobresia capillifolia*, *Kobresia pygmaea*, and *Carex moorcroftii* with a mean height of 5 cm in the undisturbed ecosystem.

Experimental design

This experiment used a paired design with two treatments. There are five blocks each with an area of approximately 40 m^2. We designated pairs of 2×2 m plots in each block with one plot assigned as the warm treatment (W) and the other as control treatment (C). The distance between blocks was more than 50 m, and the distance between the two plots in each block was more than 4 m. Two blocks were set up on the hilltop with an altitude of 4634 m above sea level, and three blocks were set up on the hillside with an altitude approximately 4633 m above sea level. We verified that the soil and vegetation characteristics for the two plots within each block were the same to guarantee comparability. Each warmed plot was heated continuously by 165×15 cm infrared radiators (Kalglo Electronics, Bethlehem, PA) with a radiation output of 150 W m^{-2}. These radiators were suspended 1.5 m above the ground since 1 June 2010. The reflector surfaces of the heaters were adjusted to distribute radiant energy evenly to the soil surface (Kimball 2005). "Dummy" heaters with the same shape and size as the infrared radiator were used to simulate the shading effect of the infrared radiator in the control plots.

A micro-meteorological station was set up near the experimental blocks to measure the features of the local microclimate, including air temperature and precipitation.

Measurement of soil moisture and temperature

EnviroSMART (Australian Sentek) probes, based on FDR (frequency-domain reflection), were installed at depths of 10, 20, 40, 60, and 100 cm in each plot to simultaneously monitor soil volumetric water content across the entire experiment. Before installing the probes, absolute calibrations were conducted for each. Five replicate samples of soil were collected 10 cm from the location where the FDR probes were placed. The gravimetric soil water content was obtained by the oven-drying method (105°C for 24 h to achieve a constant weight) and was then converted to volumetric soil water content via multiplication with the corresponding volume weight of soil. Linear regression analysis between the volumetric soil water contents obtained by FDR and by the oven-drying method was conducted to calibrate the FDR probes. Soil moisture contents were collected every 10 min by a CR1000 data logger installed in each plot.

SI-111 Apogee 20 Infrared Radiometers (Campbell Scientific, Logan, UT) were hung 80 cm above the ground to monitor soil surface temperature. Model 109SS-L Temperature Probes with an endurance range of −40 to 70°C (Campbell Scientific) were installed at depths of 20, 40, 60, and 100 cm before 15 October 2011 and were then adjusted to 5, 15, 30, 60, and 100 cm after 15 October 2011. All probes were connected to a CR1000 data logger capable of withstanding low temperatures (Campbell Scientific). Ground surface and soil temperatures were collected every 10 min by a CR1000 data logger installed in each plot.

Measurement for actual evapotranspiration

Actual evapotranspiration in this research was measured using the weighing lysimeter method. Soil augers were used to obtain 10 undisturbed soil samples with original plant cover (20 cm in diameter and 40 cm in height) in grassland near the plots. These samples were put into cylindrical PVC tanks of the same size. Then, the tanks with soil samples were put in previously prepared holes inside the plots. A measuring cup was installed under each of the soil sample tanks in order to measure the amount of leaching water. From 17 June to 2 September 2011, these tanks with soil samples were weighed at 8:00 and 20:00 each day. The actual evapotranspiration in each plot, including soil evaporation and plant transpiration, was calculated using equation 1. Then, evapotranspiration for warmed and control treatments was obtained via arithmetic mean.

$$\mathrm{ET} = \left[\frac{(\mathrm{Q}_{8:00} - \mathrm{Q}_{20:00}) - (\mathrm{W}_{20:00} - \mathrm{W}_{8:00})}{\mathrm{S}}\right]\rho + \sum_{8:00}^{20:00} \mathrm{P} \quad (1)$$

in which, ET is the actual evapotranspiration (mm), Q is the weight of the tank and soil sample (g), W is the weight of infiltration water collected in the measuring cup (g), S is the surface area of soil sample in tank (cm^2),

ρ is the water density (kg m^{-3}), and $\sum_{8:00}^{20:00} P$ is the sum of precipitation (mm) from 8:00 to 20:00.

Measurement for belowground root biomass and NPP

In contrast with the extensive studies for aboveground plant production in tundra regions, the research for belowground plant production is comparatively rare. In the QTP, however, the tough and cold climate leads plants to accumulate more production in belowground parts than in aboveground parts (Yang et al. 2009), which makes the belowground portion more sensitive to the climate change. Our prior research also shows that short experimental warming does not cause a significant change in aboveground biomass (Xu et al. 2015). Therefore, only the response of the belowground production to warming, including root biomass and NPP, was analyzed in this study.

Rooting depth has a close relation with the soil moisture because it can reflect water availability. Therefore, we measured the root biomass at different depths to understand the root response to soil moisture. Soil samples with roots were collected in the experimental plots using a 7-mm interior diameter soil auger at depths of 0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, and 40–50 cm in May, June, July, August, and September of each year. The soil samples were immediately transported to the laboratory in a cooler. In the laboratory, root and soil samples were air-dried, crumbled, and sieved. Then, larger roots were separated from the soil, and the washed soil was filtered with a 0.25-mm sieve to retrieve fine roots. Live roots were distinguished from dead roots by their color, consistency, and the presence of attached fine roots. Belowground biomass in each experimental plot was calculated by drying (48 h at 75°C to constant weight) and weighing (Yang et al. 2009). Considering the hysteretic response of vegetation to simulated warming, only root biomass in 2012 was analyzed in this research. Belowground NPP was obtained by subtracting root biomass in May 2013 from that in May 2012.

Measurement for soil characteristics

Soil samples in each plot were collected using an auger in May, June, July, August, and September of each year at depths of 0–5 cm, 5–10 cm, 10–20 cm, 20–30 cm, and 30–50 cm. The soil samples were stored at 4°C until the analyses could be performed. The samples were then dried at room temperature and passed through a sieve (1 mm diameter, IUSS, 1927 provision), and any visible living plant material was removed.

