



Effects of topography and fire on soil CO₂ and CH₄ flux in boreal forest underlain by permafrost in northeast China



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ABSTRACT

Regional quantification of soil CO₂ and CH₄ fluxes in boreal forests remains difficult because of high landscape heterogeneity and fire disturbance coupled with a sparse measurements network. Most of the work focuses on the separate effects of fire or topography, and as a result, the spatial variability in the response of soil carbon flux to fire remains unclear. A two-year field experiment was conducted in the boreal forest of the DaXing'anling Mountains to investigate the effects of topography (ridge and depression) and fire on soil CO₂ and CH₄ fluxes and to determine how the effects of fire vary with topography. The results showed that soil carbon flux to the atmosphere in this region was dominated by soil CO₂ flux. Topography had significant effect on soil carbon fluxes, with higher soil CO₂ emissions and CH₄ uptakes on the ridge than in the depression, whether burned or not, and these topographical differences were amplified by fire. Fire significantly increased soil CO₂ emissions and CH₄ uptakes both in the depression and on the ridge. However, the factors that determined soil CO₂ and CH₄ fluxes and the extent of the response to fire varied with topography. Although the depression released less soil carbon to the atmosphere, the increase in Q₁₀ of soil CO₂ flux and the permafrost degradation following fire in the depression indicated stronger positive feedbacks to climate warming. To concluded, topography regulated the effects of fire on soil carbon fluxes and might control the post-fire soil carbon flux feedbacks to climate warming. Therefore, large-scale predictions of soil carbon fluxes in response to fire in the boreal region must explicitly incorporate topographic features.

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1. Introduction

Boreal forests store 1095 Pg of carbon, accounting for more than one-third of the stored terrestrial carbon stocks and contributing greatly to the global carbon cycle (Bradshaw and Warkentin, 2015). These regions are particularly vulnerable to climate change because of the large carbon stocks and the predominance of permafrost. Although models project that some of the carbon released from permafrost will be offset by increases in Arctic and boreal primary productivity (Abbott et al., 2016; Schuur et al., 2009), a recent expert assessment survey indicated that biomass would offset little or none of permafrost carbon release because of water stress and fire disturbance, which are factors that are not adequately incorporated in current models (Abbott et al., 2016). Moreover, carbon loss from fire could increase four-fold by the end of the century (Abbott

et al., 2016); thus fire should receive more research attention in determining the carbon balance in boreal forest.

Soil carbon fluxes always vary spatially in response to topographic position (Paré and Bedard-Haughn, 2012; Wang et al., 2001; Webster et al., 2008). First, topography controls the vertical and lateral redistribution of soil water. Wetlands generally act as a CO₂ sink and CH₄ source, whereas well-drained areas can be much weaker CO₂ sinks or even sources but serve as CH₄ sinks due to their contrasting hydrology (Dai et al., 2012; Stielstra et al., 2015) and different methanotroph communities (Christiansen and Romero, 2015). Second, topographic position is an important factor controlling the distribution of permafrost (Jafarov et al., 2013), vegetation and carbon storage in boreal forests (Jafarov et al., 2013; Wang et al., 2001). Moreover, topographic features can affect the successional trajectory and permafrost dynamics following fire in boreal forests (Cai et al., 2013; Jafarov et al., 2013; Johnstone et al., 2010). Therefore, given the spatial variations in soil carbon flux and biotic and abiotic factors, the effects of fire on soil carbon flux are expected to vary with topography.

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Soil carbon fluxes are limited by substrate availability and the physical environment, which are both altered by fire (Burke et al., 1997; Morishita et al., 2015; O'Neill et al., 2002). Fire decreases soil CO₂ flux initially by limiting soil carbon sources and microbial activity after fire (Burke et al., 1997; Kim and Tanaka, 2002), but during post-fire recovery, the soil CO₂ flux gradually recovers to a pre-burn level or even surpasses it because of vegetation recovery and higher temperature (Burke et al., 1997). These changes in biotic and abiotic factors following fire are controlled by topography (Cai et al., 2013; Jafarov et al., 2013; Johnstone et al., 2010), indicating that the effects of fire on soil CO₂ flux likely vary with topography. Soil CH₄ flux, the result of CH₄ oxidation and production processes, is primarily controlled by soil hydrology, which affects the degree of anoxia in the soil profile (Kettunen et al., 1999; Sturtevant and Oechel, 2013). Fire effects on soil CH₄ flux may vary topographically depending on the specific changes in soil hydrology and environmental conditions. Although a few have studied the effects of fire and topography on soil respiration (Mccarthy and Brown, 2006; Xu and Wan, 2008), how fire effects vary with topography remains unclear in permafrost regions in which fire-induced permafrost thawing may complicate the effects on soil CO₂ and CH₄ fluxes (O'Donnell et al., 2010).

The DaXing'anling Mountains with 86.98% forest area form the southern boundary of the boreal forests, which play an important role in the national carbon budget (Fang et al., 2001) and are sensitive to climate change (Peng et al., 2009). An increase in fire intensity and frequency has seriously affected soil carbon balance and vegetation composition of boreal forest in this region (Peng et al., 2009; Wang et al., 2001; Yu et al., 2008). The Da Xing'anling Mountains with complex topographies and severe fire disturbance provide an ideal location for investigating the responses of soil carbon fluxes to fire and the variation of these responses in different topographies.

In this study, burned and unburned sites on a ridge (BR and UR) and in a depression (BD and UD) in a boreal larch forest in the DaXing'anling Mountains were selected to explore the effects

of fire and topography on soil CO₂ and CH₄ fluxes. The objectives of this study were to: 1) quantify differences in soil CO₂ and CH₄ fluxes between the ridge and depression; 2) determine how the responses of soil CO₂ and CH₄ fluxes to fire vary with topography; and 3) evaluate the effects of topography and fire on the sensitivity of soil CO₂ flux to climate warming.

2. Material and methods

2.1. Study sites

The study area is in the DaXing'anling Mountains (51.89°N, 121.91°E) in northeast China and has a terrestrial monsoon climate with a long, severe winter. The annual average temperature is −3.6°C with an average temperature of −29.8°C in the coldest month, January, and an average temperature of 18.1°C in the hottest month, August. The annual precipitation is approximately 500 mm, more than 60% of which occurs between June and August. The soil type is classified as Gelisols according to USDA or as Crysolis in WRB (Bockheim, 2015).

