

EFFECTS OF N FERTILIZATION ON SOIL MICROBIAL RESPIRATION IN *LARIX GMELINII* PLANTATION

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Abstract. Soil organic carbon decomposition is regulated by soil physical and chemical properties, such as soil nitrogen (N) and soil substrate quality. In this study, soil samples from both N fertilization and control plots were collected at two depths in a *Larix gmelinii* plantation to determine if N addition elicits consistent responses in microbial respiration in bulk and rhizosphere soil, and to determine the temporal and spatial dynamics of soil organic carbon decomposition. Soil bulk and rhizosphere microbial respiration were determined using the NaOH solution absorption method. Soil microbial biomass was determined by a modified CHCL₃ fumigation-extraction method. The greatest soil bulk and rhizosphere microbial respiration occurred in July. Soil rhizosphere microbial respiration was higher than bulk respiration at 0–10 cm and 10–20 cm. The biggest reductions in soil microbial respiration induced by fertilization were 15.0% (bulk) and 19.6% (rhizosphere) at 0–10 cm in July, and 6.4% (bulk) and 7.9% (rhizosphere) at 10–20 cm in September. Fertilization did not influence the rhizosphere priming effect except for at 10–20 cm in May. Structural equation modeling revealed that soil microbial biomass carbon (MBC) and nitrogen (MBN) contributed directly to soil microbial respiration. Moreover, soil total N and organic carbon content were associated with soil microbial respiration through MBC and MBN. These results suggest that N fertilization suppresses soil organic carbon decomposition by decreasing soil microbial biomass, while C input induced by root exudates determined the rhizosphere priming effect, not soil microbes in the rhizosphere.

Keywords: *soil microbe, rhizosphere, soil N availability, soil organic carbon decomposition*

Introduction

Soil is a large organic carbon pool ($1.5 \cdot 10^{18}$ g of C), containing twice the total C in the atmosphere (Schlesinger, 1997). The decomposition of soil organic carbon occurs via the microbial assimilation process known as soil microbial respiration, which is one of the most important processes in global carbon cycling (Schimel and Schaeffer, 2012), response to the primary decomposed ability of new carbon associated to soil by plant (Schlesinger, 1997). Therefore, the decomposition ratio of soil C pools is regulated by soil physical and chemical properties (Xu et al., 2016). Soil nutrient availability, particularly that of nitrogen (N), has been suggested as a key driver of soil organic carbon decomposition (Zhou et al., 2014), such that the soils with a high C:N ratio showing lower decomposition rates (Xu et al., 2016). Recent studies have shown that nitrogen addition reduced soil microbial respiration induced by the negative effects of N application on soil microbial abundance and composition (Zhang et al., 2018), as well as that of soil microbial activity by shifting the metabolic capabilities of soil bacterial communities (Ramirez et al., 2012). These results suggest that N addition slows soil organic carbon decomposition by decelerating microbial mineralization. Therefore, a better

understanding of soil microbial responses to N addition is critical to predicting soil carbon sequestration in terrestrial ecosystems.

Soil substrate quality controls the soil organic carbon mineralization and efficiency of soil organic carbon microbial assimilation (Manzoni et al., 2008, 2012), with a higher substrate quality leading to higher microbial assimilation, large microbial biomass (Blagodatskaya et al., 2011), and a higher ratio of microbial carbon to soil organic carbon (Xu et al., 2014). Plant root exudates and other labile root-derived rhizodeposit are important substrates for soil microbes (Haichar et al., 2014). For example, the soil adjacent to roots has larger C mineralization rates than bulk soil in undisturbed temperate forest sites (Phillips and Fahey, 2007). A meta-analysis showed that input of labile organic C to the rhizosphere can stimulate soil organic carbon decomposition by 59% (Huo et al., 2017), and this process may be regulated by changes in the size and composition of the microbial community (Dorodnikov et al., 2009; Talbot et al., 2008). This is likely because there is 14–31% higher microbial biomass (Blagodatskaya et al., 2014) and an order of magnitude higher microbial activity and abundance in the rhizosphere than in bulk soil (Kuz'yakov and Xu, 2013). However, few studies have investigated the rhizosphere soil microbial activity when there is no more ongoing labile organic C input under N addition.

Therefore, the present study was conducted to determine if N addition elicits consistent responses in microbial respiration in bulk and rhizosphere soil, and to determine the temporal and spatial dynamics of soil organic carbon decomposition. To accomplish this, soils were collected from a larch plantation (*Larix gmelinii*) during the growing season and incubated under laboratory conditions. We expected that soil microbial activity under N fertilization would mitigate any increases in soil organic carbon decomposition induced by rhizosphere microbes. We also hypothesized that changes in microbial biomass would result in concurrent changes in soil microbial respiration.

