Forest Soil Autotrophic and Heterotrophic Respiration under Different Mycorrhizal Strategies and their Responses to Temperature and Precipitation

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ABSTRACT

Mycorrhizal symbiosis between plant roots and mycorrhizal fungi are almost ubiquitous. These interactions contribute a largely to soil autotrophic respiration (R_A), influence soil heterotrophic respiration (R_H) and respond strongly to such climatic changes as temperature and precipitation. The aim of the present study was to explore how variation of temperature and precipitation influence R_A and R_H in global forest ecosystems that are classified by the mycorrhizal type of the dominant plants. The results show slight variation for R_A and significant change for R_H among different mycorrhizal strategy types. In forests with predominating arbuscular mycorrhiza (AM) the R_A and R_H are trifling higher than in non-AM type forests. The responses of R_A and R_H to temperature and precipitation were highly variable among different mycorrhizal strategies. For example, the changes of R_A and R_H are more dependent on precipitation than temperature in AM-forest, and temperature accounted more for their variations in forests of the other three mycorrhizal types. As far as we know, this study was the first to evaluate the influence of different mycorrhizal strategies on forest R_A and R_H and their response to temperature and precipitation.

Key words: soil autotrophic respiration, soil heterotrophic respiration, mycorrhizal strategy, temperature, precipitation.

Forests, as the main body of the terrestrial ecosystem, store vast amounts of carbon both above- and below-ground [Dixon, 1994] and they constitute a vital sink for atmospheric CO_2 on a global scale [IPCC, 2001]. 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 (belowground autotrophic respiration, R_A) and of heterotrophic

respiration (R_H) [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, 2008]. The realization that soils are a possible source of atmospheric CO_2, together with the continuous increase in atmospheric CO_2 concentrations, has lead to enormous interest from numerous ecologists [Gaumont-Guay et al., 2009; Bond-Lamberty, Thomson 2010; Raich et al., 2002]. Soil respiration (R_s), as the most uncertain component of many climate change models [Jones et al., 2003], is influenced by many factors, e. g., temperature and precipitation [Reichstein et al., 2003; Luo, 2006; Shi et al., 2003].

Mycorrhizal fungi play crucial roles in the regulation of terrestrial CO_2 fluxes [Zhu, 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, 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. Mycorrhizal fungi receive carbon from their host plants in exchange for nutrient transfer to the roots, which benefits plant growth. Previous studies have demonstrated the role of mycorrhizae in regulating root respiration [Shi et al., 2003; Burton et al., 2002; Hughes et al., 2008] and soil respiration [Langley et al., 2005; Heinemeyer et al., 2007; Moyano et al., 2008; Vargas, Allen, 2008]. Hughes et al. pointed out that mycorrhizal symbiosis is vital for the accurate prediction of future rates of CO_2 release from plants and soils [Hughes et al., 2008]. Further, they emphasized that the accuracy of current C cycle and climate models are very poor and restricted without mycorrhizal data.

Previous studies have shown that respiratory CO_2 release from mycorrhizae might be greater than from non-mycorrhizal roots [Valentine, Kleinert, 2007; Nottingham et al., 2010], and that mycorrhizae largely contribute to soil respiration [Högberg et al., 2001]. Furthermore, Vargas et al. have also demonstrated that ecosystem CO_2 fluxes of different mycorrhizal strategy-dominated forest types are differentially influenced by precipitation and temperature [Vargas et al., 2010]. Shi et al. confirmed that forest Rs presented varied responses to changes of temperature and precipitation under different mycorrhizal strategies [Shi et al., 2012].

Many studies have focused on how temperature and precipitation influence R_A and R_H at large, even global scales [Boone et al., 1998; Wang et al., 2010]. These studies have focused on the categorical classifications by forest type (e. g., evergreen forests and deciduous forests; conifer forests and deciduous forests) [Wang et al., 2010; Luyssaert et al., 2007] or biome (e. g., boreal, temperature and tropical) [Bond-Lamberty, Thomson, 2010] but have ignored the potential role of the belowground interactions and feedbacks that may influence the R_A and R_H. Consequently, it remained unclear whether environmental factors influence R_A and R_H 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 [Hughes et al., 2008].

In this study we used a recently compiled global forest R_s database [Wang et al., 2010] to investigate the dependency of the forest R_A and R_H on temperature and precipitation. With the help of this data 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 into global climate research.