Ridge and depression are two typical topographies in the DaXing'anling Mountains with distinct vegetation composition, permafrost and soil properties (Tables 1 and 2). The depression and ridge sites had similar stand age (117 ± 5 years) and disturbance history with developed mature *Larix-Ledum* forest and *Larix-Rhododendron* forest, respectively (Wang et al., 2001). In 2008, an extremely intense fire caused by lightning strikes burned approximately 478 ha of forest and resulted in 100% mortality of overstory and ground cover and combustion of approximately 5 cm of forest floor. We chose the burned sites on a ridge and in a depression in this fire scar with comparable fire severity. The burned sites were adjacent to the undisturbed sites (less than 1 km), and the burned and unburned sites had similar soil parameters and physical conditions before the fire. Seven years after the wildfire, many of the dead trees were still standing, and many shrubs less than 3 m and grasses had recovered in the burned sites (Table 1).

Table 1
Topographical conditions, organic layer depth, active layer thickness, water table position and vegetations at the study sites (mean ± standard error, n = 5).

		UD	BD	UR	BR
Slope aspect		SE	SE	SE	SE
Slop position		Toe-slop	Toe-slop	Middle-slop	Middle-slop
Organic layer depth (cm)		35 ± 2 a	33 ± 1 a	13 ± 1 b	7 ± 1 c
Active layer thickness (cm) ^a		44 ± 3 b	59 ± 1 a	–	–
Water table position (cm) ^b		−17.1 ± 0.8 b	−22.7 ± 1.6 a	–	–
Tree layer	Dominant species	<i>Larix gmelinii</i>	–	<i>Larix gmelinii</i>	–
	Density (trees ha ^{−1})	625	–	1450	–
	Mean height (m)	16.4	–	16.9	–
	Mean d. b. h. (cm)	17.1	–	13.2	–
Shrub layer	Canopy density	0.6	–	0.8	–
	Dominant species	<i>Ledum palustre</i>	<i>Betula fruticosa</i> ; <i>Alnus hirsuta</i> ; <i>Ledum palustre</i>	<i>Rhododendron dauricum</i>	<i>Populus davidiana</i> ; <i>Betula platyphylla</i>
Ground cover	Coverage (%)	80	95	90	60
	Dominant species	<i>Calamagrostis</i> ; <i>Carex</i> ; <i>Sphagnum</i>	<i>Calamagrostis</i> ; <i>Carex</i> ; <i>Sphagnum</i>	<i>Polytrichum</i>	<i>Carex</i>
	Coverage (%)	91	60	46	35

UD, BD, UR and BR represent the unburned depression site, burned depression site, unburned ridge site and burned ridge site, respectively.

Mean d. b. h.: mean diameter at breast height.

“–”: not determined.

The different letters indicate significant differences in means at $P < 0.05$ (Tukey's honest significance test).

^a The active layer thickness was measured on early September by digging holes to the permafrost, which were not detected at the ridge sites, because we do not find the permafrost at 3 m depth.

^b Mean water table position of the measurement period. Water table position within the depression sites was measured manually once a week synchronizing with soil carbon flux measurement.

2.2. Experimental design

The depression and ridge sites were located in typical *Larix-Ledum* forest and *Larix-Rhododendron* forest, respectively. These two forest types have distinct soil properties, permafrost and vegetation composition associated with the topography and are distributed widely in the Daxing'anling Mountains (Wang et al., 2001). Therefore, the sites represented these two topographies in this region. At each site, three polyvinyl chloride collars (21.4 cm in diameter and 15 cm in height) were randomly placed at a distance of more than 10 m to measure soil CO₂ and CH₄ fluxes. Small understory plants and seedlings that grew within the collars were clipped to remove the effect of aboveground plant respiration (Webster et al., 2008). Mosses were allowed to grow because removing them would result in excessive disturbance of the soil surface (Webster et al., 2008). Clipping occurred at least 24 h before measurements to minimize pulses of decomposition resulting from clipping. All soil collars remained in place.

2.3. Soil CO₂ and CH₄ flux measurements

Soil CO₂ and CH₄ fluxes were measured using an Ultra-portable Greenhouse Gas Analyzer (UGGA) that consisted of a laser off-axis integrated cavity output spectroscopy analyzer (Los Gatos Research, CA, USA). Air within the chamber was mixed by a battery-operated fan in the chamber, and passed through tubing with an internal diameter of 4 mm to the analytical box. After the non-destructive analysis, the air went back to the chamber. Concentrations of CH₄, H₂O, and CO₂ and the air temperature and pressure inside the chambers were recorded. The gas concentration data were collected at a 5 s rate, and the data acquisition continued for 300 s for each chamber, but the first 50 s and the last 30 s of gas concentration data were not used to calculate the soil CH₄ and CO₂ fluxes.

Diurnal measurements of soil CO₂ and CH₄ fluxes in the UD, BR, BD and UR sites were taken on August 1 and 13 and September 18, 21, 2015, every 2 h from 08:00 to 20:00 and every 3 h from 20:00 to the next day 08:00. Based on these diurnal patterns, the soil CO₂ and CH₄ flux measurements were taken between 08:00 and 11:00 local time in the order BD, BR, UD and UR on each sampling day, which represented the daily mean flux. The Measurements were taken from June to October in 2015 and from May to November in 2016. We divided the measurement period into three seasons, spring (May to June), summer (July to August) and autumn (September to November), which are related to soil physical conditions and plant phenology (Du and Fang, 2014). Soil CO₂ and CH₄ flux were measured twice per week in the spring, and once per

week in the summer and autumn, for a total of 45 measurements at each sampling point.

The soil temperature sensitivity of the soil CO₂ flux was calculated for each chamber using Van't Hoff's temperature coefficient, Q₁₀, which expresses the increase in soil CO₂ flux for a warming of 10 °C (Lloyd and Taylor, 1994). Cumulative soil CO₂ and CH₄ fluxes from June 17 to October 17 in 2015 and 2016 for each chamber were obtained by interpolating the soil CO₂ and CH₄ fluxes between sampling dates and then computing the sum of the average fluxes as follows (Zhang et al., 2015):

$$F_c = \sum F_{m,k} \Delta t_k$$

where F_c is the cumulative soil CO₂ or CH₄ flux in the sampling period; $\Delta t_k = (t_k - t_{k-1})$ is the time sequence of the field measurements across the study period; and $F_{m,k}$ is the average soil CO₂ or CH₄ flux over the interval (t_{k-1}, t_k) .

