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Factors controlling soil microbial respiration during the growing season in a mature larch plantation in Northern Japan

Laiye Qu[1,2] · Satoshi Kitaoka[3] · Takayoshi Koike[4]

Abstract

Purpose Soil microbes contribute significantly to soil respiration (SR) in boreal forests; however, there is limited knowledge on microbial contributions from long field investigations. The objective of this study was to estimate soil microbial respiration, as well as its primary controlling factors, for a period of three consecutive years.

Materials and methods A trenching method was used to distinguish soil microbial respiration (R_{Mic}) in a 55-year-old mature Japanese larch (*Larix kaempferi*) plantation in Northern Japan; the soil in which developed originally from volcanic soils containing pumice. We used a portable CO_2 detection system to measure the soil respiration rate during the growing season. Environmental factors, soil physiochemical characteristics, and soil microbial biomass carbon and nitrogen (MBC and MBN) were analyzed to explain the seasonal variations of SR and R_{Mic}.

Results and discussion The results showed that the estimated contribution of soil microbes to SR was 78, 62, and 55% during the three successive years, respectively. Respiration attributable to decomposition of aboveground litter contributed approximately 19% to SR. The major environmental factor that affected R_{Mic} was soil temperature at 5 cm depth, which accounted for more than 70% of the seasonal variation in R_{Mic} observed. There were close relations among MBC, MBN, and soil water content, but the soil water content showed no significant relation with R_{Mic}.

Conclusions The R_{Mic} to SR varied from 78 to 55% following 3 years of trenching treatments. Our results demonstrated the important role of soil microbes on soil respiration in this larch forest. Soil temperature was the major positive factor that influenced R_{Mic}, while soil water content had no significant effect. Global warming will increase the loss of C into the atmosphere by increasing the R_{Mic}, and could accelerate climate change.

Keywords Aboveground litter · Japanese larch forest · Soil microbial biomass · Soil microbial respiration · Soil temperature

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1 Introduction

Crowther et al. (2016) found that considerable losses of soil carbon attributable to the effects of global warming are occurring in high-latitude areas. Boreal forests, including larch species in the Northern hemisphere, constitute a large CO_2 sink (Luo and Zhou 2006). Larch species are a dominant tree that is distributed widely throughout the eastern Eurasian continent (Osawa et al. 2010), and the Japanese larch (*Larix kaempferi*) is one of the most important plantation species in Northern

Japan, Northeast China, Far East Russia, and Korea (Koike et al. 2000; Hirano et al. 2003; Masyagina et al. 2010). Extensive larch forests may be an important component in the global carbon cycle because this species has a high-growth rate and high-specific gravity for timber use. Determination of variations in soil respiration (or soil CO_2 efflux: SR) and its components will provide more detailed information about the way in which environmental factors in larch forests influence soil respiration. Further, in view of the spatial-temporal variations in soil respiration, this information is needed at the local scale from diverse ecosystems and climate zones to construct global carbon budgets models (Raich and Schlesinger 1992; Rayment and Jarvis 2000; Law et al. 2001; Jiang et al. 2005; Tang and Baldocchi 2005; Luo and Zhou 2006).

SR is estimated to represent 60–80% of the total ecosystem respiration in boreal forests (Raich and Potter 1995; Chapin et al. 2002; Luo and Zhou 2006; Kim 2013). In addition, SR is one of the primary pathways of carbon loss from ecosystems to the atmosphere and can influence net ecosystem production of forests strongly. Organisms (plants, microbes, and animals) that live in the soil drive the processes of soil respiration. As we know well, SR is the sum of heterotrophic (microbe) and autotrophic (root) respiration (Liang et al. 2004). The proportion of SR from microbe and root contributions may vary seasonally, and between ecosystems (Hanson et al. 2000). As mentioned above, because larch species are distributed widely in the Northern hemisphere (Osawa et al. 2010), our microbial respiration data for larch forests will contribute further to estimations of carbon cycling.

