

RESEARCH ARTICLE

The rhizosphere effect on soil gross nitrogen mineralization: A meta-analysis

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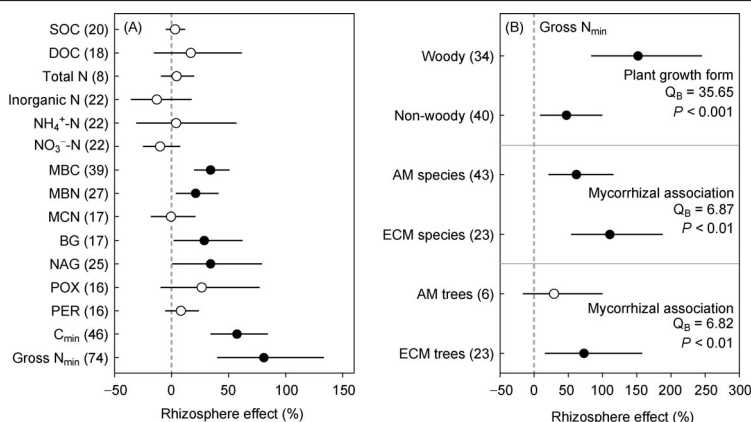
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HIGHLIGHTS

- We performed a meta-analysis to synthesize the rhizosphere effect on soil gross nitrogen mineralization rate.
- It was 81% on average, being significantly higher in woody (than non-woody species) and in ECM associated species (than AM associated species).
- It was positively correlated with the rhizosphere effects on soil C mineralization rate, microbial biomass nitrogen, phenol oxidase activity and root biomass.
- Its variations were mainly controlled by soil microbial variables and plant factors rather than climatic factors.

GRAPHICAL ABSTRACT



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ABSTRACT

Rhizosphere effects play crucial roles in determining soil carbon (C) and nitrogen (N) cycling. However, the rhizosphere effect on soil gross nitrogen (N) mineralization (N_{min}) has not been quantitatively assessed on the global scale. Here we performed a meta-analysis of compiled data from 24 publications and 37 species to synthesize the rhizosphere effect on soil gross N_{min} and its influencing factors. We found that the rhizosphere effect significantly enhanced soil gross N_{min} by 81% on average. Such rhizosphere effect was significantly higher in woody species than in non-woody species, and higher in ECM (ectomycorrhizal) associated species than in AM (arbuscular mycorrhizal) associated species. Moreover, the variations of the rhizosphere effect on soil gross N_{min} were correlated with those on soil C mineralization, phenol oxidase activity and root biomass rather than with other plant (growth form and mycorrhizal association) and climatic (mean annual temperature and precipitation) factors. These results support the 'microbial activation' and 'microbial N mining' hypotheses of rhizosphere effects and indicate the coupling of soil C and gross N mineralization in the rhizosphere. Overall, these findings provide novel insights into the rhizosphere effect on soil gross N_{min} among plant growth forms and mycorrhizal associations, and improve our mechanistic understanding of soil N dynamics in the rhizosphere.

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1 Introduction

It has been widely known that plant roots greatly affect soil carbon (C) and nutrient cycling in the rhizosphere through plant–soil interactions (Koranda et al., 2011; Kuzyakov and Xu, 2013; Cheng et al., 2014). The intense rhizosphere processes make a difference in physical, chemical or biological properties between rhizosphere soils and root-free bulk soils, which are described as rhizosphere effects (Phillips and Fahey, 2006; Finzi et al., 2015). Such effects are normally assessed via the comparison of soil organic matter (SOM) decomposition rate in the presence or absence of living roots (Cheng and Kuzyakov, 2005; Kuzyakov, 2010; Dijkstra et al., 2021), which is termed rhizosphere priming effect (RPE) (Kuzyakov, 2002; Cheng et al., 2014). Nitrogen (N) is widely regarded as the key limiting nutrient for plant growth in terrestrial ecosystems (Lebauer and Treseder, 2008; Frank and Groffman, 2009; Li et al., 2021), and soil N cycling is complicated, involving many simultaneously occurring transformation processes (Holz et al., 2016). Given the method challenges in measuring soil gross N mineralization rate (N_{\min}) (Murphy et al., 2003), there is much less attention about rhizosphere effects on soil gross N_{\min} compared to those on soil C mineralization rate (C_{\min}) (Kuzyakov, 2002; Booth et al., 2005; Zhu et al., 2014; Yin et al., 2018; Sun et al., 2021).

A recent meta-analysis assessed the direction and magnitude of rhizosphere effects on soil gross N_{\min} and other indices of C and N cycling mediated by microbes (Finzi et al., 2015). It showed that rhizosphere processes could accelerate soil N mineralization, and thus the rhizosphere effect on soil gross N_{\min} was significantly positive in all ecosystems. However, the sample size of soil gross N_{\min} was small ($n = 11$) and woody species ($n = 8$) dominated the database in that study (Finzi et al., 2015). Hence, a comprehensive and updated meta-analysis is urgently needed to consider the general patterns of rhizosphere effects on soil gross N_{\min} by including a larger number of species and more sufficient study cases.

