

Response of soil respiration under different mycorrhizal strategies to precipitation and temperature

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Abstract

The symbiotic associations between plant roots and mycorrhizal fungi are almost ubiquitous. These interactions can produce a large amount of soil respiration (R_s) and respond strongly to such climatic changes as temperature and precipitation. The objective of the present study was to explore how interannual variations in environmental factors (i.e., temperature and precipitation) and biotic factors (leaf area index, LAI) influence soil respiration and its temperature sensitivity (apparent Q_{10}) in global forest ecosystems that are classified by the mycorrhizae of the dominant plants. Based on a global forest database, the mycorrhizal strategy of tree species over 200 site-years was determined. The R_s on the global scale was largely controlled by temperature. When the mycorrhizal strategy was considered, the responses of the R_s to the mean annual temperature (MAT), mean annual precipitation (MAP) and LAI were highly variable among different mycorrhizal strategies. For example, the R_s was explained mainly by the LAI for arbuscular mycorrhizal (AM) and AM+ ectomycorrhizal (ECM) types and by the MAT for ECM and ECM+EEM (ectendomycorrhizal) +NM (non-mycorrhizal) types. The apparent Q_{10} of the R_s was not significantly different. This study was the first to evaluate the influence of different mycorrhizal strategies on forest R_s on the global scale. The mycorrhizal strategy plays an important role in the interpretation of the current soil respiration data.

Keywords: Soil respiration, mycorrhizal strategy, temperature, precipitation, leaf area index.

1. Introduction

After photosynthesis, soil respiration (R_s) accounts for the second largest carbon (C) flux in most ecosystems: 60–90% of the total ecosystem respiration (Longdoz *et al.*, 2000). Forest soil respiration arising from root activity and the associated mycorrhizal fungi (Hanson *et al.*, 2000; Subke *et al.*, 2006) is the primary pathway by which plant-fixed carbon dioxide (CO_2) is released back into the atmosphere (Gaumont-Guay *et al.*, 2009). Because of the large annual carbon fluxes between forest ecosystems and the atmosphere (Bonan, 2008), these ecosystems are likely to influence the global carbon balance in response to the projected climate change (Savage *et al.*, 2008). The realization that soils are a possible source of atmospheric CO_2 , together with the continuous increase in atmospheric CO_2 concentrations, has led to enormous interest from numerous ecologists (Raich *et al.*, 2002; Gaumont-Guay *et al.*, 2009). R_s , as the most uncertain component of many climate change models (Jones *et al.*, 2003), is influenced by many factors, e.g., the temperature, precipitation and leaf area index (LAI) (Reichstein *et al.*, 2003), but the effect of biological variables on respiration and the interaction of biotic and abiotic factors remain poorly understood on the global scale.

Mycorrhizal fungi play crucial roles in the regulation of terrestrial CO_2 fluxes (Zhu and Miller, 2003); these fungi are obligate symbionts that form mutualistic relationships with plant roots known as a mycorrhiza. In terrestrial ecosystems, symbiotic associations between plant roots and mycorrhizal fungi are nearly ubiquitous, with 90% of all plant species forming mycorrhizae (Smith and Read, 2008). Indeed, the prevalence of these relationships has led to the assertion that “the majority of plants, strictly speaking, do not have roots; they have mycorrhizae” (<http://www.kent.ac.uk/bio/beg/>). Mycorrhizal fungi receive carbon from their host plants (Hobbie, 2006) in exchange for nutrient transfer to the roots, which benefits plant growth. Previous studies have demonstrated the roles of mycorrhizae in soil respiration (Högberg *et al.*, 2001; Langley *et*

al., 2005; Heinemeyer *et al.*, 2007; Moyano *et al.*, 2008; Vargas and Allen, 2008). Although respiratory CO_2 release from mycorrhizae might be greater than from non-mycorrhizal roots (Valentine and Kleinert, 2007; Nottingham *et al.*, 2010), the mycorrhizal status is rarely considered when examining the scaling relationships between the R_s and its impact factors. The global predominance of mycorrhizal associations and their key role in soil C input means that the mycorrhizal influence on the R_s represents an important deficiency in our knowledge.

