



Predicting plant response to arbuscular mycorrhizas: The role of host functional traits



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ABSTRACT

The arbuscular mycorrhiza (AM) is among the most ubiquitous symbiosis in the world. A meta-analysis of 759 articles (1978–2012) was conducted to test whether ecologically important host plant traits (N-fixation and C-fixation pathway) affect the response of the plant to mycorrhizal colonization. We found that the effect of N-fixation on mycorrhizal growth response (MGR) depended on whether the plant was woody or a forb. N-fixing forbs had a higher MGR than non-N-fixing forbs, but the reverse was true for woody plants. Moreover, C₄-grasses had significantly higher MGR than C₃-grasses, but no significant difference was found between C₃ and C₄ forbs, or between C₃ and C₄ woody species. Overall, woody species had higher MGR than any other functional group. These results demonstrate that MGR does depend on host functional characteristics, but neither N-fixation capacity nor C-fixation pathway are apparently fundamental controllers of MGR. Instead, it would appear possible that these traits influence MGR only insofar as they influence more fundamental functions such as P demand and P supply.

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1. Introduction

Arbuscular mycorrhizal (AM) fungi form symbiosis with roots of the vast majority of terrestrial plants. Engaging in the symbiosis facilitates nutrient uptake by the plant, and may also provide a suite of other benefits such as increasing tolerance to drought, salt and heavy metal stress, and enhancing resistance to fungal pathogens, nematodes and herbivores (Smith and Read, 2008). While these effects may increase plant growth in many plant species, response to mycorrhizal colonization is certainly not uniform among plant species (Koide, 1991). In this article we, therefore, address whether specific functional traits of plants help to explain this variation in response.

The magnitude and direction of what has been called ‘mycorrhizal growth response’ (MGR, Maherali, 2014) is context-dependent, varying with a number of factors including phosphorus availability, AM fungus community composition, level of drought stress and the presence of fungal pathogens (Maherali and Klironomos, 2007; Hoeksema et al., 2010; Yang et al., 2015). Nevertheless, plant traits must also influence MGR (Koide, 1991), but our understanding of the effects of host plant traits on MGR is poorly developed and controversial, especially for the capacity to fix N and the C-fixation pathway.

In previous studies some authors have suggested that N-fixation influences MGR. One hypothesis to explain the effect of N-fixation on MGR is based on the notion that N-fixation in legumes has a large P requirement that can be satisfied by AM fungi (Veresoglou and Rillig, 2014). However, Wang & Qiu (2006) reported that some plants in the Fabaceae are only weakly mycorrhizal, and Hoeksema et al. (2010) surprisingly found that N-fixing plants exhibited smaller MGR than non-N-fixing plants. What might explain this apparent discrepancy?

Others have suggested that C₄ plant species have higher MGR

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than C₃ plant species (Hetrick et al., 1990, 1991; Veresoglou and Rillig, 2014). Lugo et al. (2003) found that C₄ grasses associated with Paris-type mycorrhiza had higher rates of colonization than C₃ grasses with Arum-type mycorrhiza. Hartnett et al. (1993) found that AMF played major roles at the seedling stage for C₃ grasses and at later stages for C₄ grasses. Nevertheless, the reason for clear differences between C₄ and C₃ plant species in their MGR is still controversial (Hoeksema et al., 2010). Thus, as determinants of MGR, the ability to fix nitrogen and the carbon fixation pathway remain unresolved.

Although previous meta-analyses have examined the effects of N-fixation and C-fixation on MGR, the data utilized were overwhelmingly from articles published in English. There is, however, a large body of mycorrhiza research published in Chinese during the last several decades (Gai et al., 2006). From 2014 forward, use of the search term “mycorrhiza* AND meta-analysis” on 28 July 2015 in the Web of Science database produced 18 meta-analyses, only two of which included data from Chinese papers (Yang et al. 2014, 2015). Thus, it seems necessary to conduct a more comprehensive meta-analysis by including data from the Chinese literature.

In this study, we conducted meta-analyses of 759 articles, among which were included those from the Chinese literature. Our purpose was, to reexamine the effects of plant functional traits, particularly the ability to fix N and C-fixation pathway, on MGR. Using this more inclusive dataset, we hoped to clear up controversies surrounding the effect of N-fixation and C-fixation pathway on MGR. In particular, we hypothesized that: (1) N-fixation capability is a general determinant of MGR, and its effect is not dependent on plant functional type; and (2) C-fixation pathway is also a general determinant of MGR, and its effect on MGR does not depend on plant functional type. All of the selected trials were those performed in the greenhouse. Controlled, greenhouse experiments have several advantages including completely non-mycorrhizal control plants, identified fungal and host species, and known and repeatable environmental conditions.

