


RESEARCH ARTICLE

Mycorrhization enhances plant growth and stabilizes biomass allocation under drought

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Abstract

Plants and their symbionts, such as arbuscular mycorrhizal (AM) fungi, are increasingly subjected to various environmental stressors due to climate change, including drought. As a response to drought, plants generally allocate more biomass to roots over shoots, thereby facilitating water uptake. However, whether this biomass allocation shift is modulated by AM fungi remains unknown. Based on 5691 paired observations from 154 plant species, we conducted a meta-analysis to evaluate how AM fungi modulate the responses of plant growth and biomass allocation (e.g., root-to-shoot ratio, R/S) to drought. We found that AM fungi attenuate the negative impact of drought on plant growth, including biomass production, photosynthetic performance and resource (e.g. nutrient and water) uptake. Accordingly, drought significantly increased R/S in non-inoculated plants, but not in plants symbiotic with established AM fungal symbioses. These results suggest that AM fungi promote plant growth and stabilize their R/S through facilitating nutrient and water uptake in plants under drought. Our findings highlight the crucial role of AM fungi in enhancing plant resilience to drought by optimizing resource allocation. This knowledge opens avenues for sustainable agricultural practices that leverage symbiotic relationships for climate adaptation.

KEYWORDS

arbuscular mycorrhizal (AM) fungi, biomass allocation, drought, global change, meta-analysis, plant biomass

1 | INTRODUCTION

Understanding resource allocation in plants among different organs has been an important topic in plant ecology (Enquist & Niklas, 2002; McCarthy & Enquist, 2007; Weiner, 2004). Among the proposed resources, biomass appears to be the most viable variable for quantifying resource allocation in plants (Bazzaz et al., 1987). On the one hand, biomass allocation is a fundamental strategy to optimize plant

growth rate, enhance survival, and improve adaptability to changing environments (Puglielli et al., 2021). According to the optimal partitioning theory, plants optimize their performance by investing more biomass to organs that capture the most limiting resource (Bloom et al., 1985). Compared with plants grown in nutrient-poor conditions, for example, those growing in nutrient-rich environments typically increase biomass allocation to shoots over roots, resulting in a lower root-to-shoot ratio (R/S hereafter), for enhancing light

Bo Tang and Jing Man contributed equally to this work.

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interception (Poorter et al., 2012). On the other hand, the R/S is thought to be a crucial parameter in estimating terrestrial carbon storage (Mokany et al., 2006), given that plant biomass is one of the terrestrial carbon reservoirs (Houghton et al., 2009).

Drought, a critical aspect of climate change, significantly limits plant growth by reducing soil water and nutrient availability (IPCC, 2021; Schimel, 2018). Plants have to employ diverse strategies to cope with this challenge. Plants generally increase the R/S under drought for acquiring more water and nutrients from soil (Eziz et al., 2017). In addition, plants can form symbiotic associations with arbuscular mycorrhizal (AM) fungi (Martin et al., 2017) to mitigate drought stress (Abdalla et al., 2023; Augé, 2001; Cosme, 2023; Marro et al., 2022; Shi et al., 2023). Within plant-mycorrhiza symbiosis, AM fungi acquire nutrients from soil by extensive hyphal networks and deliver them to the host plants in exchange for sugar and lipids (Johnson, 2010; Lanfranco et al., 2018). While both strategies can improve plant adaptation to drought, their significance for plant growth differs. The biomass allocation strategy (e.g., higher R/S under drought) is at the expense of shoot biomass, which might reduce the potential for plants to capture aboveground resources (e.g., light) used for photosynthesis (Poorter et al., 2012), thereby affecting plant growth. However, plants may tend to be less dependent on this strategy under drought when the resource benefits provided by AM fungi are sufficient to meet the growth of host plants (Frew, 2023). Unfortunately, whether and how AM fungi modulate the response of plant growth and their R/S to drought remains largely unknown. Such information is critical to our understanding and prediction of the role of AM fungi in responses of plant growth and biomass allocation to drought. While previous studies have explored the effects of AM fungi on the responses of plant growth to drought, these case studies typically involve only a single pair of plants, for example, plants inoculated with AM fungi and their non-inoculated counterparts. Because most studies have focused on only a few plant species, we lack a comprehensive understanding of the general effects of AM fungi on plants under drought conditions. Furthermore, the isolated results from these individual studies make it challenging to evaluate the significance of experimental variables, such as the biological traits of plants and the experimental procedures used.

Meta-analysis offers a quantitative approach to integrating results from different experiments, allowing us to answer broad questions by accounting for variations among studies in terms of replication levels and data dispersion, and providing quantitative estimates of experimental effects (Gurevitch & Hedges, 1999). Therefore, meta-analysis has been widely employed to improve our comprehensive understanding of scientific issues across numerous independent studies and to identify knowledge gaps (Gurevitch et al., 2018). Since the phylogeny among tested plant species can influence the results of a meta-analysis (Chamberlain et al., 2012), it is necessary to introduce phylogenetic relatedness into any meta-analysis including multiple plant species. Here, we compiled a dataset consisting of 5691 paired observations regarding the responses of R/S, biomass, nitrogen (N) and phosphorus (P) uptake, water