Previous studies have focused on how environmental and biological factors i.e., temperature, precipitation and LAI influence soil respiration (Reichstein *et al.*, 2003; Bond-Lamberty and Thomson, 2010; Wang *et al.*, 2010) at large, even global scales. These studies have focused on the categorical classifications by forest type (e.g., evergreen forests and deciduous forests; conifer forests and deciduous forests) (Luyssaert *et al.*, 2007) or biome (e.g., boreal, temperate and tropical) (Bond-Lamberty and Thomson, 2010) but have ignored the potential role of the belowground interactions and feedbacks that may influence the R_s . Consequently, it is unclear whether environmental factors influence R_s differently in vegetation types dominated by different mycorrhizal plants across large geographical distances. The failure to examine properly the role of colonization in determining root respiration means that the current interpretations of the root and soil respiration data might be flawed.

In this study, we use a recently compiled global forest C-flux database (Luyssaert *et al.*, 2007) to investigate the dependency of the forest annual R_s on the temperature, precipitation and LAI. With this information, we classified the study sites by the mycorrhizal strategy of their dominant plants. We expect that classifying those sites according to their dominant mycorrhizal strategy will provide a new insight into how to incorporate other belowground factors in global climate research.

The goal of this study was to improve the understanding of the functional role of mycorrhizal associations in soil respiration. We hypothesize that the temperature, precipitation and LAI may differentially regulate R_s in different mycorrhizal strategy-dominated systems. We expect that patterns may emerge across large geographical distances in forests dominated by different mycorrhizal strategies.

2. Materials and Methods

Data sets

This work is based on a global forest C-flux database developed by Luyssaert *et al.* (2007), which included forest carbon-flux data of tree species, R_s , LAI, mean annual temperature (MAT) and mean annual precipitation (MAP). The mycorrhizal strategy of each species was ascertained and classified according to published literature (e.g., Smith and Read, 2008). When tree species were reported to associate with more than one mycorrhizal type, they were classified as an A mycorrhizal type+B mycorrhizal type+C mycorrhizal type+D mycorrhizal type combination. For example, a tree was classified as an arbuscular mycorrhiza (AM) + ectomycorrhiza (ECM) combination when it was reported to associate with both AM and ECM mycorrhizal fungi. The mycorrhizal strategy of 257 site-year tree species was cleared, including the following 7 mycorrhizal strategies: (1) AM (45); (2) AM+ECM (62); (3) AM+ECM+EEM (ectendomycorrhiza) (3); (4) AM+ECM+EEM+NM (non-mycorrhiza) (4); (5) ECM (102); (6) ECM+EEM (23); and (7) ECM+EEM+NM (18). Both AM+ECM+EEM and AM+ECM+EEM+NM types were removed because of insufficient data. We then matched the mycorrhizal type with the R_s . In total, five mycorrhizal strategies, including (1) AM (41), (2) AM+ECM (44), (3) ECM (86), (4) ECM+EEM (12), and (5) ECM+EEM+NM (17), were used in this study because of the default of R_s data. Fur-

thermore, the relationship between the LAI and R_s was analyzed under different mycorrhizal strategies.

Data analysis

At the global scale, the R_s is linearly correlated with the MAT and MAP (Schimel *et al.*, 2001; Raich *et al.*, 2002; Wang *et al.*, 2010). To test whether the response of the R_s to the MAT varied depending on different mycorrhizal strategies and whether they presented a linear correlation, we analyzed their relationship using the linear and exponential regression of the SPSS software package version 13.0 (SPSS, Chicago, IL). We also analyzed the data using linear regression to characterize the responses of the R_s to the MAP and LAI under different mycorrhizal strategies.

To test for differences of the temperature sensitivity (apparent Q_{10}) of the R_s under mycorrhizal strategies, the apparent Q_{10} of all site-years and each mycorrhizal type were calculated by the MAT. The apparent Q_{10} values were subjected to a Chi-Square Test under the different mycorrhizal-strategy forests to examine whether the variability depended on the mycorrhizal strategies of the tree species.

3. Results

When all of the mycorrhizal-type forests were considered, the R_s increased significantly with increasing MAT, with a linear regression of $R_s^2=0.2421$ ($p<0.001$) and an exponential regression of $R_s^2=0.2562$ ($p<0.001$) (Figure 2). The exponential model simulated the relationship between MAT and R_s better than the linear model. Regarding the different mycorrhizal strategy-dominated forests, the MAT markedly influenced the R_s in the forests associated with AM+ECM, ECM, and ECM+EEM+NM mycorrhizal types (Figure 2). The effect of the MAT explained the variation of 42%, 34% and 39% of the R_s in the AM+ECM, ECM, and ECM+EEM+NM forests,

whereas no significant correlation between the MAT and R_s was observed in the AM- and ECM+EEM+NM-dominated forests. In contrast, the linear model was more suit-

able for AM and AM+ECM than the exponential model. Conversely, the exponential model better explained the ECM, ECM+EEM and ECM+EEM+NM types.