The aim of this study was to improve the understanding of the functional role of mycorrhizal associations in forest R_A and R_H. We hypothesize that temperature and precipitation may differentially regulate R_A and R_H in different mycorrhizal strategy-dominated systems. We expect that patterns may emerge across large geographical distances in forests dominated by different mycorrhizal strategies.

This work is based on a global forest R_s database developed by Wang et al. [2010], which included forest R_s, R_A, R_H, mean annual temperature (MAT) and mean annual precipitation (MAP). Further, the dominating forest species were matched with above parameters according to corresponding references. The mycorrhizal strategies of each species were ascertained and classified according to published literature [Smith, Read, 2008; Wang, Qiu, 2006]. When tree species were reported to associate with more than one mycorrhizal type, they were classified as an A mycorrhizal type + B 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 strategies of 105 R_A and R_H with their corresponding MAT and MAP were used in this study, including the following 4 mycorrhizal strategies: 1) AM (16), 2) AM + ECM (16), 3) ECM (63), and 4) ECM + EEM (10).

Data analysis

At the global scale, the R_s are linearly correlated with the MAT and MAP [Raich et al., 2002; Shi et al., 2012; Wang et al., 2010]. We also analyzed the data using linear regression to characterize the responses of the R_A and R_H to the MAT and MAP under different mycorrhizal strategies with the SPSS software package version 13.0 (SPSS, Chicago, IL). We calculated respectively path coefficients of MAT and MAP to R_A and R_H because change of MAT is usually correlated with MAP.

RESULTS AND DISCUSSION

Analysis of variance revealed that there were not significant differences in R_A as it showed practically no difference among different mycorrhizal strategy types (Fig. 1). R_A in AM + + ECM dominated forest was highest with 497 g C m^{-2} yr^{-1}, which was negligibly higher than in other three mycorrhizal dominated forests: AM (412 g C m^{-2} yr^{-1}), ECM (390 g C m^{-2} yr^{-1}), and ECM + EEM (397 g C m^{-2} yr^{-1}). However, R_H exhibited marked differences among different mycorrhizal dominated forests. R_H in ECM dominated forest with 409 g C m^{-2} yr^{-1} was significantly lower than in AM and AM + + ECM dominated forests with 537 g C m^{-2} yr^{-1} and 539 g C m^{-2} yr^{-1}, respectively. The R_A and R_H in forests with AM domination (AM and AM+ECM) were somewhat higher than in non-AM type forests (ECM and ECM + EEM), although significant differences were only observed for R_H.

The responses of R_A and R_H to change of MAT were varied in different mycorrhizal dominated forests (Fig. 2). When all of the four forest types were considered, the R_A and R_H increased significantly with increasing MAT except for ECM + EEM dominated forest. In
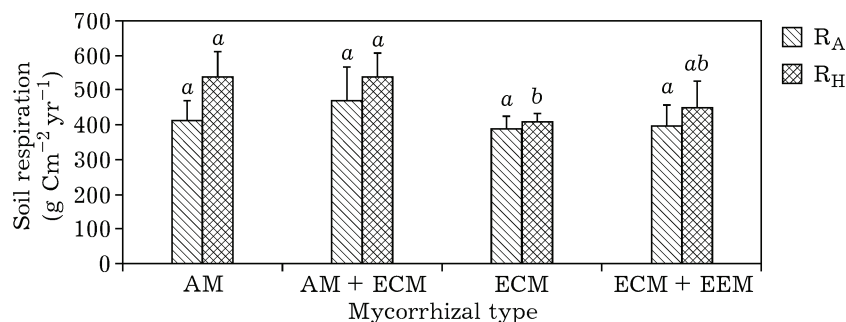

Fig. 1. Soil autotrophic (R_A) and heterotrophic respiration (R_H) under different mycorrhizal strategy-dominated forests.