SOC (Soil organic carbon) was measured via the potassium dichromate oxidation titration method (Walkley 1947). Soil LC (labile carbon) was measured using the method of Blair et al. (1995). Briefly, 5 g of soil was placed in a plastic centrifuge tube to which 25 mL of 0.333 mol L^{-1} $KMnO_4$ was added. The centrifuge tube was tumbled for 1 h at room temperature, centrifuged for 5 min at 2,000 rpm, and then, the supernatant was diluted with distilled water (1:250). A blank sample without soil was also processed using the same process as for the soil samples. The diluted and blank samples were read on a split-beam spectrophotometer at 565 nm to examine the change in $KMnO_4$ concentration, and this change was used to estimate the labile C content. Ammonium nitrogen (NH_4^+-N), nitrate nitrogen (NO_3^--N), and total nitrogen (TN) were measured in a VarioEL elemental analyzer using the Kjeldahl method (Li et al. 2012). As with the root biomass, only soil characteristics from 2012 were analyzed in this research.

Measurement for soil respiration

Soil respiration, including autotrophic respiration (R_a) from plant roots and heterotrophic respiration (R_h) from litter and soil organic matter, was measured in May, June, July, August, and September of 2012. To measure the total soil respiration (R_s), PVC collars of 5 cm in height and 10 cm in diameter with an area of 80 cm^2 were permanently inserted 2–3 cm into soil at the center of each plot. Small living plants were removed at the soil surface at least 1 day before measurements to eliminate the effect of aboveground biomass respiration. To measure the heterotrophic respiration, 50-cm-long PVC tubes (10 cm in diameter and 80 cm^2 in area) were inserted in each plot near the shallow collars prior to measurement. The deep PVC tubes cut off old plant roots (mainly distributed at depths of 0–30 cm) and prevented new roots from growing inside the tubes. R_h recording began 3 months after the deep collar had been inserted via measuring CO_2 efflux above the deep tubes. R_a was calculated as the difference between R_s and R_h, which was measured once or twice a month between 10:00 and 15:00 h (local time) using an Li-Cor 6400 portable photosynthesis system attached to soil CO_2 flux chamber (Li-Cor, Inc., Lincoln, NE).

Statistical analyses

One-way ANOVAs and paired t-tests were used to evaluate the significant differences in warmed and control plots for all of the factors analyzed herein. Basing on multiple linear regression methods, the relationships between soil moisture, air and soil temperatures, precipitation, and evapotranspiration were analyzed to identify the main factors affecting the soil moisture change. Pearson's bivariate correlations and two-tailed partial correlation analysis were used to analyze the relations among soil temperature, soil moisture, root biomass, belowground NPP, SOC, TN, NH^{+4}-N, NO^{+3}-N, and soil respiration. Path analysis was used to understand the direct and indirect effects of soil moisture on belowground C processes. All of these analyses were performed using SPSS 16.0 (SPSS Inc., Chicago, IL) for Windows.

Results

Temperature, precipitation, and soil moisture

Infrared heaters significantly ($P < 0.001$) increased the ground surface temperatures and soil temperatures at 60 cm depth by 2.31°C and 1.12°C in 2011, and 2.71°C and 0.41°C in 2012, respectively (Fig. 1C and D). The annual precipitations were 442 mm and 417.7 mm in 2011 and 2012. During the growing season (from May to September), the precipitations were 421.40 mm and 399.40 mm in 2011 and 2012 (Fig. 1B). Infrared heaters significantly ($P < 0.001$) decreased annual average soil volumetric moisture at 10 cm depth by 1.26% and 0.44% in 2011 and 2012, and significantly ($P < 0.001$) increased them at 60 cm depth by 4.26% and 4.97% in 2011 and 2012, respectively. From Figure 2, it can be seen that heater-induced soil warming significantly ($P < 0.01$) increased average soil volumetric moisture in the deep layer (40–100 cm) over both years and the growing seasons of 2011 and 2012. There was no significant soil moisture change in the interlayer between top and deep layers. An elevated soil temperature significantly ($P < 0.01$) decreased soil volumetric moisture in the top layer in the growing seasons of both 2011 and 2012 as well as the whole year of 2011.

Paired *t*-test results reflecting the infrared heater-induced differences in temperature and moisture between control and warmed plots are shown in Table 1.

Actual evapotranspiration

During 17 July to 2 September 2011, the daily average evapotranspiration levels were 2.80 ± 0.21 mm and 3.15 ± 0.26 mm in control and warmed plots, respectively. Infrared heaters nonsignificantly ($P > 0.05$) increased evapotranspiration by 0.36 mm. Based on the precipitation during 8:00 to 20:00 of each day, days were divided into the categories of rainy (with the rain fall above 0.1 mm) and sunny. Infrared heaters nonsignificantly ($P > 0.05$) increased evapotranspiration by 0.17 mm and 0.52 mm for rainy days and sunny days, respectively.

Root biomass and NPP

The growing season average root biomasses in 2012 were 3021.74 and 3095.04 g m^{-2} in control and warmed plots, respectively. Infrared heaters nonsignificantly ($P > 0.05$) increased the total root biomass in the 0–50 cm depth by 73.30 g m^{-2}. However, heaters caused different changes in root biomass between the upper and the deeper soil layer (Fig. 3A and Table 2). In the top soil layer (0–10 cm depth), root biomass in warmed plots was significantly ($P < 0.05$) lower than that in control plots (203.82 g m^{-2} difference). In contrast, the root biomass in 30–40 cm layer of warmed plots was significantly ($P < 0.001$) higher than that in control plots (141.98 g m^{-2} difference). Heater-induced decreases in the upper layer root biomass and increases in the deeper root biomass resulted in the upper layer root biomass percentage of the total root biomass to decrease from 80.90% to 72.88% and increased the deeper root biomass percentage from 19.10% to 33.30%.

Belowground NPP levels were 273.56 g m^{-2} yr^{-1} and 308.11 g m^{-2} yr^{-1} in control and warmed plots, respectively. Infrared heaters nonsignificantly ($P > 0.05$) increased the belowground NPP by 34.55 g m^{-2} $year^{-1}$. Similar to the pattern of root biomass in the different soil layers, belowground NPP levels were significantly ($P < 0.01$) higher in warmed plots than that in control plots by 28.67 g m^{-2} $year^{-1}$and 12.16 g m^{-2} $year^{-1}$ for 30–40 cm depth and 40–50 cm depth, respectively. In the upper soil layer, heaters caused a decrease in belowground NPP, but the difference was not significant (Fig. 3B).

