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RESEARCH PAPER

Changes in the non-growing season soil heterotrophic respiration rate are driven by environmental factors after fire in a cold temperate forest ecosystem

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Abstract

• ***Key message*** During the non-growing season, environmental factors changed after fire, leading to significantly increased non-growing season soil heterotrophic respiration (R_h) and potentially decreasing the amount of net C stored in cold temperate forest ecosystems of China.

• ***Context*** Intensifying forest fire regimes are likely to influence future C budgets of forest ecosystems. However, the mechanism of fire disturbance on the components of non-growing season soil respiration rate (R_s) and its environmental factors are not fully understood, creating uncertainties for future C sink estimates under climate change scenarios.

• ***Aims*** This study examined the effects of recent fire on non-growing season (November 2017 to April 2018) R_s, its heterotrophic (R_h) and autotrophic (R_a) components, and Q_{10} in a cold temperate forest in northeast China.

• ***Methods*** Soil CO_2 effluxes (including R_h and R_a) were measured using an Li-8100 portable automatic measuring system for soil C flux (Li-Cor, Inc.; Lincoln, NE, USA). Soil temperature and moisture were measured using a temperature probe (Licor p/n8100–201) and soil volumetric water content probe (ECH20 167 EC-5; p/n 8,100,202), respectively, at a depth of 5 cm; snowpack depth was measured with a ruler.

• ***Results*** During the non-growing season, fire significantly increased the R_h by approximately 47% in burned stands. The Q_{10} of R_h significantly increased from 2.39 in the unburned stands to 3.12 in the burned stands. An interaction between soil temperature and snowpack depth was the driving environmental factor controlling the non-growing season soil respiration and its components after fire disturbance.

• ***Conclusion*** Fire is a potent factor on the components of the soil respiration and should not be ignored in forest ecosystem C cycling, especially during the non-growing season as it is vulnerable to micro-environmental variation. Long-term studies involving diverse ecosystems are required to better elucidate mechanisms that have been found during the non-growing season R_s under an increasing trend of fire occurrence.

Keywords Fire disturbance · Soil respiration · Soil temperature · Snowpack depth · Forest

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Contribution of the co-authors Long Sun: Conceptualization, Methodology. **Tongxin Hu**: Data curation, Writing – original draft, Software. **Xu Dou**: Visualization, Investigation. **Fei Li**: Software, Validation. **Haiqing Hu**: Supervision, Writing – review & editing.

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1 Introduction

Forest ecosystems are predominantly sinks for atmospheric CO_2 (Gower et al. 2001; Trumbore et al. 2015). However, disturbances caused by climatic extremes and human activities (e.g., wildfire, storm, drought, prescribed burning, nitrogen addition, and land use management) can significantly and rapidly affect the C cycle of forest ecosystems and its feedback to the atmospheric system (Fang et al. 2018; Frank et al. 2015; Hu et al. 2017b; Plaza-Álvarez et al. 2017; Sheng et al. 2009). In recent years, extreme climate events, such as intensified El Niño and drought, which are associated with climate warming, have meant that the frequency, severity, and burn area of wildfires are expected to increase in the near future (Abatzoglou and Williams 2016; Santin et al. 2016; Seidl et al. 2017). Quantifying the effect of forest fire disturbance on the C dynamics of forest ecosystems is a key component for lowering the uncertainties associated with C sink estimates (Kasischke and Stocks 2000; Liu et al. 2014; Schimel and Baker 2002).

Soil respiration (R_s) is the sum of soil autotrophic respiration (R_a) (from root systems and root-associated microorganisms) and soil heterotrophic respiration (R_h) (from the decomposition of organic material by free-living microbes) (Chen et al. 2016b; Davidson and Janssens 2006; Luo and Zhou 2006). Soil respiration is the second largest C efflux (80–98 Pg C·yr^{-1}) in terrestrial ecosystems and the global R_h from soils has been estimated at 53–57 Pg C·yr^{-1} (Bond-Lamberty and Thomson 2010). A recent study observed that the soil surface R_h:R_s ratio significantly increased from 0.54 to 0.63 between 1990 and 2014 due to environmental change (Bond-Lamberty et al. 2018). Functionally, disturbance (e.g., wildfires) can have significant effects on soil respiration components such as R_h and while the control of soil respiration components by some environmental factors has been identified, how each environmental factor interacts with disturbance remains an open question (Harmon et al. 2011).

Many studies have focused on forest soil respiration during the growing season (Chen et al. 2016a; Decina et al. 2016; Pries et al. 2016; Zhou et al. 2016) and have estimated the annual soil respiration by assuming that the respiration efflux is near zero during the non-growing season (Fahnestock et al. 1998). However, other studies have shown that the non-growing season soil respiration could account for 2–37% of annual soil respiration and that it significantly affects the C balance of forest ecosystems (Brooks et al. 2005; Wang et al. 2006; Wang et al. 2013; Wang et al. 2014b). Forest fire disturbance can alter both the input and output of organic C stored in the soil. Thus, a remaining challenge is to understand the variation and dominating environmental factors of the non-growing season R_s and its components (R_h and R_a) after fire disturbance (Song et al. 2018). In particular, the response of R_h to forest fire might be the key factor influencing the amount of net C stored in forest ecosystems.

The degree of influence of fire on the soil C pool depends on fire severity and duration (Marañón-Jiménez et al. 2011). Soil respiration and its components are potentially controlled by the variation of soil environmental factors after fire disturbance (Pereira et al. 2016). For instance, forest fires can affect soil respiration by decreasing vegetation cover and increasing albedo, which can increase soil temperatures and litter decomposition rates (Jiang et al. 2015; Throop et al. 2017). Additionally, fire can increase soil hydrophobicity, which may indirectly control the components of soil respiration by reducing soil moisture infiltration and increasing surface runoff (O'Donnell et al. 2009). Previous studies have indicated that soil temperature and moisture are the dominant environmental factors of soil respiration variation during the growing season (Raich and Schlesinger 1992; Yi et al. 2020).

The northern hemisphere has a greater area of winter snow compared to the southern hemisphere, and snow in the north is much more vulnerable to climate change (Cohen and Entekhabi 1999; Danco et al. 2016). Snow creates an insulating layer that might increase soil temperature, and soil temperature and moisture changes after disturbance have a strong effect on the snow-cover depth (Groisman et al. 1994; Uchida et al. 2005). The interaction effect between environmental factors can change biological and chemical processes such as microbial decomposition, enzyme and rhizosphere organism activity (Monson et al. 2006; Tucker et al. 2014). However, few studies have focused on the effect of environmental factors on the components of the soil respiration during the non-growing season, leading to great uncertainty about the variation in soil respiration during the non-growing season (Barba et al. 2018; Hibbard et al. 2005; Rustad et al. 2001).

In the present study, we used a *Quercus mongolica* forest immediately after fire disturbance. The objectives of the study were to determine how wildfires affect the non-growing season components of soil respiration and to determine the dominating environmental factors that drive variation in soil respiration after fire disturbance. We postulated that the components of soil respiration are potentially controlled by interactions among soil environmental factors such as soil temperature, soil moisture and snow depth that are altered by a fire event. In a previous study, a forest fire was found to significantly decrease R_a (Hu et al. 2017b); thus, we hypothesized that the non-growing season total R_s was dominated by soil R_h after fire disturbance. As snowpack is an important environmental factor during the non-growing season and is vulnerable to temperature change, we further postulated that snowpack depth may be related to fire disturbance and that it will influence the components of the non-growing season soil respiration (R_h and R_a).