Soil microbes play a key role in the litter decomposition and nutrient cycling in ecological processes. However, precise estimates of microbial contributions that vary according to site characteristics in deciduous conifer forests and the way in which they are influenced by abiotic and biotic factors in the field are still needed to further our understanding of carbon budgets in forest ecosystems in the Northern hemisphere (Yanagihara et al. 2006; Masyagina et al. 2010).

Three principal methods have been used to estimate each component of soil respiration (Kuzyakov and Larionova 2006; Sapronov and Kuzyakov 2007): integration of components contributing to in situ forest soil efflux (i.e., litter, roots, and soil: e.g., Gansert 1994); comparison of soils with and without root exclusion (Bowden et al. 1993; Hart and Sollins 1998), and use of stable or radioactive isotope methods (Lin et al. 1999). All methods, however, have indicated that microbial respiration (R_{Mic}) contributes from 10 to 90% of the total soil respiration, depending on vegetation type, environment, and season (e.g., Kim 2013). These are due, in part, to methodological differences, such as closed system, flow system, and aerodynamics (Buchmann 2000; Masyagina et al. 2006; Liang et al. 2010), as well as site-to-site variation (Yanagihara et al. 2006; Masyagina et al. 2010). For larch forest stands, some of the main questions regarding soil

heterotrophic respiration involve the fact that R_{Mic} undergoes large temporal variations. Thus, the question is: how do abiotic factors, such as soil temperature, moisture and physical-chemical characteristics, and biotic factors (e.g., soil microbial biomass) influence the heterotrophic respiration rate during the growing season of larch forest in the field?

Therefore, based on these previous studies, we thus investigated the dynamic variations of R_{Mic} in a mature Japanese larch plantation. Our objectives were to (1) determine the seasonal variation of soil heterotrophic respiration during the growing season for 3 years after applying the trenching method, (2) estimate the relative contributions of soil microbes to the total soil respiration, and (3) determine the factors that control R_{Mic}.

2 Materials and methods

2.1 Site description

We carried out our study in a Japanese larch plantation approximately 55 years old (as of 2005) in the Tomakomai National Forest (42° 44′ N, 141° 31′ E), Hokkaido, Japan (Hirano et al. 2003), in which the altitude ranges from 115 to 140 m a.s.l. Japanese larch (Larix kaempferi) is the dominant species and is interspersed with Ezo-spruce (Picea jezoensis) and broad-leaved species (birch, oak, magnolia, etc.; Liang et al. 2004, 2010). In 1999, the overstory density was 1000 stems ha^{-1}, the total basal area was 23.5 m^2 ha^{-1}, and the aboveground biomass averaged 145 m^3 ha^{-1}. In 2000, the average tree height was approximately 19.0 m. The forest canopy had a mean depth of 8.9 m, and a leaf area index (LAI; square meter projected leaf area per square meter ground area) of approximately 2.0. The forest was covered predominantly by buckler fern (Dryopteris crassirhizoma), with occasional bracken (Dryopteris expansa) and Japanese spurge (Pachysandra terminalis); it also was composed, in part of oak seedlings (Quercus mongolica var. crispula), Magnolia (Magnolia hyporeuca), carpinus (Carpinus cordata), and a dwarf type of bamboo (Sasa senanensis; Yanagihara et al. 2006). In autumn of 2004, after experiments, severe typhoon damage destroyed the study site.

The site was characterized by a humid continental climate, with cold winters and cool summers, but no predominantly wet or dry seasons. The topography of the site was essentially flat, with gentle slopes of not more than 1–2°. The soil at the site is classified according to the WRB system as "Tephric Regosols" that originated from volcanic ash soil from the eruption of Mt. Tarumae (1667 and 1739 BC). Its humus contained granule litter of woody plants and the dwarf Sasa bamboo: its thickness of O1 (L)/O2 (F) was 1~3 cm and also was characterized by a very thin H layer.

The soil pH was approximately 5.0 as detected by a pH sensor (Horiba, Tokyo, Japan), and was poor in nutrients. Total carbon and nitrogen were 48 ± 2% and 1.2 ± 0.2%, respectively, as determined by a nitrogen and carbon analyzer (Shimadzu NC900, Kyoto, Japan). Moreover, the soil is highly porous (Lin et al. 1999; Ohashi et al. 2000), and the litter layer was 1–2 cm thick at most. The estimated root biomass of 13.1 Mg ha^{-1} was confined primarily to a narrow soil zone (10–15 cm) between the overlying layer of litter and the underlying, water-deficient, porous pumice. Sapronov and Kuzyakov described the soil profiles in more detail (Sapronov and Kuzyakov 2007).