Soil organic carbon, nutrient levels, and soil respiration

Figure 4 shows the average SOC, TN, C:N, LC, NH_4^+-N, and NO_3^--N in different soil layers during the growing season of 2012 in the control and warmed plots, respectively. Infrared heaters nonsignificantly changed SOC, TN, and LC at the depth of 0–30 cm, but significantly ($P < 0.05$) increased them by 1.58 g kg^{-1}, 0.13 g kg^{-1}, and 0.31 g kg^{-1} at the depth of 30–50 cm (Fig. 4A, B, D and Table 1). In addition, experimental warming did not cause significant change for the growing season average C:N, NH_4^+-N, and NO_3^--N at the depth of 0–50 cm in 2012.

Figure 5 shows the growing season average soil respiration values (R_s) in 2012 in control and warmed plots, respectively. Infrared heaters significantly ($P = 0.004$) increased R_s by 0.68 μ mol m^{-2} sec^{-1}, nonsignificantly ($P = 0.729$) increased soil R_h by 0.07 μ mol m^{-2} sec^{-1}, and significantly ($P = 0.000$) increased soil R_a by 0.56 μ mol m^{-2} sec^{-1}.

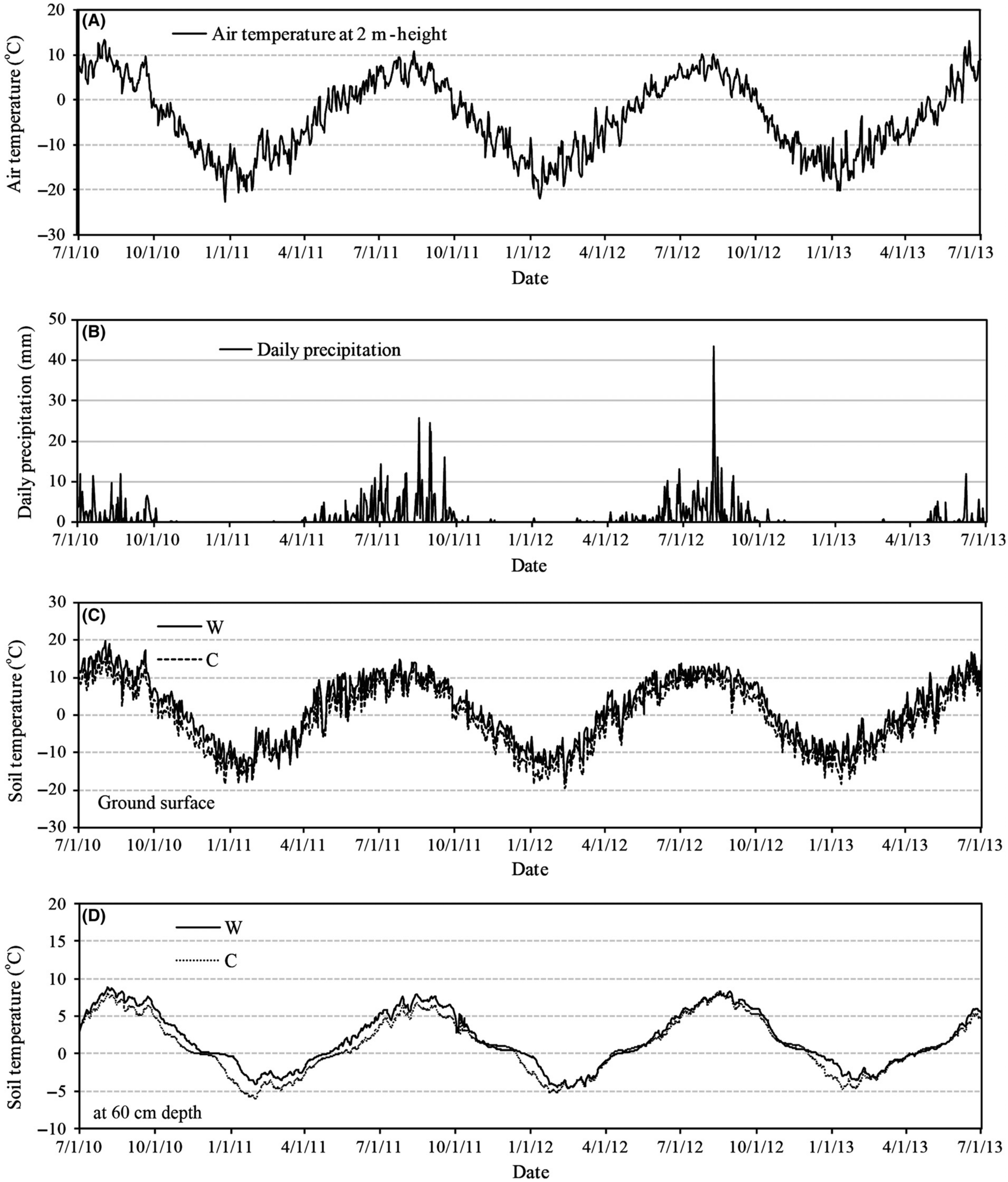

Figure 1. (A) Daily average air temperature and (B) Daily precipitation at the experimental site as well as (C) ground surface temperatures and (D) soil temperatures at 60 cm depth measured in the warmed (solid line) and control (dotted line) plots during the research period (1 July of 2010 to 1 July 2013).

Relationship among measured factors

Table 2 presents the multiregression analysis results and indicates the significance of each factor affecting the soil moisture at different depths and treatments. It can be seen that evapotranspiration has less influence on soil moisture in both warmed and control plots. However, precipitation plays an important role in affecting soil