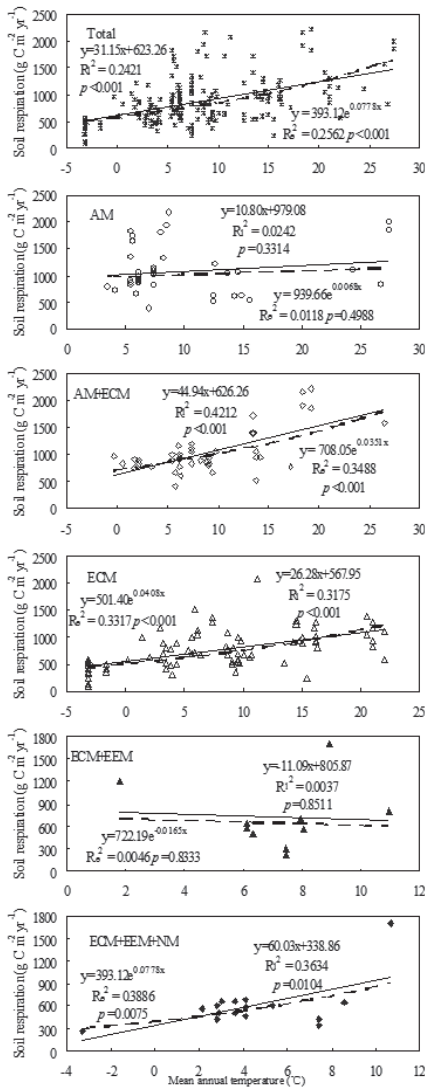


Figure 1. Relationship between soil respiration and mean annual temperature under different mycorrhizal strategy-dominated forests. The real and broken lines indicate linear and exponential regression, respectively.

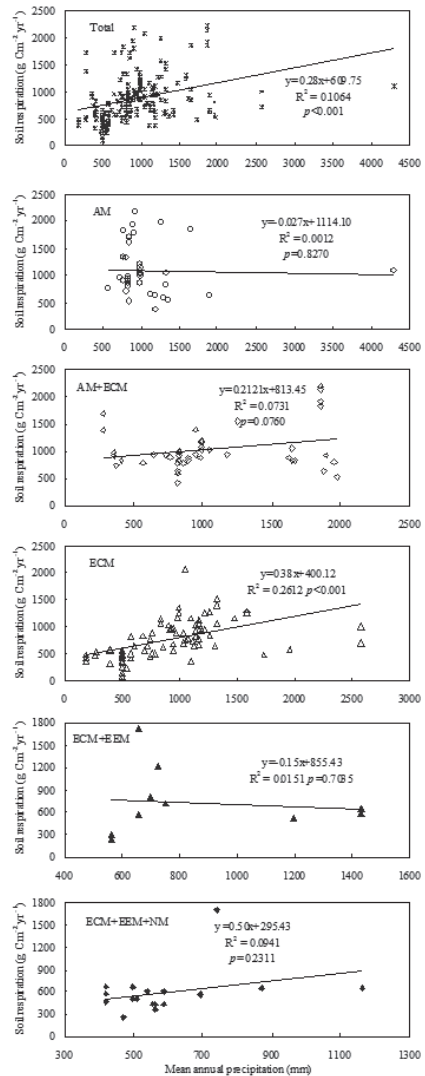


Figure 2. Relationship between soil respiration and mean annual precipitation under different mycorrhizal strategy-dominated forests.

Similar to the MAT, the R_s responded linearly to the MAP for all of the site-years, although it only explained 11% ($p < 0.001$) of the variation of R_s (Figure 3). When different mycorrhizal-type forests were considered, the effect of the MAP on the R_s was only significant in the ECM ($R^2 = 0.2612, p < 0.001$) forest. In contrast, when only the ECM type affected by both the MAT and MAP was considered, the effect of the MAT explained 8% more of the variation in the R_s than the effect of the MAP. There were no significant linear relationships between the MAP and R_s in the other four mycorrhizal-type forests.