2 Materials and methods

2.1 Study area

The present study was conducted at the Maoershan Forest Ecosystem Research Station, northeast China (45°20′–45°25′ N, 27°30′–127°34′ E, 400 m above sea level). The parent material is granite bedrock, and the soil is classified as a Haplumbrepts in the United States Soil Taxonomy (Soil Survey Staff 2014). The climate is continental monsoon with a dry and cold winter. The annual total precipitation varies from 600 mm to 800 mm, of which ~50% falls between June and August (summer dominated). The mean annual, maximum, and minimum air temperatures are 2.7 °C, 18.0 °C, and −12.1 °C, respectively. During the sampling years (2017–2018), the maximum and minimum air temperatures were 32.5 °C and −31.2 °C, respectively. Snowpack lasted for 154 days, with the snowpack depth varying from 0 to 31.2 cm, with a mean depth of 14.1 cm. The dominate tree species of our research stand is *Q. mongolica* (> 80% total basal area) and mixed with naturally regenerated tree species that include *Betula platyphylla* and *Populus davidiana*. The dominant herb species during the study period were *Anisodus acutangulus*, *Adenocaulon himalaicum*, *Dryopteris crassirhizoma*, and *Aegopodium alpestre*.

2.2 Site description

In the present study, the non-growing season experimental period was from mid-November 2017 to mid-April 2018 and was approximately 150 days. The definition of the non-growing season follows that of previous phenological studies (Piao et al. 2007; Xu et al. 2017), meta-analysis of the winter ecosystem (Wang et al. 2011) and C flux research of temperate Korean Pine (*Pinus koraiensis* Sieb. et Zucc.) in the Maoershan area (Wang et al. 2013). The first span of at least 5 days with daily mean air temperatures below 5 °C was defined as the start of the non-growing season. Similarly, the first span of 5 days with daily mean air temperatures above 5 °C was defined as the end of the non-growing season. The freeze-thaw cycle (FTC) period in spring was defined as 5 cm of soil above 0 °C (i.e., the start of the snowmelt), to the end of the non-growing season (i.e., the snow completely melted). The non-growing season included the snow-cover winter period and the FTC period (Table 1).

In April 2016, forest fires caused by lightning occurred at Maoershan Forest Ecosystem Research Station, northeast China. The total area burned was approximately 500 ha and provided an opportunity for us to study the effects of fire disturbance on soil respiration and its components. The burn severity was moderate in the burned area; severity was determined by the depth of the burned organic soil, the consumption of the aboveground biomass, tree mortality, and the bark char height (Keeley 2009). In the burned area, approximately 50% of the understory shrubs were burned, the bark char height was 1.8–2.4 m and tree mortality was approximately 36%. We selected three replicate stands in the burned area to conduct our investigation and selected nearby unburned areas as the control stands. The size of each stand was 400 m^2 (20 m × 20 m) and all stands were established in April 2017. The specific information of the stands and soil characteristic is shown in Table 2. The leaves of *Q. mongolica* were persistent; a large number of leaves did not fall off the trees and instead existed in the canopy even in the non-growing season, which led to the difference in canopy coverage between the control and the burned stands in the non-growing season.

3 Soil CO_2 efflux and its environmental factors

Soil CO_2 effluxes (including R_h and R_a) were measured using an Li-8100 portable automatic measuring system for soil C flux (Li-Cor, Inc.; Lincoln, NE, USA). Five polyvinylchloride (PVC) soil rings (internal diameter 19 cm and height 7 cm) for measuring R_s were randomly placed in each stand. A trenching approach was used to separate R_h and R_a. Three trenched plots in each stand were dug down to either bedrock or to a maximum depth of 80 cm, each encompassing an area of 1.5 m × 1.5 m. All roots within the trenches were severed and plastic lining was installed to inhibit root and mycorrhizal in-growth, and ground vegetation was absent (Liu et al. 2016; Zeng et al. 2016). All PVC rings remained in the same position throughout the study period. Soil CO_2 effluxes measured from trenched plots were assumed to be R_h. R_a was calculated as the difference between the mean values of R_s and R_h in each stand. All trenched plots were established in May 2016, approximately 12 months before the measurement of soil respiration and its components, to ensure that the disturbance caused by trenching on soil respiration and its components had subsided. The soil CO_2 efflux measurement method in the corresponding unburned control stands was the same as

Table 1 Timing of the non-growing season, winter period, and spring freeze-thaw cycle (FTC) period

	Duration	Days
Non-growing season	Mid-November 2017 to mid-April 2018	150
Winter period	Mid-November 2017 to mid-March 2018	120
FTC period	Mid-March 2018 to mid-April 2018	30

Table 2 Basic information of research stands. Values are the means (±standard deviation) of three replicates with repeat measurements ($n = 3$)

Stand type	Stand number	DBH (cm)	Height (m)	Canopy cover (%)	OML (cm)	Bulk density (g cm^{-3})	TC (g kg^{-1})	TN (g kg^{-1})	pH	$N\text{-}NH_4^+$ mg/kg	$N\text{-}NO_3^-$ mg/kg	AP mg/kg	AK mg/kg
Burned stand	Stand 1	14.58 ± 0.55	14.68 ± 0.58	74 ± 1	5.55 ± 0.13	0.66 ± 0.03	122.68 ± 8.76	6.94 ± 1.19	4.68 ± 0.11	23.54 ± 2.18	7.98 ± 0.55	43.72 ± 3.57	20.99 ± 2.41
	Stand 2	10.49 ± 0.64	9.28 ± 0.93	72 ± 1	6.74 ± 0.02	0.57 ± 0.03	135.14 ± 8.08	6.11 ± 0.46	4.20 ± 0.19	20.78 ± 1.48	10.74 ± 0.51	36.78 ± 3.17	13.18 ± 2.97
	Stand 3	13.82 ± 0.93	11.53 ± 0.63	74 ± 1	6.32 ± 0.42	0.51 ± 0.01	140.62 ± 6.66	6.75 ± 0.30	4.66 ± 0.02	21.53 ± 1.13	4.80 ± 1.29	30.83 ± 2.61	14.15 ± 1.77
Control stand	Stand 1	13.17 ± 0.76	11.02 ± 0.12	93 ± 1	11.56 ± 1.02	0.84 ± 0.04	119.74 ± 7.89	5.05 ± 0.34	4.55 ± 0.16	14.46 ± 2.87	8.31 ± 0.47	24.8 ± 2.62	16.68 ± 2.71
	Stand 2	16.98 ± 0.42	14.84 ± 0.23	88 ± 3	10.55 ± 0.65	0.80 ± 0.01	124.34 ± 5.88	5.98 ± 0.63	3.83 ± 0.10	12.34 ± 2.70	6.22 ± 0.85	38.88 ± 3.53	13.48 ± 1.69
	Stand 3	11.45 ± 0.63	10.65 ± 0.48	90 ± 2	9.58 ± 0.45	0.83 ± 0.03	105.66 ± 4.48	3.94 ± 1.27	4.62 ± 0.01	13.38 ± 1.28	8.35 ± 0.53	37.67 ± 1.96	11.17 ± 1.70

DBH, diameter at breast height; OML, depth of the organic material layer; TC, total carbon; TN, total nitrogen; AP, available phosphorus; AK, available potassium that for the burned stands. Soil CO_2 effluxes were measured monthly from November to April in 2017–2018. The measurement time lasted approximately two minutes for each soil respiration ring. Each measurement was conducted from 9:00 am to 11:00 am for a total of 48 (30 non-trenched soil rings for R_s + 18 trenched soil rings for R_h) measurements over 2 days.