2.2 Experimental design

The three experimental areas were at least 100 m apart. Each area received three treatments that began in April 2001. A 0.6 × 0.6 m plots were marked out in four directions approximately 1.0 m from the trunk of the tree, the plots contained no trees and shrubs. We assigned the following classifications to the plots randomly: control plots (control), which remained undisturbed; no-root plots (NR), where root growth was excluded, and no-root-no-litter plots (NRNL), where root growth was excluded and aboveground litter was removed.

We excluded roots from the NR and NRNL plots by making trenches approximately 50-cm deep and installing four corrugated plastic sheets (0.60 m × 0.45 m) to prevent root entry. Because there was a pumice layer at a depth of approximately 50–60 cm, roots were found only at a depth of approximately 0–20 cm. The trenches were back-filled with the same soil, including the dead roots. All understory plants, dominated by buckler fern, were removed by cutting at their base, and were continually clipped throughout the experiment in both the trenched and control plots.

2.3 Soil respiration measurements

The soil respiration rate was measured using a LI-6400 portable gas exchange measurement system (Li-Cor Inc., Lincoln, NE, U.S.A.) attached to a null balance soil flux chamber (LI-6400-09). All vegetative growths were removed from inside the collars. We followed the method of collar insertion as proposed by Wang (2005) carefully.

We measured soil respiration rates from May 1 to October 31 during the growing season from 2001 to 2003 according to the ontogeny of Japanese larch in Hokkaido. The monthly measurements typically were taken at 12:30 and ended at 16:00 during the 3 years of growing seasons.

The respiration measured in the NRNL plots was the result of decomposition of the mineral soil (R_{SOM}), and the difference between respiration in the NR and NRNL plots permitted us to estimate the contribution of litter decomposition (R_{Litter}); R_{Mic} was then estimated as the difference between respiration in the control plot and NR plots. We obtained 90 points (3 plots × 3 areas × 10 replications) for soil respiration per month.

2.4 Physicochemical and microbiological parameters

We monitored the soil temperature with four auto-logged thermometers (RT-30S; Espec Mic. Corp., Aichi, Japan) installed in random locations approximately 0.5 m from the plots. The thermometers were set to record soil temperature at a depth of 5 cm at 30 min intervals from May 2001 to November 2003. In addition, the soil temperature was measured at a depth of 5 cm with portable sensors (Li-Cor thermocouple) that were inserted adjacent to the soil collars at the time each soil respiration measurement was taken.

A soil core sampler (Daiki Rika Kogyo Co. Ltd., Saitama, Japan; 100 cm^3 volume) was used to sample the soil each time respiration was measured. Thereafter, soil volumetric water content was calculated by weighing the fresh soil before and after it was dried in an oven for 48 h at 105 °C.

Soil microbial biomass carbon (MBC) and nitrogen (MBN) were measured in the control plots during the growing season. Five cores that had been extracted monthly using the core sampler were stored at 5 °C prior to determining the microbial biomass using the fumigation method. Carbon in the 0.5 mol L^{-1} K$_2$SO$_4$ solution was measured with a UV-Persuate TOC-5000A soluble C analyzer (Elementar GmbH, Hanau, Germany), and K$_{EC}$-factor of 0.43 was used to calculate carbon. The N content was measured using a method described by Brookes et al. (1985). K$_{EN}$-factor of 0.54 was used in the nitrogen calculations.

