Science of the Total Environment 805 (2022) 150362

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Responses of AM fungal abundance to the drivers of global climate change: A meta-analysis

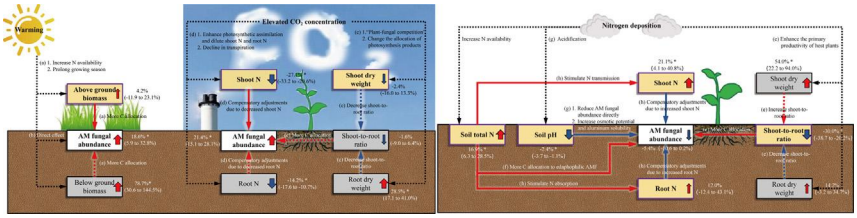
Han Hu [a,b,1], Liyuan He [c,1], Huanfei Ma [a,b], Jieying Wang [a,b], Yi Li [a,b], Jun Wang [a,b,d], Yaoxin Guo [e], Chengjie Ren [f], Hongying Bai [a,b], Fazhu Zhao [a,b,*]

[a] Shaanxi Key Laboratory of Earth Surface System and Environmental Carrying Capacity, Northwest University, Xi'an 710127, Shaanxi, China
[b] College of Urban and Environmental Sciences, Northwest University, Xi'an 710127, Shaanxi, China
[c] Biology Department, San Diego State University, San Diego, CA 92182, USA
[d] State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Institute of Soil and Water Conservation, Chinese Academy of Sciences and Ministry of Water Resources, Yangling 712100, China
[e] College of Life Sciences, Northwest University, Xi'an 710127, Shaanxi, China
[f] College of Agronomy, Northwest A&F University, Yangling 712100, Shaanxi, China

HIGHLIGHTS

- RR of AM fungal abundance decreases with the degree of eCO_2.
- 4 °C is the critical point that warming effects to AM fungal abundance.
- N fertilizer input rate and ecosystem type determined AM fungal abundance.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 1 February 2021
Received in revised form 23 August 2021
Accepted 11 September 2021
Available online 16 September 2021

Editor: Yucheng Feng

Keywords:
AM fungal abundance
Warming
Elevated CO_2 concentration
N addition
meta-analysis
Ecological consequence

ABSTRACT

Arbuscular mycorrhizal fungi (AMF), playing critical roles in carbon cycling, are vulnerable to climate change. However, the responses of AM fungal abundance to climate change are unclear. A global-scale meta-analysis was conducted to investigate the response patterns of AM fungal abundance to warming, elevated CO_2 concentration (eCO_2), and N addition. Both warming and eCO_2 significantly stimulated AM fungal abundance by 18.6% (95%CI: 5.9%–32.8%) and 21.4% (15.1%–28.1%) on a global scale, respectively. However, the response ratios (RR) of AM fungal abundance decreased with the degree of warming while increased with the degree of eCO_2. Furthermore, in warming experiments, as long as the warming exceeded 4 °C, its effects on AM fungal abundance changed from positive to negative regardless of the experimental durations, methods, periods, and ecosystem types. The effects of N addition on AM fungal abundance are −5.4% (−10.6%–0.2%), and related to the nitrogen fertilizer input rate and ecosystem type. The RR of AM fungal abundance is negative in grasslands and farmlands when the degree of N addition exceeds 33.85 and 67.64 kg N ha^{-1} yr^{-1}, respectively; however, N addition decreases AM fungal abundance in forests only when the degree of N addition exceeds 871.31 kg N ha^{-1} yr^{-1}. The above results provide an insight into predicting ecological functions of AM fungal abundance under global changes.

© 2021 Elsevier B.V. All rights reserved.

1. Introduction

Arbuscular mycorrhizal fungi (AMF), colonizing the roots of over 80% of terrestrial plants species (Cotton, 2018), confer considerable services to their host plants in exchange for photosynthetically derived carbon such as promoting nutrient uptake (Smith et al., 2011; Thirkell et al., 2016), pathogen resistance (Cameron et al., 2013), water relations

* Corresponding author at: Shaanxi Key Laboratory of Earth Surface System and Environmental Carrying Capacity, Northwest University, Xi'an 710127, Shaanxi, China.
E-mail address: zhaofazhu@nwu.edu.cn (F. Zhao).
[1] These authors made equal contributions.

https://doi.org/10.1016/j.scitotenv.2021.150362
0048-9697/© 2021 Elsevier B.V. All rights reserved.

(Auge, 2001), and heavy metal tolerance (Hildebrandt et al., 2007). Furthermore, AMF can also extend beyond direct effects on host plants to ecosystem mechanisms such as increasing crop yield (Zhang et al., 2019), reducing soil erosion (Dodd et al., 2000), regulating plant diversity (Bever et al., 2010; Yang et al., 2014), and affecting other soil biota (Nuccio et al., 2013; Rillig et al., 2001; Zhang et al., 2017). AM fungal abundance, indicating the number of AM fungi in microbial community, can not only show the growth and metabolism of AM fungal community, but also imply the growth of host plants and even the stability of ecosystem (Cotton, 2018; Zhang et al., 2019). A low AM fungi abundance is often accompanied by the lack of services provided by AM fungi, inhibiting the growth of host plants. Conversely, a high AM fungi abundance can promote host plant growth. Therefore, it is of important ecological significance to explore AM fungi abundance.

Since the industrial revolution, the anthropogenic activity-induced increase in carbon dioxide (CO_2) levels are from 280 to 400 ppm and its concentration is predicted to further double by 2100 (Betts et al., 2016; IPCC, 2013). Due to ongoing fossil fuel emissions, the concentration of CO_2 in atmosphere is expected to rise from a current value of 400 μL L^{-1} to 700–1000 μL L^{-1} by the end of this century (Betts et al., 2016). Concurrently, the increased emissions of nitrogenous gases such as nitrous oxide, oxides of nitrogen and ammonia, have led to large perturbations of the terrestrial N cycle (Galloway et al., 2004; Phoenix et al., 2006). Additionally, it is estimated that because of greenhouse gas accumulation, global surface air temperature will increase by 1.1–4.8 °C by the end of this century (Chen et al., 2020; IPCC, 2013). Such the drivers of global climate change have profound consequences on terrestrial ecosystems (Cotton et al., 2015). However, although the responses of aboveground organisms to such global climate changes have been extensively studied, relatively little is known about the sensitivity and response pattern of AM fungal responses to these shifts (Weber et al., 2019). Considering a wide range of distribution and multiple ecological functions of AM fungi (Han et al., 2020), the responses of AM fungal abundance to the drivers of global climate change will inevitably affect global carbon and nutrient cycles, plant communities and considerable ecosystem processes (Cotton, 2018; Han et al., 2020).

Currently, there is no consensus on how AM fungal abundance responds to such the drivers of global climate change although many meta-analyses have been conducted to investigate such responses (Cotton et al., 2015; Cotton, 2018; Dong et al., 2018; Han et al., 2020). For instance, several studies suggested that effects of N addition on AM fungal abundance are negative (Han et al., 2020; Treseder, 2004; Zhang et al., 2018; Zhou et al., 2017), insignificant (Weber et al., 2019; Egerton-Warburton and Allen, 2000) or positive (Eom et al., 1999; Jefwa et al., 2006; Porras-Alfaro et al., 2007; Zheng et al., 2014; Kim et al., 2015). Same as N addition effects, inconsistent results of the effects of elevated CO_2 concentration on AM fungal abundance have been also reported, including positive effects (Cotton et al., 2015; Cotton, 2018; Becklin et al., 2016; Jakobsen et al., 2016; Dong et al., 2018; Treseder, 2004), negative effects (Goicoechea et al., 2014) and insignificant effects (Tang et al., 2006). Such various and even controversial conclusions reflect the fact that previous studies often focus on AM fungal abundance responses to a single driver but ignore the discrepancies in experimental variables (such as experimental duration, experimental methods), climate variables (such as mean average air-temperature, mean annual precipitation) and especially relevant abiotic and biotic variables (such as aboveground biomass, belowground biomass, shoot and root dry weights). These disparities will hinder us from understanding how the drivers of global climate change affect AM fungal abundance. Filling up this critical knowledge gap will contribute to predict the ecological consequences of changes in AM fungal communities and forecast their implications on climate change (Cotton et al., 2015; Cotton, 2018; Dong et al., 2018; Han et al., 2020).

Targeting this current knowledge gap and research needs, this paper presents a comprehensive analysis to assess the responses of AM fungal abundance to the drivers of global climate change including warming, elevated CO_2 and nitrogen addition. Specifically, the objectives of this study are: (1) what are the response patterns of AM fungal abundance to warming, elevated CO_2 and nitrogen addition? (2) What are the most important relevant variables of the effects of warming, elevated CO_2 and nitrogen addition on AM fungal abundance? (3) What are the potential mechanisms behind the response patterns?

2. Materials and methods

2.1. Data source and extraction

Peer-reviewed works that conducted warming, elevated CO_2 and N addition experiments and measured indices of AM fungal abundance were searched using Web of Science (http://apps.webofknowledge.com), Google Scholar (http://scholar.google.com/) and China National Knowledge Infrastructure with English abstracts (http://www.cnki.net) until June 2019. The search terms were '(AM fungi/AMF/arbuscular mycorrhizal fungi) AND (climate change/global climate change/warming/increasing temperature/elevated CO_2/nitrogen addition/nitrogen deposition/nitrogen fertilization) AND (terrestrial/soil/land)'. We selected the searched papers by filtering following criteria: (a) the study contained at least one of the target variables representing AM fungal abundance, including neutral lipid fatty acid (NLFA), root colonization, extraradical hyphal length density and spore density; (b) ecosystem types, soil physicochemical properties, location, and climate were similar between controls and treatments; (c) the average values and sample size (n) of the treatments and the controls could be obtained; (d) among the standard deviation (SD), the standard error (SE), and the coefficient of variation (CV), at least one of which was reported; (e) experimental protocols, such as experimental method, experimental magnitude, experimental duration, and experimental period were clearly described; (f) If there were multiple publications reporting data from the same experiment, only the data from the most recent study were selected.

In total, 75 published papers with 431 cases were included (Note S1). For each study in our database, we extracted information on AM fungal abundance. Measurements from different ecosystem types, locations, and experimental conditions within a single study were treated as independent observations. If a study included multiple drivers of global climate change, such as eCO_2 vs. eCO_2 plus N addition, were also recorded separately. If a study included multiple soil layers, only data from the top soil layer were selected. In addition, available site and experimental information, such as latitude, longitude, mean annual air-temperature (MAT), mean annual precipitation (MAP), soil depth, sampling date, ecosystem type, and growing season, were recorded. Different experimental protocols such as experimental duration and device may introduce varied biases, we thus recorded the experimental duration and device of each case study and treated it as an independent variable. Based on the experimental duration of the collected data, we classified the experimental duration into three categories, i.e., <1 year, 1–5 years, and >5 years, in this study. Also, we included studies using devices such as open-top chamber (OTC), infrared heater (IH), green house (GH), growth chamber (GC), cable, and field in warming experiment. Furthermore, we recorded available vegetation and edaphic properties (a total of 25 biotic and abiotic variables), such as microbial biomass (MB), soil moisture (SM), soil pH, soil organic carbon (SOC), soil total nitrogen (TN), soil total phosphorus (TP), aboveground biomass (AGB), belowground biomass (BGB), root length (RL), total dry weigh of the plant (TDW), total dry C content of the plant (TDCC), total dry N content of the plant (TDNC), total dry P content of the plant (TDPC), leaf C (LC), leaf N (LN), leaf P (LP), shoot dry weight (SDW), shoot C (SC), shoot N (SN), shoot P (SP), root dry weight (RDW), root C (RC), root N (RN), root P (RP), shoot-to-root ratio of the plant (STR). We used the digitizing software GetData Graph Digitizer 2.26.0.20 (http://getdata-graph-digitizer.com) to extract data in

figures. When critical information was not reported in the paper, we contacted the authors for clarification. Finally, we included 431 observations for AM fungal abundance in our dataset, with 62 under warming, 200 under eCO_2, and 169 under N addition (Fig. 1).