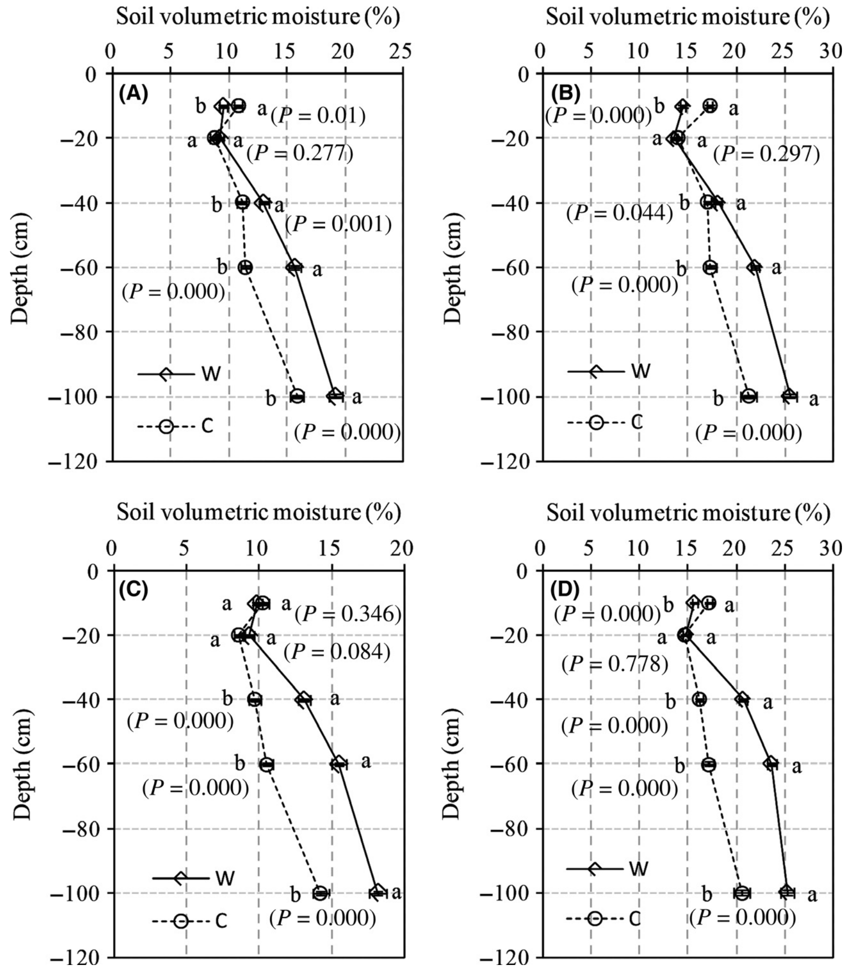

Figure 2. (A) Average soil moisture profiles in the warmed (solid line) and control (dashed line) plots in 2011, (B) the growing season of 2011, (C) 2012, and (D) the growing season of 2012. Different letters indicate statistically significant differences at the corresponding confidence interval among the two treatments as determined by ANOVA followed by a Tukey test. Error bars represent the standard error for $n = 5$.

moisture, especially top soil moisture in control treatments. Beside precipitation, the soil temperature at the depth of 60 cm has an influence on soil moisture at the 100 cm depth. Different from the weak temperature influence in control plots, infrared heaters offset the precipitation contribution and resulted a significant relation between soil temperature and moisture. The soil moisture at the 100 cm depth was significantly related to the air temperature and to soil temperature in the 0–60 cm layer.

ΔT is infrared heater-induced temperature difference (the values in the warmed plots minus that in the control plots, same hereafter), ΔSM is soil moisture difference, and ΔRBM is root biomass difference. From Figure 6A, it can be seen that ΔT did not cause the significant change ($N = 5 \times 5$) for root biomass. In contrast, there was a significant ($P < 0.05$) quadratic exponential relation between ΔSM and ΔRBM. Root biomass increased with increased soil moisture in the deep layer. However, the increase in root biomass disappeared when infrared heaters caused soil moisture content to increase above 3%. There were no significant relations between ΔSM and ΔNPP or between ΔT and ΔNPP (Fig. 6B), although the total belowground NPP in the soil profile increased with the increased soil temperature ($P = 0.148$). However, the partial correlation analysis results show that when ΔT was held as the control factor (constant), ΔSM had a marginally significant ($P = 0.052$) relation with ΔNPP. When ΔSM was held as the control factor (constant), there was still no significant ($P = 0.122$) relation between ΔT and ΔNPP. The path analysis result (Table 3) also shows the indirect influence of soil temperature via soil moisture on belowground production.

Pearson's bivariate correlations analysis results show that infrared heater-induced changes in soil temperature and moisture were significantly ($P < 0.05$) related to the changes in SOC, TN, and C:N but were not significantly ($P > 0.05$) related to the changes in LC, NH_4^+-N, and NO_3^--N. The partial correlation analysis results show that when ΔT was held as the control factor constant, ΔSM had a significant correlation with ΔSOC ($P = 0.005$) and TN ($P = 0.01$), but when ΔSM was held as the control

Table 1. Paired *t*-test results for the difference in temperature, moisture, belowground production, and carbon processes between control and warmed treatments.

Items	*t*	df	Sig.(2-tailed)
Daily average T_{surf}	84.471	1096	0.000
Daily average T_{20}	73.009	456	0.000
Daily average T_{40}	62.215	456	0.000
Daily average T_{60}	34.259	1096	0.000
Daily average T_{100}	54.354	1096	0.000
Daily average SM_{10}	−18.499	1096	0.000
Daily average SM_{20}	10.880	1096	0.000
Daily average SM_{40}	33.951	1096	0.000
Daily average SM_{60}	44.124	1096	0.000
Daily average SM_{100}	34.288	1096	0.000
Growing season average $RBM_{0–10}$	−12.275	24	0.000
Growing Season average $RBM_{10–20}$	0.627	24	0.537
Growing Season average $RBM_{20–30}$	7.374	24	0.000
Growing Season average $RBM_{30–40}$	6.609	24	0.000
Growing Season average $RBM_{40–50}$	8.990	24	0.000
Growing Season average $SOC_{30–50}$	3.475	24	0.002
Growing Season average $TN_{30–50}$	3.294	24	0.003
Growing Season average $LC_{30–50}$	2.859	24	0.009

T_{surf}, $T_{20\ cm}$, $T_{40\ cm}$, $T_{60\ cm}$, and $T_{100\ cm}$ are the soil temperatures at the ground surface and the depths of 20, 40, 60, and 100 cm; $SM_{10\ cm}$, $SM_{20\ cm}$, $SM_{40\ cm}$, $SM_{60\ cm}$, and $SM_{100\ cm}$ are soil moisture at the depths of 10, 20, 40, 60, and 100 cm; $RBM_{0–10}$, $RBM_{10–20}$, $RBM_{20–30}$, $RBM_{30–40}$, and $RBM_{40–50}$ are the root biomass at the depths of 0–10, 10–20, 20–30, 30–40, and 40–50 cm; $SOC_{30–50}$, $TN_{30–50}$, and $LC_{30–50}$ are the soil organic carbon, total nitrogen, and liable carbon at the depth of 30–50 cm.

factor, ΔT was nonsignificantly related to ΔSOC ($P = 0.196$) and ΔTN ($P = 0.225$). From Table 4, it can be seen that soil temperature was significantly related to R_s and R_h but was not significantly related to R_a in either control plots or warmed plots. However, soil moisture was significantly related to R_a in warmed plots but was not significantly related to R_h.