2. Materials and methods

2.1. Database compilation

We conducted a literature search using the popular academic databases. Three separate searches were performed with the following conditions:

Search 1: On 10 May 2012, we searched Web of Science (<http://apps.webofknowledge.com/>) and Google Scholar (<http://scholar.google.com.hk>) with the terms (arbuscular AND mycorrhiza*) AND biomass, without publication year limitations.

Search 2: On 10 May 2012, we searched the same databases in three ways, all without publication year limitations. We used the terms (mycorrhiz* AND inocul*) as in Hoeksema et al. (2010), the terms (arbuscular AND shoot AND root) as in Veresoglou et al. (2012), and the terms (mycorrhiza* AND herbivor*) as in Koricheva et al. (2009).

Search 3: On 10 May 2012, we searched for Chinese literature using the CNKI database (<http://www.cnki.net/>) with the terms (arbuscular AND mycorrhiza*).

In total the searches yielded 4325 articles. Articles were filtered using the following criteria: (1) trials included comparable mycorrhizal and non-mycorrhizal treatments; (2) trials included at least 3 replications; (3) AM fungi were identified to species; (4) trials were performed in the greenhouse; (5) trials had a duration exceeding 3 months; (6) mycorrhizal colonization of control plants was nil; (6) when the same combinations of AM fungal species and plant species appeared in different articles, different locations or times, they were treated as independent trials; (7) for factorial

experiments with AM fungi and other beneficial microbes, trials were only included in which mycorrhizal inoculation, and inoculation with those microbes did not significantly interact; (8) when time series experiments were reported only the latest data were used; (9) when the host was a legume, its roots were nodulated.

Only 759 articles (publication year from 1978 to 2012; Fig. S1) met our inclusion criteria, producing approximately 3800 trials. We extracted the mean, standard deviation (SD) or standard error (SE) and the number of replicates for shoot or total biomass. Graphed data were digitized with GetData (<http://getdata-graph-digitizer.com/>). Data presented in tables were directly extracted. When SD or SE was missing, we followed the method of van Groenigen et al. (2011). We first calculated the coefficient of variation (CV) for the trials with known SD and mean, and then averaged all CVs. The missing SD was estimated through multiplying the reported mean value by the average CV and then squaring it.

We categorized plant species as being either ‘N-fixing’ or ‘non-N-fixing’ according to Hoeksema et al. (2010) and Wang and Qiu (2006). Some plant species in our dataset were also included in Hoeksema et al. (2010), so we utilized their categorization. Wang and Qiu (2006) published a comprehensive mycorrhizal plant species list with detailed taxonomic information, and we searched it and categorized Fabaceae as ‘N-fixing’ and other plants as ‘non-N-fixing’. For the plants that we could not obtain the taxonomic information with both above methods, we wrote to the author of source references for confirmation. We also categorized plants as being either C₃ and C₄ according to Hoeksema et al. (2010) and confirmation from the author of the source reference. We further grouped our data into all combinations of N-fixing/non-N-fixing × C fixation pathway × woody/forb/grass.

2.2. Meta-analyses

We ran four separate meta-analytical models: Model 1 with N-fixing and non-N-fixing host species as predictors; Model 2 with N-fixing woody, N-fixing forb, non-N-fixing woody and non-N-fixing forb host species as predictors; Model 3 with C₃ vs. C₄ host species as predictors; Model 4 with C₃-forb, C₃-grass, C₃-woody, C₄-forb, C₄-grass and C₄-woody host species as predictors.

The natural log of the response ratio (*LnRR*) was selected as the effect size. *LnRR* was calculated as the natural log ratio of its mean value in the experimental treatment (*X_e*) and control treatment (*X_c*) (Eqn. (1)).

$$\text{LnRR} = \ln \frac{X_e}{X_c} \quad (1)$$

A positive *LnRR* value suggests that AM fungi promoted plant growth; a negative *LnRR* value suggests that AM fungi suppressed plant growth. When *LnRR* = 0, it indicates no effect of AM fungi on plant growth.

The variance of *LnRR* was estimated with the following formula:

$$v = \frac{Se}{Ne * X_e} + \frac{Sc}{Nc * X_c} \quad (2)$$

Here, *Se* and *Sc* represent the standard deviations of experimental and control treatments, respectively. *Ne* and *Nc* refer to the sampling size of experimental and control groups, respectively. *LnRR* and its variance were calculated in ‘metafor’ package version 1.9–4 (Viechtbauer, 2010) in R 3.1.3 (R Core Team, 2013).

One of the assumptions of meta-analysis is that trials are independent of each other (Gurevitch and Hedges, 1993). However, in most meta-analyses, two or more trials are extracted from a single article and so might not be independent (Yang et al., 2015). Thus, we constructed mixed effects models with article identity as a

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