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Review Paper

Rhizosphere priming effect: A meta-analysis

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ABSTRACT

Rhizosphere priming is crucial for regulating soil carbon and nitrogen biogeochemical cycles. An appreciable number of studies have been conducted to quantify the rhizosphere priming effect (RPE), and have shown that the RPE is sensitive to changes of plant and soil conditions. These diverse results across individual studies offer us an opportunity to explore for potential general patterns and variability. In this study, we conducted a meta-analysis of RPE values taken from 31 publications. Our results showed that, on average, the RPE enhanced soil organic carbon mineralization rate by 59% across all studies. The magnitudes of the RPE significantly varied among plant types and soil texture. Within plant types, woody species showed the highest RPE followed by grasses while crops had the lowest level of the RPE, indicating that plant traits and physiology may exert important controls on the RPE. Soils with finer texture tended to produce stronger RPEs than soils with coarser texture, suggesting that interactions between the rhizosphere and the soil matrix may modulate the RPE. Furthermore, the level of the RPE is positively correlated with aboveground plant biomass, but surprisingly not with root biomass which is the commonly believed key variable for influencing the RPE. In addition, the RPE increased with the length of experimental duration, which implies that the RPE may persist much longer than previously believed because it impacts stabilized soil carbon more than labile carbon as the length of experimental duration increases. Overall, the results from this meta-analysis further illustrate several complex features of the RPE and call for future attentions to decipher this complexity.

1. Introduction

Over the past decade, evidence indicates that rhizosphere processes play a crucial role in regulating soil carbon cycle (Finzi et al., 2015). The presence of live roots can suppress soil organic matter (SOM) decomposition rates by 50% or stimulate it by 380%, when compared with soil incubations without plants (Cheng et al., 2014). This phenomenon is known as the rhizosphere priming effect (RPE). Hence, the magnitude of the RPE is similar to the effects of temperature and soil moisture on SOM decomposition (Zhu and Cheng, 2011). However, our current understanding on the RPE is still mostly based on scattered published results. A meta-analysis is needed to provide a quantitative assessment on the RPE.

The RPE is a change of SOM decomposition rate due to the presence of living roots and aboveground vegetation (Kuzyakov, 2002), while the general priming effect (PE) is a change of SOM decomposition rate due to substrate additions (Löhnis, 1926; Bingemann et al., 1953). The RPE is different from the general PE in several aspects. First, simple compounds such as glucose or amino acids are often used as the trigger substrates in studying the general PE, whereas, the commonly believed substrates causing the RPE are complex mixtures of root exudates and other rhizodeposits (Kuzyakov, 2010; Haichar et al., 2014). Second, in studies of the general PE, substrates are often added once at the beginning of the incubation (but see Qiao et al., 2014), while substrates are supplied continuously during plant growth in the case of the RPE. Third, the artificially created "hotspots" (i.e. locations) of the general PE are static, while the "hotspots" in the rhizosphere are moving through the soil matrix with root growth (Kuzyakov and Blagodatskaya, 2015). Fourth, and most importantly, the RPE occurs under a suite of physical, chemical, biological and environmental interactions between plants and soils (Cheng et al., 2014; Kuzyakov and Blagodatskaya, 2015), while the general PE is often observed as a much simpler response to substrate additions (Kuzyakov et al., 2000). Because of these differences between the RPE and the

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general PE, and because meta-analyses of the general PE have recently been published (e.g. Zhang et al., 2013; Luo et al., 2016), this study strictly focuses on quantitative analysis of the RPE.

Reports published in the literature have indicated that different plant species produced different RPEs when grown in the same soil. For example, results from one study suggested that soybean (*Glycine max*) had a consistently stronger RPE than did wheat (*Triticum aestivum*) (Cheng et al., 2003). Some studies showed that grassland and crop species grown under the same condition resulted in very different magnitudes and directions of RPEs (Dijkstra et al., 2010; Shahzad et al., 2015; Wang et al., 2016). To date, however, no systematic synthesis has been done on the role of plant species in regulating the RPE. Furthermore, plant biomass (i.e. root, shoot and total) appears to have a positive linear correlation with the RPE for two plant species (*Glycine max* and *Helianthus annuus*) (Dijkstra et al., 2006; Zhu and Cheng, 2013). However, the generality of this correlation has not been tested broadly.

Significantly different levels of RPEs can also occur when the same plant species is grown in different soils (Dijkstra et al., 2006), but which soil properties lead to the differences in RPEs is unclear. Soils with high SOM content have been hypothesized to have the potential for producing higher RPEs because soils with more organic matter tend to also have more labile carbon (Kuzyakov, 2002). However, this hypothesis requires further testing as some soil incubation studies have shown that priming may actually accelerate the decomposition of both labile carbon and stabilized carbon (Fontaine et al., 2007). Some soils with lower N contents tend to have higher RPEs (Dijkstra and Cheng, 2007). But results from N fertilization experiments have indicated an inconsistent role of soil N status in regulating RPEs (Liljeroth et al., 1994; Cheng et al., 2003; Hoosbeek et al., 2006; Kumar et al., 2016). Other soil factors (e.g., soil moisture, temperature, pH value and physical characters) may also have the potential to influence the RPE, because, so far, all investigated soil variables appear to act on RPEs (Cheng et al., 2014). Therefore, sorting out potential patterns about the relationships between the RPE and soil variables requires a comprehensive analysis using all results available.