Discussion

The altered soil moisture pattern and the driving mechanism

Our results show that infrared heaters significantly decreased the moisture within the top soil (0–10 cm), increased the moisture within the deep soil layers (20–100 cm), and kept it stable in the interlayer soil at 10–20 cm depths. This pattern is more evident during the growing season (Fig. 2). Using meta-analysis methods, Rustad et al. (2001) summarized soil moisture response to experimental increase in temperature measured at 14 sites in the world and found that soil moisture was significantly lower in the heated plots than in the control plots of all of these experimental sites. Among the 14 sites, 8 were located in high latitude or altitude regions, and heating was accomplished using field open-top chambers. The warming-induced drought in the top layer of soil in our research is consistent with Rustad's meta-analysis and recently published warming experiments in tundra and alpine regions (Allison and Treseder 2008; Luo et al. 2010; Subin et al. 2013). Unfortunately, previous soil moisture monitoring efforts were mainly focused on the top layer of soil profile. Thus, we cannot compare the soil moisture pattern that we observed in the deep layer to previous research results, although the deep layer soil moisture also has an important influence on ecosystems.

Soil moisture is usually affected by precipitation, evapotranspiration, surface runoff, lateral subsurface flows, and vertical infiltration along the soil profile. Considering that the precipitation, surface runoff, and subsurface flows controlled by vegetation and soil water conductivity were the same between the warmed and the control plots in our experimental site, evaporation from the soil surface and transpiration by plants are understood to be the major factors affecting the soil moisture difference

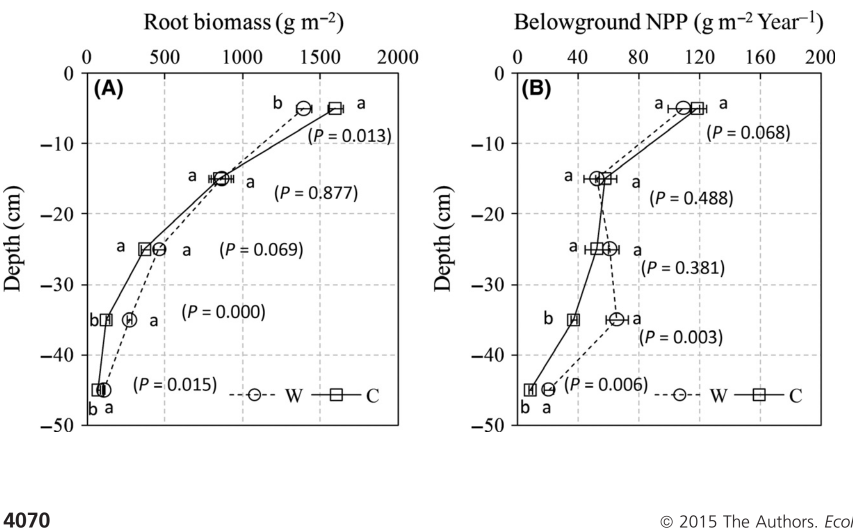

Figure 3. (A) Average root biomass during growing season of 2012 and (B) belowground net primary productivity from May 2012 to May 2013 in the warmed (dashed line) and control (solid line) plots. Different letters indicate statistically significant differences at the corresponding confidence interval among the two treatments. Error bars represent the standard error for $n = 5$.

Table 2. Multiregression analysis results among soil moisture, temperature, precipitation, and measured evapotranspiration for the warmed and control treatments from 17 June to 2 September 2011.

Treatments	Items	T_{air}	T_{surf}	T_{20}	T_{40}	T_{60}	T_{100}	P	ET	R^2
W	SM_{10}	–	–	–*	–*	+*	+**	+*	–	0.629
	SM_{20}	–	–*	–*	+*	+**	+**	+	–	0.549
	SM_{40}	–	–	+	+	+**	+**	+	–	0.734
	SM_{60}	–	–	+	+	+**	+**	+	–	0.746
	SM_{100}	+*	+**	+**	+**	+**	+	+	–	0.652
C	$SM_{10\ cm}$	–	–	–	–	+	+	+**	+	0.460
	SM_{20}	–	–	–	+	+	+	+**	+	0.445
	SM_{40}	–	–	–	+	+	+	+*	–	0.499
	SM_{60}	–	–	–	–	–	+	+*	+	0.282
	SM_{100}		–	+	+	+*	+	+	–	0.460

W signifies warmed treatment; C indicates control treatment; $SM_{10\ cm}$, $SM_{20\ cm}$, $SM_{40\ cm}$, $SM_{60\ cm}$, and $SM_{100\ cm}$ are soil moisture at the depths of 10, 20, 40, 60, and 100 cm; T_{air} means air temperature at the height of 20 cm; T_{surf}, $T_{20\ cm}$, $T_{40\ cm}$, $T_{60\ cm}$, and $T_{100\ cm}$ are the soil temperatures at the ground surface and the depths of 20, 40, 60, and 100 cm; P is the daily precipitation; and ET is the measured evapotranspiration. + indicates positive correlation and – indicates negative correlation; Asterisks denote significance at $P < 0.05$ (*) and $P < 0.01$ (**).