Several mechanisms of RPEs have been proposed, while the rhizosphere effect on soil N mineralization remains poorly understood (Kuzyakov, 2010; Cheng et al., 2014; Yin et al., 2018). Generally, microbial physiology would change under distinct C-limited or N-limited conditions, thereby affecting SOM decomposition and N mineralization (Mo et al., 2021). The ‘microbial N mining’ hypothesis postulates that microbial enzyme production would increase to promote the availability of N released from SOM under nutrient-limited conditions (Craine et al., 2007; Fontaine et al., 2011). By contrast, the ‘microbial activation’ hypothesis states that root exudates act as a source of substrates for microbes, stimulate the growth of microbes to secrete more enzymes, and enhance the decomposition of SOM (Kuzyakov, 2002; Zhu et al., 2014). These two hypotheses could explain positive RPEs, while negative RPEs may be explained by the hypothesis of ‘preferential substrate utilization’ (Cheng, 1999; Dijkstra

et al., 2013). It demonstrates that the demand of microbes for nutrients is reduced when soil mineral N is rich. Microbes thereby prefer to utilize root exudates instead of recalcitrant SOM decomposition. Collectively, soil nutrient availability and microbes play an important role in the direction and magnitude of RPEs. Moreover, some case studies revealed a positive linear relationship between primed C_{\min} and primed gross N_{\min} (Dijkstra et al., 2009; Yin et al., 2018), indicating the coupled nature of C and N mineralization. Similarly, the relationships between rhizosphere effect on soil gross N_{\min} and that on soil and microbial variables (e.g., N availability, microbial biomass and enzyme activity) need further investigation.

In addition to soil factors (e.g., soil C and N availability), plant species and mycorrhizal associations could affect soil C and N cycling via rhizosphere effects (Cheng et al., 2003; Phillips and Fahey, 2006; Sun et al., 2014). Specifically, plant species own specific adaptive traits for resource acquisition and conservation, and participate in soil nutrient cycling (Hobbie, 1992; Maire et al., 2015). Hamer and Makeschin (2009) stated that plant species may alter rhizospheric microbial community composition, indirectly influencing soil N mineralization (Henneron et al., 2020). Moreover, mycorrhizal association has been increasingly recognized as an important root biotic trait for soil carbon and nutrient cycling (Colin-Belgrand et al., 2003; Weemstra et al., 2016). Plant species mainly associate with arbuscular mycorrhizal fungi (AM-associated species or AM species hereafter) or ectomycorrhizal fungi (ECM-associated species or ECM species hereafter). These two types of plants have distinct N acquisition strategies (Read and Perez-Moreno, 2003; Brzostek et al., 2013; Yin et al., 2014), possibly causing the difference in the magnitude and direction of rhizosphere effects. A previous study reported that ECM trees exhibit greater rhizosphere effects on net N_{\min} compared to AM trees (Phillips and Fahey, 2006). However, two recent studies (Chen et al., 2018b; Han et al., 2020a) found that rhizosphere effects on C_{\min} and net N_{\min} did not vary significantly between AM and ECM mycorrhizal groups in temperate forests. Therefore, a further comparison of rhizosphere effects among plant growth forms (woody species and non-woody species) and particularly mycorrhizal associations with more sufficient data should be performed. Furthermore, plant biomass and root morphology may directly or indirectly affect soil carbon-nutrient cycling (Han et al., 2020a; Sun et al., 2021). Some studies showed a positive link between plant biomass and RPE across different plant species (Dijkstra and Cheng, 2007; Huo et al., 2017; Yin et al., 2018). However, whether this correlation exists between the rhizosphere effect on gross N_{\min} and plant biomass remains unknown.

Here we conducted a meta-analysis to assess the rhizosphere effect on soil gross N_{\min} under different plant growth forms and mycorrhizal associations. Specifically, the aims of this study were to: (i) quantify the direction and magnitude of the rhizosphere effect on soil gross N_{\min} across and within plant growth forms and mycorrhizal associations; and

(ii) investigate how the rhizosphere effects on soil C and nutrient contents, microbial biomass and enzyme activities correlate with the rhizosphere effect on soil gross N_{min} across and within plant growth forms, mycorrhizal associations and plant biomass; and (iii) evaluate how soil, plant and climatic factors jointly influence the rhizosphere effect on soil gross N_{min} . We tested two specific hypotheses: 1) soil gross N_{min} would be accelerated due to rhizosphere effects and such effects would differ among plant growth forms and mycorrhizal associations; and 2) the rhizosphere effect on soil gross N_{min} would significantly correlate with the rhizosphere effects on soil microbial variables and plant factors which explain a larger proportion of the variations of the rhizosphere effect on soil gross N_{min} than climatic factors.

2 Materials and methods

2.1 Data collection

Data were collected from peer-reviewed journal articles, up to

March 1st, 2021. In this meta-analysis, we searched on the Web of Science (ISI) and China National Knowledge Infrastructure (CNKI), using the search terms (rhizosphere effect* OR rhizosphere soil) AND (soil gross nitrogen mineral* OR soil nitrogen flux* OR soil nitrogen cycling*). Four criteria were implemented to screen appropriate articles. (a) Gross nitrogen mineralization rate measured by the ^{15}N pool dilution method was reported. (b) The rhizosphere effects were directly reported, or paired rhizosphere and bulk soils were reported simultaneously at species level. Notably, some studies included treatments with and without roots, which were regarded as rhizosphere and bulk soils, respectively. (c) The means, standard deviations (SDs) or standard errors (SEs), and sample sizes of the target variables were reported in texts, tables or figures. Finally, 24 published articles were selected from 1243 references (Fig. 1).

We extracted the sample sizes, means and SDs (or SEs) of soil gross N_{min} in both rhizosphere and bulk soils. Moreover, some important variables such as soil chemical properties (soil organic C [SOC], dissolved organic C [DOC], total N, soil NH_4^+ -N, soil NO_3^- -N), microbial biomass (microbial biomass C [MBC],