Soil temperature and moisture were measured using a temperature probe (Licor p/n8100–201) and soil volumetric water content probe (ECH20 EC-5; p/n 8,100,202), respectively, at a depth of 5 cm; snowpack depth was measured with a ruler. The measurement of soil temperature, moisture, and snowpack depth was synchronized with the measurement of soil CO_2 effluxes (Hu and Sun 2021).

3.1 Models of soil respiration and its components

An exponential model and the temperature sensitivity of soil respiration (Q_{10}) were used to describe the relationship between soil respiration and soil temperature, which was determined by fitting the exponential function (see Eq. (1) and Eq. (2) below) for burned and unburned control stands (Lloyd and Taylor 1994):

$$SR = \alpha e^{\beta T} \tag{1}$$

$$Q_{10} = e^{10\beta} \tag{2}$$

where SR is the measured total soil respiration and its components (R_h and R_a), T is the soil temperature (°C) at 5 cm, α and β are regression coefficients, e is the nature constant, and Q_{10} is the factor by which soil respiration and its components increase during a temperature increase of 10 °C.

To describe the relationship among soil respiration and soil moisture and the depth of the snowpack, linear, exponential, and quadratic functions were tested for using the data from burned and unburned control stands (Eqs. 3–8); we selected the best fitted model based on higher R^2 results (Davidson et al. 1998; Lai et al. 2012):

$$\mathrm{SR} = \alpha + \beta \mathrm{W} \tag{3}$$

$$\mathrm{SR} = \alpha e^{\beta \mathrm{W}} \tag{4}$$

$$\mathrm{SR} = \alpha + \beta \mathrm{W} + \omega \mathrm{W}^2 \tag{5}$$

$$\mathrm{SR} = \alpha + \beta \mathrm{S} \tag{6}$$

$$\mathrm{SR} = \alpha e^{\beta \mathrm{S}} \tag{7}$$

$$\mathrm{SR} = \alpha + \beta \mathrm{S} + \omega \mathrm{S}^2 \tag{8}$$

where SR is the measured total soil respiration and its components (R_h and R_a); W is the soil moisture (%) at 5 cm; S is snowpack depth (cm); and α, β, and ω are the constant values of the regression model coefficients.

3.2 Statistical analysis

Data were processed and analyzed using R statistical software version 3.5.2 (R Core Team 2018), using R packages "car" (Fox 2012), "agricolae" (Mendiburu 2017), and "lavann" (Rosseel 2012). Differences in variables between the burned and control stands were tested by analysis of variance (ANOVA) and comparisons between means were performed using the least-significant differences test. Repeated-measures ANOVA was used to determine the direct and interactive effect of fire disturbance and measurement date on soil respiration components (R_s, R_h, and R_a), soil temperature, soil moisture, and snowpack depth. Linear, exponential, and quadratic function models were used to evaluate the relationship among the soil respiration components (R_s, R_h, and R_a) and environmental factors (soil temperature, soil moisture, and snowpack depth). Structural equation modeling (SEM) was used to determine how environmental factors affected soil respiration. A conceptual meta-model was developed, including direct and indirect pathways between theoretical drivers of the components of soil respiration. Only the environmental factors that had a significant correlation with the components of soil respiration were included in the meta-model. Parameters were linked to the model either directly or as a composite variable. Non-significant P-values ($P > 0.05$) of the chi-square test in SEM suggest a good fit between the model and data. Differences were considered statistically significant at P-values < 0.05.

4 Results

4.1 The effect of fire disturbance on soil environmental factors

The average soil temperature of the non-trenched control and burned stands was −2.73 ± 1.68 °C and −0.91 ± 1.38 °C, respectively. The soil temperature of the trenched control and burned stands was −1.98 ± 2.56 °C and −0.22 ± 1.04 °C, respectively (Fig. 1a and b). The soil temperature of the non-trenched control and burned stands showed a similar variation over time, decreasing at the beginning of the non-growing season and remaining at its minimum value from December 2017 to January 2018, after which there was an increasing trend to the end of the non-growing season, reaching the maximum value from March to April 2018.

The average soil moisture of the non-trenched control and burned stands was 50.14 ± 15% and 34.98 ± 4.81%, respectively. The average soil moisture of the trenched control and burned stands was 56.10 ± 6.64% and 32.74 ± 9.87%, respectively (Fig. 1c and d). The average snowpack depth at the non-trenched control and burned stands was 14.07 ± 3.05 cm and 10.45 ± 3.30 cm, respectively. The average depth of snowpack at the trenched control and burned stands was 13.58 ± 6.64 cm and 10.74 ± 2.66 cm, respectively (Fig. 1e and f). No significant differences in soil temperature, soil moisture, or snowpack depth were detected between the trenched and non-trenched plots at the different areas (Table 3). Soil temperature was significantly higher at the fire disturbed stands than at the control stands, whereas the soil moisture and average snowpack depth were significantly lower in the fire disturbed area than in the control stands (Table 3). The measurement date had a significant effect on the soil temperature and snowpack depth; however, it did not have a significant effect on soil moisture. Therefore, soil moisture did not show a significant dynamic variation trend similar to that of soil temperature and snowpack depth during the non-growing season (Table 3).

Table 3 Results (F-values) of repeated-measures analysis of variance on the effects of fire disturbance (F), measurement date (D), trench effect (TE), and their interaction on soil temperature (T, °C), soil moisture (W, %), and snowpack depth (S, cm)

	T	W	S
F	9.975**	45.702***	22.008***
D	80.635***	0.484	85.575***
TE	1.614	0.426	0.095
F×D	0.841	0.818	2.512*
F×TE	0.002	2.066	0.921
D×TE	0.723	0.838	0.211
F×D×TE	0.587	0.415	0.01

*, **, and *** represent significance at $P < 0.05$, 0.01, and 0.001, respectively

4.2 Effect of fire disturbance on soil respiration and its components

R_s, R_h, and R_a all showed significant variation during the sampling period (Fig. 2). The R_s trend followed that of the soil temperature in that there was an increasing trend during the non-growing season (Fig. 2a). The mean values of R_s in the control and burned stands was 0.59 ± 0.19 μmol CO$_2$ m^{-2} s^{-1} and 0.72 ± 0.15 μmol CO$_2$ m^{-2} s^{-1}, respectively. The average R_s was not observably significantly different between the two treatments ($P > 0.05$; Table 4).

