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Autotrophic and heterotrophic components of soil respiration caused by rhizosphere priming effects in a plantation

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ABSTRACT

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Root-exudate inputs can stimulate the decomposition of soil organic carbon by priming microbial activity, but its ecological significance is still not fully understood. This study evaluated autotrophic respiration and heterotrophic respiration driven by roots using the ^{13}C natural abundance method in a *Robinia pseudoacacia* plantation. The results showed that the priming effect existed in deep soil of the plantation. The proportions of autotrophic respiration and heterotrophic respiration deriving from priming effect to total soil respiration varied with soil depth. Rhizomicrobial respiration (RMR) accounted for about 15% of the total soil respiration, and the rate of priming decomposition of soil organic matter (PSOM) was only about 5% of the total soil respiration. RMR was significantly positively correlated with PSOM. Heterotrophic respiration derived by the priming effect was too weak to have a positive impact on atmospheric CO_2.

Keywords: forest ecosystem; nutrient cycling; stable isotope; microorganism; carbon dioxide

Rhizosphere processes of plant-soil interactions control 50% of the total amount of CO_2 emission from the terrestrial ecosystem and affect nutrient cycling processes of the terrestrial ecosystem (Cheng et al. 2014). Thorough studies on soil priming effect have suggested that priming effect was a common phenomenon in soil and it was an important factor influencing on the decomposition of soil organic matter (SOM) (Kuzyakov 2010). Although there has been a general understanding on the occurrence of rhizosphere priming effect, its ecological significance is still not fully understood (Kuzyakov 2010).

The decomposition rate of SOM changes drastically due to the rhizosphere priming effect dependent on factors such as plant species, root morphology, the quantity and the quality of available soil substrate (Cheng et al. 2014). Autotrophic and heterotrophic respiration of the priming effect results in different feedbacks to atmospheric CO_2 concentration (Kuzyakov and Larionova 2005). Therefore, the study on rhizosphere priming effects of autotrophic and heterotrophic respiration will help us accurately assess carbon exchange between the terrestrial ecosystem and the atmosphere.

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Soil CO_2 flux can be separated into four components: root respiration; rhizomicrobial respiration (RMR); priming decomposition of SOM (PSOM), and decomposition of SOM (Kuzyakov 2006). Root respiration and RMR are driven by roots and they are called rhizosphere respiration (autotrophic respiration). PSOM together with decomposition of SOM are called heterotrophic respiration. Both RMR and PSOM are caused by the rhizosphere priming effect are produced by microorganisms. Nevertheless, RMR belongs to autotrophic respiration because some rhizomicroorganisms, especially endogenous fungi, directly use autotrophic photosynthate as a part of root (Kuzyakov and Larionova 2005). That is, RMR and PSOM are the autotrophic and heterotrophic components of soil respiration caused by rhizosphere priming effects (Kuzyakov 2006). Most of the studies on priming effect were carried out in the laboratory, and thus the results could not reflect the original ecological system (Kuzyakov 2010). So far, *in situ* study on partitioning CO_2 flux affected by the root in forests is scarce. The objectives of this study are: (1) to estimate CO_2 efflux of RMR and PSOM, and (2) to quantify the feedback of soil respiration derived by the priming effect on atmospheric CO_2 in the plantation.

MATERIAL AND METHODS

Site description. The experiment was conducted at the Xiaolangdi research station of forest ecosystem, located at the Jiyuan city, Henan province, China (35°01'N, 112°28'E, 410 m a.s.l.), with a warm temperate continental monsoon climate. The *Robinia pseudoacacia* plot was selected in the middle of the semi sunny slope.

Sampling and analysis. Soil gas sample was collected randomly from different soil depths by the soil air sampler during April–September, 2014. This equipment was drilled into the deep soil with a long thin steel tube. The end of the steel tube was filled with gauze hole. The air samplers were constructed according to the principle described by Song et al. (2016). After the gas sampling was completed, the soil and roots were sampled *in situ* from the same place where soil gas was sampled to make their $\delta^{13}C$ values comparable. Soil samples were collected in the controlled rootless (no tree) plots simultaneously. Three replicates were measured at each depth. The $\delta^{13}C$ values of CO_2, soil and root were measured using DELTA V advantage isotope ratio mass spectrometer (TFS Inc., Waltham, USA) as described by Song et al. (2016).