AM − arbuscular mycorrhizas; AM + ECM − arbuscular and ecto- mycorrhizas; ECM − ectomycorrhizas; ECM + + EEM − ecto- and ectendo- mycorrhiza; letters a and b above each bar mean the significant difference at the level of 5 % among different mycorrhizal types
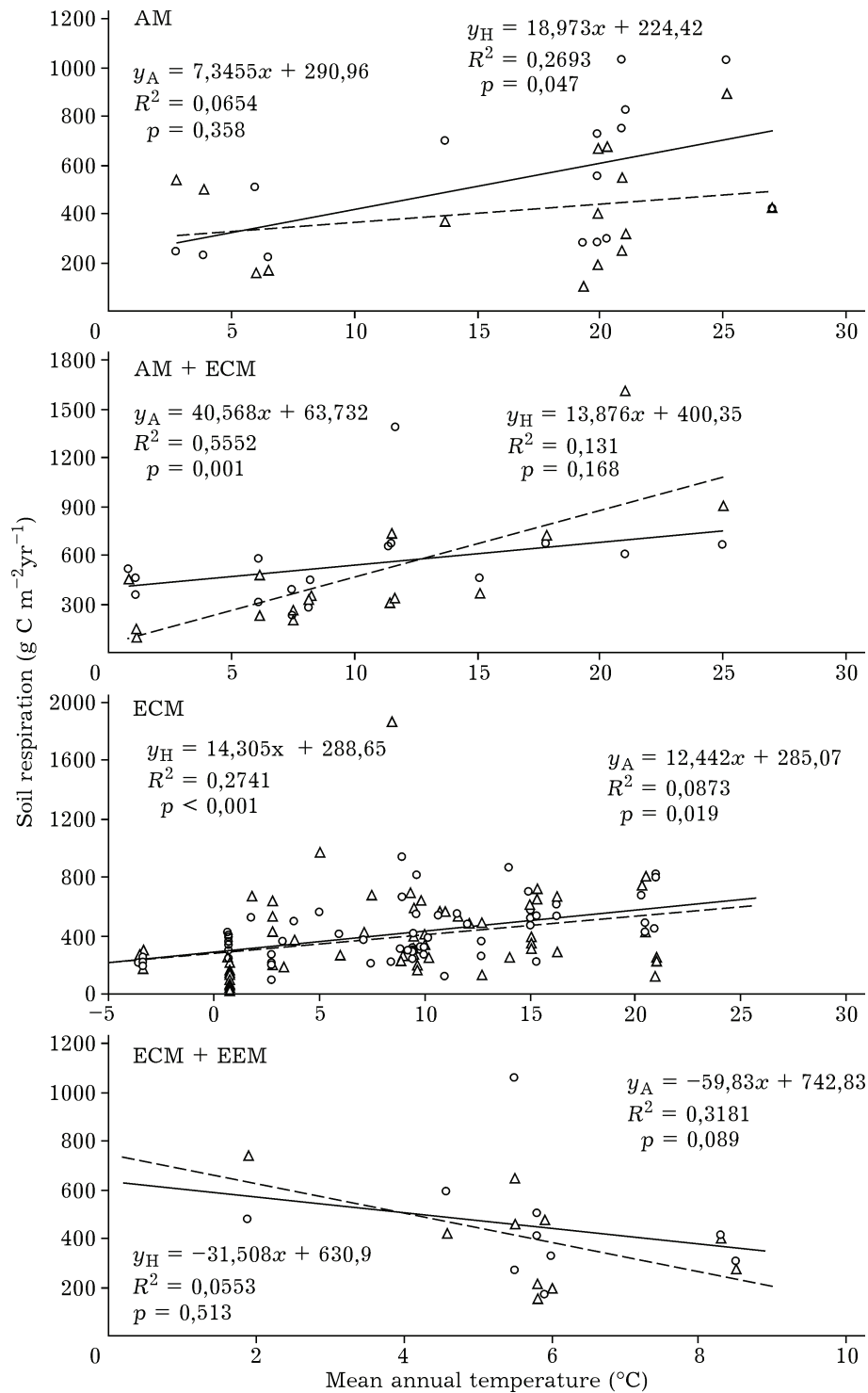
Fig. 2. The responses of soil autotrophic ($\triangle$) and heterotrophic ($\bigcirc$) respiration of forests under different mycorrhizal strategies to change of mean annual temperature. y_A (broken line) and y_H (solid line) mean the regression of soil autotrophic and heterotrophic respiration, respectively.

AM-type forest, the linear regression between R_A and MAT was not significant. However, the R_H enhanced significantly with the increase of MAT. The 26.93 % of R_H variation was explained by variation of MAT. Regarding AM+ECM forest, the responses of R_A and R_H to change of MAT were contrary to those in AM forest. MAT influenced markedly the R_A and accounted for 55.52 % of its variation. The effects of MAT on R_A and R_H were similar in ECM dominated forest. They increased with the similar rising rate significantly with the hoist of MAT. The variation of MAT explained 8.73 % and 27.41 % of R_A and R_H variation, respectively. As for the ECM + EEM forest, no significant linear relationships was observed between MAT and either R_A or R_H.