2.2. Data analysis

The meta-analysis approach was used to determine the effects of the drivers of global climate change on AM fungal abundance (García-Palacios et al., 2015; Hedges and Curtis, 1999; Groenigen et al., 2014; Zhao et al., 2017; Chen et al., 2018; Han et al., 2020). The effects of the drivers of global climate change on AM fungal abundance and relevant biotic and abiotic factors were assessed by the response ratio (*RR*):

$$RR = \ln\left(\frac{X_T}{X_C}\right) = \ln\,(X_T) - \ln\,(X_C) \quad (1)$$

where X_T are the mean values in treatment groups, including warming groups, elevated CO_2 concentration groups and N addition groups, and X_C are the control groups. The change in soil pH was calculated as $pH_{treatment} - pH_{control}$ (Tian and Niu, 2012; Han et al., 2020). The variance (v) of each RR was calculated as below:

$$v = \frac{S_T^2}{n_T X_T^2} + \frac{S_C^2}{n_C X_C^2} \quad (2)$$

where n_T and n_C are the number of replicates; and S_T and S_C are the standard deviations of means in treatment and control groups, respectively. Some included studies reported the standard errors (SE) or the coefficients of variation (CV), and they were transformed to standard deviations (SD) according to the equation:

$$SD = SE\sqrt{n} \quad (3)$$

$$SD = \frac{CV}{100\%} \times X \quad (4)$$

where n is the number of replicates and X is the mean value of a given variable. In a few studies that none of SD, SE, or CV was given, SD was assigned as 10% of the corresponding mean (Luo et al., 2006; Zhou et al., 2017; Han et al., 2020).

The weighted response ratio ($RR++$) and 95% confidence interval (95% CI) were calculated the mixed-effects using the software MetaWin (Version 2.1, Sinauer Associates, Inc. Sunderland, MA, USA). If the values of 95% CI did not overlap with zero, the effects of the given global climate driver were considered as significant ($p < 0.05$). To determine whether the responses varied among groups, the between-group heterogeneity tests (Q_B tests) were performed. If Q_B values were significant ($p < 0.05$), the responses were significantly different among groups (Liu et al., 2016). For each interpretation, the weighted response ratios ($RR++$) and their 95% confidence intervals were back-transformed and reported as percentage change following: $(e^{RR++} - 1) \times 100\%$.

The relative importance and correlation were used to assess the linkages between the response ratios of AM fungal abundance and climate (including MAT, MAP), environmental variables (including ecosystem type, growing season, soil depth, experimental duration and experimental method). The relative importance of environmental variables was calculated as the sum of Akaike weights for all the models including this factor using the corrected Akaike's Information Criteria. Cut off was set at 0.8 to distinguish between important and nonessential predictors (Terrer et al., 2016; Feng and Zhu, 2019; Chen et al., 2020). The sum of Akaike weights was calculated using the 'glmulti' and 'MuMIn' package in R 3.6.3. The correlations of environment variables were calculated as Spearman's rank correlation coefficient. This statistical significance was set at $p < 0.05$. Linear regression and quadratic regression were performed using Origin 2017. Shapiro-Wilk test was used to test data distribution using SPSS 22.0.

2.3. Risk assessment of the database used

Biases, including both publication bias and research bias, could be the most important for risk assessment of the database used. Publication

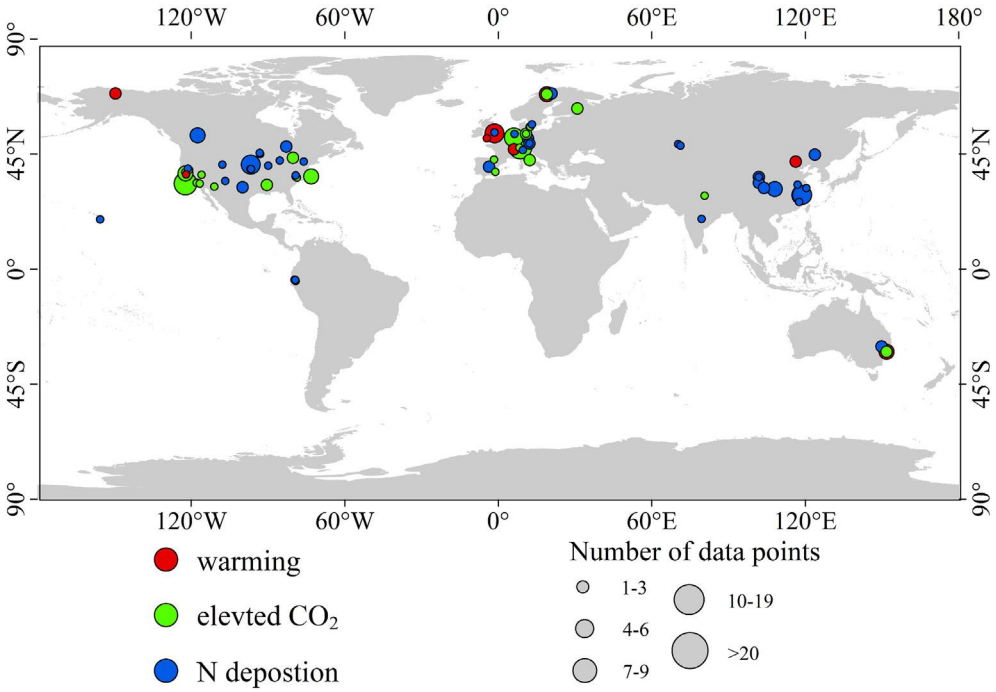


Fig. 1. Global distribution of the sites used in this meta-analysis. Red points represent warming experiments including 11 sites and 62 cases. Green points represent elevated CO_2 experiments including 37 sites and 200 cases. Blue points represent N addition experiments including 45 sites and 169 cases. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

bias usually results in an overestimated response ratio of AM fungal abundance to the drivers of global climate change since studies with positive results are more frequently accepted than those with negative results (Dong et al., 2018). The funnel plot asymmetry test by plotting standard errors against responses ratios of each observation was performed to assess publication bias. The funnel plot was performed using Origin 2017. However, research bias is a more troublesome issue since it originates from various sources (Gurevitch et al., 1999; Dong et al., 2018). For instance, NLFA and root colonization were used frequently to be the parameters for assessing AM fungal abundance in previous research since they are relatively easy to assess rather than because they are the most suitable parameters (Alberton et al., 2005; Han et al., 2020). Moreover, the objects, the methods and the experimental conditions of studies are subjectively selected by researchers, also resulting in a potentially research bias (Dong et al., 2018). To the best of our knowledge, until now, quantifying research bias has been an arduous issue since no formula or model could be fitted to predict research bias caused by human subjectivity.

3. Results

3.1. Publication bias and data distribution

In our analysis, the publication bias among these 19 variable datasets was taken into consideration, and the response ratios with publication bias were corrected by the trim-fill method (Duval and Tweedie, 2000). Fortunately, there was few publication bias in our database after correcting as the funnel plot was symmetrical (Fig. S1). The results of Shapiro-Wilk test showed that the data was abnormal distribution ($p < 0.05$, Fig. S1), therefore Spearman's rank correlation coefficient is suitable for analyzing the correlation between variables in this study.

3.2. Effects of warming on AM fungal abundance

Warming significantly increased AM fungal abundance, with a weighted response ratio of AM fungal abundance of 0.171 (95%CI: 0.057–0.284) (Fig. 2). However, the responses of AM fungal abundance were different among ecosystems types, but did not reach a statistical significant level ($p = 0.06$) (Fig. 2a). Across ecosystems, grassland (19.1%) and forest (18.7%) showed significant increases in AM fungal abundance under warming, while shrub showed no response to warming (Fig. 2). The response of AM fungal abundance to warming also varied among experimental duration, but statistically insignificant ($p = 0.10$). The AM fungal abundance significantly increased with an experimental duration of medium-term (1–5 yr) but not experiments with short-term (<1 yr) and long-term (>5 yr) in duration under warming. Warming effects on AM fungal abundance were significantly different among experimental season ($p = 0.04$). Both entire-year and growing-season warming experiments significantly enhanced AM fungal abundance, with an increase of 22.7% and 16.6% for entire-year and growing-season warming experiments, respectively. Additionally, warming methods affected the response of AM fungal abundance to warming but statistically insignificant ($p = 0.09$). Warming using infrared heater significantly promoted the AM fungal abundance, but not warming using green house and cable.

According to the results of model-averaged of the summed Akaike weights, the degree of temperature increase is the only important variable (Fig. 3a). The degree of temperature increase and the RR of AM fungal abundance are significantly negatively correlated (Fig. 3b, $p < 0.05$). Specifically, when the increased temperature is less than 4.14 °C, warming will stimulate AM fungal abundance, and when the increased temperature is greater than 4.14 °C, warming effects are negative (Fig. 3b). Moreover, the RR of AM fungal abundance only fit with the RR of AGB significantly (Fig. 4a, $p < 0.05$).

3.3. Effects of eCO_2 on AM fungal abundance

Elevated CO_2 concentration significantly enhanced AM fungal abundance, with a weighted response ratio of AM fungal abundance of 0.1943 (95%CI: 0.1408–0.2478) (Fig. 2). The responses of AM fungal abundance were all significantly different among ecosystems types, duration, periods and methods ($p < 0.01$) (Fig. 2a). Across ecosystems, eCO_2 had significant positive effects on AM fungal abundance in grassland (15.2%) and forest (31.0%), whereas it had insignificant effects on AM fungal abundance in farmland and shrub (Fig. 2). The response of AM fungal abundance to eCO_2 also varied among experimental duration ($p < 0.01$). AM fungal abundance significantly increased by 14.5%, 35.1% and 21.9%, respectively, with an experimental duration of short-term (<1 yr), medium-term (1–5 yr) and long-term (>5 yr). Elevated CO_2 concentration effects on AM fungal abundance were significantly different among experimental season ($p < 0.01$). Both entire-year and growing-period warming experiments significantly enhanced AM fungal abundance, with an increase of 37.0% and 20.0% for entire-year and growing-season warming experiments, respectively. Moreover, experimental methods affected the response of AM fungal abundance to warming statistically insignificant ($p < 0.01$). Elevated CO_2 concentration using open-top chamber, green house, and growth chamber significantly promoted the AM fungal abundance.