The dynamic patterns of R_h were similar to those of R_s and showed a similar trend to that of soil temperature (Fig. 2a and b), whereas the dynamic pattern of R_a followed that of snowpack depth, which showed a single peak and maximum values in February (Fig. 2c). The mean non-growing season R_h in the control and burned stands was 0.32 ± 0.14 μmol CO$_2$ m^{-2} s^{-1} and 0.47 ± 0.15 μmol

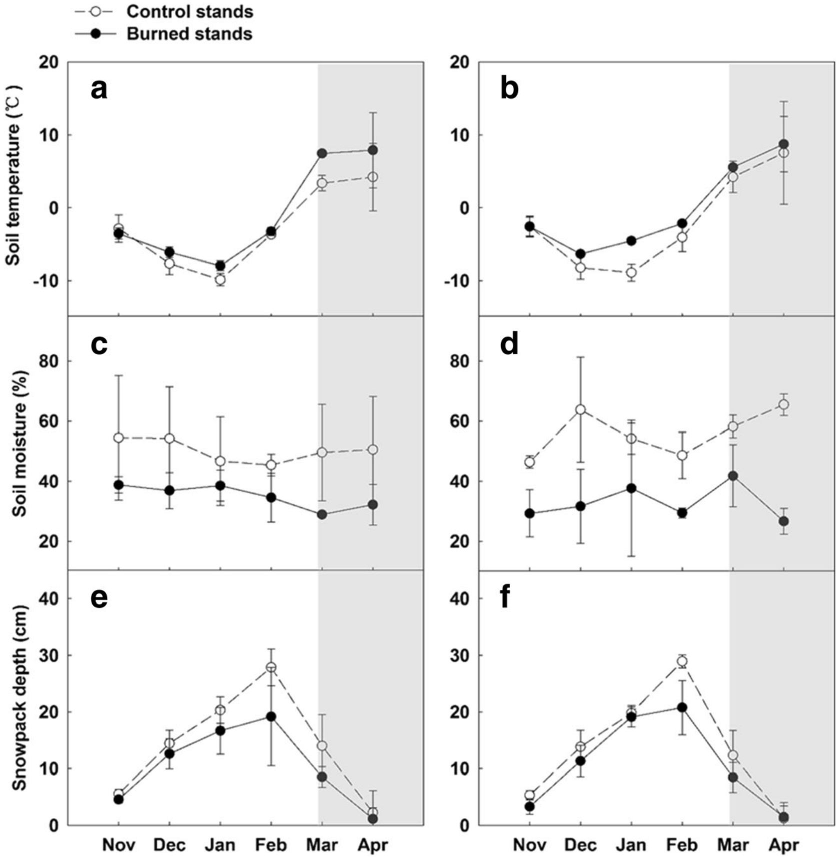

Fig. 1 Non-growing season soil temperature, soil moisture at a depth of 5 cm, and depth of snowpack measured at non-trenched (**a**, **c**, and **e**) and trenched (**b**, **d**, and **f**) plots in control and burned stands. Error bars represent standard deviations, and the shadowed period indicates the spring freeze-thaw cycle (FTC). Values represent the average of three technical replications and repeated measurements

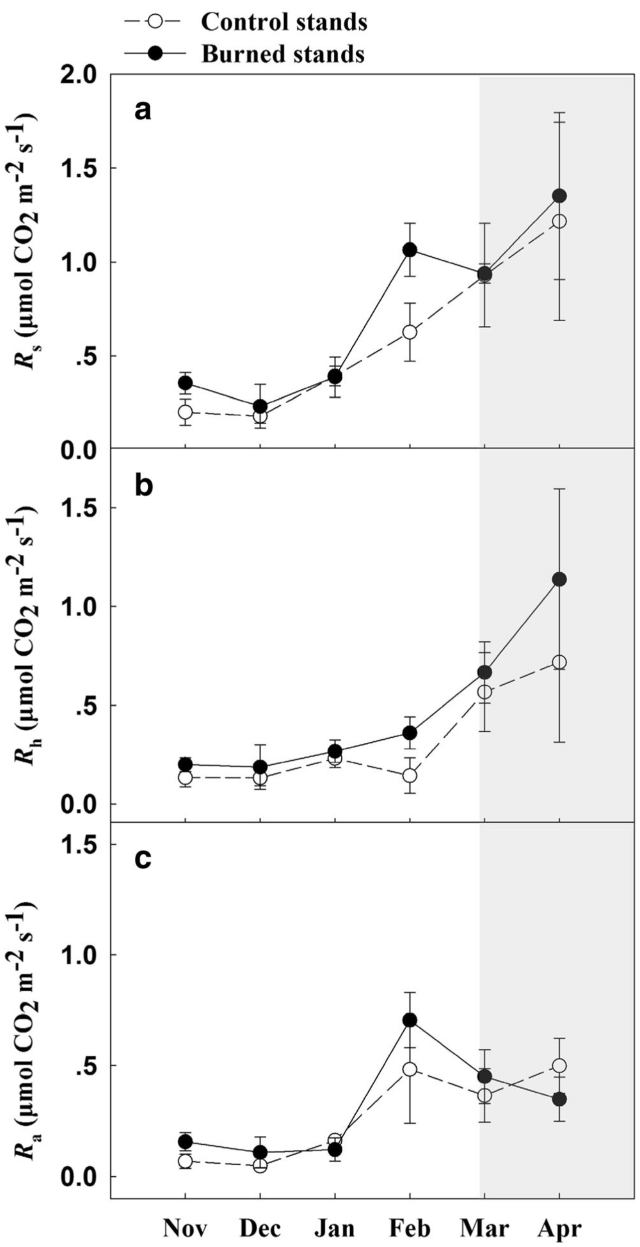

Fig. 2 Dynamic variations of the non-growing season (**a**) total soil respiration rate (R_s), (**b**) soil heterotrophic respiration (R_h), and (**c**) soil autotrophic respiration (R_a) in control and burned stands. The shadowed period indicates the spring freeze-thaw cycle (FTC). Values represent the average of three technical replications and repeated measurements with standard deviations

CO$_2$ m^{-2} s^{-1}, respectively. The average non-growing season R_h in the burned stands was significantly higher than the control stands by approximately 47% ($P < 0.05$) (Table 4). The mean non-growing season R_a in the control and burned stands was 0.27 ± 0.09 μmol CO$_2$ m^{-2} s^{-1} and 0.25 ± 0.07 μmol CO$_2$ m^{-2} s^{-1}, respectively. No significant differences were found between the R_a in the control stands and that in the burned stands ($P > 0.05$) (Table 4). Compared with the control stand, the average R_h:R_s increased from 0.57 ± 0.18 to 0.66 ± 0.19 in the burned stands (Fig. 6 in Appendix). Compared with the entire non-growing season, the FTC period increased R_s, R_h, and R_a 1.8, 1.9, and 1.6 times, respectively, in the control stands. In the burned stands, R_s and R_h increased by 1.6 and 1.9 times, respectively. There was no change between the non-growing season R_a and the FTC R_a in the burned stands (Table 6 in Appendix).

4.3 Relationships among soil respiration components and environmental factors

The exponential regressions with soil temperature as a single controlling factor for R_s, R_h, and R_a were significant ($P < 0.01$) for both control and burned stands. However, only R_h showed a significant quadratic relationship with soil moisture in the control stand (Fig. 3, Tables 5, and 7 in Appendix).