As far as the responses of R_A and R_H to change of MAP were concerned among all four mycorrhizal-type forests, the R_A only responded linearly to the MAP in AM + ECM dominated forest, and it explained 47,48 % ($p = 0.003$) of the variation of R_A (Fig. 3). The significant response of R_H to change of MAP was also only observed in ECM-type forest ($R^2 = 0.2772$ $p < 0.001$) in all mycorrhizal-type forest.

The changes of MAT and MAP are usually correlative during climate changes. The path analysis was employed to calculate the direct and indirect influence of MAT and MAP on R_A and R_H, respectively (Table 1, 2). For AM-dominated forest, R_A was more influenced by MAP with 0.4576 direct and 0.2813 indirect path coefficients, respectively (Table 1). In contrast, MAT more accounted for variation of R_A than MAP in ECM-type forest. In AM + ECM and ECM+ EEM dominated forests, the direct coefficients were higher than indirect ones. When the R_H was considered in AM-type forest, the effect of MAT was bigger (with 0.4460 direct and 0.2742 indirect path coefficients, respectively) than that of MAP (Table 2). The tendency was similar for AM+ECM and ECM +EEM forests compared to AM forests. However, the influence of MAT on RH was similar to that of MAP in ECM forest.

The novel aspect of this work is that we used a global forest data set of R_A and R_H and explored the interannual relationships between the R_A and R_H and the MAT and MAP after classifying the forests according to their mycorrhizal strategy. Previous studies have compared the responses of R_A and R_H to changes of MAT and MAP or R_s among different mycorrhizal strategies or between mycorrhizal and non-mycorrhizal strategies and their response to temperature or precipitation [Langley et al., 2005; Heinemeyer et al., 2007; Valentine, Kleinert, 2007; Högberg et al., 2001; Shi et al., 2012], but, as far as we know, this is the first study to compare the $R_{A A}$ and R_H with the MAT and MAP among global forest ecosystems based on their different mycorrhizal strategies. The present study uses a larger research scale and is aimed at increasing our understanding of the effects of mycorrhizal strategies on the components of R_s on 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].