The model-averaged of the summed Akaike weights indicated that the degree of CO_2 concentration increase is the most important variable (Fig. 3a). Although MAP and the RR of AM fungal abundance are significantly negatively correlated ($p < 0.05$), the effect of eCO_2 on AM fungal abundance is always positive in our database regardless of MAP (Fig. 3b). The correlation between the degree of CO_2 concentration increase and the RR of AM fungal abundance is quadratic polynomial ($p < 0.05$). Specifically, when the eCO_2 concentration is 60.27 ppm higher than ambient atmospheric concentration, the effect of eCO_2 on AM fungal abundance is positive, and when the eCO_2 concentration is 449.14 ppm higher than ambient atmospheric concentration, this positive effect will reach the maximum (Fig. 3b). Furthermore, the RR of AM fungal abundance increased closely with the RR of shoot N and shoot dry weight significantly (Fig. 4b, $p < 0.05$).

3.4. Effects of N addition on AM fungal abundance

N addition decreased AM fungal abundance with a weighted response ratio of AM fungal abundance of −0.0540 (95%CI: −0.1123–0.0015), but statistically insignificant ($p > 0.05$) (Fig. 2). Across ecosystems, forest (17.1%) showed significant increases in AM fungal abundance under warming, grassland (−23.2%) suggested significant decreases, while shrub and farmland showed no response to N addition (Fig. 2). The response of AM fungal abundance to warming also significantly varied among experimental durations ($p < 0.01$). The AM fungal abundance significantly increased with an experimental duration of short-term (<1 yr), but significantly decreased with an experimental duration of medium-term (1–5 yr), and not experiments with long-term (>5 yr) in duration under N addition. Additionally, experimental methods affected the response of AM fungal abundance to N addition significantly ($p < 0.01$). N addition using open-top chamber significantly promoted the AM fungal abundance, N addition using field experiment but not green house and growth chamber significantly suppressed the AM fungal abundance.

According to the results of model-averaged of the summed Akaike weights, the degree of nitrogen fertilizer input and the ecosystem types regulated the RR of AM fungal abundance (Fig. 3a). MAP is related with the RR of AM fungal abundance significant and positive (Fig. 3b, $p < 0.05$). Mean annual precipitation 814.63 mm is set as the dividing line to distinguish between positive and negative effects of N addition on AM fungal abundance (Fig. 3b). Moreover, the RR of AM fungal abundance increased closely with the RR of pH, shoot N, root N, and shoot dry weight (Fig. 4b, $p < 0.05$), and furthermore promoted the fitness with shoot-to-root ratio using quadratic fitting (Fig. 4b, $p = 0.03$).

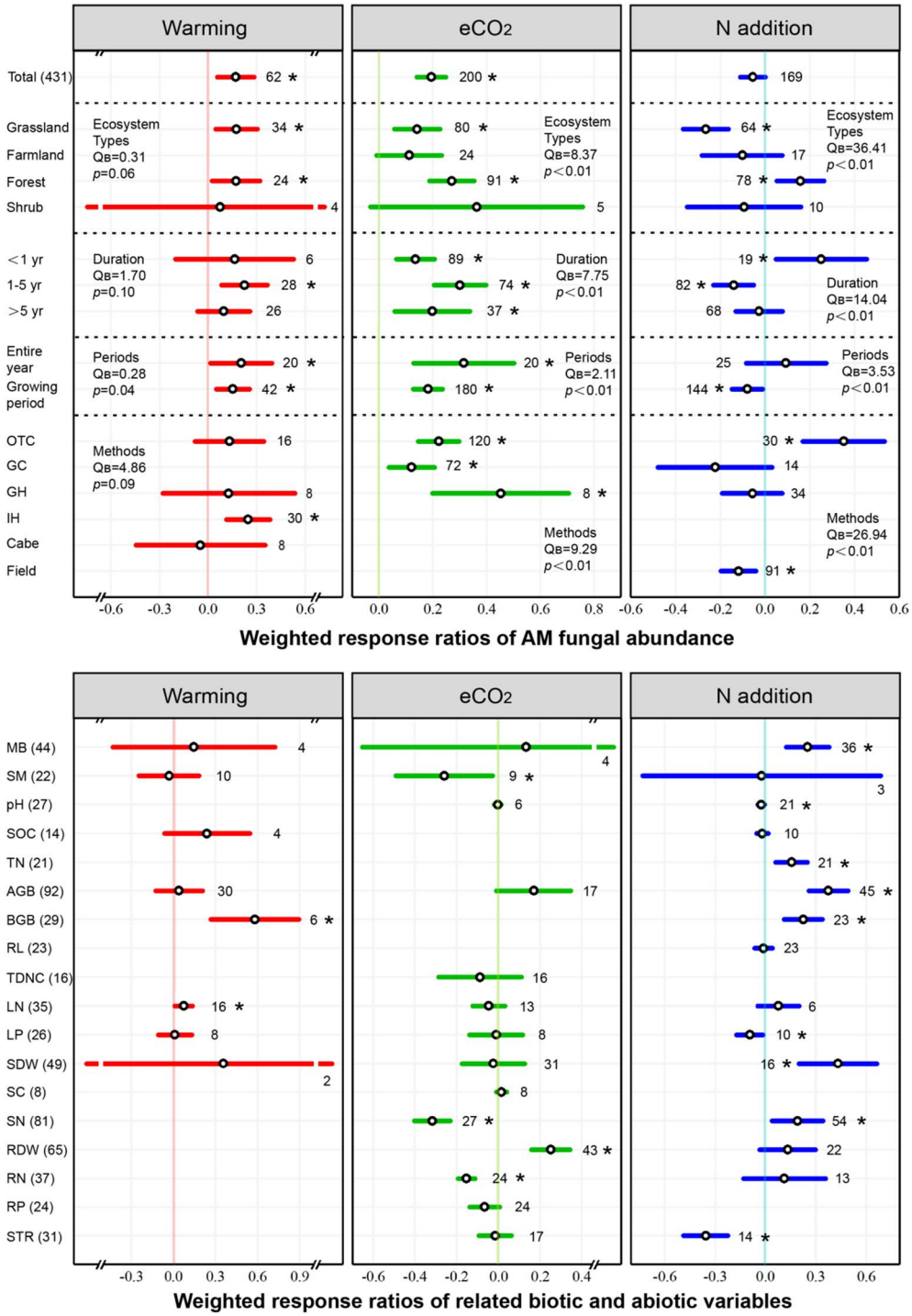


Fig. 2. Weighted response ratios of AM fungal abundance in response to warming, elevated CO_2 and N addition. MB, microbial biomass; SM, soil moisture; SOC, soil organic carbon; TN, total nitrogen; AGB, above ground biomass; BGB, below ground biomass; RL, root length; TDNC, total dry N content; LN, leaf N; LP, leaf P; SDW, shoot dry weight; SC, shoot C; SN, shoot N; RDW, root dry weight; RN, root N; RP, root P; STR, shoot-to-root ratio. The red, green and blue errors represent 95% confidence intervals (CIs) of weighted response ratios of warming experiments, increase CO_2 concentration experiments and N addition experiments. If 95% CIs did not overlap zero, the effects of climate change on variables were considered significant ($p < 0.05$, denoted by *). The numbers next to the error bar represent the sample sizes of observations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Comparison with previous studies

This study summarizes the effects of warming, eCO_2, and N addition on AM fungal abundance within the globe, and further estimates the relationship between AM fungal abundance and relevant variables under global climate change. Positive effects of warming on AM fungal abundance (Fig. 2, RR: 18.6%, 95%CI: 5.9% to 32.8%) in this study are consistent with previous regional and global studies (Cotton, 2018; Heinemeyer and Fitter, 2004; Hodge et al., 2014); eCO_2 significantly stimulated AM fungal abundance (Fig. 2, RR: 21.4%, 95%CI: 15.1% to 28.1%), consistent with earlier meta-analyses [+14.9% in the study conducted by Dong et al. (2018), +47.0% by Treseder (2004)]. However,

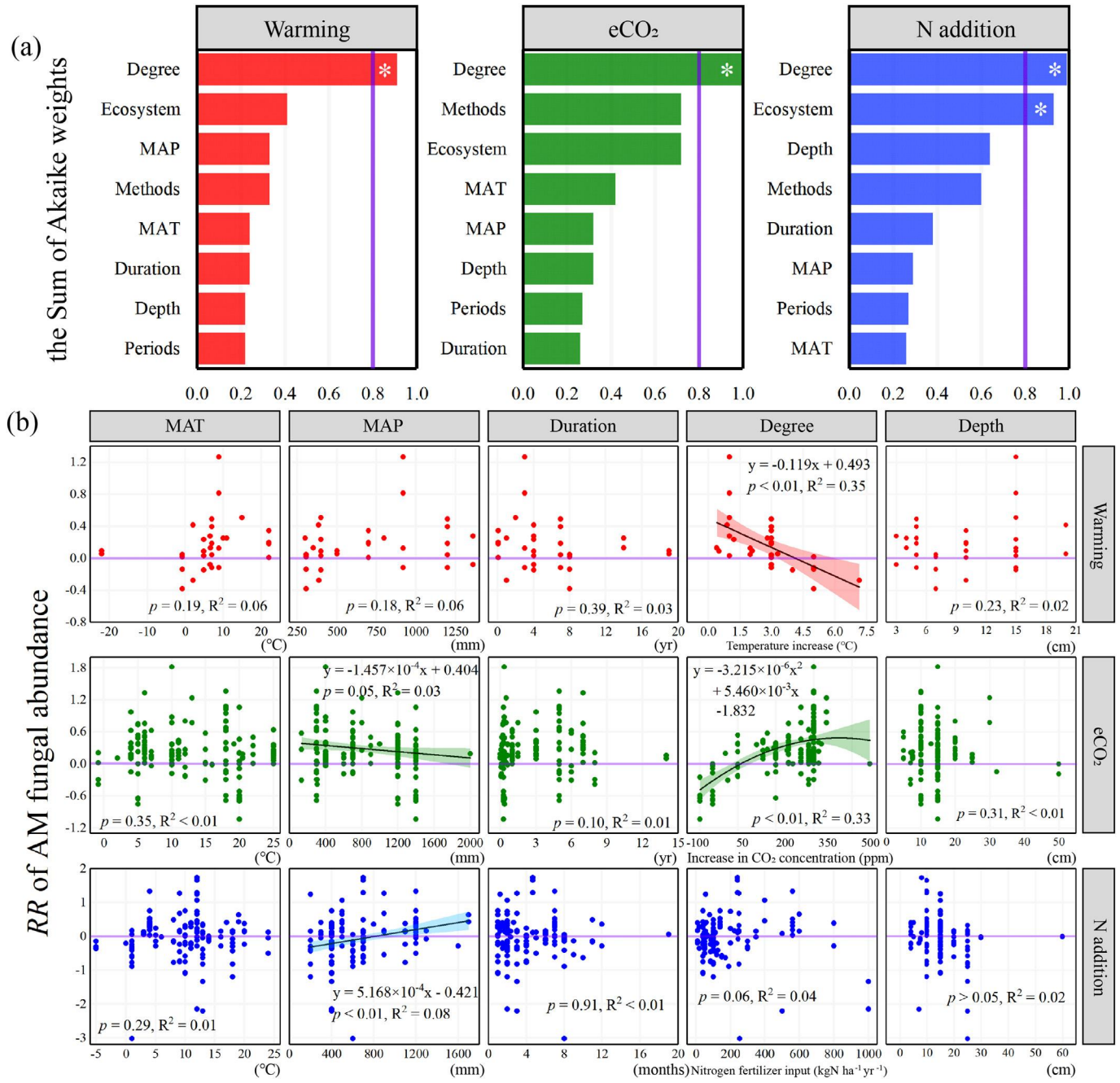


Fig. 3. Relative importance and correlations between the RR of AM fungal abundance and experimental and climate variables under the drivers of global climate change. Panel a suggested that red, green and blue columns represent the sum of Akaike weights of the RR of AM fungal abundance under warming, eCO_2 and N addition, respectively. Cut off (purple solid line) is set at 0.8 to differentiate between important and nonessential variables. If the variable is important, we denoted by *. The importance is based on the sum of Akaike weights derived from model selection using corrected Akaike's Information Criteria. MAT, MAP, Depth and Duration represent mean annual air-temperature, mean annual precipitation, soil depth and experimental duration, respectively. Periods, Methods and Ecosystem types was divided into different ranks according to the classification method in Fig. 2. Degree represent the degree of temperature rise in the warming experiment, the degree of CO_2 concentration increase in the eCO_2 experiment, and nitrogen fertilizer input in N addition experiment. Panel b showed that the correlations between the RR of AM fungal abundance and MAT, MAP, Duration, Degree. Purple solid line indicates that the RR of AM fungal abundance is 0 to differentiate between positive and negative effects. If p value smaller than 0.05, we denoted by the fitting equation and 95%CIs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