The quadratic function regressions with the snowpack depth as the single explanatory variable of R_s, R_h, and R_a were the best fitted models to describe the relationship among snowpack depth and soil respiration and its components (Fig. 3, Tables 5, and 7 in Appendix). In the control stands, snowpack depth pack showed a significant relationship with R_h and R_a; snowpack depth showed a significant relationship with soil R_s, R_h, and R_a in the burned stands (Fig. 3 and Table 5).

Based on the model fitting results, soil temperature and snowpack depth were introduced in the structural equation model to describe the relationship between R_s and its components (R_h and R_a) and soil environmental factors. All structural equation models fitted well ($P > 0.05$), explaining approximately 86.1%, 84.9%, and 66.6% of the variation for R_s, R_h, and R_a, respectively (Fig. 4).

The structural equation models revealed direct effects of environmental factors on R_s, R_h, and R_a, and also helped explain the interaction effect between soil temperature and the snowpack depth composite. The structural equation models

Table 4 Results (F-values) of repeated-measures analysis of variance of the effects of fire disturbance (F), measurement date (D), and their interaction on soil total respiration (R_s) (μmol CO$_2$ m^{-2} s^{-1}), soil heterotrophic respiration (R_h) (μmol CO$_2$ m^{-2} s^{-1}), and soil autotrophic respiration (R_a) (μmol CO$_2$ m^{-2} s^{-1})

	R_s	R_h	R_a
F	1.081	5.291*	0.01
D	81.156***	43.789***	33.047***
F×D	0.001	1.962	1.264

* and *** represent significance at $P < 0.05$ and 0.001, respectively

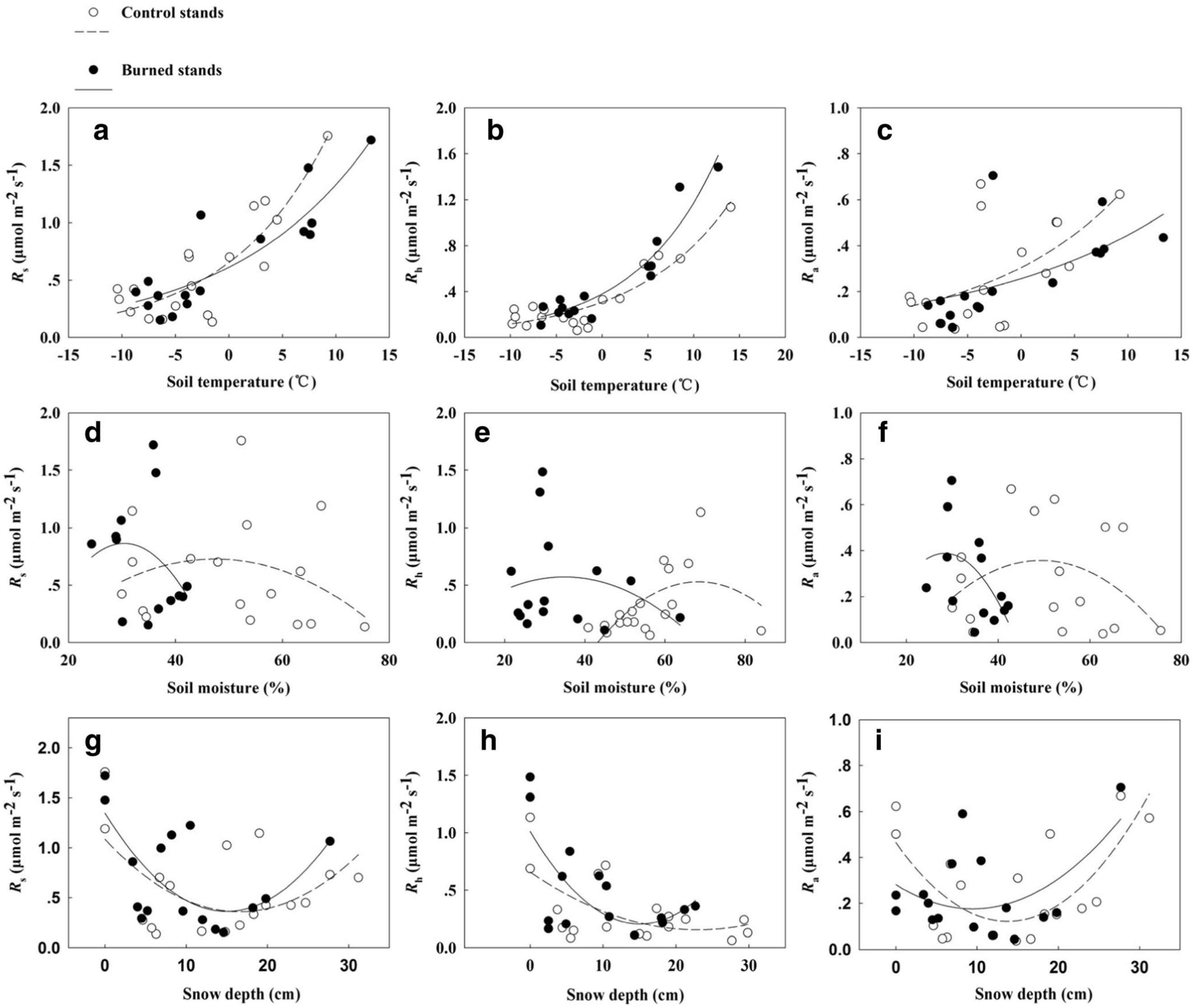

Fig. 3 Relationships between soil total respiration (R_s) and its components (R_h and R_a) and soil temperature (Fig.3a–c), soil moisture (Fig.3d–f), and snowpack depth (Fig.3g–i) in control and burned stands. Equations and statistical parameters are shown in Table 5

revealed that soil temperature directly affected R_s, R_h, and R_a (Fig. 4). Although R_s and its components (R_h and R_a) all showed significant quadratic relationships with snowpack depth, this composite only had a significant direct effect on R_s and R_a (Fig. 4).

4.4 Changes in Q_{10} induced by fire disturbance

Compared with the control stands, the Q_{10} of R_s and R_a was lower by approximately 6.8% and 15% than that in the burned stands, respectively; however, these results were not significant ($P > 0.05$) (Fig. 5 and Table 5). The Q_{10} of R_h in the burned stands was significantly greater by approximately 27.3% than that of the control stands ($P < 0.05$) (Fig. 5 and Table 5).