Materials and methods

Study site

This study was conducted at the Maoershan Experimental Station (127°30'–127°34'E, 45°21'–45°25' N) of Northeast Forestry University, Heilongjiang Province, China (Fig. 1).

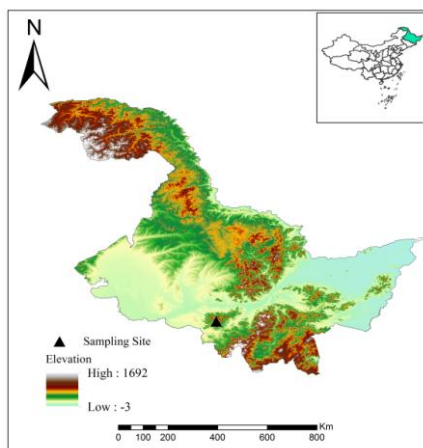


Figure 1. The sampling site of the experiment

This region is characterized by a cold, temperate-zone, continental monsoonal climate. The average annual temperature is 2.8 °C, with average daily air temperatures ranging from -19.6 °C (January) to 20.9 °C (July). The mean annual precipitation is 723 mm, with 66% (477 mm) occurring in June, July and August. Additionally, the mean annual evapotranspiration is 1,094 mm. The soil (Hap-Boric Luvisol) is usually frozen to a depth of 1 m in winter (December–April). More details about the soil in the region are given by Wang et al. (2006).

Experimental design

The experiment was designed to test the fertilization treatment effects on soil and plantations. *L. gmelinii* and *Fraxinus mandshurica* with representing 65% and 10% of conifer and hardwood plantations are both dominant species in natural forests of Northeast China and key commercial plantation specie. Two plantations were established in 1986 by planting 2-year-old seedlings using a 1.5–2.0 m planting grid. The experiment was arranged in a randomized design in each plantation in May of 2002, and all plots were 20 m×30 m. Each stand had two N (NH₄NO₃) fertilization treatments, control plots (0 g N·m⁻²·y⁻¹) and fertilized plots (10 g N·m⁻²·y⁻¹), and each treatment was applied in triplicate. The fertilizer was applied continuously on the 15th of each month from 2003 until sampling year (2014) in amounts set based on soil temperatures (Table 1). All measurements were performed after the fertilizer had been applied for two weeks. In the present experiment, only the *L. gmelinii* plantation of the parent experiment was sampled.

Table 1. Soil temperature at different soil depth of research site

Season	Soil temperature different depths (°C)			Fertilizer amount (%)
	5 cm	10 cm	20 cm	
May	12.50	9.70	8.70	15.25
June	19.50	17.20	16.30	21.00
July	22.30	20.60	19.90	27.50
August	22.10	21.00	20.80	21.00
September	14.60	16.00	14.60	15.25

Soil sampling

Six soil samples were collected from each plot using soil cores with a 6 cm inner diameter at depths of 0–10 cm and 10–20 cm in May, July, and September of 2014. Samples were separated into bulk and rhizosphere soil. To accomplish this, rhizosphere soil was collected from the soil tightly adhering to fine roots (<2 mm in diameter) as described by Wang and Zabowski (1998). Briefly, the soil not tightly adhering to roots was first removed by gently shaking the roots, then tightly adhered soil was collected by putting the roots into a paper bag and vigorously shaking them. Bulk samples were obtained from pooled soil by mixing thoroughly after fine root and rhizosphere soil removal. Soil samples were transported to the research station in a cooler (~4 °C), then sieved (<2 mm) to remove stones, coarse and fine roots and stored at 4 °C.

Soil microbial biomass

Soil microbial biomass was determined by a modified CHCl₃ fumigation-extraction method (Vance et al., 1987). The C and N content that were K₂SO₄-extracted from the CHCl₃-fumigated and unfumigated soils were estimated using a TOC-VCPH analyzer (Shimadzu, Tokyo, Japan), and soil microbial biomass C (MBC) and soil microbial biomass N (MBN) were calculated using extraction factors of 0.45 and 0.54, respectively (Brookes et al., 1985; Vance et al., 1987).