Mycorrhizal respiration, as a component of R_s, contributed to R_s to a different extent. Nottingham et al. hinted that only AM fungal mycelia accounted for 14 % of Rs and 26 % of R_A in a moist tropical forest [Nottingham et al., 2010]. Heinemeyer et al. showed that ECM fungal hyphal contribution was 25 % of R_s and 62.5 % of R_A in a 15-year-old Lodgepole pine forest [2007]. However, our results indicated that the R_A was not significantly different among four mycorrhizal strategy forests, and R_H presented a significant variation in different mycorrhizal dominated forests. The reason for no difference in R_A among different mycorrhizal-type forests is possibly connected with the contribution of each mycorrhizal type to Rs in forest ecosystems. The studies in AM and ECM forest made by Nottingham et al. [2010] and Heinemeyer et al. [2007], respectively, confirmed our deduction. Previous studies compared mycorrhizal with non-mycorrhizal treatments and neglected the function of different mycorrhizal strategies [Heinemeyer et al., 2007; Nottingham et al., 2010]. The variations of R_H in different mycorrhizal-dominated forests existed perhaps due to mycorrhizospheric microbes because numerous studies had shown that there were abundant microbial communities in mycorrhizosphere [Veresoglou et al., 2012; Herman et al., 2012; Högberg, Högberg, 2002].
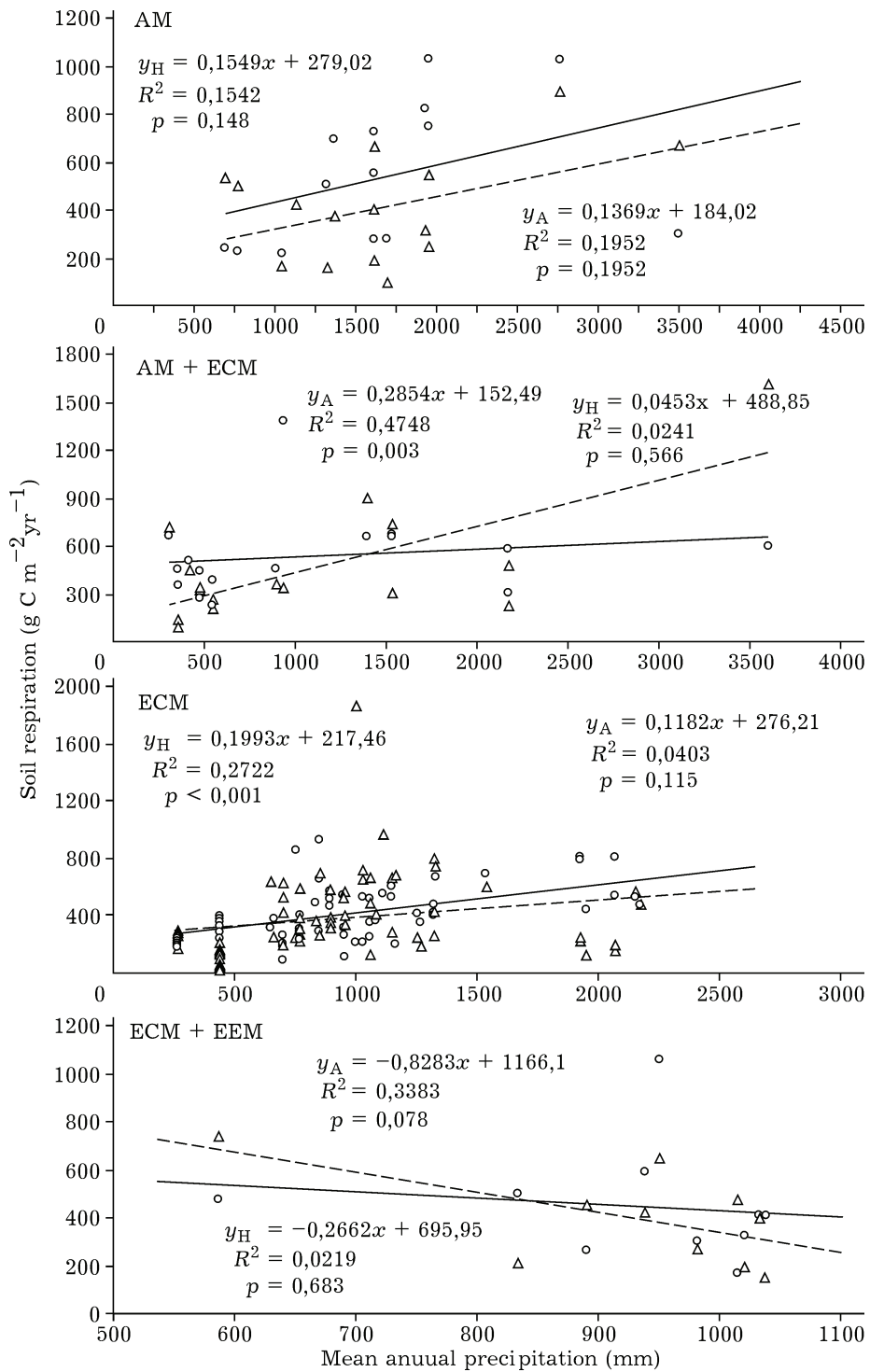
Fig. 3. The responses of soil autotrophic (△) and heterotrophic (○) respiration of forests under different mycorrhizal strategies to change of mean annual precipitation. y_A (broken line) and y_H (solid line) mean the regression of soil autotrophic and heterotrophic respiration, respectively

Coefficients of path-analysis between mean annual temperature and precipitation and soil autotrophic respiration of forests under different mycorrhizal strategies

Mycorrhizal types	Variables	Path coefficient		
		Direct	Indirect	Total
AM	MAT	-0,0256	0,2813	0,2558
	MAP	0,4576	−0,0157	0,4419
AM + ECM	MAT	0,5492	0,1960	0,7452
	MAP	0,4498	0,2392	0,6891
ECM	MAT	0,2877	0,0077	0,2954
	MAP	0,0118	0,1889	0,2007
ECM+EEM	MAT	−0,2837	−0,2803	−0,5640
	MAP	−0,3620	−0,2197	−0,5817