5 Discussion

5.1 Seasonal variation of the non-growing season soil respiration and its components

In the present study, the mean R_s during the non-growing season in the temperate *Q. mongolica* forest was 0.59 ± 0.19 µmol CO_2 m^{-2} s^{-1}. This result was higher than that of a previous study that found that the non-growing season R_s in a boreal forest ecosystem of China was 0.29 ± 0.06 µmol CO_2 m^{-2} s^{-1} (Hu et al. 2017a). This difference might be due to a lower temperature occurring in the higher latitudes of China. We found synchronous responses to R_s and R_h with a peak in mid-April, whereas R_a tended to follow the dynamics of snowpack depth, which showed a single peak curve with maximum values occurring in February (Fig. 2). In agreement with our hypothesis, R_h

stemming from the microbial decomposition of soil organic matter was the dominant component during the non-growing season R_s. Several studies indicated that R_h dominated R_s during the non-growing season (Gaumont-Guay et al., 2008; Hanson et al., 2000; Jiao and Wang, 2019; Savage et al., 2013; Tucker et al. 2014). At the same time, the non-growing season R_h accounted for a larger proportion of R_s than in the growing season (Ruehr and Buchmann, 2010; Shi et al., 2012; Tang et al., 2005). This may be caused by a difference in how R_h and R_a respond to soil environmental changes (Li et al., 2013; Zou et al., 2018). Our results indicated that R_h was more sensitive to environmental changes than R_a in the non-growing season. Despite the low temperature in the non-growing season, soil microbes were still active and were the dominant biotic controller of the non-growing season R_h due to the regulatory effect of snowpack depth (Yi et al., 2020). Several studies have shown that the duration and depth of snow cover can significantly influence soil temperature and that correspondingly, soil temperature can manipulate snow depth, which could therefore significantly influence R_s and its components (Gavazov et al. 2017; Nobrega and Grogan 2007; Reinmann and Templer 2018; Uchida et al. 2005). Our finding highlights that the interaction coupling effect between soil temperature and snowpack depth must be considered when studying the components of non-growing season R_s (Gao et al. 2018).

5.2 Effects of fire disturbance on non-growing season soil respiration and its components

Our findings show that fire has different effects on non-growing season R_s. Non-growing season R_h was significantly increased by approximately 47% after fire disturbance and R_h:R_s increased from 0.57 to 0.66, whereas the non-growing season R_a showed no change after fire. This result is in agreement with our hypothesis that the non-growing season R_s was dominated by R_h after fire disturbance. The non-growing season R_s increased after fire disturbance; however, this increasing trend was not significant for the non-growing season R_a after fire disturbance. There are several reasons to explain our findings, the first being that fire changes the quality and quantity of detritus, which may promote higher decomposition rates by microbes. Our results agree with the finding from a previous study of increased R_s in a boreal forest of interior Alaska after prescribed burning, which was mainly attributed to higher R_h after fire disturbance (Kim 2013). Fire burned the vegetation and soil organic layer, which increased the availability of nutrients, thus promoting microbial activity and changing the decomposition rate (Song et al. 2017; Wüthrich et al. 2002). Second, post-fire environmental factors control the variation of components of non-growing season R_s after fire disturbance. Forest fires decrease the forest canopy, which will directly increase the soil temperature after fire disturbance (Munozrojas et al. 2016). Owing to the persistent leaves of *Q. mongolica*, canopy cover of the burned stands was lower than that of the control stands in the non-growing season, which directly led to the higher surface solar radiation of non-growing season in the burned stands. In the present study, soil temperature significantly increased by approximately 2 °C after fire disturbance and snowpack depth and organic material layer depth were significantly decreased in the burned stands. Recent studies have shown that non-growing season R_s is almost entirely driven by microbial decomposition, which is a temperature-dependent biological process, and that soil temperatures between −2 °C and 0 °C

Table 5 Parameters of the equations for the relationship of soil respiration and its components (R_s, R_h, R_a) (μmol CO_2 m^{-2} s^{-1}) with soil temperature (T), soil moisture (W), and snowpack depth (S) (cm) for the control and burned stands.

Factor	Control stands				Burned stands			
	Equation	R^2	*P*	Q_{10}	Equation	R^2	*P*	Q_{10}
f(T)								
	R_s=0.512$e^{0.093T}$	0.459	***	2.53 ± 0.58	R_s=0.5623e0.0859 T	0.686	***	2.36 ± 0.55
	R_h=0.2773$e^{0.0873T}$	0.546	***	2.39 ± 0.47	R_h=0.3619e0.1144 T	0.84	***	3.12 ± 0.57
	R_a=0.2365$e^{0.0989T}$	0.311	***	2.69 ± 0.70	R_a=0.2129e0.0827 T	0.549	***	2.29 ± 0.58
f(W)								
	R_s=−0.7126+0.0608 W-0.0006W^2	0.075	NS		R_s=−2.1717+0.1997 W-0.0033W^2	0.102	NS	
	R_h=−3.4022+0.1151 W-0.0008W^2	0.373	*		R_h=−3.4022+3.5239 W-5.0490W^2	0.062	NS	
	R_a=−0.7044+4.3104 W-4.3739W^2	0.124	NS		R_a=−0.8713+0.0889 W-0.0019W^2	0.287	NS	
f(S)								
	R_s=1.0853–0.0879S+0.0027S^2	0.293	NS		R_s=1.3473–0.1315S+0.0044S^2	0.454	*	
	R_h=0.6576–0.0439S+0.0010S^2	0.343	*		R_h=1.011–0.1071S+0.0036S^2	0.442	*	
	R_a=0.4654–0.05S+0.0018S^2	0.51	**		R_a=04088–0.04146S+0.0019S^2	0.386	*	

Statistically significant levels: NS, not significant; *, **, and *** represent significant at $P < 0.05$, 0.01, and 0.001, respectively

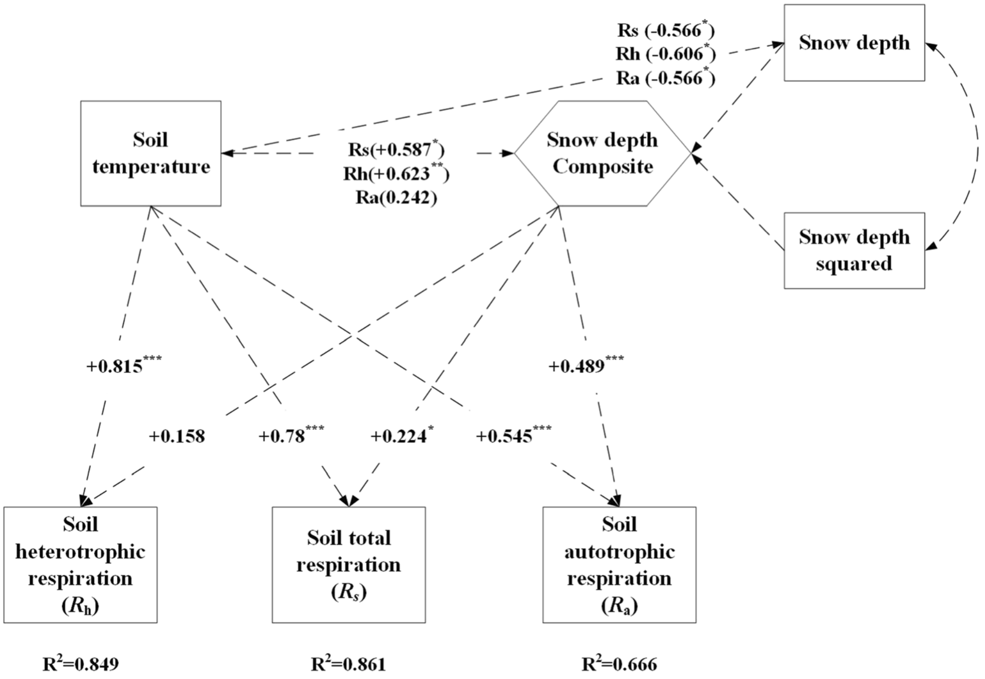

Fig. 4 Structural equation model describing the influence of soil temperature and snowpack depth as drivers of soil total respiration (R_s) and its components (R_h and R_a) after fire disturbance. Solid boxes represent observed variables, while the hexagonal box depicts a composite variable (to account for a polynomial model structure). Single and double headed arrows represent relationships and correlations between variables, respectively; the strength and sign of relationships and correlations are depicted by standardized path coefficient. *, **, and *** represent significance at $P < 0.05$, 0.01, and 0.001, respectively

strongly affect substrate supply and soil microbial activity (Monson et al. 2006; Tucker 2014). We therefore suggest that higher soil temperature and changed substrate supply from burned debris may be driving the increase of non-growing season R_h:R_s after fire.