Soil microbial respiration

The microbial (basal) respiration (including bulk and rhizosphere soil) was determined based on the soil CO₂ emissions over a 10 d incubation period. Briefly, 20 g soil samples adjusted to 60% of the water holding capacity were incubated in 1000 cm³ gas-tight jars at 20 °C ± 2 °C. The CO₂ was then absorbed by NaOH solution (0.05 M) and CO₂ was determined by single end-point titration with HCl following addition of 400 µl of 0.5 M BaCl₂, and precipitated as barium carbonate, after which the amount of CO₂ was calculated (Bekku et al., 1997; Phillips and Fahey, 2007).

Soil properties

Soil total C and N were determined using a FlashEA 1112 elemental analyzer (Thermo Finnigan, Italy). Soil pH was measured in a 1:5 soil: water solution using a FiveEasy pH meter (Mettler-Toledo Ltd., Mississauga, Canada). Soil NO₃⁻-N and NH₄⁺-N were extracted using 2 M KCl and were determined with an 8500 series flow injection autoanalyzer (Hach Company, Loveland, USA).

Data analysis

Repeated measures ANOVA was conducted to assess the effects of fertilization on soil microbial respiration using the SPSS statistical software 11.5 (SPSS Inc., Chicago, USA). When the results of ANOVA demonstrated a statistically significant difference, Tukey's test was conducted to assess the effects of fertilization treatments. A *P* < 0.05 was considered to indicate statistical significance.

Structural equation modeling (SEM) was used to evaluate the general hypothesis that soil microbial biomass (C, N), soil organic carbon, total N, NO₃⁻-N, NH₄⁺-N and pH influence soil microbial respiration in response to fertilizer application. We constructed an a priori model including possible causal relationships among predictors. Those eight predictors in the initial model were treated as observed variables. Mardia's test was then used to estimate the multivariate normality of the dataset, and the model fit was assessed using the χ²-test, comparative fit index (CFI), and root mean square error of approximation (RMSEA). Analyses were performed with the SPSS AMOS 21.0 software (SPSS Inc., Hong Kong, China) using the robust maximum likelihood estimation procedures.

Results

Soil microbial respiration

Soil bulk and rhizosphere microbial respiration showed similar seasonal dynamics as soil temperature, with the greatest respiration rate occurring in July (*Fig. 2*). Soil

microbial (bulk and rhizosphere) respiration varied with soil depths. Specifically, the surface (0–10 cm) soil microbial respiration rate was about 4.0 times (bulk: 3.1–4.9) and 3.9 (rhizosphere: 3.1–4.6) greater than that at 10–20 cm ($P < 0.05$). Soil rhizosphere microbial respiration was 6.6% (control) to 6.8% (fertilized) and 10.0% (fertilized) to 11.7% (control) higher than the bulk respiration at 0–10 cm and 10–20 cm ($P > 0.05$), respectively. Additionally, the priming effects were positive, being about 6.7% and 10.9% at 0–10 cm and 10–20 cm (Fig. 2; Table 2).

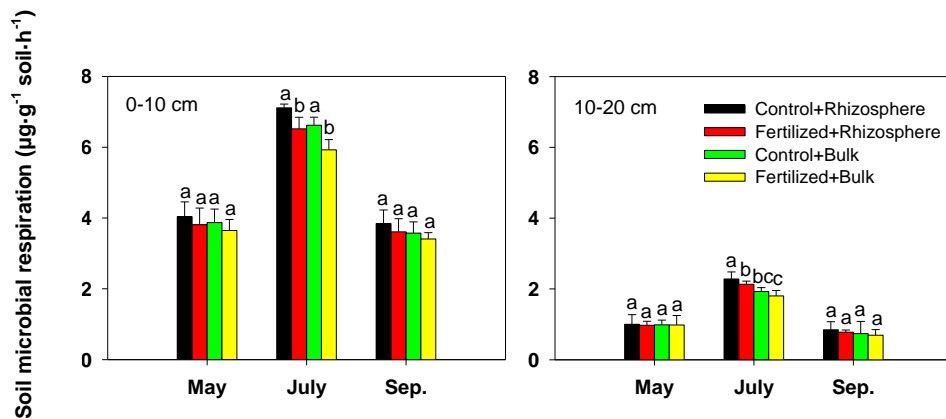


Figure 2. Seasonal dynamical of soil rhizosphere and bulk respiration at surface and subsurface layer

Table 2. Repeated measurement ANOVA of fertilizer and rhizosphere on soil microbial respiration