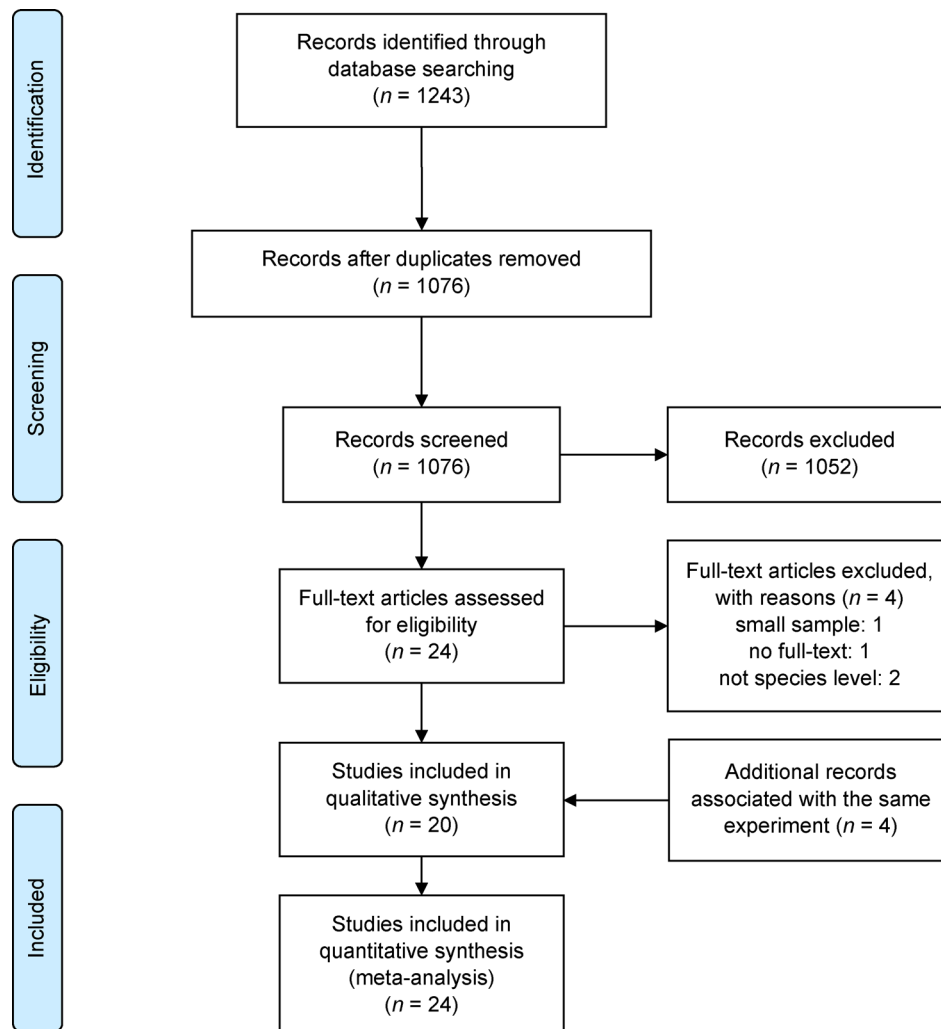


Fig. 1 Meta-analysis flow diagram.

microbial biomass N [MBN]), enzyme activities (β -1,4-glucosidase [BG], β -1,4-N-acetyl-glucosaminidase [NAG], phenol oxidase [POX] and peroxidase [PER]) and C_{\min} were collected. Most of the data would be directly attainable, and some in figures were obtained by the software GetData (version 2.25). In addition to these target variables, we also recorded the site information (latitude, longitude, mean annual temperature (MAT), mean annual precipitation (MAP)) and experiment information (experimental types, rhizosphere soil sampling methods; Table S1). The site information was obtained as much as possible from the original articles or relevant studies, otherwise they were searched from the climatic database at <https://power.larc.nasa.gov/data-access-viewer/>. For each species, plant growth forms were categorized as woody and non-woody. Mycorrhizal types were mainly categorized into arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM), which were confirmed according to Wang and Qiu (2006) and Soudzilovskaia et al. (2020). In case the mycorrhizal type of the species was not available, it was categorized according to the mycorrhizal type of other species in the same genus (Keller and Phillips, 2019; Soudzilovskaia et al., 2020). Notably, we regarded plant species having both AM and ECM fungal associations or unknown fungal associations as “others” (Table S2). We also collected other plant variables, including plant root biomass, shoot biomass and total biomass. Moreover, experiment types were divided into field (e.g., Meier et al., 2015) and pot/greenhouse (e.g., Zhu et al., 2014) in terms of experiment settings. The inconsistent sampling methods for rhizosphere soil may confound the real differences in rhizosphere effects within and among species. A previous study comparing different methods to measure rhizosphere effect showed that the root-shaking method generated stronger rhizosphere effects compared with the root-chamber method (Ding et al., 2019). Therefore, we divided soil sampling methods (rhizosphere and bulk soil separation method) into shaking (e.g., Phillips and Fahey, 2006) and other methods (others), according to the description of each study. The other methods include rhizobox (e.g., Pokharel et al., 2021) and distance measurement (e.g., Herman et al., 2006). In total, 37 species and 390 observations from 23 study sites were included in this meta-analysis. The distribution of study sites was created by the software ArcGIS (version 10.2.2) and presented in Fig. S1.

2.2 Statistical analysis

To indicate the rhizosphere effects on soil gross N_{\min} and other variables, we used the natural log of the response ratio (RR) as an effect size (Hedges et al., 1999; Luo et al., 2006):

$$RR = \ln\left(\frac{\overline{X}_R}{\overline{X}_B}\right) = \ln(\overline{X}_R) - \ln(\overline{X}_B) \quad (1)$$

where \overline{X}_R and \overline{X}_B are the mean values of a specific variable in rhizosphere soil and bulk soil, respectively. The corresponding pooled variance (v) was calculated as follows:

$$v = \frac{S_R^2}{n_R \overline{X}_R^2} + \frac{S_B^2}{n_B \overline{X}_B^2} \quad (2)$$

where n_R and n_B are the sample sizes; and S_R and S_B are the standard deviations of means in rhizosphere soil and bulk soil groups, respectively. For 3 studies that did not report SDs or SEs, we approximately assigned the SDs as the means of all other SDs (Bai et al., 2013; Feng and Zhu, 2019). Values of $RR > 0$ indicate positive rhizosphere effects, while values of $RR < 0$ indicate negative rhizosphere effects.