Although the R_s increased significantly with an enhancement of the LAI, the R_s presented a weak correlation with the LAI ($R^2 = 0.0614, p = 0.0129$) (Figure 3). The effect of the LAI on the R_s was strong in the AM, AM+ECM and ECM forest types, explaining 68%, 61%, and 23% of the R_s variations, respectively. Unlike the AM+ECM and ECM forests, a significant negative effect of the LAI on the R_s ($R^2 = 0.6792, p < 0.001$) was found for the AM-dominated forest (Figure 3).

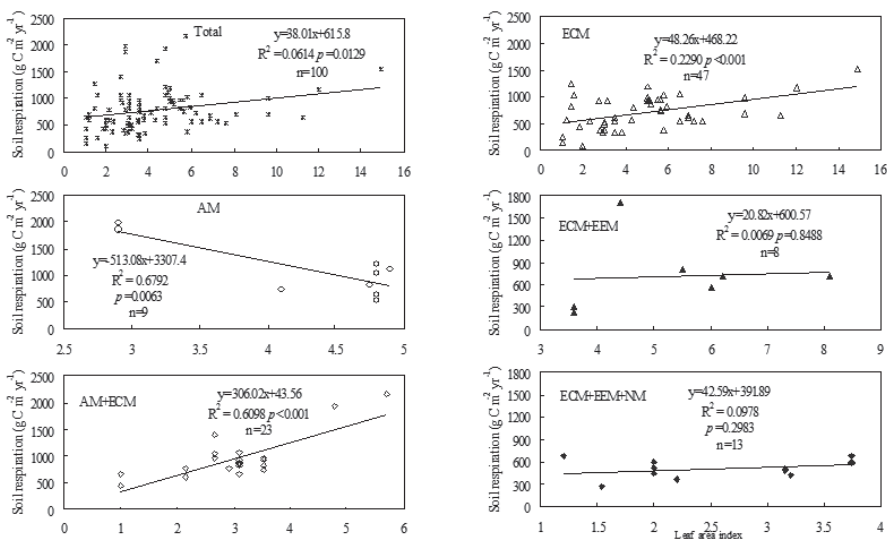


Figure 3. Relationship between soil respiration and leaf area index under different mycorrhizal strategy-dominated forests.

The apparent Q_{10} of the R_s was 1.47 when all of the mycorrhizal types were considered (Figure 4). The apparent Q_{10} changed from 0.85 to 2.18 depending on

the different mycorrhizal-dominated forests, whereas no significant difference was observed among them ($\chi^2=0.8571$, $p=0.9306$).

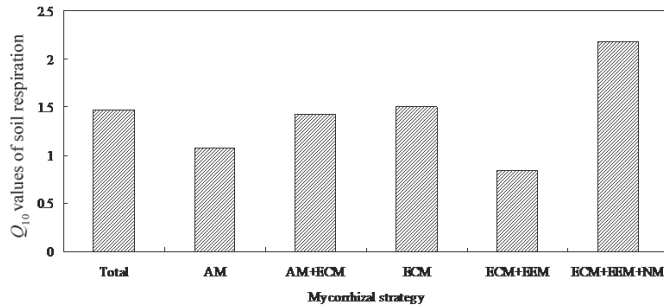


Figure 4. Q_{10} values of soil respiration under different mycorrhizal strategy-dominated forests. $\chi^2=0.8571$, $p=0.9306$, $df=4$

4. Discussion

The novel aspect of this work is that we used a global R_s data set and explored the interannual relationships between the R_s and the MAT, MAP and LAI after classifying the forests according to their mycorrhizal strategy. Previous studies have compared the R_s of mycorrhizal or non-mycorrhizal strategies and their response to temperature (Högberg *et al.*, 2001; Langley *et al.*, 2005; Heinemeyer *et al.*, 2007; Valentine and Kleinert, 2007), but, to our knowledge, this is the first study to compare the R_s with the MAT, MAP and LAI among global forest ecosystems based on their mycorrhizal strategies. The present study used a larger research scale and is aimed at increasing our understanding of the effects of mycorrhizal strategies on the R_s at the global scale. Therefore, we expected to gain a better comprehension of the role of mycorrhizae in R_s for correctly interpreting the current root and soil respiration data (Hughes *et al.*, 2008).