2.5 Statistical analyses

All statistical analyses were performed with the SAS package (SAS Institute Inc. 2016) and R packages. All sampling points were used as the statistical units to analyze the seasonal and annual variation of SR and R_{Mic}. A repeated measures ANOVA was conducted to determine whether there were significant differences between R_{Mic} and environmental factors and microbial parameters. Multiple regression analysis also was used to determine the relations between respiration rate and each of the following factors: soil temperature at 5 cm, volumetric water content, MBC, and MBN. We used the equation for the regression analysis of soil temperature and R_{Mic}:

$$R_{Mic} = ae^{bT} \tag{1}$$

where R_{Mic} is the soil microbial respiration rate at soil temperature T at a depth of 5 cm, a is the soil microbial respiration rate at a soil temperature of zero (Celsius), and the (positive) coefficient b corresponds to the R_{Mic} sensitivity to temperature (Luo and Zhou 2006).

Path analysis is an extension of the regression model, which is usually depicted with a figure in which one directional arrows indicate causation. A path coefficient is a standardized regression coefficient that shows the direct effect of an independent variable on a dependent variable in the path model. We established a path model of R_{Mic} for the data from 2001 to 2003 to indicate the direction and strength of effects on R_{Mic}. Path analysis was conducted using the Lavaan package (Rosseel 2012) in R.

3 Results

Figure 1 shows the soil temperatures measured at a depth of 5 cm after trenching between May and October from 2001 to 2003. Soil temperature increased steadily until mid-summer and reached a maximum of 19.4 °C on August 23 in 2001, 19.6 °C on August 10 in 2002, and 19.8 °C on September 3 in 2003. From this peak, the soil temperature declined until the end of October in each of the 3 years. Table 1 shows the mean monthly soil temperatures (at 5 cm depth), soil water content, precipitation, and soil microbial respiration from May to October for the 3 years.

Soil respiration rates from NRNL, NR, and control plots increased from May to July or August, and then decreased during the autumn (Fig. 2). The peak efflux of R_{Mic} rate, as measured from the NR plot, occurred in July or early August each year. Based on the data taken over the 3 years, the variance in R_{Mic} was associated closely with soil temperature at 5 cm depth, where there was a significant exponential relation between the two (Fig. 3).

The values of R_{Litter} ranged from 8 to 32% over the 3 years (Fig. S1, Electronic Supplementary Material); however, the average of R_{Litter} per year was approximately 19% (Table 2). The contributions of R_{SOM} to the total soil respiration were estimated to be 59% in 2001, 42% in 2002, and 35.6% in 2003, respectively. The contribution of R_{SOM} to total soil
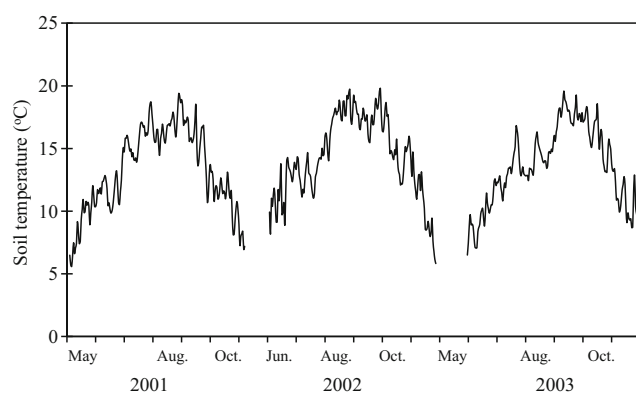

Fig. 1 Monthly change of soil temperature at 5 cm depth during the growing season in May to October in 2001, 2002, and 2003

respiration was greater than that of R_{Litter} (Table 2). R_{Mic} to total soil respiration was 78, 62, and 55% from 2001 to 2003.

Table 3 shows the correlation between soil volumetric water content and soil microbial biomass in the control plot. As can be seen, soil water content influenced MBC and MBN significantly. There also was a strong correlation between soil microbial biomass carbon and nitrogen (Table 3). However, there was no significant seasonal variation in soil microbial biomass neither carbon nor nitrogen with soil temperature.

Path analysis indicated that soil temperature at 5 cm depth had a direct strong positive effect on R_{Mic}, while soil MBC was correlated negatively with R_{Mic} (Fig. 4). Soil MBN had an indirect effect on R_{Mic} by influencing soil MBC.