status, and photosynthetic performance for both plants inoculated with AM fungi and their non-inoculated counterparts to drought, from 320 studies involving 154 plant species. Based on this dataset, we conducted a phylogenetically informed meta-analysis to address the following questions: (i) How do AM fungi regulate the responses of plant biomass and R/S to drought? (ii) What are the mechanisms underpinning such responses? In general, drought reduces soil moisture and soil nutrient (e.g. N and P) availability (Schimel, 2018), restricting plant growth (Figure 1). We hypothesize that AM fungi may mitigate the negative effects of drought on plant growth (indicated by total biomass, Figure 1) by sustaining plant nutrient and water uptake during drought conditions (Abdalla et al., 2023; Augé, 2001). According to the optimal partitioning theory, plants tend to allocate more biomass toward roots (red arrows in Figure 1) when belowground resources are limiting (Bloom et al., 1985). However, the importance of such a strategy may be reduced under drought when plants form a symbiotic relationship with AM fungi which improves the access of plants to belowground resources (Frew, 2023). Therefore, we also hypothesize that AM fungi could mitigate the negative effects of drought on shoot biomass (Figure 1). Given these points, we finally hypothesize that AM fungi could stabilize plant R/S under drought (Figure 1).

2 | MATERIALS AND METHODS

2.1 | Literature search and screening

We conducted literature searches using the *Web of Science* (<http://apps.webofknowledge.com/>) and *China Knowledge Resource Integrated Databases* (www.cnki.net/) in October 2023, with the following keyword combinations for topic search: ("arbuscular mycorrhizal fung*" OR "AM fung*" OR "AMF" OR "AM symbios*") AND ("drought" OR "water deficit" OR "water stress*" OR "climate change") AND ("plant growth" OR "plant biomass" OR "nitrogen uptake" OR "phosphorus uptake" OR "nutrient uptake" OR "water uptake" OR "water transfer" OR "photosynthe*" OR "root biomass*" OR "stem biomass*" OR "leaf biomass*" OR "shoot biomass*" OR "biomass allocation" OR "*mass fraction" OR "root shoot ratio" OR "pathogen resistance" OR "pathogen protection" OR "chemical defen*" OR "herbivore defen*" OR "osmotic adjustment" OR "stomatal regulation" OR "physiological processes" OR "stoichiometry" OR "C:N" OR "C:P" OR "N:P" OR "C:N:P"). In the *Web of Science*, databases used for our search included the Web of Science Core Collection, Chinese Science Citation Database, Current Contents Connect, Derwent Innovations Index, KCI-Korean Journal Database, MEDLINE and SciELO Citation Index. After removing duplicate records, we obtained a total of 1981 papers. Afterwards, we reviewed the titles, abstracts, and main texts of these papers. To avoid bias, studies compiled in our dataset had to meet the following criteria: (1) Studies must include both an inoculated group (with AM fungi, including both single and mixed species) and their non-inoculated counterparts, and both groups had to be identical except for the

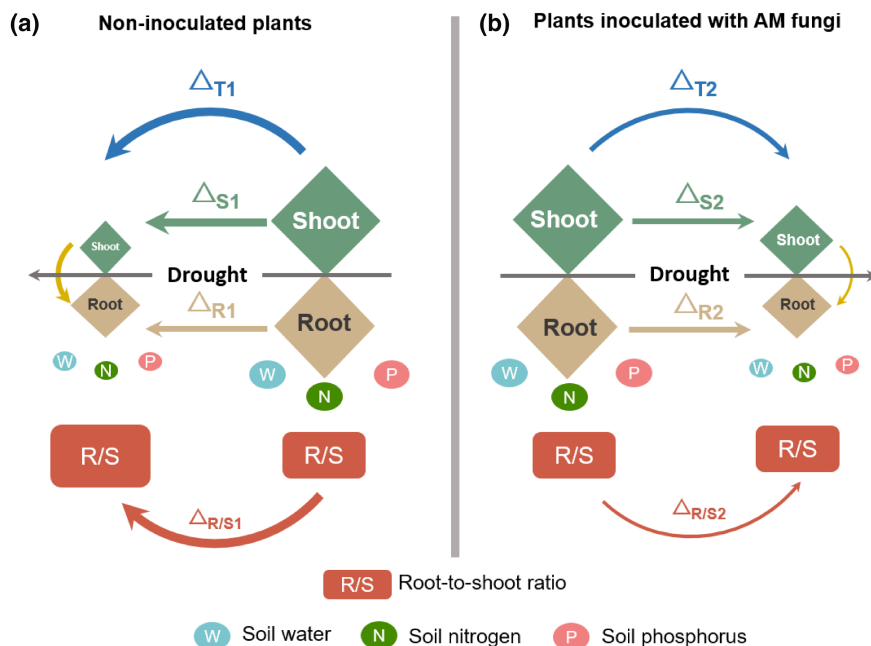


FIGURE 1 The potential responses of plant biomass and root-to-shoot ratio (R/S) for both non-inoculated plants (a) and plants inoculated with AM fungi plants (b) to drought. Drought typically decreases the availability of soil water and soil nutrients, for example, nitrogen (N) and phosphorus (P), therefore inhibits plant growth. Because AM fungi play an important role in maintaining water and nutrient supply to host plants under drought, we hypothesize that AM fungi could attenuate the negative effects of drought on plant growth (indicated by total biomass; that is, $\Delta_{T1} > \Delta_{T2}$). According to the optimal partitioning theory, plants generally tend to invest more biomass to roots over shoots, acquiring water and nutrients under drought (red arrows). However, the importance of this strategy might be reduced under drought when plants are symbiotic with AM fungi, which could improve the access of plants to belowground resources. Given this, we hypothesize that AM fungi could attenuate the negative impact of drought on shoot biomass ($\Delta_{S1} > \Delta_{S2}$). As a consequence of these processes, we finally hypothesize that AM fungi could stabilize the root-to-shoot ratio (R/S) in plants response to drought (e.g., $|\Delta_{R/S1}| > |\Delta_{R/S2}|$).