our results showed insignificant responses of AM fungal abundance to N addition (Fig. 2, RR: −5.4%, 95%CI: −10.6% to 0.2%), inconsistent with Zhang et al. (2018) who indicated the negative and significant response (RR: −24.4%, 95%CI: −42.8% to −6.0%). This inconsistency may result from three factors. First, our dataset included more indicators of AM fungal abundance. In the research of Zhang et al. (2018), two indicators of AM fungal abundance (NLFA standing for living AM fungi in soils and root colonization representing the biomass of AM fungi in host roots) were included, while in our meta-analysis, besides the above two indicators, extraradical hyphal length density and spore density in soils were also taken into account. Recent research implied that extraradical hyphal length density and spore density in soils have been demonstrated to be less affected by N addition than NLFA and root colonization (Han et al., 2020). Therefore, the negative effects of Zhang et al. (2018) may result in overestimation. Second, the data on AM fungal abundance in Zhang et al.'s (2018) meta-analysis is mainly derived from the N

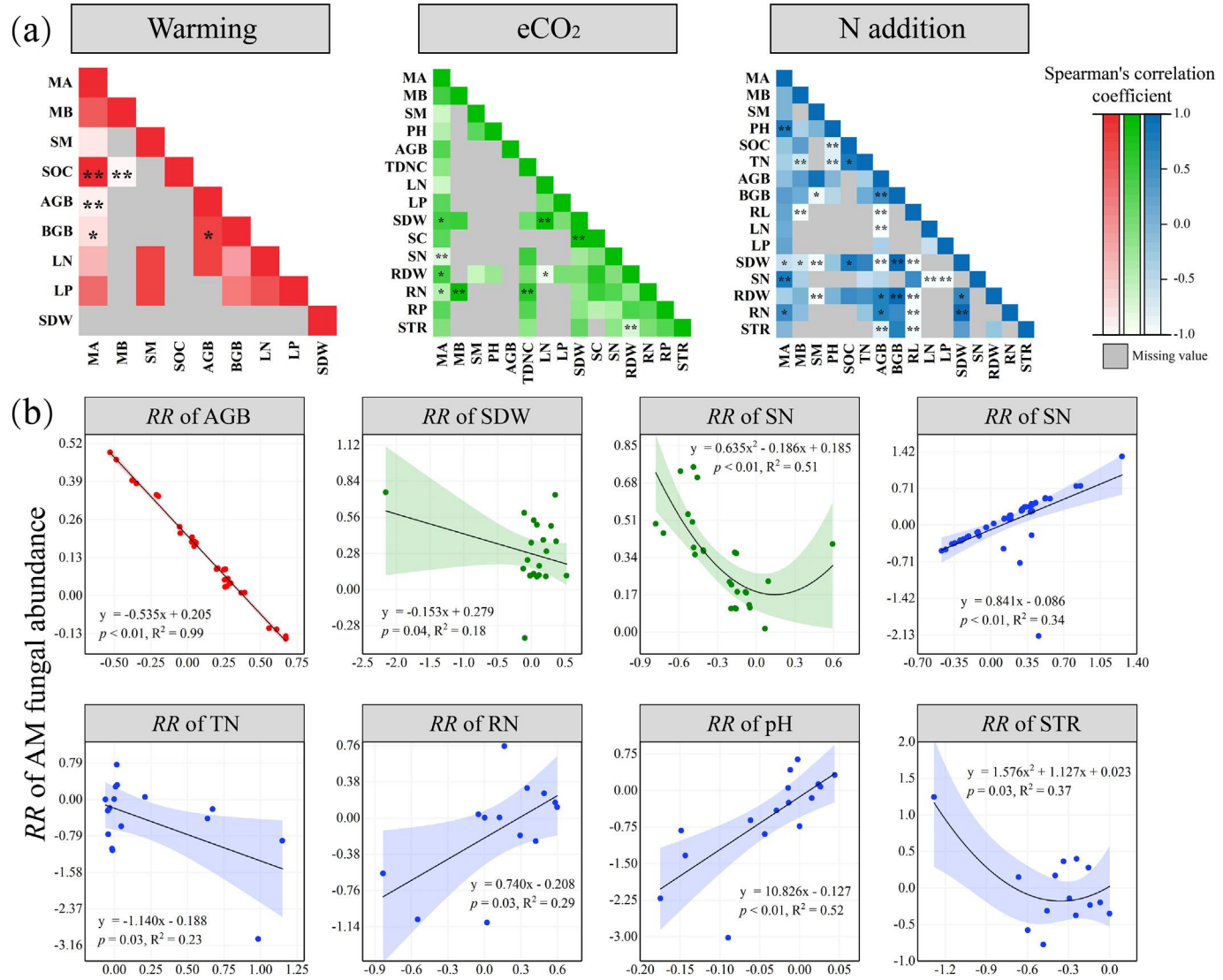


Fig. 4. Relationships between the response ratios (RR) of AM fungal abundance and its relevant biotic and abiotic variables under the drivers of global climate change. Panel a shows Spearman's correlation coefficients between the RR of AM fungal abundance and its relevant biotic and abiotic variables under warming, eCO_2 and N addition. MA, AM fungal abundance; MB, microbial biomass; SM, soil moisture; SOC, soil organic carbon; TN, total nitrogen; AGB, above ground biomass; BGB, below ground biomass; RL, root length; TDNC, total dry N content; LN, leaf N; LP, leaf P; SDW, shoot dry weight; SC, shoot C; SN, shoot N; RDW, root dry weight; RN, root N; RP, root P; STR, shoot-to-root ratio. If p value smaller than 0.05 and 0.01, we denoted by * and **, respectively. Panel b shows the significant correlations between the RR of AM fungal abundance and its significant relevant variables based on the results of Panel a. Light red, light green and light blue areas represent the 95% CIs under warming, CO_2 concentration increase and N addition, respectively. When p value is larger than 0.05, the correlation is considered insignificantly, and please refer to Table S5 for detailed information about the insignificant correlations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

addition experiments. The experimental duration of more than one month and a high level of N fertilizer input rate may lead to the overestimation of the negative effect of N addition on AM fungal abundance. Our results implied that when the duration of N addition is less than one month and N fertilizer input rate is less than 396.38 kgN ha^{-1} yr^{-1} (Table S4), the RR of AM fungal abundance increased with N fertilizer input rate. Third, our database included a total of 78 forests covering 46.1% of all ecosystem types. Under N addition, the average RR of AM fungal abundance forests was positive significantly (Fig. 2) and the RR of AM fungal abundance in forests is negative when the N fertilizer input rate exceeds 871.31 kg N ha^{-1} yr^{-1} (Table S4).

4.2. Relevant variables and their potential mechanisms

The consistent decrease in the RR of AM fungal abundance with the degree of warming, in contrast to the positive effects reported from the majority of similar warming studies (Compant et al., 2010; Heinemeyer and Fitter, 2004; Hodge et al., 2014). Our results showed that under the scenario of warming, the degree of warming was the most important variable for the RR of AM fungal abundance (Fig. 3a), and the average RR of AM fungal abundance and the degree of warming were negatively correlated (Fig. 3b). Interestingly, we found that taking the degree of warming as the X-axis and the RR of AM fungal abundance as the Y-axis, the zero points of the fitting equation with an experimental duration of 1–5 years, more than 5 years were 3.92 °C, 4.19 °C, respectively; the zero points of the fitting equation with an experimental ecosystem type of grasslands and forests were 4.59 °C, 4.28 °C, respectively; the zero points of the fitting equation with an experimental period of the entire year and only growing periods were 4.59 °C, 3.91 °C, respectively; the zero points of the fitting equation with an experimental method of OTC and IH were 4.53 °C, 4.10 °C, respectively (Table S2); the zero point of the fitting equation of the average effects of all warming cases in our dataset was 4.14 °C (Fig. 3b). Therefore, in our meta-analysis, the zero points of all significant fitting equations were around 4 °C, which implied that in the warming experiments, as long as the degree of warming exceeded around 4 °C, the effects of warming on AM fungal

abundance changed from positive to negative regardless of the experimental durations, methods, periods and ecosystem types. A possible explanation is that slight experimental warming (less than 4 °C) will change the structure and allocation of the AM hyphal network, with a switch from more vesicles (representing storage energy in cooled soils) to more extensive extraradical hyphal networks (representing growth in AM fungi in warmed soils), increasing AM fungal abundance (Hawkes et al., 2008) (Fig. 5a); however, when the AM fungi are exposed to experimental warming of more than 4 °C, warming will decrease soil water availability, resulting in an imbalance of soil available N:P owing to the greater mobility of the inorganic N (such as nitrate and ammonia) compared to P (Wilson et al., 2016). Previous studies demonstrated that the decline in soil available N:P harms AM fungal colonization (Wilson et al., 2016; Ostertag, 2001; Yoneyama et al., 2012). Therefore, excessive warming (more than 4 °C) suppresses the AM fungal abundance via decreasing soil water availability and soil available N:P (Fig. 5b).