Our results indicate that, at the global scale, the R_s presents a significant correlation with the MAT, MAP

and LAI, a finding that was consistent with previous evidence (Reichstein *et al.*, 2003; Luyssaert *et al.*, 2007; Bond-Lamberty and Thomson, 2010; Wang *et al.*, 2010). However, when the regression relationship between the R_s and MAT included AM mycorrhizal forests (all site-years, AM, AM+ECM), the exponential relationship was more suitable than a linear one, which contradicted previous many conclusions (Schimel *et al.*, 2001; Raich *et al.*, 2002; Wang *et al.*, 2010). The reasons for this result require further investigation through the collection of additional data because no exponential model was employed in the above studies. The contribution of the MAT was larger than the MAP on the interannual variability of the R_s , with the exception of for the ECM+EEM mycorrhizal-dominated forest. This finding conflicted with the previous conclusion that the MAP had a larger contribution than the MAT on R_s . However, the interpreter ratio (26%) of the MAT was similar to the finding (26%) of Wang *et al.* (2010) for a global forest ecosystem; in contrast, our finding was lower than that (42%) of Bond-Lamberty and Thomson (2010) for a global forest ecosystem and

the conclusion (76%) reported by (Raich *et al.*, 2002) at a global scale. These discrepancies may be due to the difference of the methods employed during the data measurements and data analyses because diverse measurement methods cause variations of the R_s (Wayson *et al.*, 2006) and the previous discrepancy also presented among many previous studies (Raich *et al.*, 2002; Reichstein *et al.*, 2003; Bond-Lamberty and Thomson, 2010; Wang *et al.*, 2010). In addition, the mycorrhizal status was considered as the first selection level in this study. As a result, we removed those data for which the mycorrhizal status of the corresponding tree species was never reported, which also may account for the differences. Our finding showed that there is a significant positive correlation between the R_s and LAI when all of the site-years were taken into account, supporting the conclusion of Reichstein *et al.* (2003). However, our interpretation ratio of the LAI to the R_s (6%) was dissimilar the finding (69%) of Reichstein *et al.* (2003). This distinction may be due to the difference of region studied; the study of Reichstein *et al.* was conducted in 17 different forest and shrubland sites in Europe and North America. In addition, the mycorrhizal strategy most likely exerted an important influence. The LAI explained different variation of the R_s with changes of the mycorrhizal strategies. Furthermore, Reichstein *et al.* (2003) presented significant negative relationship ($r = -0.8241$) with the AM-dominated forest.

The Q_{10} (1.47) was similar to the finding (1.5) of Bond-Lamberty and Thomson (2010) in which the Q_{10} was calculated by air temperature in the two studies. When the Q_{10} was considered under different mycorrhizal strategies, we found that, although the Q_{10} fluctuated according to the mycorrhizal strategy, the variation was not significant among the different mycorrhizal strategies. This finding confirmed the conclusions of the majority of studies (Langley *et al.*, 2005; Atkin *et al.*, 2009). However, Koch *et al.* (2007) showed that the Q_{10} of the R_s increased 20% when *Pi-*

cea abies was colonized by ECM fungi (*Piloderma croceum*) compared to non-mycorrhizal plants.

The effects of the mycorrhizal strategy on the ecosystem response to climate change have triggered the interest of ecologists (Zhu and Miller, 2003; Vargas *et al.*, 2010). However, to our knowledge, there was only one report involving mycorrhizal associations and ecosystem respiration at large scales. Moreover, this study only compared different AMs and ECMs on ecosystem CO_2 fluxes (Vargas *et al.*, 2010). By reviewing previous literature, we found no report on the response of the forest R_s to climate changes based on the mycorrhizal strategy at the global scale, although much research have reported the contribution of mycorrhizal fungi to the R_s under conditions of control pot or field experiments (Högberg *et al.*, 2001; Langley *et al.*, 2005; Hughes *et al.*, 2008). Furthermore, there was no study on the effect of different mycorrhizal types on the R_s and its Q_{10} and comparing the values between mycorrhizal and non-mycorrhizal species (Högberg *et al.*, 2001; Langley *et al.*, 2005; Hughes *et al.*, 2008). This is the first study to evaluate the R_s in response to the MAT, MAP, and LAI and the change of the Q_{10} based on multiple mycorrhizal types in global forest ecosystems. Clearly, considerable research effort is required in the future to allow a full quantitative investigation of the function of mycorrhizal associations at a global ecosystem scale.

Acknowledgements

This study was financially supported by the National Natural Science Foundation of China (Grant 40971150), the Chinese Postdoctoral Science Foundation (20090450004, 20103018), the open fund of Laboratory for Earth Surface Processes, Ministry of Education (2011004), and the Science Foundation Fostering Innovative Ability of Henan University of Science and Technology (2009CZ0006).

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