Source	df	0-10 cm		10-20 cm	
		F value	P value	F value	P value
Sampling time (S)	2	235.045	0.000	114.102	0.000
Fertilized (F)	1	8.371	0.045	1.153	0.050
Rhizosphere (R)	1	6.544	0.060	5.145	0.045
S×F	2	1.372	0.722	0.293	0.238
S×R	2	1.119	0.343	2.347	0.503
S×F×R	2	0.039	0.654	0.001	0.728
Error	8				

Effect of fertilization on soil microbial respiration

Fertilization decreased soil bulk and rhizosphere microbial respiration, while its effects on soil microbial respiration varied with sampling time and soil depth (Fig. 2; Table 2). The greatest reductions in soil microbial respiration induced by fertilization of 15.0% (bulk) and 19.6% (rhizosphere) occurred in July at 0–10 cm, and by 6.4% (bulk) and 7.9% (rhizosphere) at 10–20 cm in September (Fig. 2; Table 2). Fertilization did not influence the rhizosphere priming effect at 0–10 cm and 10–20 cm during the growing season except during May at 10–20 cm (Fig. 2).

Relationship between soil properties and soil microbial respiration

Structural equation modeling revealed that the predictors explained 88% of the variation in soil microbial respiration (R_{mic}) (Fig. 3). Soil MBC and MBN contributed directly to soil microbial respiration, and the response of soil microbial respiration to MBC and MBN differed. Soil total N (STN) and organic carbon (SOC) content were associated with soil microbial respiration through MBC and MBN. It should be noted that fertilization influenced soil microbial respiration indirectly through soil NO_3^- -N and pH.

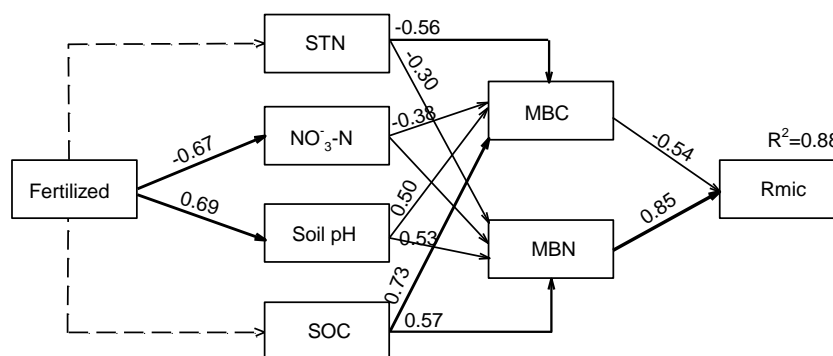


Figure 3. Structural equation model relating fertilization on soil microbial respiration ($\chi^2 = 14.385$; $df = 28$; $P = 0.695$; $CFI = 1.000$; $RMSEA = 0.000$). Note: Rectangles represent observed variables; ovals represent latent variables; arrow thickness represents the magnitude of the path coefficient. Solid line arrows represent significant paths ($P < 0.05$), dot lines represent not significantly different ($P > 0.05$). STN: Soil total N; SOC Soil organic carbon; MBC: Soil microbial biomass carbon; MBN: Soil microbial biomass nitrogen; R_{mic} : Soil microbial respiration

Discussion

Soil microbial respiration

Soil microbial respiration showed significant seasonal and soil depth effects. Specifically, the respiration rate was $2.04\text{--}4.87 \mu\text{gC}\cdot\text{g}^{-1} \text{soil}\cdot\text{h}^{-1}$ and $1.90\text{--}4.27 \mu\text{gC}\cdot\text{g}^{-1} \text{soil}\cdot\text{h}^{-1}$ in rhizosphere and bulk soil, respectively, which is consistent with the results of other studies (Ananyeva et al., 2008; Olsson et al., 2005). These seasonal dynamics differed from those of the MBC and MBN (Table 3). This likely occurred because of interspecific competition between plants and microbes for nutrients (Kuzyakov and Xu, 2013), especially for N. In July, soil conditions are beneficial to both soil microbes and plant growth. Soil microbes showed higher respiration rate, indicating they were taking more nutrients for their own and plant growth, leading to decreased biomass accumulation (Fig. 2; Table 3). Soil microbes might utilize available N more effectively than plants in the short-term, while plants might be more competitive in the long run (Kuzyakov and Xu, 2013). Moreover, temporal dynamics of soil microbial biomass are associated with alternating periods of microbial death and growth, which has important consequences for soil nutrient dynamics and soil microbial biomass turnover (Wardle, 1998). The soil microbial respiration rate decreased with declining soil microbial biomass turnover, leading to the accumulation of soil microbial biomass in September (Table 3). Finally, soil microbial biomass and activity determined the soil microbial respiration rates (Xu et al., 2017). A higher soil microbial metabolic quotient ($q\text{CO}_2$),

which is defined as the microbial respiration per unit of microbial biomass, indicates higher respiration consumption of carbon and lower construction carbon. The results of the present study showed that the qCO_2 value in July was higher than in May and September at depths of both 0–10 and 10–20 cm (Table 4). In general, if microbes are more active during that period, cumulative maintenance respiration should be greater, and the population size should be lower (Brown et al., 2004).