4 Discussion

There were clear seasonal changes in soil respiration rate in trenched and control plots from May to October for the 3 years (Fig. 1). R_{Mic} was obtained from the NS plots, which increased from May and reached a peak in July or August, then declined gradually until October (Table 1). In a study site near ours, Liang et al. (2010) showed that SR was stable at 0.50–0.55 μmol m^{-2} s^{-1} during the snowy season until mid-March, and then increased gradually up to 0.8 μmol m^{-2} s^{-1} when the snow melted (April 17). Mean SR for the snowy season of 127 days was 0.56 ± 0.12 μmol m^{-2} s^{-1}(mean ± SD). Thus, SR was much smaller and stable during the snowy season compared to the growing season, and seasonal changes in SR and R_{Mic} occurred mainly during the growing season.

There was a significantly exponential relationships between soil temperature at 5 cm depth and R_{Mic} ($R^2 = 0.702$). Thus, the soil temperature is the most important factor that influences root growth (Qu et al. 2009) and soil microbial respiration (Liang et al. 2010; Karhu et al. 2014; Li et al. 2017). With increasing global temperatures, we might predict an increasing soil CO_2 efflux contributed by soil.

We found that the contribution of R_{Litter} largely was constant (as a percentage) from year to year over the 3 years (Table 2). According to the 3 years of data, R_{Litter} was much higher in the autumn, when new litterfall increased, and the temperature (approximately 10–14 °C) might still promote aboveground litter decomposition. This result suggested that litter decomposition contributes importantly to the soil CO_2 efflux (Hanson et al. 2000). However, during the first year after trenching, dead roots severed by the trenching usually decomposed faster than SOM, possibly giving rise to pulsed releases of CO_2 after the trenching. As a result, the increased contribution of R_{SOM} to SR in the first year, compared to the second and third years, may have underestimated the root respiration's contribution to SR based on simple subtraction of the CO_2 efflux measured between trenched and control

Table 1 Climate data recorded during the growing season at a Japanese larch forest in Northern Japan. The growing season is defined as from May 1 to October 31

Year	Month	Mean soil temperature (°C)	Mean soil water (%)	Mean soil microbe respiration rate ($\mu mol\ m^{-2}\ s^{-1}$)	Precipitation (mm)
2001		13.2	45.2	3.1	154.9
	May	9.2	48.1	2.4	163.3
	June	12.3	38.9	2.6	20.1
	July	15.9	48.0	3.7	125.7
	August	17.0	46.0	4.3	194.2
	September	14.7	44.9	3.2	242.9
	October	10.3	45.1	2.2	183.3
2002		14.2	40.3	1.9	110.9
	May	11.1	36.6	2.2	36.5
	June	12.8	34.7	1.7	72.2
	July	16.8	43.9	2.6	146.6
	August	17.6	43.7	2.5	189.2
	September	15.5	36.8	1.7	114.7
	October	11.0	46.1	0.8	106.2
2003		13.5	41.9	2.8	129.4
	May	9.5	35.9	2.2	36.6
	June	13.3	35.7	2.3	89.3
	July	14.2	38.7	3.3	106.1
	August	17.2	37.5	4.3	191.8
	September	15.7	57.2	3.5	219.9
	October	10.6	46.3	1.0	132.4

plots (see Table 2). Consequently, R_{Mic} accounted for a slightly larger fraction of total SR (>50%) in this forest. In temperate forests, the estimated contribution of R_{Mic} to total SR varies from 45 to 67% in broad-leaved forests and 38–65% in coniferous forests (Nakane et al. 1996; Striegl and Wickland 1998; Lin et al. 1999; Ohashi et al. 2000; Rey et al. 2002; Lee et al. 2003; Wang 2005; Wang et al. 2008). These authors concluded that the contribution of R_{Mic} to the total SR may approach approximately 50% in all forest types when soil organic carbon is in a steady state. Therefore, our results are consistent with other reports of measurements at

similar altitudes (~130 m a.s.l.) in coniferous forests around the world. We found that soil microbial respiration rate was greater than root respiration during the 3 years indicating the important contribution of soil microbial communities to CO_2 emissions. In fact, using an automated closed-type chamber system, Liang et al. (2004) also estimated that heterotrophic respiration accounted for 57% of SR within 1 year in the same larch forest.