factor of AM fungal inoculation. (2) We excluded the inoculation of AM fungi in combination with other microorganisms that were not controlled for; this was done to mitigate potential confounding effects; that is, we included studies where microbes included in the AM fungal inoculum were added to the control, as is common practice in AM fungal research. (3) Studies in which the non-inoculated group was established using fungicides (e.g. benomyl) were excluded; this was due to the non-target effects of fungal inhibitors, which could eliminate other fungal groups, including pathogens. (4) Drought and control conditions had to be implemented for both the inoculated group and their non-inoculated counterparts. (5) Due to the presence of AM fungal spores in soil, the experimental soils had to be sterilized; in case where the soil condition was unknown, we further assessed AM root colonization within the non-inoculated group; only studies demonstrating colonization rates below 1% were compiled into our dataset; studies lacking information on both soil condition and AM colonization were excluded. (6) The study had to report at least one variable of interest (or provided data that allowed us to calculate such a variable), including plant biomass (e.g. total biomass, shoot biomass and root biomass), R/S, plant nutrients uptake (e.g. N and P uptake), plant water status (e.g. relative water content and water content) and photosynthetic performance (e.g. photosynthetic rate, maximal photochemical efficiency [Fv/Fm] and total chlorophyll content). It should be noted that we only compiled

the data on total nutrient uptake rather than tissue nutrient concentrations, given the potential influence of the “dilution effect” caused by plant biomass. However, when a study reported data on both the nutrient concentrations and biomass, then nutrient uptake can be calculated (for more details, see sections below). (7) The means and sample sizes of target variables had to be either reported or could be derived from the information provided in the article, including the text, tables, figures, and supplementary information. (8) The name of the plants used for the experiment needed to be reported. The article selection process followed the PRISMA guidelines (Figure S1).

2.2 | Data collection

After screening, a total of 320 papers met the set criteria. For each study, we collected means and sample size of our variables of interest; as sample size, we gathered either standard deviation (SD), standard error (SE) or 95% confidence interval (CI) if reported. Unspecified error bars were recorded as SE. If a study reported data at various time points, we only extracted the last time point to mitigate potential temporal autocorrelation. If a study reported data for multiple manipulations (e.g. different drought intensities and inoculants), we treated them as independent observations. Data from figures were digitized using the software WebPlotDigitizer 4.1 (<https://>

automeris.io/WebPlotDigitizer/). In addition, we recorded the name of tested plant species, experimental duration and drought intensity. Finally, our dataset consisted of 5691 paired observations covering 154 plant species.

To test whether the effects of AM fungi on responses of plants to drought were dependent on plant traits, we collected the following biological traits by cross-referencing their names with multiple databases: life form (woody vs. non-woody), lifespan (annuals vs. perennials) and domestication (wild vs. crop). First, we followed the World Flora Online (www.worldfloraonline.org) to harmonize Latin names of tested plant species. Second, we obtained the information on plant life form and lifespan from the original text or the following databases, including PLANTS (<http://plants.usda.gov/>), Plants of the World Online (<https://powo.science.kew.org/>) and Plants for a Future (<https://pfaf.org/>). For the species not included in the database, we conducted online searches to acquire this information. Finally, we categorized a species as a crop species in the narrow sense if it is documented as a source of human food following the World Economic Plants (WEP) database (<https://npgsweb.ars-grin.gov/gringlobal/taxon/taxonomysearchWEP>).

2.3 | Effect size and variance

We used the natural log response ratio (lnRR), a metric commonly used in meta-analysis, to assess the effect sizes of drought on variables:

$$\lnRR = \ln \frac{X_D}{X_W} = \ln X_D - \ln X_W, \quad (1)$$

where X_D and X_W represent the arithmetic mean values of variables in the drought treatment and control, respectively. A positive lnRR value indicates a positive effect of drought on the variables, whereas a negative value indicates the opposite. The variance (v) for each lnRR was calculated as follows:

$$v = \frac{SD_D^2}{N_D X_D^2} + \frac{SD_W^2}{N_W X_W^2}, \quad (2)$$

where SD_D and SD_W are the SD in the drought treatments and control, respectively. N_D and N_W represent the sample size in the drought treatments and control, respectively. If a study reported SE, the corresponding SD was computed as:

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

where n is the sample size. If a study provided only 95% confidence intervals (CI), the SD was calculated as:

$$SD = (CI_u - CI_l) \sqrt{n} / 2Z_{\alpha/2}, \quad (4)$$

where CI_u and CI_l are the upper and lower limits of the 95% CI, respectively. $Z_{\alpha/2}$ represents the Z score for a given level of significance (e.g., 1.96 at $\alpha=0.05$). If a study reported the biomass of multiple organs of

a plant (e.g., leaf, stem, and root biomass), their sum was considered as total biomass. We calculated the corresponding SD according to the method of error propagation:

$$SD_{\text{sum}} = \sqrt{SD_a^2 + SD_b^2 + SD_c^2}, \quad (5)$$

where SD_{sum} represents the new SD for the sum values, with SD_a , SD_b , and SD_c as the values of each organ of plant biomass. We used the same method to calculate the SD of shoot biomass, when a study reported both leaf and stem biomass rather than shoot biomass. If a study did not report R/S, but root and shoot biomass, we propagated SD for the calculated R/S, as follows:

$$SD_{R/S} = X \sqrt{\left(\frac{SD_R}{\text{Mean}_R}\right)^2 + \left(\frac{SD_S}{\text{Mean}_S}\right)^2}, \quad (6)$$