In this study, the responses of R_A and R_H to changes of MAT and MAP were similar in the same mycorrhizal-type forest (Fig. 2, 3). They increased with the hoist of MAT and MAP in AM, AM + ECM and ECM forests, and decreased in ECM + EEM forests. The finding was in accord with the responses of total Rs to changes of MAT and MAP [Shi et al., 2012]. R_A was more dependent on MAP than MAT in AM forests. In contrast to R_H, R_A was more sensitive to change of MAT than MAP (Fig. 2, 3; Table 1, 2). The possible mechanism was that AM only influenced the rate but not the temperature sensitivity of soil respiration [Langley et al., 2005]. In addition, R_A was more dependent on photosynthesis than on temperature [Heinemeyer et al., 2007; Нцgberg et al., 2001; Bhupinderpal et al., 2003; Edwards et al., 2004]. Root respiration [Luo et al., 2001; Hartley et al., 2007] and root-associated respiration of AM fungi [Heinemeyer et al., 2006] were reported to be relatively insensitive to temperature when compared with R_H. This higher dependence on photosynthetic substrate supply may therefore reduce the dependence of R_A on temperature [Kirschbaum, 2006]. Among AM + ECM and ECM forests, MAT accounted more for variation of R_A and R_H than MAP (Fig. 2, 3; Table 1, 2). There can be two reasons for that. Firstly, ECM fungi could improve the temperature sensitivity of R_A [Koch et al., 2007]. Moreover, the temperature sensitivity of ECM was different among the different ECM fungal species [Malcolm et al., 2008]. Secondly, the ECM species were more sensitive to change of MAT than AM species [Burton et al., 2002].

Coefficients of path-analysis between mean annual temperature and precipitation and soil heterotrophic respiration of forests under different mycorrhizal strategies

Mycorrhizal types	Variables	Path coefficient		
		Direct	Indirect	Total
AM	MAT	0,4460	0,0729	0,5189
	MAP	0,1185	0,2742	0,3927
AM + ECM	MAT	0,3632	−0,0013	0,3620
	MAP	−0,0029	0,1582	0,1553
ECM	MAT	0,3182	0,2054	0,5236
	MAP	0,3129	0,2089	0,5217
ECM + EEM	MAT	−0,3011	0,0659	−0,2351
	MAP	0,0851	−0,2331	−0,1480

The mycorrhizal status was considered 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 or for which any one of the parameters including MAT, MAP, R_A and R_H was absent. Therefore, future study needs to cite more published data. Nevertheless, the tendencies of R_A and R_H with the MAT and MAP should remain valid during each mycorrhizal-type forest because the trend of R_A and R_H in each mycorrhizal-type forest was similar to previous studies with different source data [Shi et al., 2012].

CONCLUSIONS

The effects of the mycorrhizal strategy on the ecosystem response to climate change have triggered the interest of ecologists [Zhu, Miller, 2003; Vargas et al., 2010; Shi et al., 2012]. However, as far as we know, there was only one report involving mycorrhizal associations and Rs at large scales [Shi et al., 2012]. Having reviewed previously published literature, we found no report on the response of the forest R_A and R_H to climate changes based on the mycorrhizal strategy at the global scale, although many researches have reported the contribution of mycorrhizal fungi to the R_s under conditions of control pot or field experiments [Hughes et al., 2008; Langley et al., 2005; Högberg et al., 2001; Veresoglou et al., 2012]. Furthermore, there was no study on the effect of different mycorrhizal types on the R_A and R_H. This is the first study to evaluate the R_A and R_H and their response to the MAT and MAP 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.

Certainly, the datasets analysed in the study were not too big based on existing data. Therefore, the response of R_A and R_H to changes of MAT or MAP in different mycorrhizae-dominated forests needs to be carefully studied further with the accumulation of data.

REFERENCES

Bhupinderpal S., Nordgren A., Ottosson Löfvenius M., Högberg M. N., Mellander P. E., Нцgberg P. Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year // Soil Biol. Biochem. 2003. Vol. 27. P. 753.

Bonan G. B. Forests and climate change: forcings, feedbacks, and the climate benefits of forest // Science. 2008. Vol. 320. P. 1444.

Bond-Lamberty B., Thomson A. Temperature-associated increases in the global soil respiration record // Nature. 2010. Vol. 464. P. 579.

Boone R. D., Nadelhoffer K. J., Canary J. D., Kaye J. P. Roots exert a strong influence on the temperature sensitivity of soil respiration // Ibid. 1998. Vol. 396, P. 570.

Burton A. J., Pregitzer K. S., Ruess R. W., Hendrick R. L., Allen M. F. Root respiration in North American forests: effects of nitrogen concentration and temperature across biomes // Oecologia. 2002. Vol. 131. P. 559.

Dixon R. K. Carbon pools and flux of global forest ecosystems //Science. 1994. Vol. 263. P. 185.

Edwards E. J., Benham D. G., Marland L. A., Fitter A. H. Root respiration is determined by radiation flux in atem perate grass land community // Glob. Change Biol. 2004. Vol. 10. P. 209.