Furthermore, our results also indicated that (1) warming stimulated AM fungal abundance (RR: 18.6%, 95CI%: 5.9%–32.8%), accompanied by the increased AGB (+4.2%) and BGB (+78.7%) (Fig. 2); and (2) AM fungal abundance significantly correlated with AGB and BGB under warming (Fig. 4a). This may be due that host plant growth benefits from warming via elevating soil N availability and prolonging growing season (Sherry et al., 2007; Chen et al., 2020; Lu et al., 2011; Takatoshi and Anne, 2016; Zhang et al., 2015). Such benefit drives host plants to allocate more C to AM fungi for improving N availability of host plants (shown in Fig. 5c, Heinemeyer and Fitter, 2004; Hodge et al., 2014; Shi et al., 2017; Kim et al., 2015; Yang et al., 2013; Qin et al., 2020). Although we found that AM fungal abundance is more relevant with AGB than BGB (Fig. 4a), we cannot infer the relative importance of AGB and BGB to AM fungal abundance since we collected 30 responses ratios of AGB but only 6 response ratios of BGB under warming scenarios (Fig. 2). Overall, warming has both positive effects (Fig. 5a, c) and negative effects (Fig. 5b) on AM fungal abundance. When the degree of warming

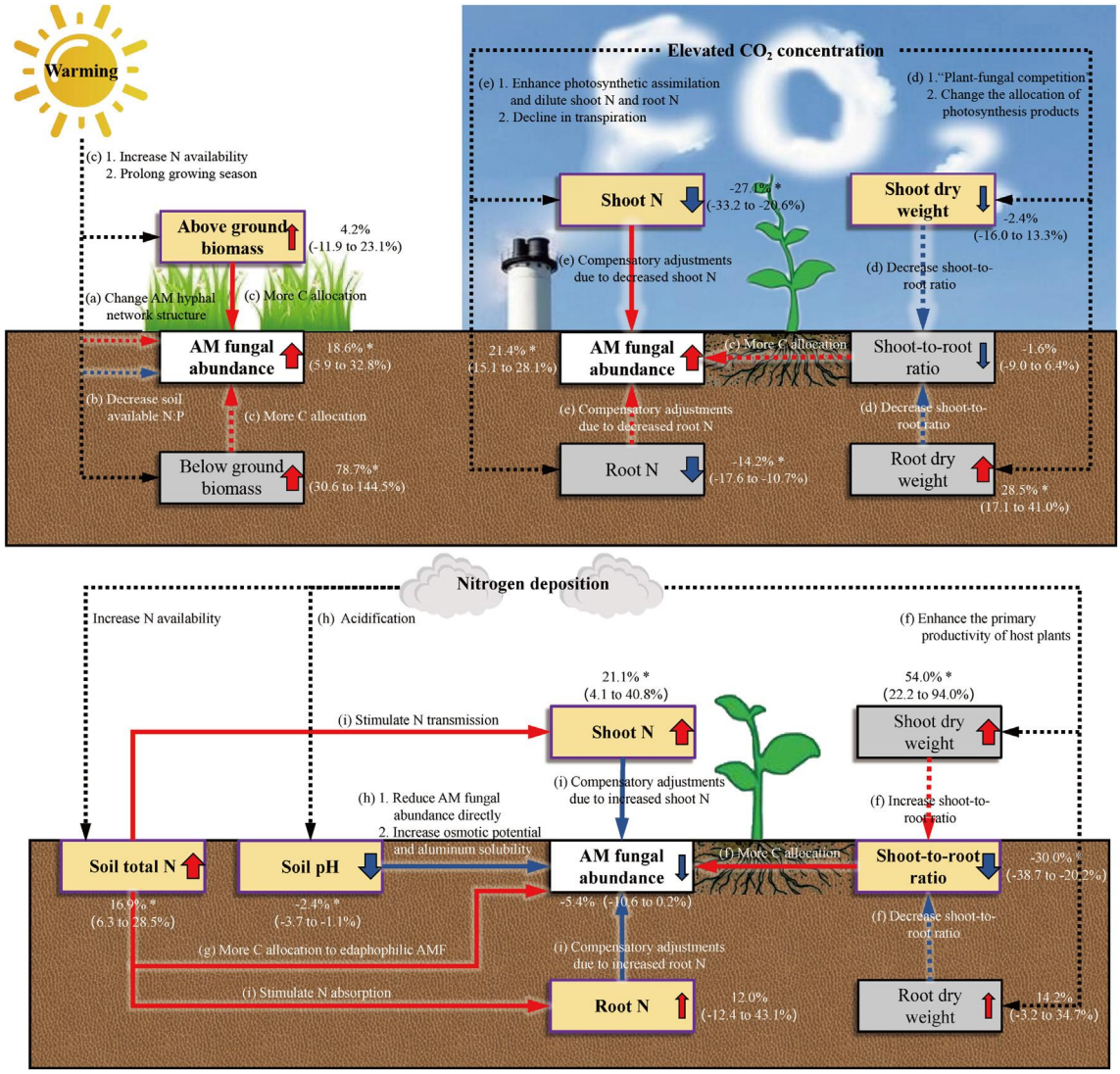


Fig. 5. Potential mechanism of global climate change effects on AM fungal abundance. Panel A, B and C show potential mechanism of effects of warming, elevated CO_2 and N addition on AM fungal abundance, respectively. Significance and structure are derived from Fig. S4. The white boxes represent AM fungal abundance, the yellow boxes and the grey boxes represent the significant and insignificant relevant variables with AM fungal abundance, respectively. The red up arrows and blue down arrows in boxes represent positive and negative responses, respectively. The thick arrows and narrow arrows in boxes represent significant and insignificant, respectively. The numbers next to each box represent weighted percentage change and its corresponding lower and upper 95% CIs, respectively. The asterisk (*) represent global climate change effects on the variable was significant ($p < 0.05$). The red arrows and blue arrows outside boxes represent the positive and negative effects, respectively. The solid arrows and dashed arrows outside boxes represent the significant and insignificant correlations with AM fungal abundance, respectively. The black dashed arrows outside boxes represent the effects of the global climate driver on these variables. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

is less than 4 °C, the positive effect will be greater than the negative effect.

Same as the warming experiments, the degree of eCO_2 concentration is also the most important variable for the RR of AM fungal abundance (Fig. 3a). Consistent with most previous studies, both positive effect of eCO_2 on AM fungal abundance (Fig. 2, RR: 21.4%, 95%CI: 15.1%–28.1%) and a positive correlation between the RR of AM fungal abundance and the degree of eCO_2 concentration (Fig. 3b) were found in our study. Interestingly, the RRs of AM fungal abundance to eCO_2 of less than 1 year, 1–5 years, and more than 5 years were +14.5%, +35.1%, and +21.9%, respectively (Fig. 2). The mechanism of progressive nitrogen limitation (PNL) could explain these results. PNL describes the stimulation of host plants and their AM fungal symbionts by eCO_2 leads to increases in N sequestration in plant and SOM, eventually resulting in a progressive reduction in soil N availability (Luo et al., 2004; Long and Drake, 1991; Dong et al., 2018). ECO_2 accelerates the N immobilization rates of host plants and their AM fungal symbionts, which depletes the soil available N (Finzi et al., 2006). The decline in N availability constrains the eCO_2 fertilization effect on plant growth over longer timescales, and optimal utilization strategy of mycorrhizal mutualistic partners by plants lead to the mycorrhizal-induced PNL, which suppresses the positive responses of AM fungal abundance to eCO_2 (Kummel and Salant, 2006; Alberton and Kuyper, 2009; Liang et al., 2016; Dong et al., 2018). In detail, photosynthesis of mycorrhizal plants is stimulated by eCO_2 in a short period, whereas the initial stimulation of photosynthesis is reduced by prolonged exposure to eCO_2 (Dong et al., 2018). Therefore, the less positive response of AM fungal abundance to eCO_2 of more than 5 years than 1–5 years (Fig. 2) may be attributed to downregulate photosynthesis, caused by the prolonged eCO_2-induced excess carbohydrate accumulation or decreased N content rather than the direct effect of eCO_2 (Dong et al., 2018; Chapin et al., 1987).

Moreover, significant correlations between the RR of AM fungal abundance and the RRs of shoot N, root N, shoot dry weight, and root dry weight (Fig. 4b) were found in our study. These results may be attributed that changes in CO_2 concentration would modulate the allocation of nutrient and carbohydrate by host plants and their AM fungal symbionts via altering the relative degree of nutrient and carbohydrate limitations in host plants (Becklin et al., 2016; Johnson, 2010). Here, two potential mechanisms of such modulation have been proposed (Fig. 5d and e). First, plant-fungal competition for resource induced by eCO_2 drives the decline in shoot-to-root ratio of host plants, increasing the AM fungal abundance (Fig. 5d). Under low CO_2 concentration (340–400 μL L^{-1}), AM fungi could promote CO_2 assimilation of host plants by enhancing the nutrient uptake that is necessary for host plants to maximize photosynthetic capacity (Becklin et al., 2016). However, under high CO_2 concentration (It refers to a CO_2 concentration higher than 540 ppm, but this critical point varies depending on different host plants, for example, AM fungi decreased the growth of *T. ceratophorum* plants but still increased the growth of *T. officinale* plants at the CO_2 concentration of 1000 ppm), the relationship between host plants and AM fungi shifts from cooperation to competition for resource especially nutrients (Becklin et al., 2016). Such plant-fungal competition would suppress the enhancement of photosynthesis of host plants as well as constraining the response of host plant growth to eCO_2. The increased AM fungal abundance could enhance the carbohydrate sink strength within host plants without providing additional nutrient benefits, which results in the host plant growth depressions (Becklin et al., 2016; Alberton et al., 2007; Johnson, 2010). Such competition has been confirmed to be usually accompanied by a decline in shoot-to-root ratio of host plants because the shoot-to-root ratio depends on nutrient and environmental conditions and implies resource allocation strategy of host plants and their AM fungal symbionts (Rogers et al., 1996; Dong et al., 2018; Klironomos et al., 2005; Veresoglou et al., 2012). Our results that eCO_2 decreased shoot-to-root ratio by 1.6% (Fig. 2) suggested more C allocation from host plants to AM fungi under the scenario of eCO_2. Second, eCO_2-induced decreases in shoot N, while root N drives compensatory adjustments of host plants to AM fungi (Fig. 5e). Two possible reasons could explain the decline in shoot N and root under eCO_2: (1) eCO_2 enhances photosynthetic assimilation of host plants with more C and secondary compound production, which dilutes the N contents of shoot and root (Gifford et al., 2000; Kuehny et al., 1991; Loladze and Elser, 2011); (2) host plants exposed to the eCO_2 atmosphere close stomas, resulting in the decline in transpiration, which decreases the delivery of mobile N to root and limits plant N acquisition that lags behind the accelerated C acquisition (Mcdonald et al., 2002; Pozo et al., 2007). Thus, declines in shoot N and root N under eCO_2 atmosphere due to enhancement photosynthetic assimilation and decline in transpiration elicit compensatory adjustments to increase the AM fungal abundance. Compensatory adjustments include (1) increase in root mycorrhizal infection, (2) change in root morphology and architecture, (3) better root absorption capacity to nutrient, and (4) a higher nutrient-use efficiency that can meet the increased nutrient demand of plant (Alberton et al., 2005; Dong et al., 2018; Pang et al., 2006; Bassirirad et al., 2001).