where $SD_{R/S}$ indicates the SD value for the newly calculated R/S; X is mean value of the new R/S; Mean_R and Mean_S are the mean values of root and shoot biomass, with the SD_R and SD_S as the SD values of root and shoot biomass, respectively. If a study did not report total nutrient uptake, but nutrient concentration and biomass, their product was treated as total nutrient uptake, and the corresponding SD was calculated as follows:

$$SD_T = \sqrt{\text{Mean}_C^2 SD_C^2 + \text{Mean}_B^2 SD_B^2 + SD_C^2 SD_B^2}, \quad (7)$$

where SD_T is the SD value for calculated total nutrient uptake. Mean_C and Mean_B are the mean values of nutrient concentration and biomass, with the SD_C and SD_B as the SD values of nutrient concentration and biomass, respectively. In cases where SD, SE, or 95% CI were not reported in our dataset, the Bracken1992 approach was employed to impute missing SD using the R package *metagear* (Lajeunesse, 2016).

2.4 | Data analysis

All statistical analyses were carried out in R (R Development Core Team, 2019). First, to assess whether plants exhibit an overall positive or negative response to drought irrespective of their mycorrhizal status (e.g., inoculated with AM fungi or not), we employed a mixed-effects model (restricted maximum likelihood approach, REML) to calculate weighted mean of the lnRR ($\overline{\lnRR}$) using the R package *metafor* (Viechtbauer, 2010). In the mixed-effects model, the $\overline{\lnRR}$ was calculated as follows:

$$\overline{\lnRR} = \frac{\sum_{i=1}^k \lnRR_i * w_i}{\sum_{i=1}^k w_i}, \quad (8)$$

where k indicates the number of study, and \lnRR_i represents the lnRR of the i th study. The w_i is the weighing of i th study, which was calculated according to the Equations (9) and (10):

$$w_i = \frac{1}{v_i}, \quad (9)$$

$$v_i = v + \tau^2, \quad (10)$$

where v_i is the variance of i th study, v represents the variance within study and τ^2 indicates the variance between studies. It should be noted that if a study simultaneously reported two or more variables related to plant water status (e.g. water content and water use efficiency) or photosynthetic performance (e.g. photosynthetic rate, Fv/Fm and total chlorophyll content), we first ran a mixed effects model at the level of this study to obtain an estimate of effect size ($w_i = 1/v$ within this model). This estimate was then used for the calculation of $\ln\overline{RR}$. The $\ln\overline{RR}$ was considered statistically significant if the 95% CI around the mean did not overlap with zero. Because certain studies provided multiple effect sizes, we conducted a hierarchical meta-analysis to control for non-independence within this dataset. To address this issue, we treated the *id* of the effect size nested within the *study* as a random factor in the mixed-effects model. Given that the non-independence of the data from the same tested plants, species identity was also considered a random factor in the mixed-effects model. In order to mitigate the potential non-independence of effect sizes stemming from plant species with shared evolutionary history (Chamberlain et al., 2012), we integrated the phylogenetic relatedness among the examined plant species into the mixed-effects model by including the variance-covariance matrix of species relatedness as an additional random factor. To generate this matrix, we initially constructed a phylogenetic tree for the examined plant species based on the Open Tree of Life (OTL) database (Hinchliff et al., 2015) and the R package *rotl* (Michonneau et al., 2016). The phylogenetic tree was subsequently converted into an ultrametric tree using Grafen's method (Grafen, 1989) with the R package *ape* (Paradis et al., 2004). Finally, a variance-covariance matrix was computed from the ultrametric tree, capturing the phylogenetic relatedness among plant species (Paradis et al., 2004). It should be noted that although both the species identity and phylogenetic effect are specific to each species, the former indicates the non-phylogenetic component (Nakagawa & Santos, 2012). Furthermore, both the factors should be accounted for in meta-analysis involving multi-species datasets (Cinar et al., 2022). For simplicity in interpretation, the $\ln\overline{RR}$ was reverted to its original scale and presented as a percentage change (%), as follows:

$$\text{Percentage change (\%)} = (e^{\ln\overline{RR}} - 1) \times 100, \quad (11)$$

Second, to test the potential role of AM fungi in regulating the responses of plants to drought (e.g., whether plants inoculated with AM fungi and their non-inoculated counterparts differ significantly in their responses to drought), mycorrhizal status of tested plants (e.g. inoculated with AM fungi or not) were treated as a moderator in the mixed-effects model. We employed a pooled estimation approach within the mixed-effects model to calculate the $\ln\overline{RR}$ and its corresponding 95% CIs for each level of this moderator. In these models, the overall heterogeneity of effect sizes can be divided

into two components: heterogeneity explained by moderators incorporated in the model (Q_M) and residual heterogeneity (Q_E). The significance of the moderator was tested using the Q_M statistics (Koricheva et al., 2013).

Third, to examine whether the influence of AM fungi on plant responses to drought was contingent upon plant life form (woody vs. non-woody), datasets were divided into two subsets (for woody and non-woody plants, respectively). In each subset, we used the mentioned above models to calculate the $\ln\overline{RR}$ and its corresponding 95% CIs for the moderator of mycorrhizal status. Similarly, the Q_M statistics were used to evaluate the significance of this moderator. The same methods were performed for plant lifespan (annuals vs. perennials) and domestication (wild vs. crop).