In some experiments, when data points were repeatedly measured at different times under the same treatment, they were aggregated by the following equations (Liao et al., 2008; Huo et al., 2017):

$$M = \sum_{i=1}^j \frac{M_i}{j} \quad (3)$$

$$SD = \sqrt{\frac{\sum_{i=1}^j SD_i^2 (n_i - 1) n_i}{(\sum_{i=1}^j n_i - 1) \sum_{i=1}^j n_i}} \quad (4)$$

where M is the overall aggregated mean and SD is the associated standard deviation under the particular treatment; j is the number of repeated measurement ($j \geq 2$), M_i , SD_i and n_i are the mean, standard deviation and sample size on the i th sampling time, respectively. After the removal of time-dependency, the pooled data points of soil gross N_{\min} for rhizosphere soil and bulk soil groups were reduced from 86 to 74.

The weighted response ratio (RR_{++}) and its corresponding 95% confidence intervals (CIs) were calculated using the *rma.mv* function in the ‘metafor’ package on mixed-effects model (Viechtbauer, 2010). For some case studies consisting of multiple experiment sites that may contribute more than one effect size, the variable “site” was set as a random factor in the model (Chen et al., 2018a; Feng and Zhu, 2021). The rhizosphere effect on a given variable was considered to be significant ($P < 0.05$) if the 95% CIs of RR_{++} did not overlap zero. To test whether rhizosphere effects differed in plant and mycorrhizal groups, the between-group heterogeneity (Q_B) test was performed. A significant Q_B indicates the rhizosphere effect shows significant differences among groups (Liu et al., 2016). For a better interpretation, the RR_{++} and its 95% CIs were transformed to the percentage change(%) by the following formula: $(\exp(RR_{++}) - 1) \times 100\%$. Such percentage change is equal to the rhizosphere effect (%) calculated by the relative change of a variable between paired rhizosphere and bulk soils ($[\text{rhizosphere} - \text{bulk}]/\text{bulk}$). Moreover, the publication bias was tested using Kendall’s tau rank correlation and Spearman’s rank correlation between individual response ratios and their corresponding variance of each variable (Dieleman and Janssens, 2011).

We first conducted the Pearson correlation analysis to explore the relationships between the rhizosphere effect on soil gross N_{\min} with bulk soil properties and rhizosphere effects on other biogeochemical variables. We also performed the simple linear regression analysis to examine the specific

relationships between the rhizosphere effect on soil gross N_{min} and certain soil variables (DOC, MBN, POX and C_{min}), plant variables (root biomass, shoot biomass and total biomass) and climatic variables (MAT and MAP), using the original value instead of aggregated value. Furthermore, a weighted random-forest analysis was carried out to identify the relative importance of the variables that influenced the rhizosphere effect on soil gross N_{min} , including soil continuous variables (e.g., rhizosphere effects on soil properties and microbial activities), plant variables (e.g., plant growth forms, mycorrhizal associations and root biomass) and climatic variables (MAT and MAP) (Jiao et al., 2018; Terrer et al., 2019; Han et al., 2020b). The importance of a variable was expressed as the increase in the mean square error (%IncMSE) and higher MSE% values implied more important predictors. All statistical analyses were performed using the R platform (version 3.6.2).

3 Results

3.1 Rhizosphere effects on soil gross N_{min}

Across all studies, soil gross N_{min} was significantly enhanced in rhizosphere soil compared to bulk soil, and the overall average rhizosphere effect was 81% with the 95% CIs from

40% to 134% ($n = 68$; Fig. 2). In addition, the rhizosphere effects on variables of soil biogeochemical processes were mostly positive, being significant for microbial biomass C (34%), microbial biomass N (21%), β -1,4-glucosidase (29%), β -1,4-N-acetyl-glucosaminidase (34%) and C_{min} (57%). However, the rhizosphere effects on other variables were non-significant (Fig. 2A).

There were significant differences in the rhizosphere effect on soil gross N_{min} among plant growth forms and mycorrhizal associations (Fig. 2B). The rhizosphere effect on soil gross N_{min} was larger in woody species (152%) compared to non-woody species (47%), and it was larger in ECM species (111%) than in AM species (62%). Similarly, ECM trees exhibited a stronger rhizosphere effect on soil gross N_{min} compared with AM trees (73% vs. 29%). In contrast, the rhizosphere effect on soil gross N_{min} did not vary with experimental types and soil sampling methods (Fig. S2). Notably, there was no significant publication bias for the rhizosphere effects on all variables (Table S3).

3.2 Factors influencing the rhizosphere effect on soil gross N_{min}

Correlation analysis showed that the rhizosphere effect on soil gross N_{min} had no significant correlation with the rhizosphere