Among the drivers of global climate change, the effect of N addition on AM fungal abundance has received the most attention (Cotton, 2018). Our results suggested that both the experimental ecosystem type and the degree of N addition were important (Fig. 3a). The RR of AM fungal abundance was negative in grassland, farmland, and shrub (RRs: −23.3%, −9.8%, and −9.0%, respectively) whereas positive in the forest (RR: 17.1%) (Fig. 2). Furthermore, the RR of AM fungal abundance in grasslands and farmlands is negative when the degree of N addition exceeds 33.85 and 67.64 kg N ha^{-1} yr^{-1}, respectively; however, N addition decreases AM fungal abundance in forests only when the degree of N addition exceeded 871.31 kg N ha^{-1} yr^{-1} (Table S4). The relatively low abundance of edaphophilic AM fungi and the relatively high abundance of rhizophilic AM fungi in forest ecosystem type (Yuan et al., 2018; Weber et al., 2019). Rhizophilic AM fungi, such as Glomeracea (Table S1), is favored under N addition (Treseder et al., 2018; Weber et al., 2019) and can be even able to persist or thrive under high N (Lilleskov et al., 2019), but edaphophilic AM fungi, such as Gigasporaceae (Table S1), would be suppressed under N addition (Weber et al., 2019; Han et al., 2020).

Notably, our result implied the negative but insignificant effect of N addition on AM fungal abundance (Fig. 2), which is inconsistent with the results of several recent meta-analyses (Treseder et al., 2018; Zhang et al., 2018; Han et al., 2020) or field research (Antoninka et al., 2011; van Diepen et al., 2011; Liu et al., 2012). Mechanically, the fundamental reason for such inconsistency may be attributed to the fact that the effect of N addition on AM fungal abundance is comprehensive (Fig. 5), and previous meta-analyses overestimated the negative effects or ignored the positive effects. We found that such a comprehensive effect comprising of four single effects (shown in Fig. 5f, g, h, i, respectively). First, N addition normally enhances the primary productivity of AM plants (Phillips et al., 2013; Thomas et al., 2010; Pan et al., 2020), resulting in the C-richness and shifts fungal community in favor of AM fungi over ECM fungi (Averill et al., 2018; Averill et al., 2019) (Fig. 5f). In our study, the increased shoot and root dry weight (+54.0% and + 14.2%) and the decreased shoot-to-root ratio (−30.0%) demonstrated that the high available N would improve the ability of the AM fungal to transfer N to host plants, augmenting benefits of host plant investment, such as C allocation into AM fungi (Johnson et al., 2015; Verlinden et al., 2018). This positive effect indicates that N addition may elicit a positive feedback loop in which AM fungal enhancement of N uptake would promote the allocation of host plant C to AMF for the acquisition of other resources, resulting in an increased AM fungal abundance (Pan et al., 2020). Second, N addition leads to an imbalance of N:P of host plants, which drives host plants to invest more C to edaphophilic AM fungi, since edaphophilic AM fungi contribute to P uptake of the host plants (Fig. 5g, Weber et al., 2019; Mosse and Phillips, 1971; Dong et al., 2018; Treseder, 2004; Staddon et al., 2004).

Response of edaphophilic AM fungi to N addition follows this mechanism to ensure N:P balance of host plants and their AM fungal symbionts. When the host plants and their AM fungal symbionts are in the N-limitation, edaphophilic AM fungi limit the protein synthesis rates to reduce N consumption. While under P-limitation, edaphophilic AM fungi constrain RNA production rates to reduce P consumption (Loladze and Elser, 2011; Alberton et al., 2005; Dong et al., 2018; Han et al., 2020). Third, soil acidification decreases AM fungal abundance both directly and indirectly (Fig. 5h). Soil acidification from excessive N addition would usually reduce root colonization, spore production, and extraradical hyphal growth (Han et al., 2020; Clark, 1997), inhibit enzymatic activities (Zhang et al., 2018), and decrease SOC decomposition (Janssens et al., 2010; Lee and Jose, 2003). Moreover, the decreased microbial biomass C following soil acidification results in a greater osmotic potential and an increased aluminum solubility that is toxic to AM fungi (Vitousek et al., 1997). Finally, compensatory adjustments due to increased shoot N and root N can suppress AM fungal growth. N addition can increase soil total N and supplement N availability (An et al., 2008; Weber et al., 2019), which will stimulate N absorption and transmission and increase shoot N and root N of host plants, and led to the compensatory adjustments that reduce AM fungal abundance (Zhang et al., 2018) (Fig. 5i). Overall, the former two effects (Fig. 5f, g) are positive on AM fungal abundance, the latter two effects are negative (Fig. 5h, i), therefore the comprehensive effect composed by such 4 single effects changes with a specific context. This means that we could not simply determine the effects of N addition on AM fungal abundance without considering the difference in a specific context such as ecosystem types.

4.3. Uncertainties and research need

Sources of uncertainties should be noted when interpreting results in this meta-analysis. First, uncertainty may derive from the uneven spatial distribution of data. Specifically, we reviewed a total of 431 cases, of which 36.0% were in North America, 33.6% in Europe, 24.6% in Asia, 4.4% in Oceania, and the remaining 1.4% in South America (Fig. 1). More importantly, more than 85% of the experiments were conducted in mid-latitudes, whereas very few experiments were in low-latitudes and particularly high-latitudes. Instead of simply extrapolating results from this analysis (mostly from mid-latitudes) to low-latitudes and high-latitudes, we took into account various environmental conditions, including climate, precipitation, carbon storage, and the sensitivity to the drivers of global climate change (Chen et al., 2020). As a consequence, more experimental results from low or high latitude areas are needed to better understand the responses of AM fungal abundance to the drivers of global climate change in the future. Second, the studies in our database employed a wide range of experimental methods, which could also be a source of uncertainty. Previous meta-analyses suggested that open-top chamber (OTC) and infrared heater (IH) techniques would only increase the temperature of surface soil, but barely warm the subsoil by more than 30 cm, where more than half of the total SOC in the whole soil profile is stored (Jackson et al., 2017; Chen et al., 2020). Although our analysis indicated that the effects of any single driver of global climate change on AM fungal abundance did not depend on the experimental method (Fig. 3a), uniform research techniques would facilitate comparisons between experiments. Third, due to data limitations, we cannot further divide the data into subgroups, and the differences between subgroups will also become one of the sources of uncertainty. For instance, as introduced by Han et al. (2020), AM fungi have intra- and extra- radical structures, which can be subdivided "in root" and "in soil" guilds with different responses to climate change. Moreover, differences in sampled soil types, soil layers, and measurement methods of the same variable may contribute to the uncertainty of the results. For instance, in our study, there are 65 cases related to dry root weights, of which 24.6% used 60 °C for 2 days to determine dry root weights, 4.6% used 60 °C for 5 days, 9.2% used 65 °C until the weight was constant, 1.5% used 70 °C for 2 days, 10.8% used 75 °C for 3 days, 6.2% used 80 °C for 1 day, 27.7% used 80 °C for 4 days, and 15.4% used 105 °C until the weight was constant. Therefore, we suggest conducting multi-site comparison studies that employ the same measurement method, which is conducive to understanding the role of AM fungi in regulating the growth of host plants under global changes. Lastly, the small sample size in some groups could be another source of uncertainty. For example, only 4 cases of shrubs under warming and 5 cases of shrubs under eCO_2 were included in our database, indicating that future researchers should pay more attention to the response of AM fungi abundance on global climate change in the shrub ecosystem.

5. Conclusions

Overall, this meta-analysis reveals the response patterns of AM fungal abundance to the drivers of global climate change including warming, eCO_2, and N addition on a global scale, and provides unparalleled insights into how AM fungal community will change in the future. We also explicitly suggested that the degree of warming, eCO_2, and N addition is the most important variable for the RR of AM fungal abundance. Specifically, although both warming and eCO_2 stimulate AM fungal abundance, the RR of AM fungal abundance decreased with the degree of warming while increased with the degree of eCO_2. Furthermore, in warming experiments, as long as the degree of warming exceeded around 4 °C, the effects of warming on AM fungal abundance changed from positive to negative regardless of the experimental durations, methods, periods, and ecosystem types; however, in N addition experiments, the effects of N addition on AM fungal abundance are often highly context-specific, especially the nitrogen fertilizer input rate and ecosystem type. We highlight that the shoots and roots of plant hosts and their mutual relationship may be the predictor for the growth of AM fungal communities. Taken together, the results provide a framework for understanding the responses of AM fungal communities to the drivers of global climate change, and contribute to developing a theoretical model to better predict ecological functions of AM fungal communities under global changes.

CRediT authorship contribution statement

Han Hu: Writing – original draft. **Liyuan He:** Writing – review & editing. **Huanfei Ma:** Data curation. **Jieying Wang:** Software. **Yi Li:** Data curation. **Jun Wang:** Conceptualization. **Yaoxin Guo:** Conceptualization. **Chengjie Ren:** Conceptualization. **Hongying Bai:** Conceptualization. **Fazhu Zhao:** Supervision, Funding acquisition, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was financially supported by the 2021 first funds for central government to guide local science and technology development in Qinghai Province (No. 2021ZY002), the China Postdoctoral Science Foundation (No. 2019M650276), and the Chinese Academy of Sciences "Light of West China" Program for Introduced Talent in the West, the National Natural Science Foundation of China (Grant No. 31570440, 31270484), and the Key International Scientific and Technological Cooperation and Exchange Project of Shaanxi Province, China (Grant No. 2020KWZ-010).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2021.150362.

References

Alberton, O., Kuyper, T.W., 2009. Ectomycorrhizal fungi associated with Pinus sylvestris seedlings respond differently to increased carbon and nitrogen availability: implications for ecosystem responses to global change. Glob. Chang. Biol. 15, 166–175.

Alberton, O., Kuyper, T.W., Gorissen, A., 2005. Taking mycocentrism seriously: mycorrhizal fungal and plant responses to elevated CO2. New Phytol. 167, 859–868.

Alberton, O., KuyperAntonie, T.W., Gorissen, 2007. Competition for nitrogen between Pinus sylvestris and ectomycorrhizal fungi generates potential for negative feedback under elevated CO2. Plant Soil 296 (1-2), 159–172.

An, G.H., Miyakawa, S., Kawahara, A., Osaki, M., Ezawa, T., 2008. Community structure of arbuscular mycorrhizal fungi associated with pioneer grass species Miscanthus sinensis in acid sulfate soils: habitat segregation along pH gradients. Soil Sci. Plant Nutr. 54, 517–528.

Antoninka, A., Reich, P.B., Johnson, N.C., 2011. Seven years of carbon dioxide enrichment, nitrogen fertilization and plant diversity influence arbuscular mycorrhizal fungi in a grassland ecosystem. New Phytol. 192, 200–214.

Auge, R.M., 2001. Water relations, drought and vesicular-arbuscular mycorrhizal symbiosis. Mycorrhiza 11, 3–42.

Averill, Colin, Dietze, Michael, C., Bhatnagar, Jennifer, M., 2018. Continental-scale nitrogen pollution is shifting forest mycorrhizal associations and soil carbon stocks. Glob. Chang. Biol. 24 (10), 4544–4553.

Averill, C., Bhatnagar, J.M., Dietze, M.C., Pearse, W.D., Kivlin, S.N., 2019. Global imprint of mycorrhizal fungi on whole-plant nutrient economics. Proc. Natl. Acad. Sci. 116, 201906655.

Bassirirad, H., Gutschick, V.P., Lussenhop, J., 2001. Root system adjustments: regulation of plant nutrient uptake and growth responses to elevated CO2. Oecologia 126, 305–320.

Becklin, K.M., Mullinix, G.W.R., Ward, J.K., 2016. Host plant physiology and mycorrhizal functioning shift across a glacial through future CO2 gradient. Plant Physiol. 172, 789–801.