Fourth, we used subset analysis to test whether the influence of AM fungi on plant responses to drought was dependent on experimental duration and drought intensity. In this meta-analysis, experimental duration was divided into two subgroups: short (<50 days) and long term (>50 days). Similarly, drought intensity was grouped by low (<45%; referring to the changes in soil moisture under drought compared to normal conditions) and high intensity (>45%). Within each subset, the mixed-effects model was used to calculate the $\ln\overline{RR}$ and its corresponding 95% CIs for the moderator of mycorrhizal status, and the Q_M statistics were used to evaluate the significance of the moderator.

Finally, due to the higher likelihood of publishing statistically significant results compared to non-significant ones, publication bias might affect the outcomes of meta-analysis. We first employed a funnel plot to explore the potential of publication bias, and asymmetry of the funnel plot was subsequently assessed through Egger's regression test (Egger et al., 1997). If asymmetry was identified, we used the Rosenberg fail-safe number to further evaluate the potential impact of unpublished articles on our conclusions. In addition, we assessed the robustness of our results by performing a leave-one-out analysis using the "leave1out" function within the R package *metafor* (Viechtbauer, 2010). The quality of this meta-analysis was evaluated following the checklist of quality criteria proposed by Koricheva and Gurevitch (2014).

3 | RESULTS

3.1 | AM fungi enhance plant growth and stabilize biomass allocation under drought

In this meta-analysis, we compiled 5691 paired observations from 320 studies on 154 plant species (Figure 2a). As expected, our meta-analysis showed that drought reduced total plant biomass (-31.4%, 95% CI [-39.3%, -22.3%]), as well as root (-29.6%, 95% CI [-34.8%, -24.0%]), and shoot biomass (-32.4%, 95% CI [-40.5%, -23.2%]) when mycorrhizal status of tested plants was not considered (Figure 2b). Furthermore, we observed a tendency toward higher R/S in response to drought (7.3%, 95% CI [-0.9%, 16.1%], $p = .08$; Figure 2b). Regarding plants inoculated with AM fungi, our

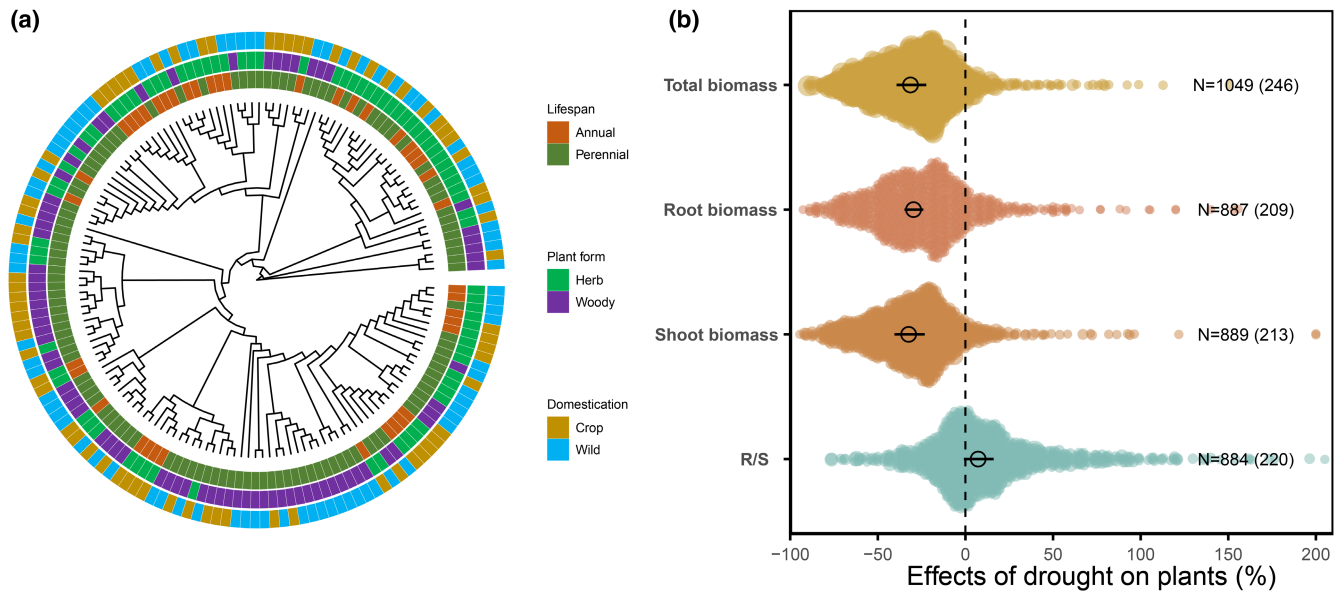


FIGURE 2 Phylogenetic tree of plant species included in the study (a), and responses of plant total biomass, root biomass, shoot biomass, and root-to-shoot ratio (R/S) to drought (b). (a) This phylogenetic tree is generated on the basis of 154 plant species from the studies involving the effects of AM fungi on plant responses to drought. The phylogenetic relatedness among these plant species is incorporated in the meta-analysis. Plants in the phylogenetic tree are shown with their lifespan (annual vs. perennial), plant form (herb vs. woody), and domestication (crop vs. wild). (b) The overall effects of drought on plant total biomass, root biomass, shoot biomass and R/S, regardless of mycorrhizal status in these plants. Circles and error bars are mean estimate and 95% confidence intervals (CIs), respectively. If the 95% CIs do not overlap with zero, a significant effect of drought ($p < .05$) was considered. The dots indicate the individual effect size and are scaled by their precision (e.g., $1/\text{variance}$). N corresponds to the sample size, with numbers of studies given in parentheses.

results suggested that the total ($Q_M = 15.1$, $p < .001$; [Figure 3a](#)) and shoot biomass ($Q_M = 13.7$, $p < .001$; [Figure 3b](#)) of plants inoculated with AM fungi was significantly higher than that of their non-inoculated counterparts in response to drought ([Figure 3](#)). However, no significant difference was detected for root biomass between inoculated and non-inoculated plants ($Q_M = 1.9$, $p = .169$; [Figure 3b](#)). In addition, we found that drought significantly increased the R/S in non-inoculated plants (12.2%, 95% CI [3.5%, 21.7%]; [Figure 3d](#)), but not in plants inoculated with AM fungi (4.2%, 95% CI [-3.8%, 12.7%]; [Figure 3d](#)). Finally, R/S of inoculated plants was significantly lower than that of their non-inoculated counterparts ($Q_M = 16.0$, $p < .001$; [Figure 3d](#)).