Table 3. Soil microbial biomass C and N (mean \pm SE) at surface and subsurface layer

Soil depths	Sampling time	Treatment	MBC (mg/kg)	MBN (mg/kg)
0-10 cm	May	Control	670.85 \pm 77.68	143.16 \pm 17.63
		Fertilized	447.34 \pm 41.68	78.23 \pm 9.38
	July	Control	731.71 \pm 32.18	204.67 \pm 24.67
		Fertilized	435.01 \pm 25.28	95.17 \pm 13.16
	September	Control	1106.59 \pm 40.36	223.52 \pm 4.99
		Fertilized	864.08 \pm 47.30	122.28 \pm 20.03
10-20 cm	May	Control	406.29 \pm 49.79	82.38 \pm 6.28
		Fertilized	285.57 \pm 5.13	58.88 \pm 7.28
	July	Control	450.61 \pm 34.71	107.51 \pm 12.07
		Fertilized	241.33 \pm 31.19	64.47 \pm 13.65
	September	Control	732.95 \pm 52.50	128.51 \pm 9.39
		Fertilized	649.26 \pm 37.39	97.94 \pm 9.53

Table 4. Soil microbial respiration metabolic quotient (qCO_2)

	Month	0-10 cm		10-20 cm		0-20 cm	
		Control	Fertilized	Control	Fertilized	Control	Fertilized
Metabolic quotient (qCO_2) $mgCO_2-C \cdot g^{-1}(C_{mic}) \cdot h^{-1}$	May	5.77	8.15	2.42	3.44	4.51	6.31
	July	9.05	13.62	4.07	7.47	7.23	11.44
	Sep.	3.23	3.94	1.01	1.06	2.34	2.71

Fertilization effect

Soil nitrogen availability strongly influences the growth and abundance of soil organisms. The addition of N has been shown to affect microbial growth, abundance and composition, as well as soil microbial activity (Bowden et al., 2004; Phillips and Fahey, 2007; Zhang et al., 2018), which is consistent with our finding that fertilization decreased soil microbial respiration (Fig. 2). There are several explanations for these results. First, N fertilization decreased the number of colony forming units of bacteria, fungi, and actinomycetes in our research plot by 98%, 63% and 61%, respectively (Jia et al., 2009). Because the number of colony forming units of soil microbes was positively related to soil pH (Compton et al., 2004), which declined from 5.18 (control plot) to 4.35 (fertilized plot) in this larch plantation. Moreover, the SEM results revealed that fertilization influenced soil microbial respiration indirectly through soil pH. Second, N fertilization decreased soil microbial biomass (Table 3). Soil MBC and MBN contributed directly to soil microbial respiration (Fig. 3). Because soil microbial biomass turnover was fast under lower soil pH, it would be slower under higher pH

(Wardle, 1998). Third, the soil microbial respiration metabolic quotient ($q\text{CO}_2$) is increasingly being used as an index of ecosystem development and disturbance (Wardle and Ghani, 1995). Nitrogen fertilization increased $q\text{CO}_2$ by 42% (the average of the growing season) at both 0–10 and 10–20 cm. The increasing $q\text{CO}_2$ indicates that microbes invested more in consuming carbon instead of construction carbon. These findings suggested that soil microbes may change their strategy by increasing the function per unit of soil microbial biomass in high nutrient soil. Therefore, N fertilization decreased microbial respiration because of reduced microbial demand for mining of soil organic carbon for N uptake.