Betts, R.A., Jones, C.D., Knight, J.R., Keeling, R.F., Kennedy, J.J., 2016. El Nino and a record CO2 rise. Nat. Clim. Chang. 6, 806–810.

Bever, J.D., Dickie, I.A., Facelli, E., Facelli, J.M., Klironomos, J., Moora, M., Rillig, M.C., Stock, W.D., Tibbett, M., Zobel, M., 2010. Rooting theories of plant community ecology in microbial interactions. Trends Ecol. Evol. 25, 468–478.

Cameron, D.D., Neal, A.L., van Wees, S.C.M., Ton, J., 2013. Mycorrhiza-induced resistance: more than the sum of its parts? Trends Plant Sci. 18, 539–545.

Chapin III, F., Stuart, Bloom, Arnold, J., Field, Christopher, B., 1987. Plant responses to multiple environmental factors. Bioscience 37, 49–57.

Chen, J., Luo, Y., Garcia-Palacios, P., Cao, J., Dacal, M., Zhou, X., Li, J., Xia, J., Niu, S., Yang, H., Shelton, S., Guo, W., van Groenigen, K.J., 2018. Differential responses of carbon-degrading enzyme activities to warming: implications for soil respiration. Glob. Chang. Biol. 24, 4816–4826.

Chen, Y., Feng, J., Yuan, X., Zhu, B., 2020. Effects of warming on carbon and nitrogen cycling in alpine grassland ecosystems on the Tibetan Plateau: a meta-analysis. Geoderma 370, 114363.

Clark, R.B., 1997. Arbuscular mycorrhizal adaptation, spore germination, root colonization, and host plant growth and mineral acquisition at low pH. Plant Soil 192, 15–22.

Compant, S., van der Heijden, M.G.A., Sessitsch, A., 2010. Climate change effects on beneficial plant-microorganism interactions. FEMS Microbiol. Ecol. 73, 197–214.

Cotton, T.A., 2018. Arbuscular mycorrhizal fungal communities and global change: an uncertain future. FEMS Microbiol. Ecol. 94.

Cotton, T.E., Fitter, A.H., Miller, R.M., Dumbrell, A.J., Helgason, T., 2015. Fungi in the future: interannual variation and effects of atmospheric change on arbuscular mycorrhizal fungal communities. New Phytol. 205, 1598–1607.

Dodd, J.C., Boddington, C.L., Rodriguez, A., Gonzalez-Chavez, C., Mansur, I., 2000. Mycelium of arbuscular mycorrhizal fungi (AMF) from different genera: form, function and detection. Plant Soil 226, 131–151.

Dong, Y., Wang, Z., Sun, H., Yang, W., Xu, H., 2018. The response patterns of arbuscular mycorrhizal and ectomycorrhizal symbionts under elevated CO2: a meta-analysis. Front. Microbiol. 9, 1248.

Duval, S., Tweedie, R., 2000. A nonparametric "trim and fill" method of accounting for publication bias in meta-analysis. J. Am. Stat. Assoc. 95, 89–98.

Egerton-Warburton, L.M., Allen, E.B., 2000. Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. Ecol. Appl. 10, 484–496.

Eom, Ahn-Heum, Hartnett, C.David, Wilson, W.T.Gail, Figge, Deborah, A.H., 1999. The Effect of Fire, Mowing and Fertilizer Amendment on Arbuscular Mycorrhizas in Tallgrass Prairie. American Midland Naturalist.

Feng, J., Zhu, B., 2019. Global meta-analysis of soil respiration and its components in response to phosphorus addition. Soil Biol. Biochem. 135, 38–47.

Finzi, A.C., Moore, D.J.P., DeLucia, E.H., Lichter, J., Hofmockel, K.S., Jackson, R.B., Kim, H.S., Matamala, R., McCarthy, H.R., Oren, R., Pippen, J.S., Schlesinger, W.H., 2006. Progressive nitrogen limitation of ecosystem processes under elevated CO2 in a warm-temperate forest. Ecology 87, 15–25.

Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S.P., Asner, G.P., Cleveland, C.C., Green, P.A., Holland, E.A., Karl, D.M., Michaels, A.F., Porter, J.H., Townsend, A.R., Vorosmarty, C.J., 2004. Nitrogen cycles: past, present, and future. Biogeochemistry 70, 153–226.

García-Palacios, P., Vandegehuchte, M.L., Shaw, E.A., Dam, M., Post, K.H., Ramirez, K.S., Sylvain, Z.A., De Tomasel, C.M., Wall, D.H., 2015. Are there links between responses of soil microbes and ecosystem functioning to elevated CO2, N deposition and warming? A global perspective. Glob. Chang. Biol. 21, 1590–1600.

Gifford, R.M., Barrett, D.J., Lutze, J.L., 2000. The effects of elevated [CO2] on the C:N and C:P mass ratios of plant tissues. Plant Soil 224, 1–14.

Goicoechea, N., Baslam, M., Erice, G., Irigoyen, J.J., 2014. Increased photosynthetic acclimation in alfalfa associated with arbuscular mycorrhizal fungi (AMF) and cultivated in greenhouse under elevated CO2. J. Plant Physiol. 171, 1774–1781.

Groenigen, K.J.V., Qi, X., Osenberg, C.W., Luo, Y., Hungate, B.A., 2014. Faster decomposition under increased atmospheric CO2 limits soil carbon storage. Science 344, 508–509.

Gurevitch, Jessica, Hedges, Larry, V., 1999. Statistical issues in ecological meta-analyses. Ecology 80, 1142–1149.

Han, Y., Feng, J., Han, M., Zhu, B., 2020. Responses of arbuscular mycorrhizal fungi to nitrogen addition: a meta-analysis. Glob. Chang. Biol. 26 (12), 7229–7241.

Hawkes, C.V., Hartley, I.P., Ineson, P., Fitter, A.H., 2008. Soil temperature affects carbon allocation within arbuscular mycorrhizal networks and carbon transport from plant to fungus. Glob. Chang. Biol. 14, 1181–1190.

Hedges, L.V., Curtis, G.P.S., 1999. The META-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156.

Heinemeyer, A., Fitter, A.H., 2004. Impact of temperature on the arbuscular mycorrhizal (AM) symbiosis: growth responses of the host plant and its AM fungal partner. J. Exp. Bot. 55, 525–534.

Hildebrandt, U., Regvar, M., Bothe, H., 2007. Arbuscular mycorrhiza and heavy metal tolerance. Phytochemistry 68, 139–146.

Hodge, Angela, Barrett, Gracie, Campbell, Colin D., 2014. The direct response of the external mycelium of arbuscular mycorrhizal fungi to temperature and the implications for nutrient transfer. Soil Biol. Biochem. 78, 109–117.

IPCC, 2013. Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Computational Geometry 18, 95–123.

Jackson, R.B., Lajtha, K., Crow, S.E., Hugelius, G., Kramer, M.G., Pi?Eiro, G., 2017. The ecology of soil carbon: pools, vulnerabilities, and biotic and abiotic controls. Annu. Rev. Ecol. Evol. Syst. 48 annurev-ecolsys-112414-054234.

Jakobsen, I., Smith, S.E., Smith, F.A., Watts-Williams, S.J., Clausen, S.S., Grønlund, M., 2016. Plant growth responses to elevated atmospheric CO2 are increased by phosphorus sufficiency but not by arbuscular mycorrhizas. J. Exp. Bot. 6173–6186.

Janssens, I.A., Dieleman, W., Luyssaert, S., Subke, J.A., Reichstein, M., Ceulemans, R., Ciais, P., Dolman, A.J., Grace, J., Matteucci, G., 2010. Reduction of forest soil respiration in response to nitrogen deposition. Nat. Geosci. 3, 315–322.

Jefwa, J.M., Sinclair, R., Maghembe, J.A., 2006. Diversity of glomale mycorrhizal fungi in maize/sesbania intercrops and maize monocrop systems in southern Malawi. Agrofor. Syst. 67, 107–114.

Johnson, N.C., 2010. Resource stoichiometry elucidates the structure and function of arbuscular mycorrhizas across scales. New Phytol. 185, 631–647.

Johnson, N.C., Wilson, G.W.T., Wilson, J.A., Miller, R.M., Bowker, M.A., 2015. Mycorrhizal phenotypes and the law of the minimum. New Phytol. 205.

Kim, Y.-C., Gao, C., Zheng, Y., He, X.-H., Yang, W., Chen, L., Wan, S.-Q., Guo, L.-D., 2015. Arbuscular mycorrhizal fungal community response to warming and nitrogen addition in a semiarid steppe ecosystem. Mycorrhiza 25, 267–276.

Klironomos, J.N., Allen, M.F., Rillig, M.C., Piotrowski, J., Makvandi-Nejad, S., Wolfe, B.E., Powell, J.R., 2005. Abrupt rise in atmospheric CO2 overestimates community response in a model plant-soil system. Nature 433, 621–624.

Kuehny, J.S., Peet, M.M., Nelson, P.V., Willits, D.H., 1991. Nutrient dilution by starch in CO2-enriched chrysanthemum. J. Exp. Bot. 42, 711–716.

Kummel, M., Salant, S.W., 2006. The economics of mutualisms: optimal utiliztion of mycorrhizal mutualistic partners by plants. Ecology 87, 892–902.

Lee, K.H., Jose, S., 2003. Soil respiration, fine root production, and microbial biomass in cottonwood and loblolly pine plantations along a nitrogen fertilization gradient. For. Ecol. Manag. 185, 263–273.

Liang, J., Qi, X., Souza, L., Luo, Y., 2016. Processes regulating progressive nitrogen limitation under elevated carbon dioxide: a meta-analysis. Biogeosciences 13, 2689–2699.

Lilleskov, E.A., Kuyper, T.W., Bidartondo, M.I., Hobbie, E.A., 2019. Atmospheric nitrogen deposition impacts on the structure and function of forest mycorrhizal communities: a review. Environ. Pollut. 246, 148–162.

Liu, Y., Shi, G., Mao, L., Cheng, G., Jiang, S., Ma, X., An, L., Du, G., Johnson, N.C., Feng, H., 2012. Direct and indirect influences of 8 yr of nitrogen and phosphorus fertilization on Glomeromycota in an alpine meadow ecosystem. New Phytol. 194, 523–535.

Liu, L., Wang, X., Lajeunesse, M.J., Miao, G., Piao, S., Wan, S., Wu, Y., Wang, Z., Yang, S., Li, P., 2016. A cross-biome synthesis of soil respiration and its determinants under simulated precipitation changes. Glob. Chang. Biol. 22, 1394–1405.

Loladze, I., Elser, J.J., 2011. The origins of the Redfield nitrogen-to-phosphorus ratio are in a homoeostatic protein-to-rRNA ratio. Ecol. Lett. 14, 244–250.

Long, S.P., Drake, B.G., 1991. Effect of the long-term elevation of CO2 concentration in the field on the quantum yield of photosynthesis of the C3 sedge, Scirpus olneyi. Plant Physiol. 96, 221–226.

Lu, M., Yang, Y., Luo, Y., Fang, C., Zhou, X., Chen, J., Yang, X., Li, B., 2011. Responses of ecosystem nitrogen cycle to nitrogen addition: a meta-analysis. New Phytol. 189 (4), 1040–1050.