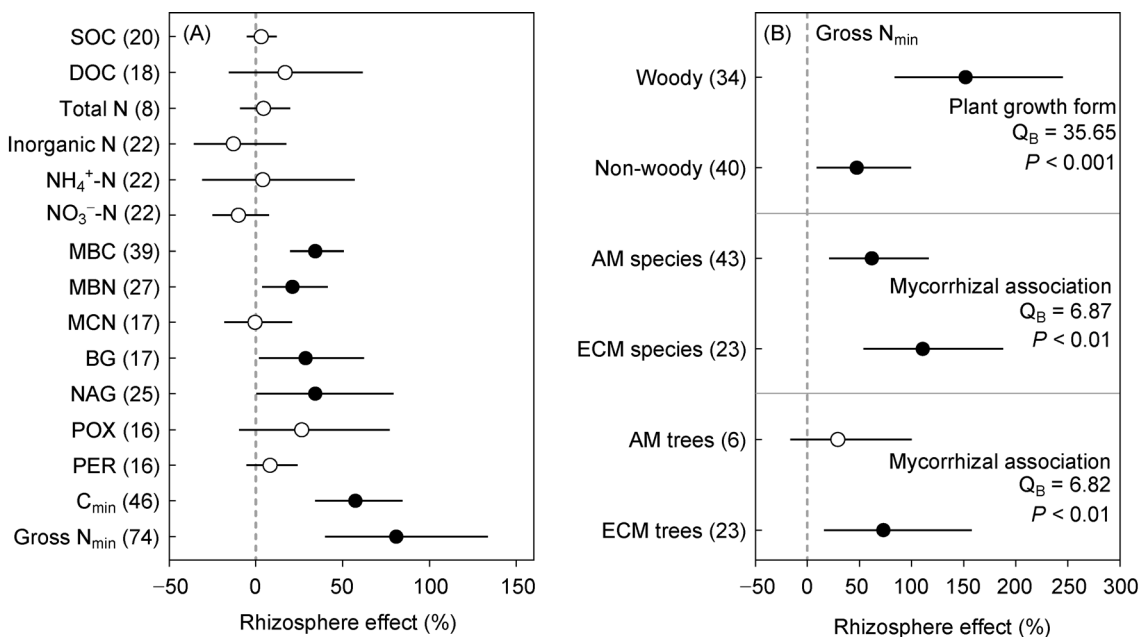


Fig. 2 Rhizosphere effects (%) on soil variables and biogeochemical processes. Rhizosphere effects (%) are calculated as the percentage change transformed by weighted response ratio, which is similar to the relative change between rhizosphere and bulk soils ([rhizosphere – bulk]/bulk). SOC: soil organic carbon (C), DOC: dissolve organic C, NH_4^+ -N: ammonium nitrogen (N), NO_3^- -N: nitrate N, MBC: microbial biomass C, MBN: microbial biomass N, BG: β -1,4-glucosidase, NAG: β -1,4-N-acetyl-glucosaminidase, POX: phenol oxidase, PER: peroxidase, C_{min} : C mineralization rate, N_{min} : N mineralization rate. The numbers in parentheses indicate sample sizes of observations. Plant growth forms represent woody and non-woody species. Mycorrhizal association represents arbuscular mycorrhizal (AM) and ectomycorrhizal (ECM) fungi. The sample size for each group is in parentheses. Error bars represent 95% confidence intervals (CIs) of weighted response ratio. If 95% CIs do not overlap with zero the rhizosphere effect is considered significant ($P < 0.05$, denoted by solid points), otherwise is considered nonsignificant ($P > 0.05$, denoted by open points). Q_B represents the heterogeneity in rhizosphere effect among groups, and the significant value of Q_B indicates significant differences among groups ($P < 0.05$).

effects on other soil variables (Table S4) or most properties of bulk soils (Table S5). The rhizosphere effect on soil gross N_{\min} had significantly positive relationships with the rhizosphere effects on soil dissolved organic C in non-woody species ($R^2 = 0.261$, $P = 0.011$; Fig. 3A) and AM species ($R^2 = 0.219$, $P = 0.033$; Fig. 3E). It was also positively correlated with the rhizosphere effects on microbial biomass N ($R^2 = 0.124$, $P = 0.038$) and phenol oxidase activity ($R^2 = 0.252$, $P = 0.048$) across all species (Fig. 3A, 3B). Furthermore, the rhizosphere effect on soil gross N_{\min} significantly increased with the rhizosphere effect on soil C_{\min} ($R^2 = 0.130$, $P = 0.005$; Fig. 3D). The positive relationships were consistent within each plant growth forms or AM species (Fig. 3D, 3H), but the regression slopes were different (woody>non-woody). The relationship between the rhizosphere effect on soil gross N_{\min} and root biomass was significantly positive ($R^2 = 0.117$, $P = 0.017$), but not for shoot biomass or total biomass (Fig. 4). Moreover, for climatic factors, the rhizosphere effect on soil gross N_{\min} had no significant correlation with MAT and MAP within and across different experimental types (Fig. S3).

Results from the weighted random forest analysis showed that the model explained 54% of the variations for the rhizosphere effect on soil gross N_{\min} (Fig. 5). Among the multiple variables, the significantly important moderates were the rhizosphere effect on soil C_{\min} (20% IncMSE, $P < 0.001$), phenol oxidase activity (13% IncMSE, $P < 0.001$) and root biomass (14% IncMSE, $P < 0.01$). Relatively, other variables such as climatic factors, plant growth forms and mycorrhizal associations were of minor importance.

4 Discussion

Based on 24 published studies, this meta-analysis provided a comprehensive synthesis of the rhizosphere effect on soil gross N_{\min} overall and across different plant growth forms (woody and non-woody) and mycorrhizal associations (AM and ECM). Consistent with previous studies, our results demonstrated that the rhizosphere effect on soil gross N_{\min} was significantly positive. It significantly varied among plant growth forms and mycorrhizal associations, but not among experimental settings (pot vs. field) and rhizosphere soil sampling methods (shaking vs. others). In addition, we highlighted the positive relationship between the rhizosphere effect on soil gross N_{\min} and the rhizosphere effect on soil C_{\min} within and across different types of plant growth forms. The rhizosphere effects on oxidative enzyme (phenol oxidase) activity, C_{\min} and root biomass were also important moderators affecting the variations in the rhizosphere effect on soil gross N_{\min} . Taken together, these novel findings reveal the changes and drivers in soil gross N_{\min} affected by rhizosphere processes, and improve our mechanistic understanding of soil nitrogen transformations in the rhizosphere.