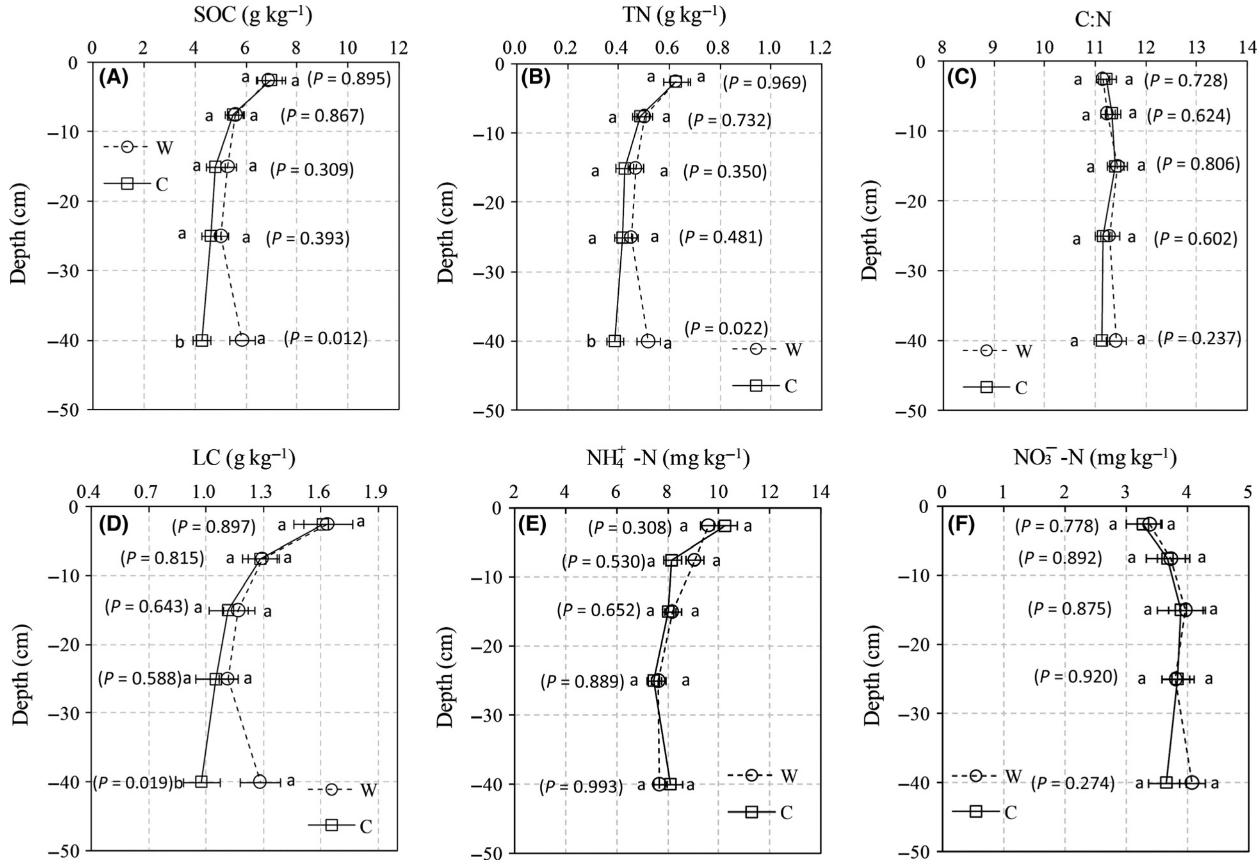

Figure 4. (A) Average soil organic carbon, (B) total nitrogen, (C) ratio of soil organic carbon to total nitrogen, (D) liable carbon, (E) ammonium nitrogen, and (F) nitrate nitrogen in the warmed (dash line) and control (solid line) plots during the growing season of 2012. Different letters indicate statistically significant differences at the corresponding confidence interval among the two treatments as determined by ANOVA followed by a Tukey test. Error bars represent the standard error for $n = 5$.

between warmed and control plots in this research (Porporato et al. 2004; Diffenbaugh 2005; Rodriguez-Iturbe et al. 2006; Dermody et al. 2007). However, 3 years of infrared heater warming did not cause significant change in evapotranspiration, although it was higher in warmed plots than in control plots. This perhaps can be attributed

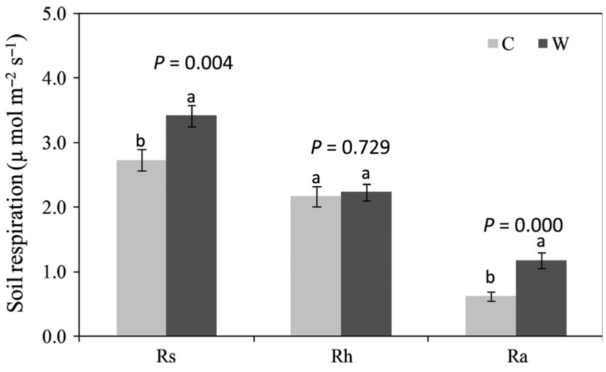

Figure 5. Average soil respiration, heterotrophic respiration, and autotrophic respiration in warmed (black bar) and control (gray bar) plots during the growing season of 2012. Different letters indicate statistically significant differences at the corresponding confidence interval among the two treatments as determined by ANOVA followed by a Tukey test. Error bars represent the standard error for $n = 5$.

to a reduced water supply for evapotranspiration from the top soil and plants in our study area. The annual average top soil moisture content was less than 10% in warmed plots and 11% in control plots. Additionally, sandy soil texture with low water-holding capacity in the study area perhaps inhibits the uplift of water. However, the significant soil moisture difference between warmed and control plots reveals that there are factors affecting soil moisture besides evapotranspiration.

The study area is located in the permafrost region with an active layer (the seasonally thawing layer of ground above the permafrost) approximately 2.5 m in thickness. The soil in the active layer freezes from October to April and melts from May to September. Infrared heater-induced warming increases the thawing period and thickness of the active layer (Xue et al. 2014). This increased the annual average soil moisture by 2.00% ($P < 0.001$) and the growing season average soil moisture by 2.08% ($P < 0.001$) in the 0–100 cm depth from 1 July 2010 to 1 July 2013. The liquid water released from frozen soil moves to surface under the force of evapotranspiration and moves downward to roots under the force of gravity. The amount and rate of water flowing down into the deep layer depends mostly on the hydraulic conductivity of the soil which is determined by soil texture and aggregate structure. As mentioned in the experimental site description, the content of sand with larger particle size occupies more than 90% of the soil in our experiment site. Usually, water moves much more readily through sandy soils than through clay soils or compacted soils (English et al. 2005; Bormann 2012). We speculate that the thawing water moves down into the deep soil and causes the soil moisture in warmed plots to significantly increase under 20 cm depth. The decrease of soil moisture in the top layer of the warmed plots might result from evapotranspiration and infiltration. The simple multiregression analysis results shown in Table 2 support this speculation very well. Therefore, we concluded that the infrared heater-induced increase in soil temperature caused the soil moisture decrease in the top layer and increase in the deep layer. The seasonal freeze–thaw cycles in the active layer played an important role, and the poor soil texture intensified the process (Baumann et al. 2009). The increasing evapotranspiration also contributed to the reduction of soil moisture in the top layer but was not enough to cause significant change.