In contrast, we found no clear relation between soil volumetric water content and SR or R_{Mic} as was found in Dahurian larch in northeast China (Jiang et al. 2005). However, because

Fig. 2 Monthly change in the control and trenched plots during the growing season in May to October in 2001, 2002, and 2003. *Control* control plot, *NRNL* no-root-no-litter plot, *NR* no-root plot
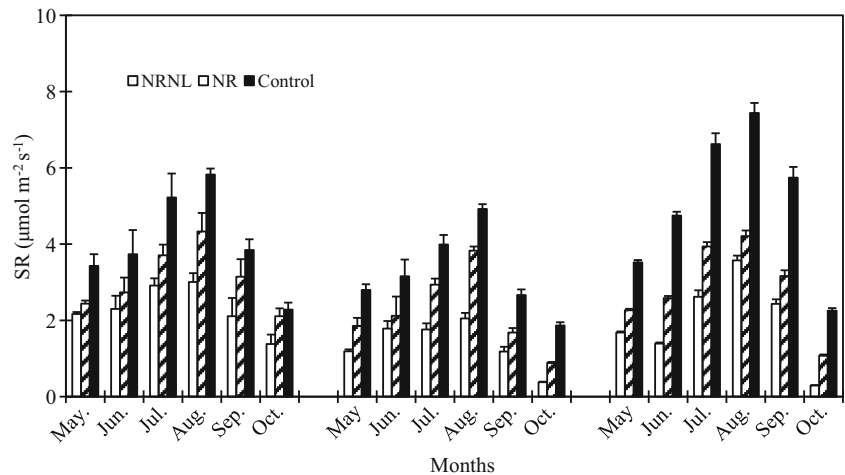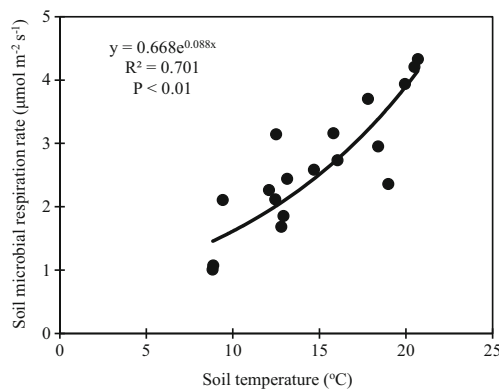
Fig. 3 The exponential relationship between soil respiration (SR) or soil microbial respiration (R_{Mic}) and soil temperature at 5 cm depth over 3 years. Data shown are the mean values for each month

there was abundant precipitation, and no predominantly wet or dry season in this plantation, there was always substantial volumetric soil water content (normal range of 35–45%). Thus, the soil water content was higher than in northeast China. These moist conditions promote root and microbial activity throughout the entire growing season. Although soil volumetric water content was correlated strongly with soil MBC and MBN (Table 3), the path analysis did not show that soil water content or precipitation influenced MBC and MBN significantly (Fig. 4). This result requires further investigation.

Buchmann (2000) conducted a series of root exclusion experiments with staggered start times that permitted comparison between roots cut recently and those that had been dead for up to 6 months. In this study, we assumed that soil disturbance and residual root decomposition contributed little to underground respiration after the plots had been trenched for one growing season, or for 1 year. Thus, R_{Mic} in the first year may have increased because of the root trenching. Lee et al. (2003) found a similar tendency in a cool-temperate deciduous forest in central Japan showing that the contribution of decomposition of residual roots to SR was 14–52% in the trenching year, but was 7–8% in the succeeding year. Moreover, soil moisture may increase in

Table 2 The contribution of microbes from mineral soil, aboveground litter, and total microbe to SR during growing season from 2001 to 2003. The growing season is defined as Table 1

Year	R_{Litter}/SR (%)	R_{SOM}/SR (%)	R_{Mic}/SR (%)
2001	19.6 ± 3.8	58.6 ± 1.8a	78.2 ± 3.2a
2002	19.4 ± 2.2	42.2 ± 3.7b	61.6 ± 2.0b
2003	18.8 ± 3.7	35.6 ± 4.8b	54.5 ± 2.6b