Respiration caused by priming effect. The contributions of root-derived autotrophic respiration (RDR) and SOM-derived heterotrophic respiration (SDR) to total soil respiration were calculated using a linear two source isotopic mixing model. At the deep soil depths (> 40 cm), the high $\delta^{13}C$ values resulted from C input of the original native land. Corn (C_4) was cropped for many years before land use conversed to a C_3 plantation.

$$f_{RDR} = (\delta^{13}C_G - \delta^{13}C_{SOM})/(\delta^{13}C_R - \delta^{13}C_{SOM}) \quad (1)$$

$$f_{SDR} = 1 - f_{RDR} \quad (2)$$

$$Q_T = Q_{RDR} + Q_{SDR} \quad (3)$$

Where: $\delta^{13}C_G$, $\delta^{13}C_{SOM}$, $\delta^{13}C_R$ – $\delta^{13}C$ values of soil CO_2, SOM-derived respiration and root-derived respiration; f_{RDR}, f_{SDR} – proportions of root-derived respiration and SOM-derived respiration to soil CO_2; Q_T, Q_{RDR}, Q_{SDR} – amount of total CO_2 effluxes, root-derived respiration and SOM-derived respiration (Pausch and Kuzyakov 2012).

Following the calculation method of Kuzyakov (2005), the proportion of RMR (f_{RMR}) is given as:

$$f_{RMR} = \frac{(\delta^{13}C_{MO} - \delta^{13}C_{SOM})(\delta^{13}C_G - \delta^{13}C_R)}{(\delta^{13}C_R - \delta^{13}C_{SOM})(\delta^{13}C_{MO} - \delta^{13}C_R)} \quad (4)$$

Where: $\delta^{13}C_{MO}$ – $\delta^{13}C$ value of SOM. The isotopic fractionation was considered as described by Werth and Kuzyakov (2009).

The fractionation caused by soil microbial respiration existed between the root and its reference SOM (Pausch and Kuzyakov 2012). Since the $\delta^{13}C$ value of the root was the same as that of root-derived CO_2, the fractionation of SOM in the rhizosphere resulted from heterotrophic decomposition (Werth and Kuzyakov 2010). Therefore, the amount of PSOM (Q_{PSOM}) can be calculated using the following mass balance:

$$F_{RS} = \delta^{13}C_{RSOM} - \delta^{13}C_R \quad (5)$$

$$\delta^{13}C_{RIR} = \delta^{13}C_R + F_{RS} \quad (6)$$

$$Q_{RMR} = f_{RMR}Q_T = f_{rh}Q_{RIR} \quad (7)$$

$$f_{rh} = (\delta^{13}C_{RIR} - \delta^{13}C_{SOM})/(\delta^{13}C_R - \delta^{13}C_{SOM}) \quad (8)$$

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$$Q_{PSOM} = Q_{RIR} - Q_{RMR} \tag{9}$$

Where: $\delta^{13}C_{RSOM}$, $\delta^{13}C_{RIR}$ – $\delta^{13}C$ values of SOM originate from roots and root-impacted respiration (i.e. RMR + PSOM); F_{RS} – fractionation between the rhizosphere and root-impacted respiration, or with the opposite sign, between the root and root reference SOM (Equations (5) and (6) are the mass balance); Q_{RMR}, Q_{RIR} – amounts of RMR and root-impacted respiration; f_{rh} – proportion of RMR to root-impacted respiration.

Statistics. The values presented in the figures are given as means ± standard errors of means (± SEM). The R package for SIAR was used as the method described by Parnell et al. (2010). Statistical analyses were performed with IBM SPSS statistics 19.0 (IBM Inc., New York, USA).

RESULTS AND DISCUSSION

Variations of rhizosphere priming respiration with soil depth. The proportions of RMR (f_{RMR}) and PSOM (f_{PSOM}) varied with depth and had a steep gradients (Figure 1). The ratio of C to N of SOM did not linearly vary with the depth (Figure 2), suggesting that the mobilization and accumulation of N changed with the depth (Song et al. 2017). The values of f_{RMR} and f_{PSOM} were affected by the available C and N of the soil in the *Robinia pseudoacacia* plantation. Rhizosphere priming effect was mainly controlled by the availability of soil nutrient (Dijkstra et al. 2013). Trees could more effectively transport photosynthetic products to the deep underground through the root, and hence causing a great priming effect that was significantly positively correlated with root exudates (Tefs and Gleixner 2012, Yin et al. 2014).