3.2 | Effects of biological traits of tested plants and experimental factors on the role of AM fungi

Our study revealed that herbaceous plants inoculated with AM fungi had significantly higher biomass under drought compared to non-inoculated plants ($p < .001$; [Figure S2a](#)), a trend not seen in woody plants ($p = .16$; [Figure S2a](#)). However, AM fungi buffered against the negative effects of drought on plant growth across annual and perennial species ([Figure S2b](#)), as well as in both crop and wild varieties ([Figure S2c](#)). Stabilizing effects of AM fungi on plant R/S in response to drought persist across life forms (e.g. herb vs. woody; [Figure S3a](#)), lifespan ([Figure S3b](#)), and domestication status ([Figure S3c](#)). The

positive effects of AM fungi on plant biomass in response to drought were independent of drought intensity ([Figure S4a](#)) and experimental duration ([Figure S4b](#)). Similarly, the stabilizing effects of AM fungi on plant R/S were consistent regardless of drought intensity ([Figure S5a](#)) and experimental duration ([Figure S5b](#)).

3.3 | AM fungi facilitate nutrient and water uptake by plants and photosynthesis

We found that plants inoculated with AM fungi show significantly better performance under drought than their non-inoculated counterparts for N ($Q_M = 9.3$, $p = .002$; [Figure 4a](#)) and P uptake ($Q_M = 15.4$, $p < .001$; [Figure 4b](#)) as well as for plant water status ($Q_M = 18$, $p < .001$; [Figure 4c](#)). Moreover, a similar pattern was also observed for photosynthetic performance of plants ($Q_M = 35.9$, $p < .001$; [Figure 4b](#)).

3.4 | Publications bias and sensitivity analysis

We found no evidence of publication bias for plant P uptake and R/S in responses to drought ([Table S2](#); [Figure S6](#); Egger's test: $p > .05$). Although asymmetry of funnel plots was detected for other variables in response to drought, the Rosenberg fail-safe numbers were much larger than $5k + 10$ ([Table S2](#)). These results suggest that publication bias is unlikely to be an issue for the interpretation of our

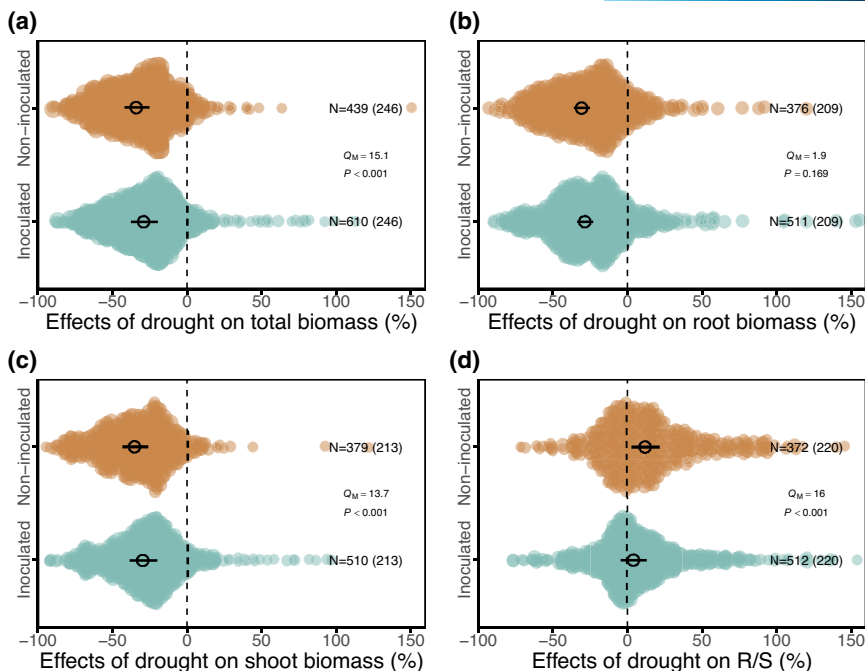


FIGURE 3 Mean effects of drought on total biomass (a), root biomass (b), shoot biomass (c), and root-to-shoot ratio (R/S, d) of plants inoculated with AM fungi (Inoculated) and their non-inoculated counterparts (non-inoculated). Circles and error bars are mean estimate and 95% confidence intervals (CIs), respectively. If the 95% CIs do not overlap with zero, a significant effect of drought ($p < .05$) was considered. The dots indicate the individual effect size and are scaled by their precision ($1/\text{variance}$). N corresponds to the sample size, with numbers of studies given in parentheses. The p -values derived from Q_M statistics show the significant responses to drought between plants inoculated with AM fungi and their non-inoculated counterparts.