4.1 Patterns of the rhizosphere effect on soil gross N_{\min}

In the presence of living roots, soil C decomposition and net N mineralization were often accelerated (Cheng and Kuzyakov, 2005; Finzi et al., 2015), while existing research focused much

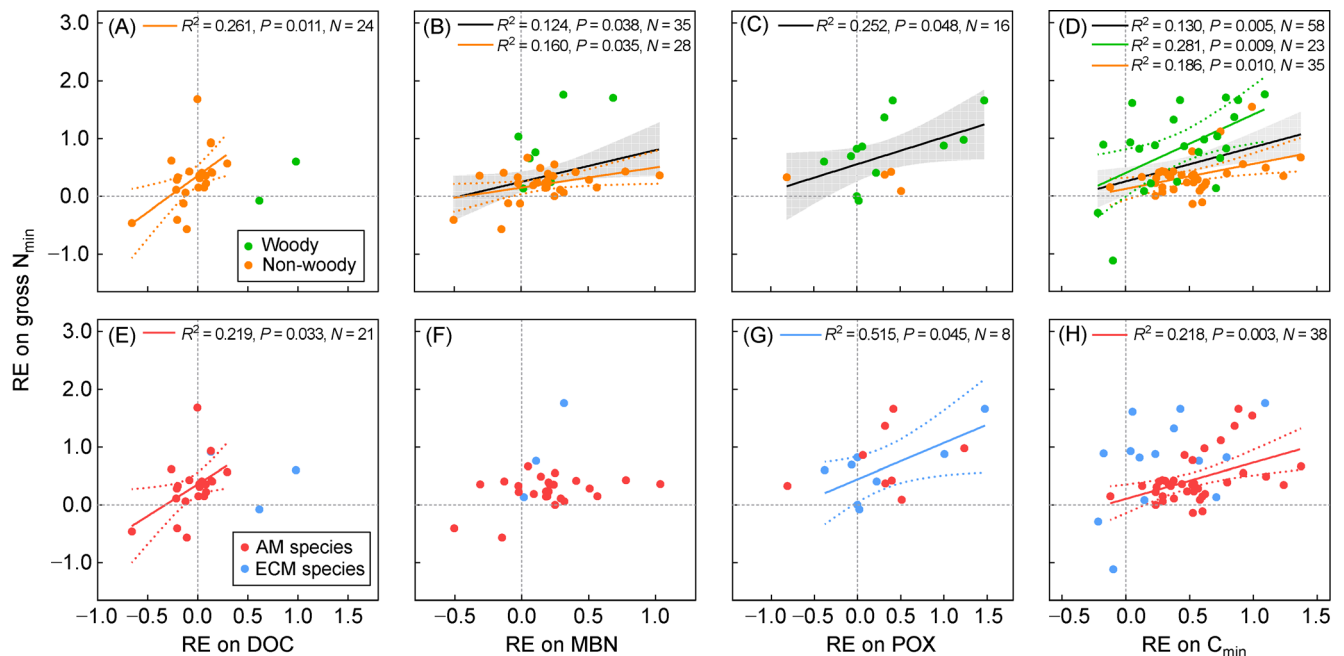


Fig. 3 Relationships of the rhizosphere effect (RE) on soil gross nitrogen mineralization rate (gross N_{\min}) with the rhizosphere effect on soil dissolved organic carbon (DOC), microbial biomass nitrogen (MBC), phenol oxidase (POX) and carbon mineralization rate (C_{\min}) across and within plant growth forms and mycorrhizal types. The RE is calculated as the natural log-transformed response ratio of rhizosphere to bulk soil. Grey area represents 95% confidence intervals and only significant relations ($P < 0.05$) are drawn with regression lines.

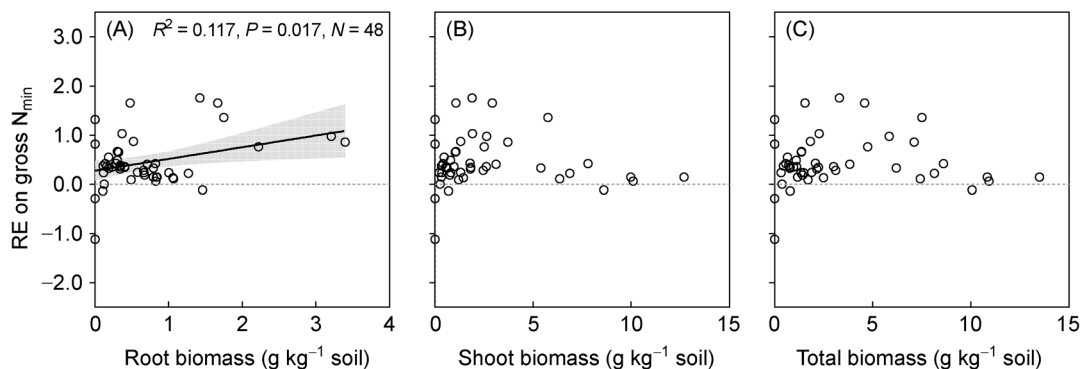


Fig. 4 Relationships of the rhizosphere effect (RE) on soil gross nitrogen mineralization rate (gross N_{\min}) with plant biomass (root, shoot and total). The RE is calculated as the natural log-transformed response ratio of rhizosphere to bulk soil. Grey area represents 95% confidence intervals and only significant relations ($P < 0.05$) are drawn with regression lines.

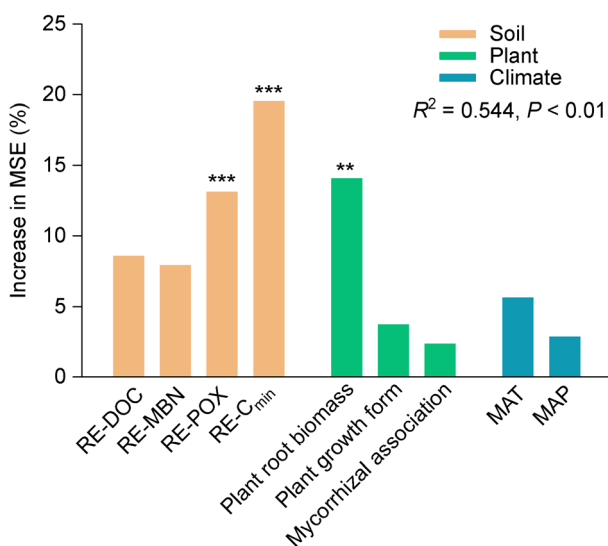


Fig. 5 Variable importance of moderators for the rhizosphere effects (RE) on soil gross mineralization rate (gross N_{\min}). Importance values are derived from a weighted random-forest analysis including variables as moderators. Percentage increases in the MSE (mean squared error) of variables were used to evaluate the importance of these predictors. DOC, soil dissolved organic carbon; MBN, microbial biomass nitrogen; POX, phenol oxidase; C_{\min} , soil carbon mineralization rate; Plant growth form (woody and non-woody); Mycorrhizal association (arbuscular mycorrhizal, ectomycorrhizal); MAT, mean annual temperature; MAP, mean annual precipitation. Significance levels are as follows: * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