The temporal dimension of the RPE is another potentially important aspect that may need a comprehensive analysis. Many studies report values of the RPE based on one or two measurements in short-term experiments with durations from weeks to a few months (e.g. Thurgood et al., 2014; Wang et al., 2016). Some longer-term studies have shown multiple RPE values during an entire growing season (e.g. Cheng et al., 2003; Shahzad et al., 2015; Mwafulirwa et al., 2016). Only two studies have experimental durations longer than a year (Bader and Cheng, 2007; Dijkstra and Cheng, 2007). Thus, it remains unclear how the length of the experimental durations may influence the reported RPE values.

Meta-analysis as an objective and quantitative methodology has complementary advantages of subjective and qualitative reviews. General reviews or syntheses on the RPE have recently been published (Dijkstra et al., 2013; Cheng et al., 2014; Finzi et al., 2015). However, meta-analysis on the RPE is lacking. In order to address the above-mentioned issues, we carried out a meta-analysis on the RPE with the following key objectives: (1) to evaluate the overall mean level of the RPE reported so far, (2) to seek relationships between the RPE and other variables (e.g., plant biomass and soil properties), and (3) to identify the time scale of the RPE. Specifically, we addressed the following research questions: (1) Is the RPE positively correlated with plant biomass (shoots, roots, and total)? (2) Do different groups of plant species (e.g., crops, grassland species, and woody species) tend to produce different levels of the RPE? (3) What soil properties show significant correlations with the RPE? and (4) Does the RPE change as the experimental duration increases?

2. Materials and methods

2.1. Data sources

In this meta-analysis, we searched for relevant articles in Web of Science database (publication years 1900–2016) using the "Advanced Search" feature and two search statements: (1) TS = rhizosphere AND TS = priming; and (2) TS = rhizosphere AND TS = decomposition AND TS = isotope ("TS", one of the "Field Tags" in the search engine, stands for "Topic"). A total of 232 articles were found by using the first search statement and 72 articles were found by using the second search statement. All found articles were further screened, and articles do not satisfy the following criteria were excluded from further analysis: (1) the article reports SOM-derived CO_2 release rate(s) separately from root-derived CO_2 (which includes rhizosphere microbial respiration utilizing rhizodeposits) using a ^{13}C or ^{14}C isotope technique; and (2) the study includes unplanted soil controls under the same environmental conditions as the planted treatments. Both criteria are required for quantitative determination of the RPE. Studies under wetland settings were also excluded (e.g. Wolf et al., 2007; Linkosalmi et al., 2015; Mueller et al., 2016), because of the drastically different soil water conditions. After these restrictions, a total of 191 quantitative measurements of the RPE from 31 published articles were identified as suitable for further analysis (Table S1).

For each study, we tabulated information on soil organic matter decomposition rates of both planted soils and unplanted soil controls (i.e. SOM-derived CO_2 efflux rates), their associated standard deviation and the sample size. We also collected other frequently reported information, including experimental settings, plant species, plant biomass, soil texture, soil organic carbon and nitrogen contents, pH, and microbial biomass (Table S2). Most of the RPE values were determined under controlled environmental conditions, so soil moisture, soil temperature and lighting intensity at the time of RPE measurements were not tabulate for further analyzing. When data were presented in figures in original publications, they were extracted by GetData (V2.20) software. In addition, we unified units among studies prior to statistical analysis.

Furthermore, for categorical variables, plant species were grouped into woody species, grassland species, crops and others; soil types were grouped according to soil texture: fine (clay loam, silty loam and loam) and coarse (sandy loam and loamy sand).

2.2. Statistical analysis

2.2.1. Average effect size of the RPE under plant and soil groups

We carried out meta-analysis using MetaWin software (Rosenberg et al., 2000) to assess the overall magnitude of the RPE as reported in the published literature and the relationship between the degree of the RPE and the associated categorical variables of plant groups and soil texture groups. Among the 191 data points of the RPE collected from 31 articles, some data points came from measurements at deferent time points (i.e. repeated measures) under the same treatment (e.g. plant species or soil type) in a particular experiment. As required by meta-analysis procedure (removal of time-dependency), we aggregated the data points from repeated measures using the following equation (Liao et al., 2008):

$$M = \sum_{i=1}^{j} \frac{Mi}{j},\ SD = \sqrt{\frac{\sum_{i=1}^{j} SD_i^2 (n_i - 1) n_i}{\left(\sum_{i=1}^{j} n_i - 1\right) \sum_{i=1}^{j} n_i}}$$

Where M is the overall aggregated mean for the particular treatment and SD is the associated standard deviation for M; j is the