Gaumont-Guay D., Black T. A., Mccaughey H., Barr A. G., Krishnan P., Jassal R. S., Nesic Z. Soil CO_2 efflux in contrasting boreal deciduous and coniferous stands and its contribution to the ecosystem carbon balance // Glob. Change Biol. 2009. Vol. 15. P. 1302.

Hanson P. J., Edwards N. T., Garten C. T., Andrews J. A. Separating root and soil microbial contributions to soil respiration: a review of methods and observations // Biogeochemistry. 2000. 48. P. 115..

Hartley I. P., Heinemeyer A., Ineson P. Effects of three years of soil warming and shading on the rate of soil respiraiton: substrate availability and not thermal acclimation mediates observed response // Glob. Change Biol. 2007. Vol. 13. P. 1761.

Heinemeyer A., Hartley I. P., Evans S. P., De la Fuente J. A. C., Ineson P. Forest soil CO_2 flux: uncovering the contribution and environmental responses of ectomycorrhizas // Ibid. P. 1786.

Heinemeyer A., Ineson P., Ostle N., Fitter A. H. Respiration of the external mycelium in the arbuscular mycorrhizal symbiosis shows strong dependence on recent photosynthates and acclimation to temperature // New Phytol. 2006. Vol. 171. P. 159.

Herman D. J., Firestone M. K., Nuccio E., Hodge A. Interactions between an arbuscular mycorrhizal fungus and a soil microbial community mediating litter de-

composition // Fems Microbiol. Ecol. 2012. Vol. 80. P. 236.

Högberg M. N., Hцgberg P. Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil // New Phytol. 2002. Vol. 154. P. 791.

Högberg P., Nordgren A., Buchmann N., Taylor A. F. S., Ekblad A., Högberg M. N., Nyberg G., Ottosson-Löfvenius M., Read D. J. Large-scale forest girdling shows that current photosynthesis drives soil respiration // Nature. 2001. Vol. 411. P. 789.

Hughes J. K., Hodge A., Fitter A. H., Atkin O. K. Mycorrhizal respiration: implications for global scaling relationships // Trends Plant Sci. 2008.Vol. 13. P. 583.

IPCC, Climate Change 2001: The Scientific Basis-Summary for Policymaker, Third Assessment Report of the IPCC, Cambridge: Cambridge University Press, 2001.

Jones C. D., Cox P., Huntingford C. Uncertainty in climate-carbon-cycle projections associated with the sensitivity of soil respiration // Tellus. 2003. Vol. 55. P. 642.

Kirschbaum M. U. F. The temperature dependence of organic-matter decomposition-still a topic of debate // Soil Biol. Biochem. 2006. Vol. 38. P. 2510.).

Koch N., Andersen C. R., Raidl S., Agerer R., Matyssek R., Grams T. E. // Temperature- respiration relationships differ in mycorrhizal and non-mycorrhizal root systems of *Picea abies* (L.) Karst // Plant Biol. 2007. Vol. 9. P. 545.

Langley J. A., Johnson N. C., Koch G. W. Mycorrhizal status influences the rate but not the temperature sensitivity of soil respiration // Plant Soil. 2005. Vol. 277. P. 335.

Longdoz B., Yernaux M., Aubinet M., Soil CO_2 efflux measurements in a mixed forest: impact of chamber distances, spatial variability and seasonal evolution // Glob. Change Biol. 2000. Vol. 6. P. 907).

Luo Y. Q., Wan S. Q., Hui D. F., Wallace L. L. Acclimatization of soil respiration to warming in a tall grass prairie // Nature. Vol. 2001. 413. P. 622.

Luo Y., Zhou X. Soil Respiration and the Environment. San Diego: Academic Press; Elsevier, CA., 2006.

Luyssaert S., Inglima I., Jung M., Richardson A. D., Reichstein M., Papale D., Piao S. L., Shulze E. D., Wingate L., Matteucci G., Aragao L., Aubinet M., Beer C., Bernhofer C., Black K. G., Bonal D., Bonnefond J. M., Chambers J., Ciais P., Cook B., Davis K. J., Dolman A. J., Gielen B., Goulden M., Grace J., Granier A., Grelle A., Griffis T., Grunwald T., Guidolotti G., Hanson P. J., Harding R., Hollinger D. Y., Hutyra L. R., Kolari P., Kruijt B., Kutsch W., Lagergren F., Laurila T., Law B. E., Le Maire G., Lindroth A., Loustau D., Malhi Y., Mateus J., Migliavacca M., Misson L., Montagnani L., Moncrieff J., Moors E., Munger J. W., Nikinmaa E., Ollinger S. V., Pita G., Rebmann C., Roupsard O., Saigusa N., Sanz M. J., Seufert G., Sierra C., ?mith M. L., Tang J., Valentini R., Vesala T., Janssens I. A. CO_2 balance of boreal, temperate, and tropical forests derived from a global data base // Glob. Change Biol. 2007. Vol. 13. P. 2509.