Fire severity has a strong effect on the components of non-growing season R_s with the effect of fire depending on severity and duration, which may account for the divergence in our R_s response to fire (Czimczik et al. 2006; Meigs et al. 2009; Nave et al. 2011; Richards et al. 2012; Song et al. 2018; Uribe et al. 2013). High severity fires have greater negative effects on ecosystem processes than that of low severity fires (Dooley and Treseder 2012; Martínez-García et al. 2017; Plaza-Álvarez et al. 2017). Previous studies have shown that the non-growing season R_s of Dahurian Larch in the high latitudes of China decreased by approximately 55% in burned stands, which may be attributed to the decrease of R_a after a high severity fire (Hu et al. 2017a). This is because high severity fires result in the understory shrubs, litter, and duff layers being completely burned, causing damage to plant roots (Hu et al. 2017a; O'Donnell et al. 2009). This result is inconsistent with the findings from our study, possibly because the fire in our study was only of medium severity. The rapid recovery of pioneer vegetation after fire promoted the recovery of plant roots, which may be the main reason why there was no significant difference in non-growing season R_a between the control and burned stands (Hart et al. 2005; Johnson and Curtis 2001).

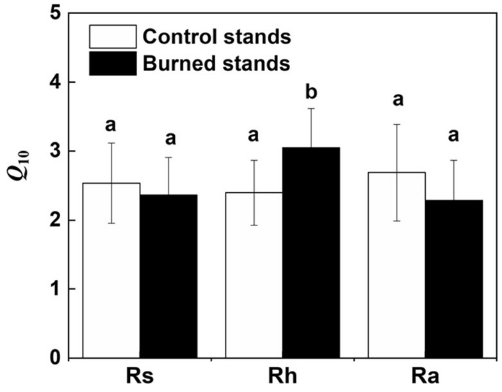

Fig. 5 Temperature sensitivity (Q_{10}) of non-growing season soil total respiration (R_s), soil heterotrophic respiration (R_h), and soil autotrophic respiration (R_a) in control and burned stands. Different letters represent significance at $P < 0.05$. Values presented represent the average of three technical replications and repeated measurements with standard deviations

Recent meta-analyses and long-term experiments have shown that global R_h is increasing, probably in response to environmental changes; therefore, climate-driven losses of soil C are currently occurring across many ecosystems, with a detectable and sustained trend emerging at the global scale (Crowther et al. 2016; Melillo et al. 2017; Wang et al. 2014a; Zhou et al. 2016). Our results indicate that an increase in forest fire frequency might accelerate the process of C loss in said ecosystems within the context of global warming and the intensification of the El Niño effect (Jolly et al. 2015; Yin et al. 2016). Fire disturbance will convert live vegetation into dead material that decomposes, changes ambient soil conditions and temporally decreases the ability of the ecosystem to gain C via plant photosynthesis, which in turn will change the relationship between net primary production (NPP) and net ecosystem production (NEP) (Keeley 2009; Smithwick et al. 2007). Fire could then drive NEP (i.e., NEP = NPP – R_h) to be negative, and the ecosystem to become a source of C to the atmosphere (Harmon et al. 2011). Thus, fire as a potent factor should not be ignored in forest ecosystems, especially during the non-growing season as it is vulnerable to micro-environmental variation.

5.3 Effect of environmental factors on non-growing season soil respiration and its components

Previous studies have reported that the components of soil respiration exponentially increased with temperature increase during both the growing and non-growing seasons (Bondlamberty et al. 2004; Mo et al. 2005; Monson et al. 2006; Yi et al. 2020). Our study showed that wildfire increased the non-growing season R_s. Consistent with our hypothesis and results from previous studies, snow depth as an insulating layer influences the non-growing season (i.e., winter) respiration (Aanderud et al. 2013; Brooks et al. 2011; Wang et al. 2010). Although snowpack depth decreased in the burned stands, it still had a significant quadratic function relationship with R_s and components after fire. Thus, the interaction between soil temperature and snowpack depth was the driving environmental factor controlling the non-growing season soil respiration and its components after fire disturbance.

Previous studies have found that higher soil moisture stimulated soil respiration when the soil water content was below optimum (Rey et al. 2011; Yohannes et al. 2011). Although we did find lower soil moisture in the burned stands, probably due to the higher solar radiation and thinner snow depth, soil moisture did not show a significant correlation with the non-growing season R_s and its components after fire disturbance. This result may be due to the non-growing season soil moisture being abundant (> 30%) in the burned stands. Therefore, the effects of soil moisture on the non-growing season R_s and its components were minor or were counterbalanced by other environmental factors after fire.

In our study, the mean Q_{10} of the non-growing season R_s were 2.53 and 2.36 in the unburned control and burned stands, respectively. The results were higher than the global scale estimate (1.69) (Zhou et al. 2009). In addition, compared with the unburned control stands, the Q_{10} of R_h was significantly greater in the burned stands (2.39 vs. 3.12), whereas there was no significant difference in Q_{10} of R_a between the unburned control stands and burned stands (2.69 vs. 2.29). These results were inconsistent with a previous study in which a high severity fire decreased the growing season Q_{10} of R_s and R_h in a forest of boreal China (Hu et al. 2017b). These contrasting results might be attributed to the high severity fire destroying the plant root structure and a loss of the labile fraction of soil organic C to the atmosphere, which restrained root and rhizosphere respiration and limited soil microorganisms activity (Conant et al. 2011; Thornley and Cannell 2001). R_h was the dominant component of the non-growing season soil respiration efflux. The mean R_h of the FTC period was 1.9 times greater than the non-growing season; R_h accounted for 71% to 84% during this period. The higher temperature and soil nutrients could provide more activation energy based on Arrhenius kinetic theory. Activation energy is one of the dominant abiotic factors that is directly related to the substrate supply (Schipper et al. 2014). More recalcitrant substrates in burned areas, which are complex molecules and have higher activation energy, should have higher temperature sensitivity than those in unburned areas (Davidson and Janssens 2006; O'Neill et al. 2006). Therefore, the higher solar radiation and temperature combined with soil nutrient content in the burned areas could promote the microbial decomposition leading to the higher non-growing season Q_{10} of R_h after fire (Mikan et al. 2002; Pan et al. 2013).

In the present study, we found that fire led to the non-growing season R_h significantly increasing after a fire disturbance. Considering that temperate and boreal forests have been experiencing a significant increasing trend of fire occurrence caused by global warming and cold months have been facing even faster warming than the growing season during the past decades (Hantson et al. 2015; Jolly et al. 2015; Piao et al. 2007; Zhang et al. 2013), our study suggests that forest fires create an increase of non-growing season R_h:R_s, which will potentially decrease the amount of net C stored in forest ecosystems.

