

Trees with different mycorrhizal types show differential drought responses at the global scale

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Abstract

Climate drying is posing severe threats to forest ecosystems across the world. Although experimental evidence suggested that tree species with different mycorrhizal types may differ in their drought responses, a quantitative global synthesis is still lacking. By compiling and analyzing global datasets of four aspects of trees' drought responses (i.e., mortality, sensitivity, growth reduction and growth recovery), we found that AM trees exhibited lower sensitivity to drought intensity variation than EM trees in the tropical zone, whereas the opposite was true in the temperate zone. In addition, growth and survival of EM trees were more strongly impacted by severe drought than AM trees in the temperate zone, potentially causing reduced EM dominance in some temperate regions under climate drying. Compared to other previously studied traits, mycorrhizal type is a better predictor of trees' drought responses than specific leaf area, seed-bearing type, and rooting depth, but a worse predictor than wood density and maximum height. This study is the first to reveal the importance of mycorrhizal type in affecting trees' drought responses at the global scale, contributing to a better understanding of the intraspecific differences in trees' drought responses and the global biogeography of plant-mycorrhizal symbiosis.

Introduction

Forests cover about 30% of the land surface across the world¹, providing important services to natural ecosystems and humankind, such as biodiversity conservation, carbon storage, food provisioning, and climate modification etc.² However, the past few decades have seen sudden and widespread forest degradation (i.e., die-back and die-off), which were commonly linked to drought and elevated temperature^{3,4}. Given that the frequency and intensity of drought events will continue to increase in the future^{5,6}, the well-being of forest ecosystems and the potential loss of valuable services accompanying forest degradation have raised more and more concerns⁷. Which traits facilitate drought avoidance or recovery of trees has been proposed as one of the burning questions that need to be resolved in face of increasing drought-induced forest degradation incidences⁸. Answering this question can help us better understand the differences in drought responses across tree species and the mechanisms shaping the large-scale patterns of drought effects on forests.

In fact, quite a few functional traits have been identified to affect drought responses of trees. For instance, larger trees generally exhibited greater mortality in drought events compared to smaller trees⁹⁻¹¹. It is also reported that species with denser wood^{11,12}, lower specific leaf area^{4,13}, and deeper roots¹⁴ may be less affected by drought stress. In addition, seed-bearing type, an important phylogeny-related trait, may also affect tree responses to drought; gymnosperms usually suffer more from drought stress than angiosperms^{15,16}. Mycorrhizal fungi are commonly believed to mitigate drought stress on trees. Various mycorrhiza-mediated effects, including enhanced water and nutrient uptake^{17,18}, increased photosynthetic rate¹⁹, altered transpiration processes^{20,21}, enhanced osmo-protection^{20,21}, and reduced oxidative damage^{18,22}, have been identified to play important roles in facilitating drought avoidance and recovery of trees. Although most tree species can form mycorrhizal association with arbuscular

mycorrhizal fungi (AM) or ectomycorrhizal fungi (EM)^{23,24}, the roles of these two types of mycorrhizal associations in trees' drought responses has not been compared at the global scale.

While both AM and EM fungi have been reported to mitigate drought effect on their host species^{25,26}, their direct responses and host-mediated indirect responses to drought were found to be largely different. In general, EM fungi may show greater abundance decrease during drought events^{27,28} and may provide less benefits for drought stress mitigation than AM fungi²⁹⁻³¹. In addition, drought stress is likely to incur opposite effects on AM and EM infection rates in root tissue³²⁻³⁵, thereby, affecting the relative contribution of AM vs. EM to the drought responses of their host species. The above evidence suggests that AM and EM trees may exhibit differential drought responses due to the distinct drought-induced changes in their mycorrhizal partners per se, as well as the interactions with their mycorrhizal partners.

So far, it is still not clear whether different mycorrhizal types have different effects on drought-induced mortality and growth performance changes of trees. Answering this question can facilitate a better understanding on the role of mycorrhizal type in trees' drought responses. In addition, because the tropical and temperate zones are respectively dominated by AM and EM trees²⁴, it is interesting to compare the potentially mycorrhizal-type-dependent drought response patterns between these two climate zones so that we may better predict the biogeographic pattern of plant-mycorrhizal symbiosis under climate drying scenarios. If the patterns are consistent across zones, the more advantageous mycorrhizal type may increase its advantage in the originally dominating zone and decrease its disadvantage in the originally subordinating zone. If the patterns are inconsistent across zones, we may expect an even stronger or a reversed biogeographic pattern of AM vs. EM trees under intensified drought stress in the future. Therefore, in the current study, by quantifying drought responses based on the ring width data from the International Tree-Ring Data Bank (ITRDB) (<https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring>) and acquiring the mortality data from the study by Greenwood et al. (2017)⁴, we explored the effects of species mycorrhizal type (AM vs. EM) on trees' drought responses at the global scale. It was our goal to address the following three questions: (1) Can mycorrhizal type explain the differential drought responses across different tree species? (2) Are the mycorrhizal-type-dependent drought responses consistent across the tropical and temperate zones? (3) Will the mycorrhizal-type-dependent drought responses affect the relative dominance of AM vs. EM trees in the tropical and temperate zones under climate drying? Furthermore, we compared the explanatory power of mycorrhizal type on trees' drought responses with other drought-related traits to see how good mycorrhizal type performs as a predictor of trees' drought responses.