Rhizosphere effect

Soil organic carbon is the source of soil microbial respiration. In rhizosphere soil, organic C derived from living roots consists of soluble and insoluble forms of organic C such as sugars, organic acids, mucilage, sloughed cell walls and root hairs, providing a carbon- and energy-rich environment (Haichar et al., 2014). This can suppress soil organic carbon decomposition by 50% or stimulate it by 380% during incubation in soil without plants (Cheng et al., 2014). Therefore, rhizosphere microbial communities, biomass, activity and abundance are distinct from those not affected by living roots (Blagodatskaya et al., 2014; Garland, 1996). The soil microbial community and biomass in the rhizosphere have been shown to be higher than in bulk soil. For example, Gram-negative, Gram-positive and fungal PLFA abundance in rhizosphere were higher by 45.4%, 33.3% and 66.7% than in bulk soil, and the average rhizosphere microbial biomass was 3.5 times more than that of bulk soil in a previous study (Paterson et al., 2007). The root exudates and other rhizodeposits can influence physical, chemical, biological and environmental interactions between plants and soils (Cheng et al., 2014; Kuzyakov and Blagodatskaya, 2015), and it is estimated that the quantity of C released in soil via root exudates ranges from 50 to 1500 $\mu\text{g g}^{-1}$ soil d^{-1} (Cheng, 1996; Jones and Darrah, 1993; Meharg and Kilham, 1991; Trofymow et al., 1987), which may induce higher microbial abundance and diversity and faster microbial growth in rhizosphere soil (Berg and Smalla, 2009; Paterson et al., 2009). Moreover, exudation rates were shown to be positively correlated with organic carbon decomposition in the rhizosphere (Yin et al., 2014). Furthermore, the amount of soil microbial biomass was not closely related to priming (Liu et al., 2017). In the present study, no significant priming effects were observed (*Fig. 4*), even though the average rhizosphere soil respiration was 6.4% (4.0–7.1%) and 11.7% (1.9–18.5%) higher than that of bulk soil at depths of 0–10 and 10–20 cm (*Fig. 2; Table 2*). These findings differ from the previous studies, which showed significantly higher basal respiration in the rhizosphere than root-free soil after glucose addition (Blagodatskaya et al., 2014). Our findings suggest that the C input induced by root exudates determined the occurrence of rhizosphere priming, not soil microbes in the rhizosphere.

The priming effect did not differ significantly between the control and fertilized (except for in May at 10–20 cm) plot in this study (*Fig. 4*). This may have been because there was no ongoing new C input in the present study. Indeed, a previous study showed that N fertilization decreased the decomposition of old and stable soil organic carbon, but did not affect newly deposited C (Zang et al., 2017). However, soil nutrient availability is one of the factors controlling priming effects between soil depths. Greater priming has been observed in low nutrient soils compared with high nutrient soils (Dimassi et al., 2014), which may explain why the rhizosphere effects in July and

September were higher at 10–20 cm than at 0–10 cm (Fig. 4). Another reason may be the lower MBC at 10–20 cm soil, because soils with a higher MBC showed less priming compared to those with a lower MBC (Wang et al., 2015). These results suggest that microbes from deeper soil were less dependent on the C input derived from roots.

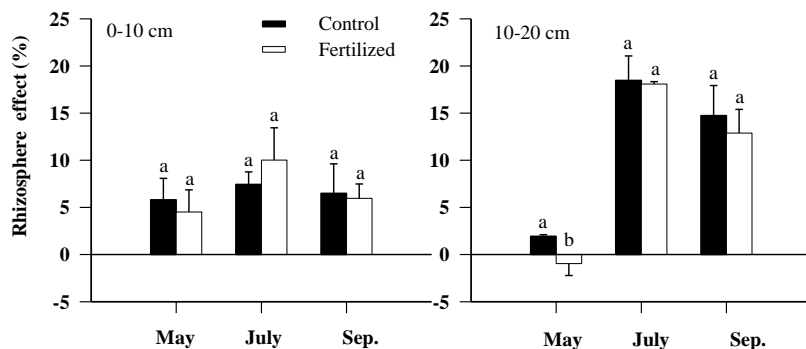


Figure 4. Effect of N fertilization on rhizosphere effect at surface and subsurface layer

Conclusion

In summary, there was no significant rhizosphere priming effect when there was no ongoing new C input to soil, even though soil rhizosphere microbial respiration was higher than bulk respiration. Nitrogen fertilization decreased soil bulk and rhizosphere microbial respiration, but did not influence the rhizosphere priming effect. Soil microbial biomass carbon and nitrogen contributed directly to soil microbial respiration. Moreover, soil total N and organic carbon content were associated with soil microbial respiration through soil microbial biomass. These results suggest that it is not the soil microbes in the rhizosphere that determined the occurrence of rhizosphere soil organic carbon decomposition (priming effect). Soil microbes may change their strategy for mining soil organic carbon under higher soil N availability.

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