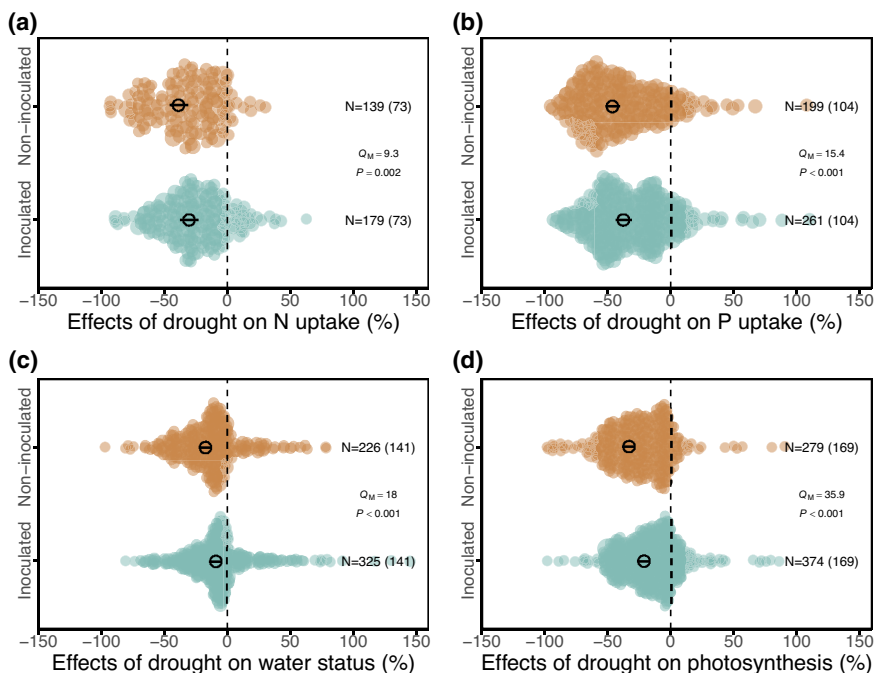


FIGURE 4 Mean effects of drought on nitrogen (N) uptake (a), phosphorus (P) uptake (b), water status (c), and photosynthetic performance (d) of plants inoculated with AM fungi (Inoculated) and their non-inoculated counterparts (non-inoculated). Circles and error bars are mean estimate and 95% confidence intervals (CIs), respectively. If the 95% CIs do not overlap with zero, a significant effect of drought ($p < .05$) was considered. The dots indicate the individual effect size and are scaled by their precision ($1/\text{variance}$). N corresponds to the sample size, with numbers of studies given in parentheses. The p -values derived from Q_M statistics show the significant responses to drought between plants inoculated with AM fungi and their non-inoculated counterparts.

results. In addition, we found that our findings are unlikely to be driven by a single influential study (Figure S7).

4 | DISCUSSION

On the basis of 5691 paired observations from 154 plant species, we conducted a phylogenetically controlled meta-analysis to test the potential role of AM fungi in plant growth and biomass allocation in response to drought. Our major finding was that AM fungi attenuate the negative impacts of drought on plant biomass. This benefit arose predominantly from AM fungi buffering against the drought-induced reductions in shoot biomass, thereby maintaining a stable R/S ratio under drought conditions. Our results suggest that this response is likely due to AM fungi enhancing nutrient (N and P) and water uptake in drought conditions, highlighting a symbiotic mechanism that could be harnessed to support plant resilience in water-limited environments.

Consistent with the first hypothesis, we found that AM fungi reduce the negative impact of drought on plant growth. Because most nutrients (e.g. N and P) used for plant growth are water soluble, drought generally reduces the availability of soil nutrients and water through processes such as dissolution, diffusion, and transport (Schimel, 2018). Therefore, negative effects of drought on plant growth have been frequently reported (Eziz et al., 2017). However, studies at the local scale or under laboratory conditions have shown that the negative impacts of drought on plant growth might be mitigated by AM fungi in several ways. First, AM fungi can modify soil structure and soil water relations (Augé, 2001), improving plant access to water when the soil undergoes drying (Abdalla et al., 2023). Second, AM fungi can acquire soil nutrients and water from the soil by extensive hyphal networks and deliver them to the host plant (Kakouridis et al., 2022). Furthermore, the hyphal pathway is considered to be a more efficient way of acquiring soil nutrients and water, due to the ability of AM hyphae to reach soil microsites that are inaccessible by plant roots (Kaiser et al., 2015). Third, AM fungi can elevate soil nutrient availability, thereby facilitating nutrient uptake by plants under drought. Although AM fungi lack the capacity to function as saprotrophs (Tisserant et al., 2013), such as secreting lytic enzymes that enhance the availability of soil nutrients by mineralization, they could facilitate nutrient cycling through interactions with free-living saprotrophs (Kaiser et al., 2015; Zhang et al., 2022). For example, hyphal exudates stimulate microbial growth and thus the enzyme production associated with soil nutrient cycling (Frey, 2019; Kakouridis et al., 2024; Zhang et al., 2022). Moreover, fructose, a constituent of hyphal exudates, has been demonstrated to function as a signal molecule, inducing the expression of genes responsible for encoding phosphatase in bacterial cells (Zhang et al., 2018). Finally, given the important role of plant nutrient (e.g., N and P) and water status in photosynthetic processes, inoculated plants with improved N and P nutrition, and water status under drought, are expected to show better photosynthetic

performance than their non-inoculated counterparts (Gavito et al., 2019; Kuyper & Jansa, 2023). Together, these processes mediated by AM fungi largely increase soil nutrient availability and facilitate the uptake of nutrients and water by plants, ultimately mitigating the negative impact of drought on plant growth.