2.4. Environmental monitoring

The soil temperature at a depth of 5 cm and the soil volumetric water content at 0–10 cm were measured near the collar simultaneously with the soil carbon flux measurements until the soil was frozen. Soil temperature was measured with a thermocouple probe connected to the UGGA (Los Gatos Research, CA, USA). The soil volumetric water content was measured using a portable MST3000+ (STEP Systems GmbH, Essen, Germany) by frequency-domain reflectometry (FDR).

2.5. Statistical analysis

Soil CO₂ flux, CH₄ flux, temperature and moisture were analyzed with repeated-measures ANOVA with time-points of measurement as within-subject comparisons and fire and topography as fixed effects. Two-way ANOVA was used for the cumulative soil CO₂ flux, CH₄ flux and Q₁₀ with fire and topography as factors. The differences in soil mean temperature, moisture, and cumulative soil CO₂ flux and CH₄ flux between 2015 and 2016 were tested by paired-samples *t*-tests. The SPSS statistical software package (version 19.0 for Windows) was used for statistical analyses with a significance level of 0.05. The relationships between soil carbon fluxes and soil temperature or soil moisture were assessed by regression analysis (linear or exponential) with Origin software (version 9.0 for Windows).

Table 2

Soil properties of the UD, BD, UR and BR sites (mean ± standard error, n = 5).

		UD	BD	UR	BR
Soil pH ^a	0–15 cm	5.18 ± 0.14 b	5.78 ± 0.08 a	5.60 ± 0.08 ab	5.70 ± 0.08 a
Soil organic C (%) ^b	0–15 cm	22.5 ± 1.3 ab	31.1 ± 3.8 a	15.1 ± 1.2 bc	7.6 ± 0.6 c
	15–30 cm	24.0 ± 2.0 ab	30.1 ± 2.9 a	8.7 ± 0.9 c	7.3 ± 0.4 c
	30–45 cm	19.5 ± 1.7 ab	29.5 ± 4.3 a	8.1 ± 0.9 b	7.2 ± 0.6 b
Soil total N (%) ^b	0–15 cm	1.2 ± 0.1 b	1.6 ± 0.1 a	0.7 ± 0.1 c	0.3 ± 0.1 d
	15–30 cm	1.6 ± 0.1 a	1.7 ± 0.1 a	0.3 ± 0.1 b	0.2 ± 0.0 b
	30–45 cm	1.2 ± 0.0 b	1.8 ± 0.2 a	0.2 ± 0.0 c	0.2 ± 0.0 c
Soil C/N ^c	0–15 cm	18.8 ± 0.3 a	19.3 ± 1.4 a	22.2 ± 1.4 a	27.5 ± 4.1 a
	15–30 cm	14.9 ± 0.3 c	17.4 ± 1.3 c	35.2 ± 9.6 ab	42.6 ± 5.2 a
	30–45 cm	16.4 ± 1.5 b	16.5 ± 1.1 b	35.0 ± 5.4 a	42.1 ± 4.3 a

UD, BD, UR and BR represent the unburned depression site, burned depression site, unburned ridge site and burned ridge site, respectively. Soil samples collected in early September of 2015 were sieved with a 2 mm mesh sieve and air-dried to measure soil pH, then ground to pass through a 0.15 mm mesh sieve to measure soil organic carbon and total nitrogen.

The different letters in a row indicate significant differences among sites at $P < 0.05$ (Tukey's honest significance test).

^a Soil pH was measured after 12 h of contact by mixing 5 g of dry soil with 50 ml of deionized water.

^b Soil organic C and total N contents were measured by dry combustion method after decarbonation (Vario Macro cube, Elementar). Values are expressed in% of the element by dry weight.

^c Soil C/N was the ratio of soil organic carbon to soil total nitrogen.

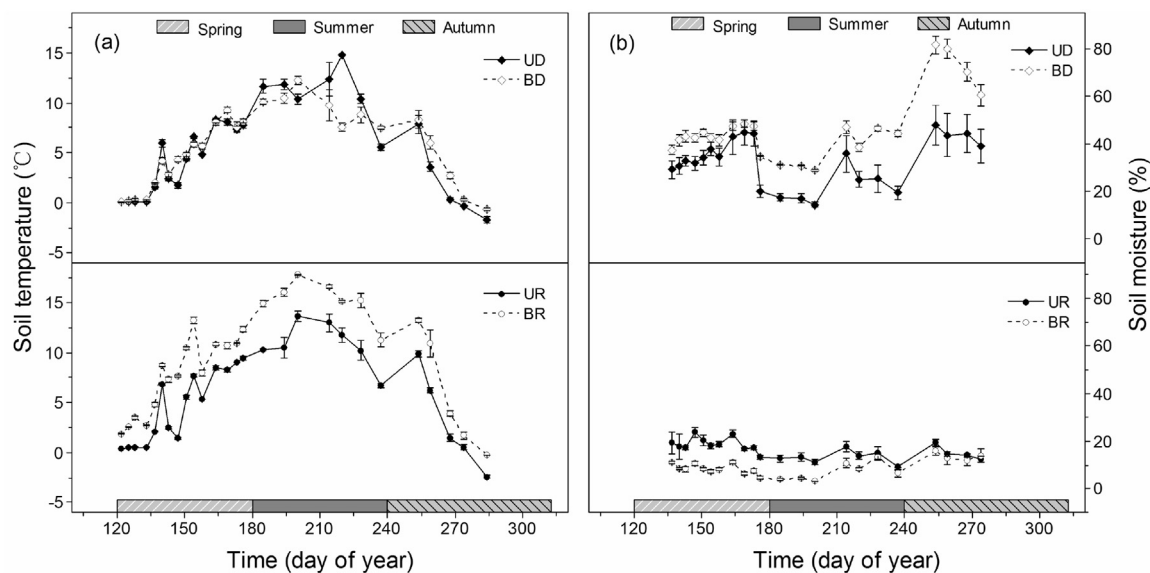


Fig. 1. Seasonal variation of soil temperature at 5 cm soil depth (a) and soil moisture at 0–10 cm soil depth (b) in boreal forest in northeast China ($n=3$). UD, BD, UR and BR represent the unburned depression site, burned depression site, unburned ridge site and burned ridge site, respectively; the points represent the mean values, and error bars represent the standard error of the mean at each site.