less on soil gross N_{\min} in the rhizosphere. Our meta-analysis showed that the rhizosphere effect on soil gross N_{\min} was significantly positive, with an increase of 81% on average compared to bulk soil ($n = 74$; Fig. 2). These results were consistent with our first hypothesis that rhizosphere effects tend to accelerate soil biogeochemical processes (particularly gross N mineralization). In comparison, the rhizosphere effect on soil gross N_{\min} in this study was lower than the result (102%, $n = 11$) in a previous work (Finzi et al., 2015). Such

difference might be partly caused by the enlarged sample size of our database (74 vs. 11). Among the C and N cycling variables associated with soil gross N_{\min} , microbial biomass (especially MBN) and enzyme activities (especially β -1,4-N-acetyl-glucosaminidase) tended to show positive rhizosphere effects (Fig. 2A). This result indicated that microbial growth and enzyme activities were stimulated by rhizosphere processes to release mineral N from SOM, which supports the 'microbial activation' hypothesis (Kuzyakov, 2002; Cheng and Kuzyakov, 2005; Kuzyakov, 2010). Specifically, the plant releases labile C substrates to the rhizosphere through root exudates and litter, stimulating the rhizosphere-associated microbial growth (Dijkstra and Cheng, 2007). In this case, microbes could produce more extracellular enzymes to access soil available N by increasing N mineralization rate (Schimel and Bennett, 2004). Thus, the N mineralization rate was higher in the rhizosphere soil compared to the bulk soil, especially in N-limiting conditions (Zhu and Cheng, 2012; Blaško et al., 2013). Moreover, many studies have reported that the C mineralization rate was stimulated in the rhizosphere and the rhizosphere effect on C_{\min} tended to be positive (Kuzyakov, 2002; Cheng and Kuzyakov, 2005; Cheng et al., 2014). Consistent with these studies, we found that the magnitude of rhizosphere effect on C_{\min} was 57% (Fig. 2A). These results demonstrate that the rhizosphere is a hotspot for SOM turnover, and root stimulation of organic matter turnover is an effective way to supply the needed nutrients of plants (Kuzyakov and Blagodatskaya, 2015).

Among plant growth forms, the rhizosphere effects on soil gross N_{\min} were all positive and the magnitude of such rhizosphere effects appeared significantly different from each other (Fig. 2B). Woody species tended to exhibit stronger rhizosphere effects than non-woody species. There were two possible explanations for this result. On one hand, there were significant differences in root morphology, physiology and nutrient requirements among plant life forms (Jones et al., 2004), which may lead to species-specific rhizosphere effects on nutrient cycling (Kuzyakov, 2002). On the other hand, woody species roots were mostly associated with ECM, while non-woody species roots were associated with AM in our data

set. Generally, ECM species would generate greater rhizosphere effects on soil gross N_{min} than AM species (Fig. 2B), thus the stronger rhizosphere effects occurred in woody species may be partly caused by the mycorrhizal association of woody plants (predominantly ECM) in this study. Furthermore, our results showed that the rhizosphere effect on soil gross N_{min} positively correlated to the rhizosphere effect on C_{min} for all plant growth forms (Fig. 3D), suggesting the strong coupling between soil C and gross N mineralization in the rhizosphere (Dijkstra et al., 2009; Zhu et al., 2014).

Plant mycorrhizal associations (particularly AM vs. ECM) have been proposed to affect belowground resource-acquisition strategies (Bergmann et al., 2020; Han and Zhu, 2021), and the different turnover rates of fungal hyphae could influence the magnitude of rhizosphere effects (Phillips and Fahey, 2006). However, the underlying mechanisms of mycorrhizal effects on rhizosphere processes remain elusive (Lin et al., 2017). Our results showed that the rhizosphere effect on soil gross N_{min} was significantly higher under ECM species than under AM species. This difference was also observed in the same plant growth form (woody species) but with different mycorrhizal associations (AM trees vs. ECM trees, Fig. 2B). Earlier studies found that ECM tree species generated greater rhizosphere effects than AM tree species due to their higher root exudation rates and different microbial community composition (Phillips and Fahey, 2006; Yin et al., 2014; Brzostek et al., 2015). Furthermore, the rhizosphere effect on soil gross N_{min} positively correlated with the rhizosphere effect on soil phenol oxidase activity in ECM species, but not in AM species (Fig. 4C). Likely, ECM roots had stronger abilities to release oxidative enzymes (Frank and Groffman, 2009; Lindahl and Tunlid, 2015), thereby leading to the greater rhizosphere effect on soil gross N_{min} in ECM species compared to that in AM species.

4.2 Potential influencing factors for the rhizosphere effect on soil gross N_{min}

There are many factors potentially affecting the rhizosphere effect, including biotic and abiotic factors (Kuzyakov, 2010; Cheng et al., 2014; Sun et al., 2014). Here we focused on soil biogeochemical variables, plant traits and climatic factors for the rhizosphere effect on soil gross N_{min} . For soil properties, our results showed that the rhizosphere effect on soil dissolved organic C significantly and positively correlated with the rhizosphere effect on soil gross N_{min} in non-woody species (Fig. 3A, Table S3), suggesting that DOC as substrate for microbial growth could facilitate microbial N mineralization. Moreover, the rhizosphere effect on soil gross N_{min} did not show significant correlations with inorganic N in the bulk soil (Table S5) or the rhizosphere effect on inorganic N (Table S4). These results seem to be inconsistent with the 'N mining' hypothesis (Craine et al., 2007; Fontaine et al., 2011; Dijkstra et al., 2013) which posits that the rhizosphere effect on soil gross N_{min} would be stronger in more N-limited soils.