In addition, we found that a positive effect of AM fungi on plant biomass in responses to drought was only observed in herbaceous plants, not in woody plants. The first plausible explanation is the pronounced biological difference between herbaceous and woody plants (Field & Pressel, 2018; Poorter et al., 2012). Herbaceous plants typically have shorter life cycles and faster growth rates, making them potentially more responsive to the effects of AM fungi (Wang & Qiu, 2006). For example, they may have adjusted resource allocation in response to drought during the seedling stage when experiments typically begin. In contrast, woody plants typically start experiments with more mature root structures and established resource allocation patterns, potentially leading to weaker effects mediated by AM fungi. Second, woody plants have complex below-ground structures, such as more extensive woody roots and deeper root systems (Comas & Eissenstat, 2009; McCormack et al., 2012), which may play a larger role under drought conditions compared to changes in absorptive fine roots that are influenced by AM fungi. Future research should prioritize conducting long-term studies on the effects of AM fungi on plant growth throughout the plant life-cycle and detailed investigations into root architecture and function under drought conditions. Understanding the differential impacts of AM fungi on herbaceous and woody plants can guide agricultural and forestry management, inform ecosystem restoration and conservation efforts, and aid in developing climate change adaptation strategies.

In line with our second hypothesis, AM fungi could mitigate drought impacts on plant shoot biomass. According to the optimal partitioning theory, plants adjust to changing environments by allocating more biomass to organs that are capable of capturing the limiting resource, thereby optimizing overall plant performance (Bloom et al., 1985; Puglielli et al., 2021). Therefore, plants might tend to invest more biomass to roots over shoots under drought, aiming to enhance nutrient and water uptake from soil (Eziz et al., 2017). However, the importance of the strategy of changing biomass allocation may be reduced (e.g., reduced R/S) when plants are associated with AM fungi (Frew, 2023), as AM fungi can partly mitigate the drought-induced negative impacts on soil nutrients and water availability for plant growth (Abdalla et al., 2023; Augé, 2001). As a result, the mitigating effects of AM fungi on plant response to drought were only observed for shoot biomass, and not for root biomass. As expected, we also found that AM fungi stabilize the R/S in plants in response to drought, which aligns with our third hypothesis. Although plants can improve their adaptability to environmental fluctuations by altering biomass allocation, for example, R/S (Bloom et al., 1985; Weiner, 2004), this may be at the expense of other functions. In this study, for example, we found that plants significantly increase the R/S in response to drought in the non-inoculated group (Figure 3d). The consequence of this allocation strategy is a reduction in shoot

biomass, which could reduce the competitiveness of plants to capture aboveground resources, for example, light for photosynthesis (Poorter et al., 2012). It is reasonable to assume that non-inoculated plants might be more prone to being eliminated from a plant community compared to plants inoculated with AM fungi in the scenario of drought. Therefore, we suggest that such stabilizing effects of AM fungi on R/S in plant responses to drought are crucial not only for plant growth but also in plant-plant interactions in a world where drought events are intensifying in intensity and frequency.

Although our study offers crucial insights into the role of AM fungi in promoting plant growth and stabilizing biomass allocation under drought, our analysis also reveals several data limitations. The majority of studies in our dataset focused on individual plants in response to drought. Consequently, the extrapolation of these findings to natural communities is subject to several uncertainties. Since the influence of AM fungi usually extends beyond individual plants, such as the documented effects on plant community dynamics (Rudgers et al., 2012) and ecosystems (Powell & Rillig, 2018), additional research is still required to comprehensively understand the effects of AM fungi on plant communities in response to drought. There is mounting evidence that we are presently experiencing a scenario where multiple global change factors occur simultaneously. Nevertheless, nearly all studies encompassed in our meta-analysis have concentrated on drought. The limited data available on the role of AM fungi in plant response to multiple global change factors hinder our ability to explore the potential mitigating effects. Furthermore, the number of global change factors significantly impacts soil functions and plant community dynamics (Rillig et al., 2019, 2024). Given this, we call for more studies to test the potential role of AM fungi in plant responses in the context of the simultaneous occurrence of multiple global change factors. By doing so, we may provide a more complete picture in which the role of AM fungi in plant responses (e.g., growth and biomass allocation) to ongoing global environmental change can be better understood and predicted.

In conclusion, our meta-analysis showed that AM fungi are beneficial for plant growth under drought through mitigating the negative impact of drought on plant shoot biomass. Moreover, we found that AM fungi stabilize the R/S in plant response to drought. The potential mechanism underlying such responses are likely the facilitation of plant nutrient (e.g., N and P) and water uptake by AM fungi, and thus the elevated photosynthetic performance under drought. All in all, this study showed that AM fungi attenuate the negative impact of drought on plant growth, and stabilize plant R/S under drought. Such positive effects highlight the crucial role of AM fungi in enhancing plant resilience to drought by optimizing resource allocation. This knowledge opens avenues for sustainable agricultural practices that leverage symbiotic relationships for climate adaptation.

AUTHOR CONTRIBUTIONS

Bo Tang: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; supervision; validation; visualization; writing – original

draft; writing – review and editing. **Jing Man:** Conceptualization; data curation; formal analysis; investigation; methodology; project administration; validation; visualization; writing – original draft; writing – review and editing. **Ferran Romero:** Writing – review and editing. **Joana Bergmann:** Writing – review and editing. **Anika Lehmann:** Writing – review and editing. **Matthias C. Rillig:** Conceptualization; funding acquisition; project administration; supervision; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at <https://doi.org/10.6084/m9.figshare.26299351>.

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