3. Results

3.1. Effects of topography and fire on soil environment factors

Both the burned and unburned ridge sites had higher soil 5 cm temperatures and lower soil 0–10 cm moisture than the depression sites, which were consistent in spring, summer and autumn (Fig. 1; Table 3). However, soil temperature and moisture of the ridge and depression differed in their responses to fire (Table 3). On the ridge, the burned site had higher soil 5 cm temperatures and lower soil 0–10 cm moisture than those of the unburned site (Fig. 1; Table 3). By contrast, in the depression, the burned site had lower soil 5 cm temperatures and higher 0–10 cm soil moisture than those of the unburned site (Fig. 1; Table 3). Moreover, the burned site in the depression had a thicker active layer and a lower mean water table position than those of the unburned site (Table 1).

3.2. Temporal variation of soil CO₂ and CH₄ fluxes

The diurnal and seasonal variation of soil CO₂ flux (single peak) was similar at all sites (Figs. 2 and 3); however, the peak of the seasonal pattern on the ridge lagged behind that in the depression (Fig. 3). The temporal variations of soil CO₂ flux were closely associated with the soil 5 cm temperatures (Fig. 4). Moreover, the temperature sensitivities (Q_{10}) of soil CO₂ flux were different among sites, which increased after fire in the depression but decreased after fire on the ridge (Fig. 4).

The diurnal variation of soil CH₄ flux was similar at all sites, and no diurnal patterns were detected in soil CH₄ flux because flux values were not significantly different during the day ($P>0.05$; Fig. 5).

Table 3

The repeated-measures ANOVA results (P values) for soil CO₂ flux, soil CH₄ flux, soil 5 cm temperature and soil 0–10 cm moisture in spring, summer and autumn.

	Soil CO ₂ flux			Soil CH ₄ flux			Soil temperature			Soil moisture		
	spring	summer	autumn	spring	summer	autumn	spring	summer	autumn	spring	summer	autumn
Time	0.000	0.000	0.000	0.000	0.349	0.212	0.000	0.000	0.000	0.000	0.000	0.019
F	0.054	0.000	0.003	0.524	0.005	0.000	0.000	0.000	0.000	0.004	0.000	0.000
T	0.004	0.000	0.000	0.296	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
F × T	0.062	0.001	0.246	0.281	0.109	0.103	0.000	0.000	0.026	0.811	0.000	0.000

Time, F and T represent the time-points of measurement, fire and topography, respectively; F × T represents the interaction of fire and topography.

Additionally, no seasonal variations in soil CH₄ fluxes in summer and autumn seasons were detected (Fig. 6; Table 3), because the seasonal variation of soil CH₄ flux was poorly correlated with soil moisture at 0–10 cm and soil temperature at 5 cm within each site.

3.3. Effects of topography and fire on soil CO₂ flux

Topography determined the magnitude of soil CO₂ flux, with higher values on the ridge and lower values in the depression, and this topographical difference was amplified by fire (Fig. 3; Table 3). Soil CO₂ emissions increased significantly after fire, except in the spring (Fig. 3; Table 3). The differences of soil CO₂ fluxes among sites were strongly correlated with soil 5 cm temperatures (Fig. 7(a)) and 0–10 cm moisture (Fig. 7(b)). Furthermore, cumulative soil CO₂ fluxes increased significantly after fire, with a greater increase on the ridge (41.6%) than that in the depression (36.4%; Fig. 8(a)). Additionally, cumulative soil CO₂ fluxes were higher in 2016 than in 2015 (Fig. 8(a)).

3.4. Effects of topography and fire on soil CH₄ flux

Soil CH₄ flux was controlled by topography with greater soil uptake of CH₄ on the ridge but with a slight uptake or emission in the depression (Fig. 6; Table 3). The soil CH₄ uptakes and its accumulations were increased after fire both on the ridge and in the depression (Figs. 6 and 8(b); Table 3). However, the fire and topography effects were not significant in the spring (Table 3). The differences in soil uptake of CH₄ among sites were significantly correlated with soil 5 cm temperatures ($R^2=0.852$; Fig. 9(a)) and soil 0–10 cm moisture ($R^2=0.869$; Fig. 9(b)).

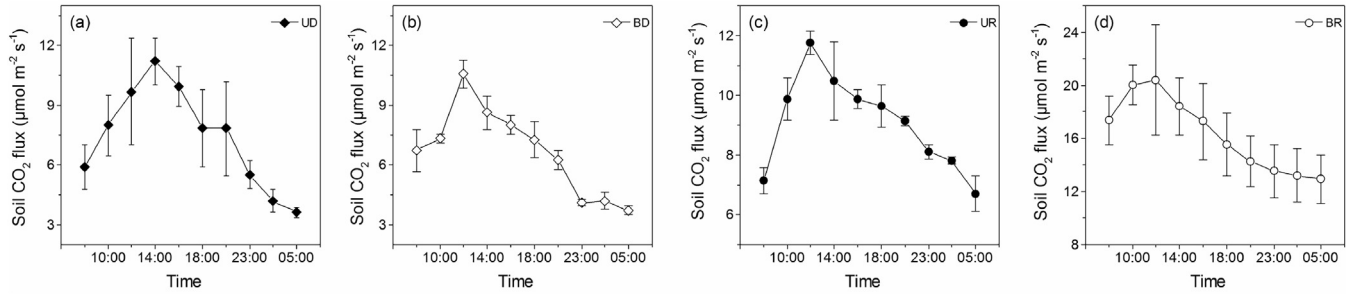


Fig. 2. Diurnal variation of soil CO₂ flux at the UD (a), BD (b), UR (c) and BR (d) sites (n=3). UD, BD, UR and BR represent the unburned depression site, burned depression site, unburned ridge site and burned ridge site, respectively; the points represent the mean values, and error bars represent the standard error of the mean at each site.