However, this result should be interpreted with caution because 1) extractable inorganic N may not be a good indicator of N availability among different soil types (Van Sundert et al., 2020), and 2) other co-varying factors may mask the relationship between soil N availability and the rhizosphere effect on soil gross N_{min} (Dijkstra et al., 2013).

Moreover, we found positive relationships between the rhizosphere effect on soil gross N_{min} and the rhizosphere effects on microbial variables such as microbial biomass N and phenol oxidase activity (Fig. 3B, 3C), indicating that rhizosphere microbes could regulate soil gross N_{min} according to their nutrient demand. These results are consistent with the 'microbial N mining' hypothesis. The oxidative enzyme (phenol oxidase) was linked to the degradation of recalcitrant SOM and changes in its activity may have significant impact on soil N mineralization (Zhu et al., 2014; Meier et al., 2015). Moreover, consistent with our results, increasing case studies demonstrated that the positive rhizosphere priming of SOM decomposition would also enhance soil gross N_{min} , and the rhizosphere effect on SOM decomposition was proportional to that on soil gross N_{min} (Zhu et al., 2014; Murphy et al., 2015; Yin et al., 2018; Jiang et al., 2021; Mo et al., 2021). In addition, climatic factors (MAT and MAP) might indirectly control the rhizosphere effect on soil gross N_{min} . However, the rhizosphere effect on soil gross N_{min} exhibited not significant relationships with MAT and MAP (Fig. S3), and MAT and MAP were not strong moderators of the rhizosphere effect on soil gross N_{min} when considering other factors such as soil and plant characteristics in the full random forest model (Fig. 5). These results suggest that climate is less important than soil microbial variables (e.g., C_{min} and oxidase) in explaining the large-scale variations of the rhizosphere effect on soil gross N_{min} . Given the relatively small coverage of climate and region in this study (Fig. S1), the role of climate on the spatial variation of rhizosphere effect on soil gross N_{min} awaits further study with more data from less-sampled regions.

Plant root traits are closely linked to rhizosphere processes, and hence may influence soil belowground processes (Bardgett et al., 2014). Our results showed that the rhizosphere effect on gross N_{min} had significant correlations with plant root biomass, while the correlations with plant shoot biomass and total biomass were not significant (Fig. 4). Similarly, previous studies found the RPE was positively correlated with root biomass. (Fu and Cheng, 2002; Dijkstra et al., 2006; Yin et al., 2018). These findings suggest that the rhizodeposition and root biomass could control rhizosphere effects on soil C and N mineralization.

Collectively, the regulation of different moderators for the rhizosphere effect on soil gross N_{min} was assessed by a random forest model. Consistent with our second hypothesis, the rhizosphere effects on C_{min} , phenol oxidase and root biomass were the three most important regulators of the rhizosphere effect on soil gross N_{min} (Fig. 5). This result suggested the dominant role of soil microbes in influencing soil gross N_{min} and the coupled relationships between C and gross N mineralization (Hart et al., 1994; Booth et al., 2005).

The rhizosphere effect on oxidative enzymes was more important to the rhizosphere effect on soil gross N_{\min} , compared to the rhizosphere effect on hydrolytic enzymes, which supports earlier studies (Zhu et al., 2014; Yin et al., 2018). Moreover, our results showed that root biomass also significantly correlated with the rhizosphere effect on soil gross N_{\min} in the model. There were significant differences in the rhizosphere effect on soil gross N_{\min} among plant growth forms and mycorrhizal associations. But compared to soil microbial factors, these plant factors and climatic factors were poor predictors and appeared less important. It should be noted that recent studies reported that plant species with different economic strategies could regulate soil C and N cycling through their rhizosphere effects (Han et al., 2020a; Henneron et al., 2020), providing evidence that plant traits other than growth forms and mycorrhizal associations should be paid attention to in future studies on rhizosphere effects.

5 Conclusions

Our meta-analysis quantitatively assessed the patterns of the rhizosphere effect on soil gross N_{\min} and compared their differences among plant growth forms and mycorrhizal associations. These results highlight that the rhizosphere process can accelerate soil gross N mineralization rate and related microbial variables (biomass and enzyme), indicating that rhizosphere effects play important roles in driving below-ground biogeochemical processes. The rhizosphere effect on soil gross N_{\min} was 81% on average, and it differed greatly among plant growth forms (woody > non-woody) and mycorrhizal associations (ECM > AM). The rhizosphere effect on soil gross N_{\min} significantly correlated with the rhizosphere effect on soil microbial biomass nitrogen and plant root biomass. Specifically, the rhizosphere effect on soil gross N_{\min} was mainly influenced by the rhizosphere effects on phenol oxidase and C_{\min} rather than by other plant (growth form and mycorrhizal association) and climatic (MAT and MAP) factors. However, as soil N mineralization and immobilization occur simultaneously, further studies should consider multiple N transformation processes comprehensively in the rhizosphere (Frank and Groffman, 2009). Moreover, further studies should explore the relative roles of plant functional traits (including leaf, fungal and root traits), soil physico-chemical and microbial properties, and environmental conditions in influencing the variations of rhizosphere effects. Taken together, these results could enrich our understanding of how rhizosphere effects regulate belowground C and N cycling in terrestrial ecosystems on a large scale, and also contribute to development of ecosystem models that consider plant-microbe interactions in the rhizosphere.

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Electronic supplementary material

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