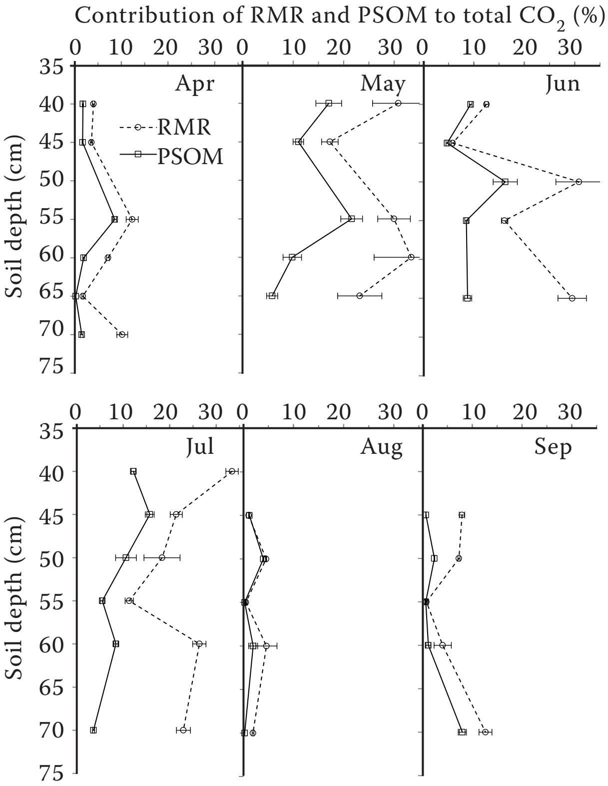

Figure 1. Variations of rhizomicrobial respiration proportion (f_{RMR}) and the priming decomposition of soil organic matter proportion (f_{PSOM}) with soil depth in the growing season

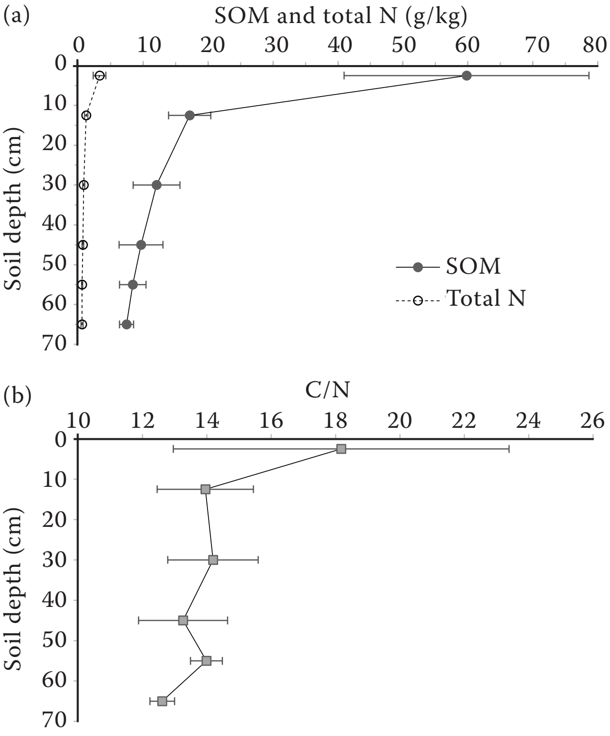

Figure 2. Variations of (a) soil organic matter (SOM) and total nitrogen (N) at the different soil depth and (b) the ratio of C to N (C/N) with soil depth

The relationship between the contribution of rhizosphere priming respiration to total soil respiration and soil depth could be explained by the competition between roots and rhizomicrobials for C and N in the rhizosphere. The plants add underground carbon inputs, promoting microbial decomposition of SOM to obtain more available nitrogen, and therefore resulting in positive priming effect (Phillips et al. 2011, Kuzyakov and Xu 2013). However, the negative priming effect occurred

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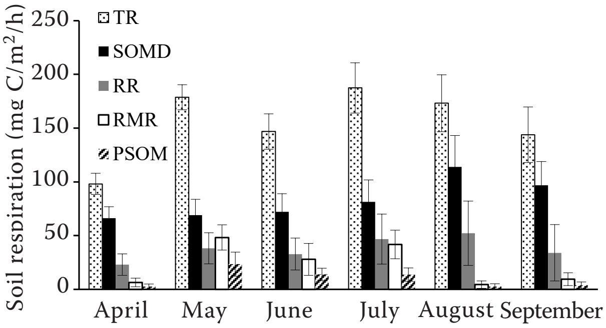