6 Conclusion

In summary, the present study explored the effects of recent fire disturbance on the components of non-growing season R_s (R_h and R_a) as well as their Q_{10} in a cold temperate forest in northeast China. Our results revealed that forest fires significantly increased the non-growing season R_h and also drove the R_h:R_s increase that was found in burned stands. The Q_{10} of R_h significantly increased in the burned stands. The interaction between soil temperature and snowpack depth was the driving environmental factor controlling the non-growing season soil respiration and its components after fire. Our study highlights that fire is a potent factor on the components of the soil respiration and should not be ignored in forest ecosystem C cycling, especially during the non-growing season as it is vulnerable to micro-environmental variation. Considering that temperate and boreal forests have been experiencing a significant increasing trend of fire occurrence caused by global warming and that cold months have been facing even faster warming than the growing season during the past decades, long-term studies involving diverse ecosystems are required to better elucidate mechanisms that have been found during the non-growing season R_s under an increasing trend of fire occurrence.

Appendix

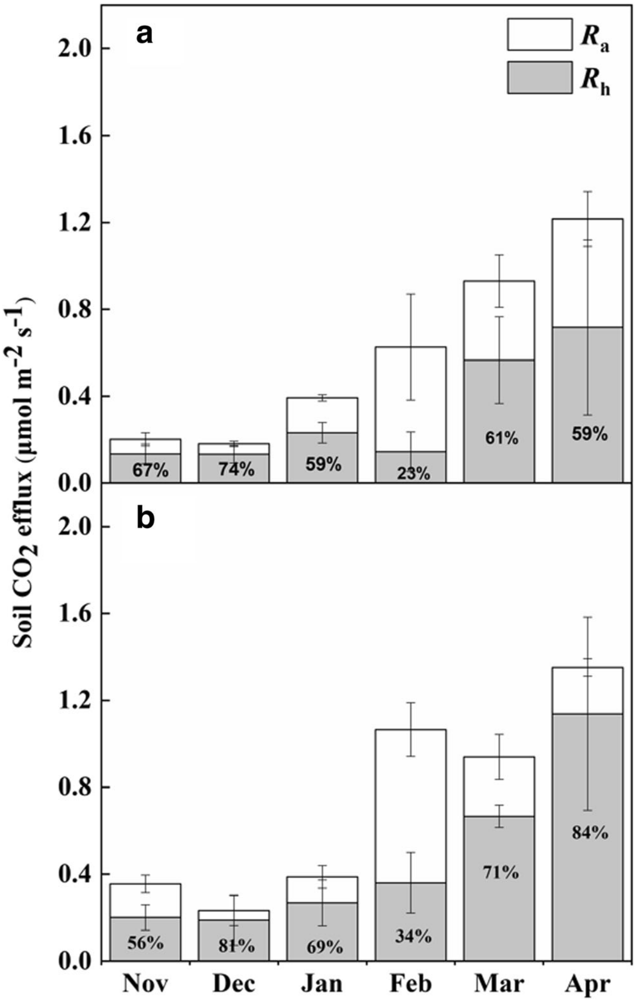

Fig. 6 Variation of the ratio of soil heterotrophic respiration rate (R_h) to soil total respiration (R_s) in the control (**a**) and burned stands (**b**). Values represent the average of three technical replications and repeated measurements with standard deviations

Table 6 Average values of R_s (μmol CO$_2$ m^{-2} s^{-1}), R_h (μmol CO$_2$ m^{-2} s^{-1}), and R_a (μmol CO$_2$ m^{-2} s^{-1}) of the non-growing season and FTC period in the control and burned stands

	Non-growing season		FTC period	
	Control stands	Burned stands	Control stands	Burned stands
R_s	0.59 ± 0.19	0.72 ± 0.15	1.07 ± 0.40	1.15 ± 0.25
R_h	0.32 ± 0.14	0.47 ± 0.15	0.64 ± 0.30	0.91 ± 0.31
R_a	0.27 ± 0.09	0.25 ± 0.07	0.43 ± 0.12	0.24 ± 0.07

Table 7 The parameters of the equations for the relationship of soil respiration and its component (R_s, R_h, R_a) with soil temperature, soil moisture, and snow depth (cm) for control and burned stands.

Factor	Control stands			Burned stands		
	Equation	R^2	*P*	Equation	R^2	*P*
f(W)						
	$R_s=0.5199+0.002\ W$	0	NS	$R_s=1.679–0.0274\ W$	0.092	NS
	$R_s=0.8502+e^{0.9646W}$	0	NS	$R_s=1.446+e^{0.9825W}$	0.085	NS
	$R_s=-0.7126+0.0608\ W\text{-}0.0006W^2$	0.075	NS	$R_s=-2.1717+0.1997\ W\text{-}0.0033W^2$	0.102	NS
	$R_h=-0.3555+0.012\ W$	0.182	NS	$R_h=0.7127–0.0062\ W$	0.031	NS
	$R_h=0.8796+e^{1.0112W}$	0.115	NS	$R_h=1.3615+e^{0.99467W}$	0.037	NS
	$R_h=-3.4022+0.1151\ W\text{-}0.0008W^2$	0.373	*	$R_h=-3.4022+3.5239\ W\text{-}5.049W^2$	0.062	NS
	$R_a=0.3130–0.0001\ W$	0	NS	$R_a=0.9059–0.01895\ W$	0.304	NS
	$R_a=1.6433+e^{0.995W}$	0.115	NS	$R_a=0.7881+e^{0.9711W}$	0.272	NS
	$R_a=-0.7044+4.3104\ W\text{-}4.3739W^2$	0.124	NS	$R_a=-0.8713+0.0889\ W\text{-}0.0019W^2$	0.309	NS
f(S)						
	$R_s=0.7301–0.01S$	0.042	NS	$R_s=0.8474–0.0148S$	0.054	NS
	$R_s=0.6711+e^{0.9831S}$	0	NS	$R_s=0.8179+e^{0.9938S}$	0.022	NS
	$R_s=1.0853–0.0879S+0.0027S^2$	0.293	NS	$R_s=1.3473–0.1315S+0.0044S^2$	0.454	*
	$R_h=0.5307–0.0154S$	0.264	*	$R_h=0.7844–0.0291S$	0.286	*
	$R_h=0.7078+e^{0.9999S}$	0.222	*	$R_h=0.7855+e^{0.8314S}$	0.183	NS
	$R_h=0.6576–0.0439S+0.0010S^2$	0.343	*	$R_h=1.011–0.1071S+0.0036S^2$	0.442	*
	$R_a=0.2226–0.0034S$	0.021	NS	$R_a=0.1725–0.0074S$	0.095	NS
	$R_a=0.4249+e^{1.0079S}$	0.029	NS	$R_a=0.4569+e^{1.00576S}$	0.019	NS
	$R_a=0.4654–0.05S+0.0018S^2$	0.51	**	$R_a=04088–0.04146S+0.0019S^2$	0.386	*

Statistical significant levels: NS, not significant; *, **, and *** represents significant at $P < 0.05$, 0.01, 0.001, respectively

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Data availability The datasets generated and/or analyzed during the current study are available in the Zenodo repository, https://doi.org/10.5281/zenodo.4549901

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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