Luo, Y., Su, B., Currie, W.S., Dukes, J.S., Finzi, A., Hartwig, U., Hungate, B., Mc Murtrie, R.E., Oren, R., Parton, W.J., 2004. Progressive nitrogen limitation to ecosystem response to rising atmospheric carbon dioxide. Bioscience 54, 731.

Luo, Y., Hui, D., Zhang, D., 2006. Elevated CO2 stimulates net accumulations of carbon and nitrogen in land ecosystems: a META-analysis. Ecology 87.

Mcdonald, E.P., Erickson, J.E., Kruger, E.L., 2002. Research note: can decreased transpiration limit plant nitrogen acquisition in elevated CO2? Funct. Plant Biol. 29.

Mosse, B., Phillips, J.M., 1971. The influence of phosphate and other nutrients on the development of vesicular-arbuscular mycorrhiza in culture. J. Gen. Microbiol. 69, 157–166.

Nuccio, E.E., Hodge, A., Pett-Ridge, J., Herman, D.J., Weber, P.K., Firestone, M.K., 2013. An arbuscular mycorrhizal fungus significantly modifies the soil bacterial community and nitrogen cycling during litter decomposition. Environ. Microbiol. 15, 1870–1881.

Ostertag, R., 2001. Effects of nitrogen and phosphorus availability on fine-root dynamics in Hawaiian montane forests. Ecology 82, 485–499.
Pan, S., Wang, Y., Qiu, Y., Chen, D., Zhang, L., Ye, C., Guo, H., Zhu, W., Chen, A., Xu, G., Zhang, Y., Bai, Y., Hu, S., 2020. Nitrogen-induced acidification, not N-nutrient, dominates suppressive N effects on arbuscular mycorrhizal fungi. Glob. Chang. Biol. 26, 6568–6580.
Pang, J., Zhu, J.G., Xie, Z.B., Liu, G., Zhang, Y.L., Chen, G.P., Zeng, Q., Cheng, L., 2006. A new explanation of the N concentration decrease in tissues of rice (Oryza sativa L.) exposed to elevated atmospheric pCO2. Environ. Exp. Bot. 57, 98–105.
Phillips, R.P., Brzostek, E., Midgley, M.G., 2013. The mycorrhizal-associated nutrient economy: a new framework for predicting carbon-nutrient couplings in temperate forests. New Phytol. 199.
Phoenix, G.K., Hicks, W.K., Cinderby, S., Kuylenstierna, J.C.I., Stock, W.D., Dentener, F.J., Giller, K.E., Austin, A.T., Lefroy, R.D.B., Gimeno, B.S., Ashmore, M.R., Ineson, P., 2006. Atmospheric nitrogen deposition in world biodiversity hotspots: the need for a greater global perspective in assessing N deposition impacts. Glob. Chang. Biol. 12, 470–476.
Porras-Alfaro, A., Herrera, J., Natvig, D.O., Sinsabaugh, R.L., 2007. Effect of long-term nitrogen fertilization on mycorrhizal fungi associated with a dominant grass in a semiarid grassland. Plant Soil 296, 65–75.
Pozo, A.D., Pérez, P., Gutiérrez, D., Alonso, A., Morcuende, R., Martínez-Carrasco, R., 2007. Gas exchange acclimation to elevated CO2 in upper-sunlit and lower-shaded canopy leaves in relation to nitrogen acquisition and partitioning in wheat grown in field chambers. Environ. Exp. Bot. 59, 371–380.
Qin, M., Zhang, Q., Pan, J., Jiang, S., Liu, Y., Bahadur, A., Peng, Z., Yang, Y., Feng, H., 2020. Effect of arbuscular mycorrhizal fungi on soil enzyme activity is coupled with increased plant biomass. Eur. J. Soil Sci. 71 (1), 84–92.
Rillig, M.C., Wright, S.F., Nichols, K.A., Schmidt, W.F., Torn, M.S., 2001. Large contribution of arbuscular mycorrhizal fungi to soil carbon pools in tropical forest soils. Plant Soil 233, 167–177.
Rogers, H.H., Prior, S.A., Runion, B.G., Mitchell, R.J., 1996. Root to shoot ratio of crops as influenced by CO2. Plant Soil 187, 229–248.
Sherry, R.A., Zhou, X., Gu, S., Arnone, J.A., Schimel, D.S., Verburg, P.S., Wallace, L.L., Luo, Y., 2007. Divergence of reproductive phenology under climate warming. Proc. Natl. Acad. Sci. 104, 198–202.
Shi, G., Yao, B., Liu, Y., Jiang, S., Wang, W., Pan, J., Zhao, X., Feng, H., Zhou, H., 2017. The phylogenetic structure of AMF communities shifts in response to gradient warming with and without winter grazing on the Qinghai-Tibet Plateau. Appl. Soil Ecol. 121, 31–40.
Smith, S.E., Jakobsen, I., Gronlund, M., Smith, F.A., 2011. Roles of arbuscular mycorrhizas in plant phosphorus nutrition: interactions between pathways of phosphorus uptake in arbuscular mycorrhizal roots have important implications for understanding and manipulating plant phosphorus acquisition. Plant Physiol. 156, 1050–1057.
Staddon, P.L., Jakobsen, I., Blum, H., 2004. Nitrogen input mediates the effect of free-air CO2 enrichment on mycorrhizal fungal abundance. Glob. Chang. Biol. 10 (10), 1678–1688.
Takatoshi, K., Anne, K., 2016. Plant nitrogen acquisition under low availability: regulation of uptake and root architecture. Plant Cell Physiol. 2016 (4), 707–714.
Tang, J., Jing, C., Xin, C., 2006. Response of 12 weedy species to elevated CO2 in low-phosphorus-availability soil. Ecol. Res. 21, 664–670.
Terrer, C., Vicca, S., Hungate, B.A., Phillips, R.P., Prentice, I.C., 2016. Mycorrhizal association as a primary control of the CO2 fertilization effect. Science 353, 72–74.
Thirkell, T.J., Cameron, D.D., Hodge, A., 2016. Resolving the 'nitrogen paradox' of arbuscular mycorrhizas: fertilization with organic matter brings considerable benefits for plant nutrition and growth. Plant Cell Environ. 39, 1683–1690.
Thomas, R., Canham, C.D., Weathers, K.C., Goodale, C.L., 2010. Increased tree carbon storage in response to nitrogen deposition in the US. Nat. Geosci. 3, 229–244.
Tian, D., Niu, S., 2012. A global analysis of soil acidification caused by nitrogen addition. Environ. Res. Lett. 10, 1714–1721.
Treseder, K.K., 2004. A meta-analysis of mycorrhizal responses to nitrogen, phosphorus, and atmospheric CO2 in field studies. New Phytol. 164, 347–355.
Treseder, K.K., Allen, E.B., Egerton-Warburton, L.M., Hart, M.M., Klironomos, J.N., Maherali, H., Tedersoo, L., Wurzburger, N., 2018. Arbuscular mycorrhizal fungi as mediators of ecosystem responses to nitrogen deposition: a trait-based predictive framework. J. Ecol. 106, 480–489.
van Diepen, L.T.A., Lilleskov, E.A., Pregitzer, K.S., 2011. Simulated nitrogen deposition affects community structure of arbuscular mycorrhizal fungi in northern hardwood forests. Mol. Ecol. 20, 799–811.
Veresoglou, S.D., Menexes, G., Rillig, M.C., 2012. Do arbuscular mycorrhizal fungi affect the allometric partition of host plant biomass to shoots and roots? A meta-analysis of studies from 1990 to 2010. Mycorrhiza 22, 227–235.
Verlinden, M.S., Ven, A., Verbruggen, E., Janssens, I.A., Wallander, H., Vicca, S., 2018. Favorable effect of mycorrhizae on biomass production efficiency exceeds their carbon cost in a fertilization experiment. Ecology 99.
Vitousek, P.M., Aber, J.D., Howarth, R.H., Likens, G.E., Tilman, D.G., 1997. Human alteration of the global nitrogen cycle: source and consequences. Ecol. Appl. 7, 739–750.
Weber, S.E., Diez, J.M., Andrews, L.V., Goulden, M.L., Aronson, E.L., Allen, M.F., 2019. Responses of arbuscular mycorrhizal fungi to multiple coinciding global change drivers. Fungal Ecol. 40, 62–71.
Wilson, H., Johnson, B.R., Bohannan, B., Pfeifer-Meister, L., Mueller, R., Bridgham, S.D., 2016. Experimental warming decreases arbuscular mycorrhizal fungal colonization in prairie plants along a Mediterranean climate gradient. Peerj 4.
Yang, W., Zheng, Y., Gao, C., He, X., Ding, Q., Kim, Y., Rui, Y., Wang, S., Guo, L.-D., 2013. The arbuscular mycorrhizal fungal community response to warming and grazing differs between soil and roots on the Qinghai-Tibetan Plateau. Plos One 8.
Yang, G., Liu, N., Lu, W., Wang, S., Kan, H., Zhang, Y., Xu, L., Chen, Y., 2014. The interaction between arbuscular mycorrhizal fungi and soil phosphorus availability influences plant community productivity and ecosystem stability. J. Ecol. 102, 1072–1082.
Yoneyama, K., Xie, X., Kim, H.I., Kisugi, T., Nomura, T., Sekimoto, H., Yokota, T., Yoneyama, K., 2012. How do nitrogen and phosphorus deficiencies affect strigolactone production and exudation? Planta 235, 1197–1207.
Yuan, T., Tao, G., Jiang, L., 2018. Arbuscular mycorrhizal fungi in the rhizospheric soil of four forest types in Fanjingshan National Nature Reserve. J. Northeast For. Univ. 046, 83–86 (in Chinese).
Zhang, B., Zhou, X., Zhou, L., Ju, R., 2015. A global synthesis of below-ground carbon responses to biotic disturbance: a meta-analysis. Glob. Ecol. Biogeogr. 24, 126–138.
Zhang, J., Tang, X., Zhong, S., Yin, G., Gao, Y., He, X., 2017. Recalcitrant carbon components in glomalin-related soil protein facilitate soil organic carbon preservation in tropical forests. Sci. Rep. 7.
Zhang, T., Chen, H.Y.H., Ruan, H., 2018. Global negative effects of nitrogen deposition on soil microbes. ISME J. 12, 1817–1825.
Zhang, S., Lehmann, A., Zheng, W., You, Z., Rillig, M.C., 2019. Arbuscular mycorrhizal fungi increase grain yields: a meta-analysis. New Phytol. 222, 543–555.
Zhao, F., Ren, C., Shelton, S., Wang, Z., Pang, G., Chen, J., Wang, J., 2017. Grazing intensity influence soil microbial communities and their implications for soil respiration. Agric. Ecosyst. Environ. 249, 50–56.
Zheng, Y., Kim, Y.-C., Tian, X.-F., Chen, L., Yang, W., Gao, C., Song, M.-H., Xu, X.-L., Guo, L.-D., 2014. Differential responses of arbuscular mycorrhizal fungi to nitrogen addition in a near pristine tibetan alpine meadow. FEMS Microbiol. Ecol. 89, 594–605.
Zhou, Z., Wang, C., Zheng, M., Jiang, L., Luo, Y., 2017. Patterns and mechanisms of responses by soil microbial communities to nitrogen addition. Soil Biol. Biochem. 115, 433–441.