Figure 3. Seasonal variation of the rates of total soil respiration (TR); decomposition of soil organic matter (SOMD); root respiration (RR); rhizomicrobial respiration (RMR) and the priming decomposition of soil organic matter (PSOM)

in the rhizosphere when plants input excessive N (Dijkstra et al. 2013, Kuzyakov and Xu 2013). When the available N was appropriated at a certain depth, the ratio of C to N of SOM larger than the adjacent soil layers significantly, both f_{RMR} and f_{PSOM} increased under the conditions of positive priming effect. As the organic matter decomposes, the positive priming effect may turn to be the negative priming effect due to the change of the rhizosphere nutrient status. The decomposition rate of the organic matter will influence on both C and N pools at each of the depth. Hence, f_{RMR} and f_{PSOM} dynamically varied at different soil depth in the whole growing season (Figure 1).

The difference of $\delta^{13}C$ values between the root and SOM at the shallow depth (< 40 cm) was too small to partition soil respiration (Susfalk et al. 2002). On the other hand, the calculation of f_{RMR} in deep soil (> 70 cm) could fail due to inactive microbial biomass (Werth et al. 2006). As a result, only the values at the 40–70 cm soil depth were tested within the confidence interval in this study.

Rhizosphere priming effect on respiration in the growing season. Leaf area was small in April and so little organic matter was transported to the underground by roots, and presumably this caused a low rate of RMR and PSOM. In May, a large amount of photosynthetic product was probably transported to the underground by roots. The r-strategists of microorganism firstly used the rhizosphere matter and available nitrogen to obtain a rapid growth and turnover (Paterson et al. 2007, Moore-Kucera and Dick 2008). Consequently, the rate of RMR reached the maximum rapidly (Figure 3), while the k-strategists of microorganism were inhibited (Fontaine et al. 2011, Pascault et al. 2013, Cheng et al. 2014), the increasing rate of PSOM was less than that of RMR and the maximal difference between the rates of PSOM and RMR occurred in May (Figure 3). With the rapid consumption of the rhizodeposits, the microbial activity of r-strategists was limited. The microbial population and the activity of k-strategists increased, leading to a stable positive priming effect in the rhizosphere (Talbot et al. 2008, Fontaine et al. 2011). As a result, the rates of RMR and PSOM were high in June and July (Figure 3). In August and September, the rates of RMR and PSOM were low (Figure 3). It was because plants reduced the demand for N so that the growth of the root and the exudation of rhizodeposits gradually decreased, resulting in a low or negative rhizosphere priming effect (Pascault et al. 2013, Cheng et al. 2014).

The effect of RMR on net ecosystem productivity was ignored when soil respiration was partitioned, and thus the autotrophic respiration was underestimated (Kuzyakov and Larionova 2005). The rate of RMR accounted for about 15% of the total soil respiration and 40% of rhizosphere respiration in the growing season. Hence, the effect of RMR on CO_2 efflux cannot be ignored in the plantation (Figure 3). The proportion of PSOM to the total soil respiration was relatively small, only about 5% of the total soil respiration in the growing season (Figure 3). The rate of RMR was larger than that of PSOM and they were significantly positively correlated with each other (Figure 4). This indicates that the

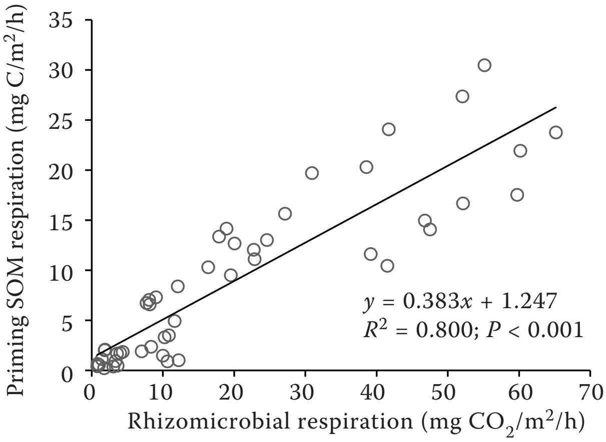

Figure 4. Relationship between rhizomicrobial respiration rate and the priming decomposition rate of soil organic matter

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rhizodeposits were the main carbon source of the rhizosphere microorganism, and the decomposition of SOM was a side-effect of N mineralization. In conclusion, heterotrophic respiration caused by priming effect was too weak, not leading to a positive feedback to atmospheric CO_2.

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