The response of the belowground parts of plants to changed soil temperature and moisture

The relations between infrared heater-induced ΔT, ΔSM, ΔRBM, and ΔNPP (Fig. 6) show that soil moisture has a more direct influence than increased temperature,

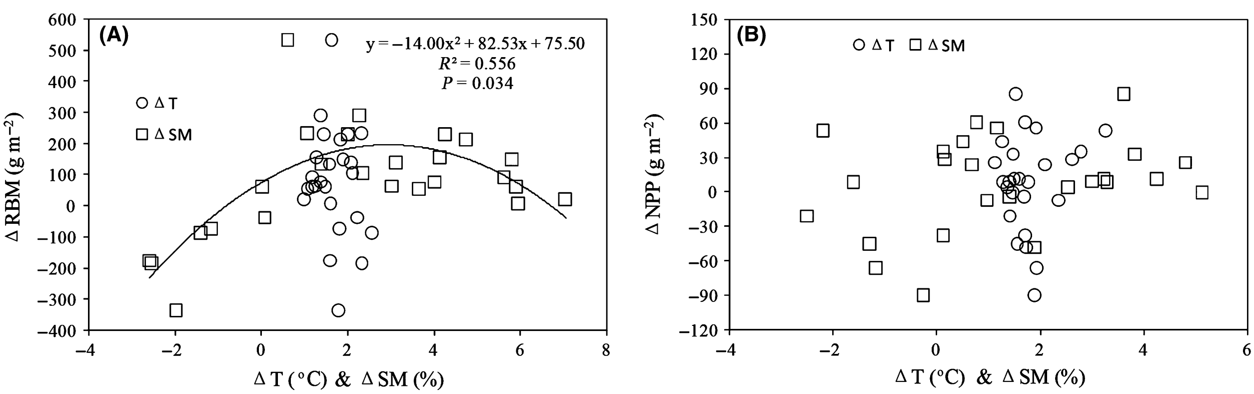

Figure 6. The relationships of (A) ΔRBM and (B) ΔNPP with ΔT and ΔSM. ΔRBM, ΔT, and ΔSM indicate infrared heater-induced difference in root biomass, soil temperature, and soil moisture, respectively.

Table 3. Path analysis results on direct effect of soil temperature (T) and indirect effect of SM (soil moisture) on RBM (root biomass) and soil LC (labile carbon).

Dependent variable	Independent variable	Direct path coefficient	Indirect path coefficient		Total effect
			SM	RB	
RBM	T	0.088	−0.520**		−0.156
	SM	0.470*			
LC	T	−0.052	−0.520**	0.088	−0.115
	SM	0.132		0.470*	
	RBM	−0.109			

Asterisks denote significance at $P < 0.05$ (*) and $P < 0.01$ (**).

although the change in soil moisture followed the rising temperature (Table 3). This result is consistent with research conducted in the alpine river valleys of the Tibetan Plateau (Li et al. 2013), on the Saana massif in northwestern Finland (Le Roux et al. 2013), and in the arid regions of the western United States (Kwon et al. 2008). There is certainly a positive relation between temperature and NPP. A newly published meta-analysis based on the data from 16 simulation experiments shows that experimental warming increased NPP by $4.40 \pm 0.25\%$ (Lu et al. 2013). However, in areas where soil moistures are low, plant growth is relatively more sensitive to soil moisture compared to rising temperature. A tiny increase in soil moisture may be reflected by increased plant growth. Our research suggests that the lower soil moisture (<15%) in the study area during the growing season is the main cause for soil moisture acting as the predominant limiting factor of plant growth. When soil moisture surpasses the field moisture capacity of 22%, the influence of soil moisture on plant growth is reduced. The exponential relationship between ΔSM and ΔRBM as well as the optimal soil moisture value beneficial to root growth, as shown in Figure 6A, supports this speculation.

The other effect of soil moisture on plant belowground production in our research is the downward extension of root biomass. There was a consistent downward trend for soil moisture, root biomass, and belowground NPP (Figs. 2, 3). In response to water stress, plants typically extend their root system into deeper soil layers with more water and reduce growth in top soil layers where water is deficient. Many observational and model results have demonstrated this pattern (Martyn et al. 1998; Jackson et al. 2000; Schenk and Jackson 2002; Chaves et al. 2003). Alpine shrubs, steppe grasses, and weeds have deeper root systems than alpine meadow grasses such as Kobresia and sedge. If warming-induced drought in top soil layers cannot be offset by increasing precipitation, alpine meadow communities might degrade into alpine steppe or shrub communities. Alpine meadow ecosystem degradation studies conducted in an alpine region (You et al. 2014) and in a northern higher latitude region (Bonfils et al. 2012) have already demonstrated this phenomenon.

The effect of soil temperature and moisture on soil C and N processes

Because soil respiration has a close relation with belowground carbon processes, we analyzed the relationships of soil temperature and moisture with soil respiration rate and its components. The significant relation between soil temperature, R_s, and R_h in control and warmed plots (Table 4) shows that soil temperature definitely affects the decomposition process of the alpine ecosystem in the permafrost regions of QTP as was found in some other

Table 4. The Pearson's correlation analysis results of soil respiration with soil temperature and moisture in different treatments during 2012 growing season.