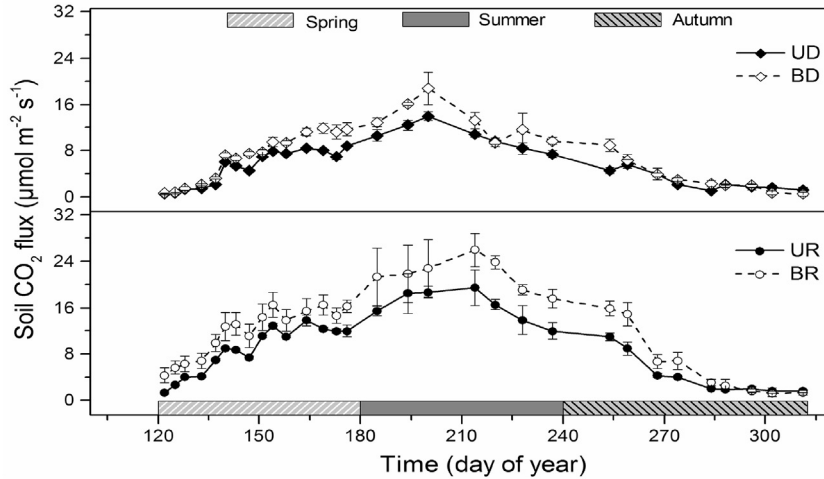


Fig. 3. Seasonal variation of soil CO₂ flux in boreal forest in northeast China (n=3). UD, BD, UR and BR represent the unburned depression site, burned depression site, unburned ridge site and burned ridge site, respectively; the points represent the mean values, and error bars represent the standard error of the mean at each site.

4. Discussion

4.1. Temporal variation of soil CO₂ and CH₄ fluxes

Diurnal variation of soil CO₂ flux was closely correlated with soil temperatures and follow a curve with a single peak (Zhang et al., 2015), which was the pattern confirmed in the present study (Fig. 2). The mean soil CO₂ fluxes at 08:00–11:00 local time were 99.9%, 99.2%, 117.4% and 115.3% of their daily mean fluxes at the

UD, UR, BD and BR sites, respectively; therefore, the daily flux at the BD and BR and the UD and BR was slightly overestimated or underestimated, respectively. Measurements in the order BD, BR, UD and UR represented their daily mean flux more accurately. The seasonal variation of soil CO₂ flux at all sites was similar to that of soil temperatures at 5 cm (Figs. 1, 3 and 4). This pattern is widely found in previous studies (O'Neill et al., 2002; Takakai et al., 2008), and soil surface temperature is the primary factor driving the diurnal and seasonal variation of soil CO₂ fluxes by affecting plant phe-

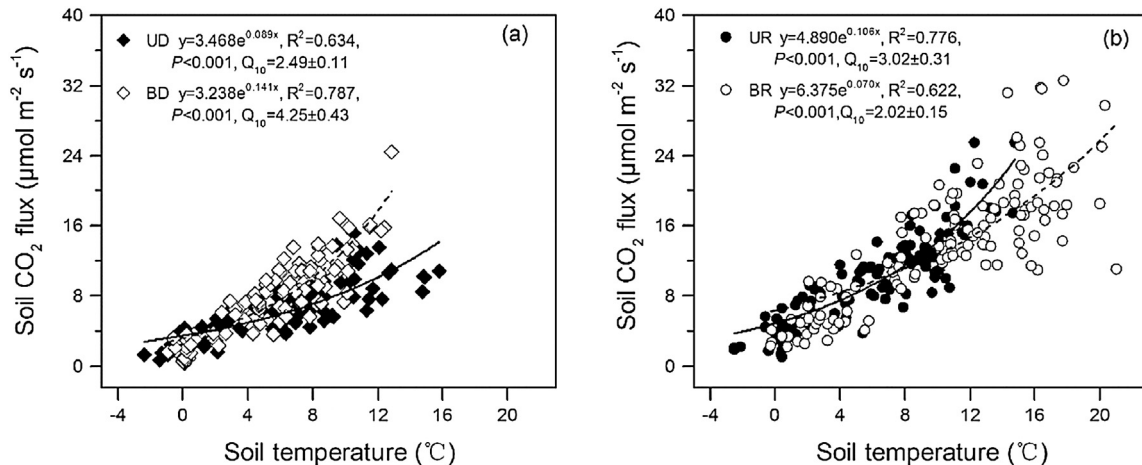


Fig. 4. Temperature sensitivity of soil CO₂ flux at the UD, BD, UR and BR sites (n=123). UD, BD, UR and BR represent the unburned depression site, burned depression site, unburned ridge site and burned ridge site, respectively.

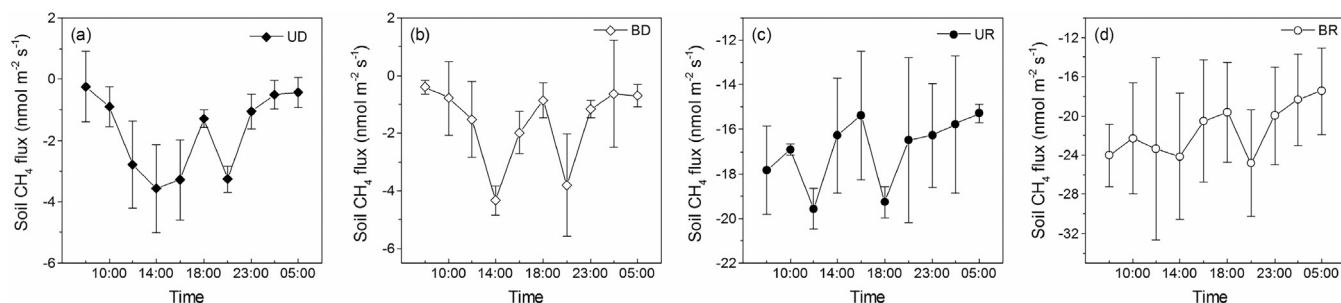


Fig. 5. Diurnal variation of soil CH₄ flux at the UD (a), BD (b), UR (c) and BR (d) sites. UD, BD, UR and BR represent the unburned depression site, burned depression site, unburned ridge site and burned ridge site, respectively; the points represent the mean values, and error bars represent the standard error of the mean soil CH₄ flux at each site (n = 3).