Malcolm G. M., López-Gutiérrez J. C., Koide R.T., Eissenstat D. M. Acclimation to temperature and temperature sensitivity of metabolism by ectomycorrhizal fungi // Ibid. 2008. Vol. 14. P. 1169.

Moyano F. E., Kutsch W. L., Rebmann C. Soil respiration fluxes in relation to photosynthetic activity in broad-leaf and needle-leaf forest stands // Agr. Forest Meteorol. 2008. Vol. 148. P. 135.

Nottingham A. T., Turner B. L., Winter K., van der Heijden M. G. A., Tanner E. V. J., Arbuscular mycorrhizal mycelial respiration in a moist tropical forest // New Phytol. 2010. Vol. 186. P. 957).

Raich J. W., Potter C. S., Bhagawati D. Interannual variability in global soil respiration, 1980−1994 // Glob. Change Biol. 2002. Vol. 8. P. 800).

Reichstein M., Rey A., Freibauer A., Tenhunen J., Valentini R., Banza J., Casals P., Cheng Y. F., Grunzweig J. M., Irvine J., Joffre R., Law B. E., Loustau D., Miglietta F., Oechel W., Ourcival J. M., Pereira J. S., Peressotti A., Ponti F., Qi Y., Rambal S., Rayment M., Romanya J., Rossi F., Tedeschi V., Tirone G., Xu M., Yakir D. Modeling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices // Global Biogeoch. Cy. 2003. Vol. 17. P. 1104).

Savage K., Davidson E. A., Richardson A. D. A conceptual and practical approach to data quality and analysis procedures for high-frequency soil respiration measurement // Funct. Ecol. 2008. Vol. 22. P. 1000.

Shi Z. Y., Zhang X. F., Wang F. Y. Influence of mycorrhizal fungi on soil respiration // Ecol. Environ. Sci. Vol. l9. 233 (2010). [in Chinese with English Abstract]

Shi Z., Wang F., Liu Y. Response of soil respiration under different mycorrhizal strategies to precipitation and temperature // J. Soil Sci. Plant Nutr. 2012. Vol. 12. P. 411.

Smith S. E., Read D. J. Mycorrhizal symbiosis. 3rd edn. New York: Academic Press, 2008.

Subke J. A., Inglima I., Cotrufo F. Trends and methodological impacts in soil CO_2 efflux partitioning: a metaanalytical review // Glob. Change Biol. 2006. Vol. 12. P. 921).

Valentine A. J., Kleinert A. Respiratory responses of arbuscular mycorrhizal roots to short-term alleviation of P deficiency // Mycorrhiza. 2007. Vol. 17. P. 137.

Vargas R., Allen M. F. Environmental controls and the influence of vegetation type, fine roots and rhizomorphs on diel and seasonal variation in soil respiration // New Phytol. 2008. Vol. 179. P. 460.

Vargas R., Baldocchi D. D., Querejeta J. I., Curtis P. S., Hasselquist N. J., Janssens I. A., Allen M. F., Montagnani L. Ecosystem CO2 fluxes of arbuscular and ectomycorrhizal dominated vegetation types are differentially influenced by precipitation and temperature // New Phytol. 2010. Vol. 185. P. 226.

Veresoglou S. D., Shaw L. J., Hooker J. E., Sen R. Arbuscular mycorrhizal modulation of diazotrophic and denitrifying microbial communities in the (mycor)rhizosphere of *Plantago lanceolata* // Soil Biol. Biochem. 2012. Vol. 53. P. 78.

Wang B., Qiu Y. L. Phylogenetic distribution and evolution of mycorrhizas in land plants // Mycorrhiza. 2006. Vol. 16. P. 299.

Wang W., Chen W. L., Wang S. P. Forest soil respiration and its heterotrophic and autotrophic components: Global patterns and responses to temperature and precipitation // Soil Biol. Biochem. 2010. Vol. 42. P. 1236.

Zhu Y. G., Miller R. M. Carbon cycling by arbuscular mycorrhizal fungi in soil-plant systems // Trends Plant Sci. 2003. Vol. 8. P. 407.