Item	Tr	T_5	T_{15}	T_{30}	T_{60}	SM_5	SM_{15}	SM_{25}	SM_{35}	SM_{45}
R_S	C	***+	***+	**+	*+	ns−	ns−	ns−	ns−	ns−
R_S	W	*+	ns+	ns+	ns+	ns−	ns−	ns−	ns−	ns−
R_S	W-C	ns−	ns−	ns−	ns−	ns+	*+	*+	ns+	ns+
R_h	C	***+	***+	***+	***+	ns−	ns−	ns−	ns−	ns−
R_h	W	***+	**+	**+	*+	ns−	ns−	ns−	ns−	ns−
R_h	W-C	ns+	ns−	ns+	ns−	ns+	ns+	ns−	ns−	ns−
R_a	C	ns−	ns−	ns−	ns−	ns−	ns−	ns−	ns−	ns−
R_a	W	ns−	ns−	ns−	ns−	***+	***+	**+	**+	**+
R_a	W-C	ns−	ns−	*−	ns−	ns+	ns+	*+	**+	*+

R_s is soil respiration; R_h and R_a are heterotrophic and autotrophic respiration; W signifies warmed treatment; C denotes control treatment; W-C indicates the difference between warmed treatment and control treatment; T_5, T_{15}, T_{30}, and T_{60} are the daily mean values of the measured soil temperatures at the depths of 5, 15, 30, and 60 cm during the soil respiration measurement dates; SM_5, SM_{15}, SM_{25}, SM_{35}, and SM_{45} are the daily mean values of the measured soil moistures at the depths of 0–10, 10–20, 20–30, 30–40, and 40–50 cm during the soil respiration measurement dates; + indicates positive correlation and − indicates negative correlation; Asterisks denote significance at $P < 0.05$ (*), $P < 0.01$ (**), and $P < 0.001$(***).

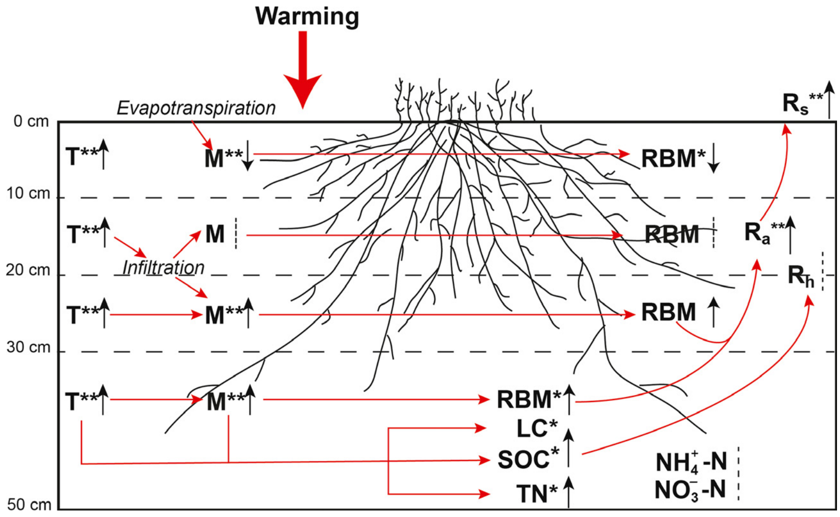

Figure 7. A diagram for the responses of belowground C processes to experimental warming in permafrost region. ↑: positive response and increase to warming; ↓: negative response and decrease to warming; vertical dot line is no significant change. *indicates statistical significance at the level of $P < 0.05$, ** indicates statistical significance at the level of $P < 0.01$. T is soil temperature; M is soil moisture; RBM is root biomass; R_s is soil respiration; R_h and R_a are heterotrophic and autotrophic respiration; SOC is soil organic carbon; LC is labile carbon; TN is total nitrogen; NH_4^+-N is ammonium nitrogen; NO_3^--N is nitrate nitrogen.

regions of the world (Karhu et al. 2014). The pattern among soil temperature, moisture, and respiration shows that warming-induced increases in soil moisture enhanced soil respiration. This is supported by two results of this research. One is that infrared heaters significantly increased R_a (Fig. 5) but not R_h. The other is that only soil moisture had a significant relation with R_a (Table 4).

In some warming experiments, the increased soil respiration was attributed to elevated soil temperature stimulating the production of plants as well as the decomposition of organic matter and litter (Boone et al. 1998; Luo et al. 2001; Schindlbacher et al. 2009). In other studies, researchers conjectured that warming-induced change in soil moisture might encourage or inhibit carbon release because the optimal combination between temperature and moisture can benefit the production and decomposition processes, but dryer or moister soil environments do not promote carbon release (Robinson et al. 1995; Rustad et al. 2001; Luo 2007; Wan et al. 2007; Luo et al. 2009; Lu et al. 2013). Our research in the permafrost regions, however, indicated that increasing soil respiration mainly resulted from the belowground growth of plants and not from the decomposition of organic matter. Elevated soil moisture played a more direct role than elevated soil temperature. The results shown in Figure 4 also support this point. Usually, the change of NH_4^+-N and NO_3^--N levels in soil can reflect the mineralization process of organic nitrogen. In our research, 3 years of experimental warming did not cause significant changes in the content of NH_4^+-N and NO_3^--N. Although soil temperature increased more evidently in the top soil layer than in deeper layers, the significant increase in SOC, TN, and LC only occurred in the deeper soil layer. The deeper layer, where root biomass was significantly increased, might thereby provide more original resources for SOC, TN, and LC.

All of these patterns and analytic results indicate that experimental warming did not significantly change the decomposition process but instead affected plant belowground production processes which depend more on increasing soil moisture (Fig. 7). This pattern can be explained by the seasonal freeze–thaw process. After the midpoint of July in every year, heating caused soil moisture in the deeper soil layer to increase beyond field moisture capacity which created anoxic conditions in the deeper soil and inhibited decomposition.

Our result is very different from previously published studies which report that experimental increases in soil temperature enhanced soil respiration. This discrepancy might arise from two reasons. The first is that the permafrost region has active layers with unique seasonal freeze–thaw cycles, leading to soil moisture having a more dominant influence on the ecosystem compared to temperature (Smith et al. 2005; Allison and Treseder 2008; Sardans et al. 2008; Baumann et al. 2009; Swenson et al. 2012; Doerfer et al. 2013). The other potential cause is that previous research focused more on changes in the top layer and omitted changes in the deeper soil layers.

Conclusions

A 3-year warming experiment in the alpine meadow system of the permafrost region shows that elevated soil temperature did not directly affect belowground carbon processes by stimulating the decomposition of litter and soil organic matter but indirectly enhanced the growing of belowground parts of plants in deeper layers via elevated soil moisture. Therefore, we conclude that elevated soil temperature-induced soil moisture change had a significant influence on the alpine ecosystem change. Freezing and thawing processes might play an important role in affecting soil moisture change. This research conducted in the permafrost region of the Qinghai–Tibetan Plateau had different results from prior research conducted in temperate or tropical regions. These results would therefore be of great use for understanding the influence of climate warming on belowground carbon processes and improving models that simulate ecosystem responses to climate change.

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Conflict of Interest

None declared.

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