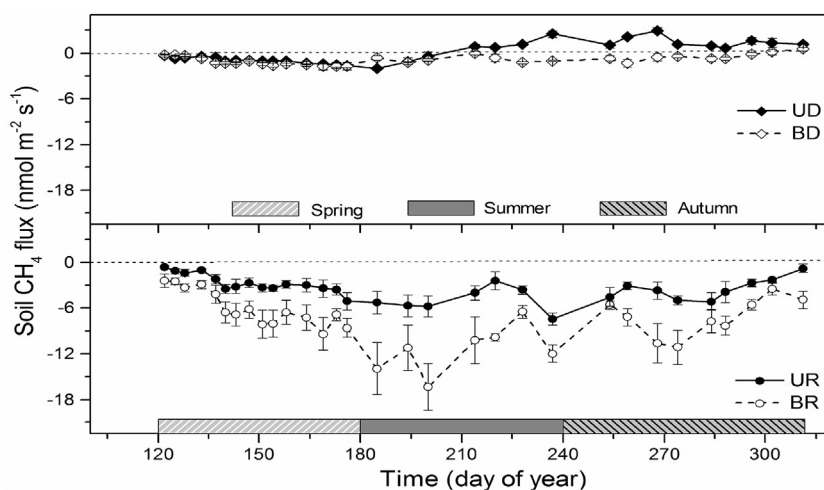


Fig. 6. Seasonal variation of soil CH₄ flux in boreal forest in northeast China (n = 3). UD, BD, UR and BR represent the unburned depression site, burned depression site, unburned ridge site and burned ridge site, respectively; the grey dash line indicates the zero lines with a change from positive (i.e., release) and negative (i.e., uptake) fluxes; the points represent the mean values, and error bars represent the standard error of the mean soil CH₄ flux at each site.

nology and microbial activity (O'Neill et al., 2002; Takakai et al., 2008). Furthermore, soil CO₂ fluxes were higher in 2016, which had higher soil temperatures than those in 2015, demonstrating that the interannual variation of soil CO₂ flux was also controlled by soil temperature. This close dependence of soil CO₂ fluxes on soil temperature in this region suggests a strong positive feedback between soil CO₂ emissions and climate warming.

We found no diurnal CH₄ flux pattern in the present study, which is consistent with previous studies (Castro et al., 1992; Rinne et al., 2007). The lack of a diurnal cycle allowed us to directly calculate the average flux for each day from the measurements, because missing data only increases the random uncertainty, but does not lead to any systematic error (Rinne et al., 2007). Yvon-Durocher et al. (2014) considered the seasonal variation of soil CH₄ flux to be

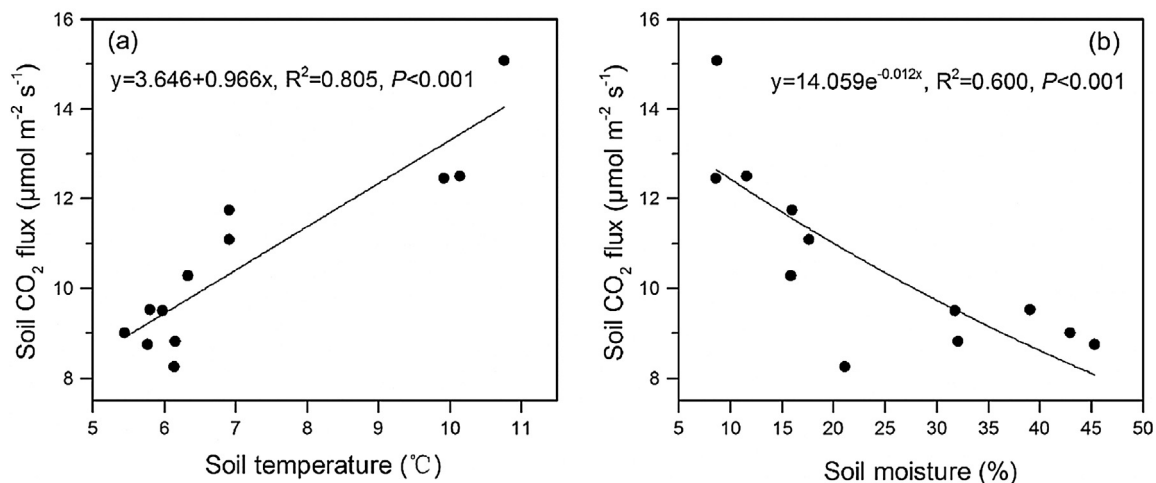


Fig. 7. The relationship between the mean soil CO₂ flux and soil 5 cm temperature (a) or 0–10 cm moisture (b) in boreal forest in Northeast China (n = 12).

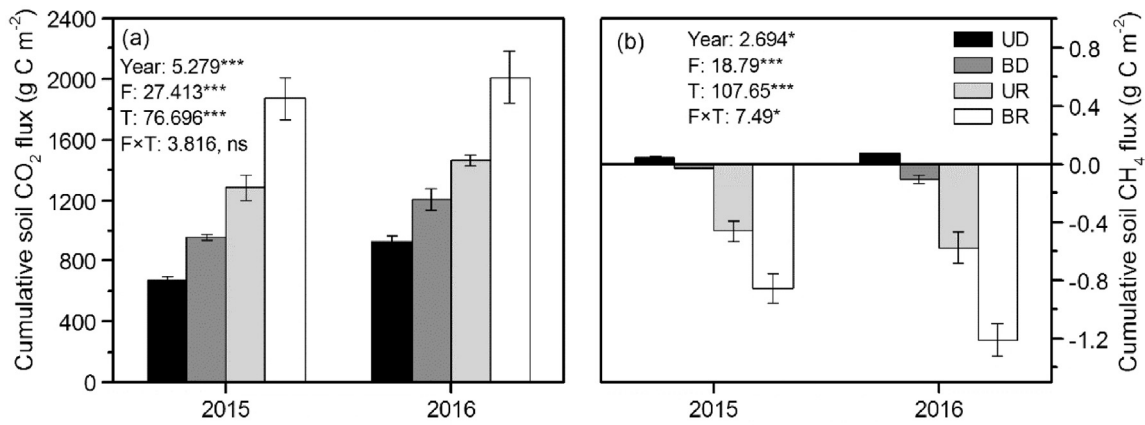


Fig. 8. Cumulative soil CO₂ (a) and CH₄ flux (b) of the measurement period in 2015 and 2016 in boreal forest in Northeast China (n=3). UD, BD, UR and BR represent the unburned depression site, burned depression site, unburned ridge site and burned ridge site, respectively; Error bars represent the standard error of the mean cumulative soil CO₂ and CH₄ fluxes at each site; F and T represent fire and topography treatment, respectively, and F × T represents their interaction; * represents significant at $P < 0.05$; ** represents significant at $P < 0.01$; *** represents significant at $P < 0.001$.