The values with different letters within the same row are significantly different ($P < 0.05$)

R_{Litter} soil respiration rate from aboveground litter; R_{SOM} soil respiration rate from mineral soil; R_{Mic} soil microbial respiration, which is the sum of R_{Litter} and R_{SOM}; SR soil respiration rate, which included soil microbial respiration and root respiration

Table 3 Pearson correlation analysis for soil microbial biomass carbon and nitrogen, soil water during the growing seasons from 2001 to 2003

	MBC	MBN	Soil water	Years	Months
MBC	1	0.589**	0.479**	−0.665**	0.061
MBN		1	0.212*	−0.184	0.185
Soil water			1	−0.113	−0.054
Years				1	−0.005
Months					1

MBC microbial biomass carbon, MBN microbial biomass nitrogen
*$P < 0.05$, **$P < 0.01$

the trenched plots, given that roots cannot extract water because transpiration ceases after root exclusion (Gavrilenko et al. 2011). In this case, the increasing soil moisture also can affect the decomposition rate. Therefore, we checked the soil water content in the trenched and control plots in 2002 and 2003. There was a slight increase of soil water content, but no significant effect in the trenching (data not shown).

The girdling method was developed to estimate the contribution of different components to soil respiration (Högberg and Högberg 2002; Wang 2005). Högberg and Högberg (2002) found that microbial biomass decreased by 30–40% 1 month after girdling, although Frey et al. (2006) reported that girdling of sweet chestnut did not affect MBC within their 37-day experiment. Subke et al. (2004) showed that microbial biomass in the AOh horizon was not affected by girdling after the litter layer was removed. The soil MBC pool size may not be correlated well with soil CO_2 efflux (Wang et al. 2003). There was no significant relationship between MBC and SR in the Chinese chestnut plantation, regardless of the treatment (Wang et al. 2014). A possible explanation for such a lack of relationship is MBC represents the size of soil microflora, which may not be related to microbial activity measured by CO_2 emissions (Zhang et al. 2014; Wang et al. 2014). Therefore, the role of MBC in determining soil CO_2 efflux may still be uncertain. We measured MBC and MBN in the control plots monthly from May to October as soil microbial biomass measurements were not available for the trenched
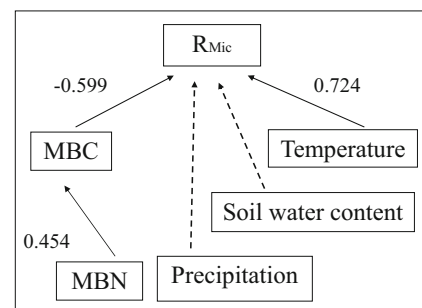

Fig. 4 The path analysis model of soil microbial respiration (R_{Mic}). Only the significant paths were presented in path diagram. MBC soil microbial biomass carbon, MBN soil microbial biomass nitrogen

plots. We found MBC had significantly negative effects on R_{Mic} in this larch forest (Fig. 4). In our experiment, MBC was high early in the growing season (e.g., May) and low in the middle of the growing season (e.g., July or August). R_{Mic} was determined directly by MBC and soil temperature in the opposite way (Fig. 4). R_{Mic} and soil temperature showed similar seasonal patterns of variation that demonstrated the critical role of soil temperature on R_{Mic} during the growing season, while we could not find the relationship between MBC and soil temperature. This may be the case because the measurements were only performed during the growing season, when soil temperature ranged from 9 to 17 °C. Thus, our results suggested that the processes of carbon cycle in larch forest are complicated, and gaps remain in our understanding of the carbon cycle with respect to soil microbial biomass and CO_2 efflux.

5 Conclusions

The R_{Mic} to SR varied from 78 to 55% after 3 years of trenching treatments. This demonstrated the important role soil microbes play in soil respiration in larch forest. The microbial metabolic biomass carbon and nitrogen were correlated with heterotrophic respiration. The soil temperature was the most significant positive factor that influenced R_{Mic}, while soil water content had no significant effect. Global warming will stimulate the loss of C into the atmosphere by increasing R_{Mic} and could accelerate climate change.

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