primarily controlled by soil temperature. However, in the present study, because the seasonal variation of soil CH₄ fluxes was poorly correlated with soil 5 cm temperatures or 0–10 cm moisture, and because both soil CH₄ uptake and emission occurred throughout the entire period, soil CH₄ flux showed no seasonal pattern.

4.2. Effects of topography on soil CO₂ and CH₄ fluxes

Soil CO₂ flux was the dominant soil carbon flux to the atmosphere at all sites, and the flux values at the unburned sites were approximately the same as the values reported for white spruce in a previous study (O'Neill et al., 2002) but higher than those for black spruce (Kim and Tanaka, 2002; O'Neill et al., 2002; Takakai et al., 2008). We found the ridge sites had higher soil CO₂ fluxes and accumulations than those of the depressions (Figs. 3 and 8(a); Table 3). This topographical difference in soil CO₂ flux has been documented previously (Dai et al., 2012; Stielstra et al., 2015), and the soil hydrological condition could be a key factor regulating this soil carbon flux (Fig. 7(b); Dai et al., 2012). First, the soil hydrological condition affects aeration and therefore determines whether the soil is aerobic or anaerobic, which affects microbial respiration (Dai et al., 2012). Second, the soil hydrological condition greatly affects the species composition and aboveground net primary production (NPP) of boreal forest ecosystems, which change nutrient avail-

ability and root respiration (Wang et al., 2003; Wang et al., 2001). Moreover, we further concluded that the seasonal frozen soil might be another important factor controlled by topographical variation that affected soil CO₂ fluxes in this permafrost region, because the seasonal frozen soil when thawed in growing season became a source of the soil CO₂ flux with high microbial and root activity. Consistent with this conclusion, active layer was less thick in the depression, and the depression had lower soil CO₂ flux than the ridge (Fig. 7(a); McConnell et al., 2013). Thus, our results are consistent with previous observations that topography affects soil CO₂ flux by affecting the soil hydrological condition; but also emphasized the effects of seasonal frozen soil associated with topography in the permafrost region.

Soil CH₄ uptake and emission were both observed at the depression site, which are similar to the observations of a previous study in northeast China (Sun et al., 2011). However, soil CH₄ uptake at the ridge site was consistent and was significantly greater than that in the depression. Similar results are reported for black spruce stands in interior Alaska (Gulledge and Schimel, 2000; Morishita et al., 2015). They assumption is that topography controls the vertical and lateral redistribution of water in the soil, which affect soil aeration, and that soil CH₄ flux is the result of active methanogenic and methanotrophic bacteria depending on the level of anoxia in soil (Kettunen et al., 1999; Kim, 2015; Sturtevant and Oechel, 2013). We

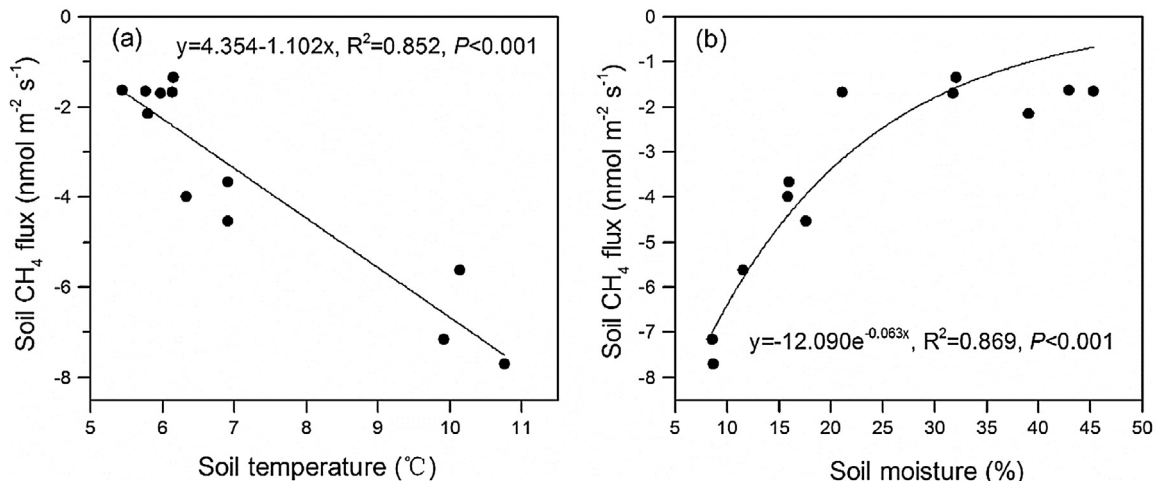


Fig. 9. The relationship between the mean soil CH₄ flux and soil 5 cm temperature (a) or 0–10 cm moisture (b) in boreal forest in Northeast China (n=12).

confirmed that topography determined the patterns of the soil CH₄ fluxes by controlling the redistribution of water in the soil (Fig. 9; Gulledge and Schimel, 2000; Kim, 2015). Additionally, Christiansen and Romero (2015) found that the magnitude of soil CH₄ oxidation and the direction of the flux, i.e., uptake or emission, are linked to the different methanotrophic communities in upland and wetland soils. Thus, topographic position might be the best predictor of CH₄ flux in taiga forest stands (Gulledge and Schimel, 2000).

4.3. Effects of fire on soil CO₂ and CH₄ fluxes under different topographies

Wildfire is a widespread disturbance influencing boreal forest ecosystems that dramatically affects the carbon budget (Balshi et al., 2009; O'Neill et al., 2003; Turetsky et al., 2010;). We found that the 7-year-old burned sites had significantly higher soil CO₂ emissions than the unburned ones (Table 3; Figs. 3 and 8(a)), which is consistent with previous observations in boreal forests (Burke et al., 1997; O'Neill et al., 2003). One possible explanation is that the early successional stage of the burned site was likely favorable to soil carbon decomposition due to greater productivity and higher quality of detritus inputs from invasion of more deciduous species (Gulledge and Schimel, 2000; Wang et al., 2003). Furthermore, fire might lead to increases in soil CO₂ fluxes in different ways depending upon soil drainage related to topography. At the "well-drained" ridge site, fire substantially increased soil temperatures, which were a crucial factor driving the increase in soil CO₂ emissions (Fig. 7; Burke et al., 1997; Morishita et al., 2015). However, in the poorly drained depression site, the increase in thickness of the active layer might be the primary factor controlling the increase in soil CO₂ fluxes after fire because of the decomposition of old organic carbon that was originally locked in the permafrost (Dorrepaal et al., 2009). In addition to thawing of the permafrost, the increase in soil moisture after fire was important to the change of soil carbon flux in the depression (Fig. 1). Similar results were observed in Alaskan lowland forests in which up to 50 cm of thaw settlement occurred after fire, which led to a further increase in moisture in the active layer (Brown et al., 2015). The deeper active layer and adequate moisture conditions in the burned depression site might increase decomposition rates and plant NPP and root biomass, which would further increase soil CO₂ fluxes (Yi et al., 2010). However, in the spring, the fire effects on soil CO₂ fluxes were not significant. The lower root respiration in spring might explain the absence of significant fire effects on soil respiration, because root respiration contributes more to soil respiration at the burned sites than at the controls (Tan et al., 2012).

Soil CH₄ fluxes are controlled by both CH₄ oxidation and production processes that depend on the degree of anoxia in the soil profile (Kettunen et al., 1999; Sturtevant and Oechel, 2013). Fire is widely reported to increase soil CH₄ uptake in boreal forests (Burke et al., 1997; Kim and Tanaka, 2002; Morishita et al., 2015; Takakai et al., 2008), which is consistent with our results (Figs. 6 and 8(b); Table 3). Soil CH₄ uptake increases after fire at well-drained ridge sites because of increases in methanotroph activity under the higher soil temperature and lower soil moisture conditions (Kim and Tanaka, 2002; Morishita et al., 2015; Takakai et al., 2008), which is a scenario supported by the relationships between soil CH₄ flux and soil 5 cm temperatures or 0–10 cm moisture in this study (Fig. 9). However, in the poorly drained depression sites, the burned depression site with higher soil moisture did not have higher CH₄ emissions than the unburned site. This result might be related to permafrost thawing after fire, which was associated with a lower water table position (Table 1) that could lead to an increased zone of methanotrophy for CH₄ oxidation and consequently, a decrease in CH₄ emissions (Lawrence et al., 2015; Turetsky et al., 2008). The interaction between fire and permafrost was emphasized by this

result, which has strong but unknown effects on the carbon balance in the permafrost regions (Abbott et al., 2016; Brown et al., 2015).

4.4. Effects of topography and fire on Q₁₀

In the present study, soil temperature at 5 cm explained 62.2–78.7% (R²) of the variability in soil CO₂ fluxes (Fig. 4), and the temperature sensitivity of the soil CO₂ flux (Q₁₀) ranged from 2.02 to 4.25, which are realistic values for a boreal forest (1.9 for alder, 2.8 for birch/aspen, 2.5–4.2 for black spruce, 3.4–12 for white spruce; Gulledge and Schimel, 2000; Kim and Tanaka, 2002).

The results on the ridge in this study are consistent with reports that Q₁₀ values are reduced after fire (O'Neill et al., 2002; Takakai et al., 2008). The significant increase in temperature at the burned ridge site might explain the decrease in Q₁₀, because the Q₁₀ decreases with increasing temperature in the temperature range of 10–20 °C (Kirschbaum, 1995). By contrast, the Q₁₀ increased after fire in the depression (Fig. 4), which might be related to the increased water content of the soil active layer, because the Q₁₀ is always higher under more adequate soil moisture conditions (Kim, 2015; Kim and Tanaka, 2002; Riveros-Iregui et al., 2007). Therefore, the increase in Q₁₀ at the burned depression site might be because of the confounding effects of adequate water on Q₁₀. The effect of moisture on Q₁₀ is clearly demonstrated by Kim (2015) who found Q₁₀ values were 2.10 under dry conditions, 2.06 in the control, but drastically increased to 107 under wet conditions. Additionally, the permafrost might interact with other environmental parameters to influence the temperature sensitivity of soil CO₂ flux in the depression (Allison et al., 2010). Thus, our results suggested that topography will regulate the effects of fire on the feedbacks of soil CO₂ flux to climate change, and emphasize that the depressions will likely have a stronger feedback response to climate warming than ridges after fire with the degradation of permafrost.

5. Conclusions

In this field study, the strong spatial and temporal variations of soil carbon fluxes in a boreal forest underlain by permafrost are highlighted. Fire significantly increased soil CO₂ emission and CH₄ uptake both in the depression and on the ridge. However, the factors driving soil CO₂ and CH₄ fluxes and the extent of the response to fire varied by topography. Furthermore, topography primarily controlled the patterns of soil CO₂ and CH₄ fluxes with higher soil CO₂ emissions and CH₄ uptakes on the ridge than in the depression, whether burned or not. Although the depression site released less soil carbon to the atmosphere, the increase in temperature sensitivity of soil CO₂ flux after fire indicated stronger positive feedbacks to climate warming in the depressions than on the ridges, which would be based on the permafrost degradation. Additionally, the degraded permafrost in depression might change plant succession and further alter the carbon budget. Therefore, topography features must be explicitly included in the predictions of the responses of soil carbon fluxes to fire at the scale of assessment, particularly in boreal forests, which have greater topography-derived differences in soil carbon effluxes than in other ecosystems. Additionally, the depressions underlain by permafrost should be a focus of attention because of likely stronger feedbacks to climate change after fire.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecoleng.2017.05.033>.

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