Methods

Drought-response dataset compilation

Global datasets of four aspects of trees' drought responses were compiled: drought-induced mortality, drought sensitivity, growth reduction by severe drought and growth recovery from severe drought.

Data of drought-induced mortality was directly acquired from the global dataset compiled by Greenwood et al. (2017)⁴, which included drought-induced annual mortality rate for 257 species from 28 studies across the world. Because our goal was to explore the differences between AM and EM trees in the tropical vs. temperate zone, we determined the mycorrhizal type of each species by referring to the recommended mycorrhizal status for plant genera in FungalRoot Database³⁶ and removed all non-AM and non-EM species from the dataset. Climate zone information for each study was determined by the geographic coordinates provided by the authors⁴. Additionally, because different drought events were caused by different levels of drought intensity, which strongly covaried with tree mortality⁴, we also extracted the data of drought intensity (i.e., Standardized Precipitation Evapotranspiration Index, SPEI) from Greenwood's dataset that was based on SPEIbase v.2.3 (2014) (https://spei.csic.es/spei_database). As a result, we obtained a dataset of drought-induced mortality for 220 species (i.e., 177 AM vs. 33 EM species) from 20 different locations (i.e., 4 tropical vs. 16 temperate locations) across the world (Fig. 1a,c).

Data of drought sensitivity, growth reduction by severe drought and growth recovery from severe drought were all calculated using ring width data and the Standardized Precipitation Evapotranspiration Index (SPEI). We first determined the mycorrhizal type for each species listed in the International Tree-Ring Data Bank (ITRDB) (<https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring>) and downloaded the total ring width of all AM and EM species that had been documented by 3 or more different studies. Similar to the mortality dataset, mycorrhizal type was also determined by FungalRoot Database (Soudzilovskaia et al. 2020)³⁶. Then, in accordance with Greenwood's dataset, we downloaded the Standardized Precipitation Evapotranspiration Index (SPEI) at a 12-month timescale from SPEIbase v.2.6 (2017) (https://spei.csic.es/spei_database) and extracted the SPEI from 1901 to 2018 for each study basing on the geographic coordinates provided by the ITRDB using the package "RNetCDF"³⁷. Because tree growth always tends to decline with age³⁸, we adopted the smoothing spline method to remove non-climatic signals from all ring width series before calculating trees' growth responses to drought³⁹. Ring width detrending was performed in R version 4.0.2⁴⁰ using the package "dplR"⁴¹⁻⁴³. For each study, growth responses to drought were calculated using the averaged detrended ring widths of all core samples. For drought sensitivity, if the correlation coefficient between ring width and SPEI based on the linear regression model for a species was statistically significant ($P < 0.05$), we used the coefficient to reflect the drought sensitivity of this species. Otherwise, the drought sensitivity of the focal species was set as "NA". All linear regressions were conducted using the R package "stats"⁴⁰. For growth reduction and recovery, we first identified the years when severe drought events occurred at each study site (i.e., when SPEI was smaller than -1.5)^{44,45}. Growth reduction by severe drought was quantified as the pairwise difference between the detrended ring width in the year before drought and that in the year of drought for all years when severe drought events occurred, so that a positive reduction value corresponds with growth reduction while a negative reduction value corresponds with growth increase. Growth recovery from severe drought was quantified as the pairwise difference between the detrended ring width in the 5th year after drought compared to that in the year of drought for all years when severe drought events occurred,

so that a positive recovery value corresponds with growth increase while a negative reduction value corresponds with growth reduction. Pairwise t-tests were adopted for calculations of growth reduction and recovery, which were conducted using the R package “stats”⁴⁰. Similarly, we determined the climate zone information basing on the geographic coordinates of each study. As a result, we obtained a dataset of species growth responses to drought for 47 species (i.e., 15 AM vs. 32 EM species) from 1186 different locations (i.e., 165 tropical vs. 1021 temperate locations) across the world (Fig. 1b,c).

Trait data collection

According to previous studies, seed-bearing type (i.e., gymnosperm vs. angiosperm)^{16,46}, wood density^{11,12}, specific leaf area^{4,13}, plant size^{9,10} and rooting depth¹⁴ are important predictors for drought responses of trees. Thus, data of these traits were collected in addition to mycorrhizal type so that we could compare the explanatory power of different traits and have a more comprehensive understanding of the relationship between trait and species drought response.

For the 260 tree species included in our drought response datasets, we directly acquired data of seed-bearing type, wood density, specific leaf area and maximum plant height (i.e., a measure of plant size) for 136 species from Greenwood’s dataset⁴. For the other 124 species that did not have available data in Greenwood’s dataset, we determined the seed-bearing type of each species based on its family; gymnosperm species were all from Pinaceae and Cupressaceae families, while all other species were angiosperms. For wood density, specific leaf area and maximum plant height, we requested public data from the TRY trait database (<https://www.try-db.org/>) (request ID 14442)⁴⁷. As a result, we obtained seed-bearing type data for all 260 species, wood density data for 136 species, specific leaf area data for 155 species, and maximum height data for 167 species. For rooting depth, we managed to acquire data for only 35 species from the Global Root Trait (GRooT) database⁴⁸. See details in supporting datasets (Data S1 and S2).

Phylogenetic tree construction

Because species taxonomy may strongly affect species’ drought responses, we constructed two separate phylogenetic trees to respectively account for the phylogenetic relatedness among the 220 species and 47 species for the mortality and growth response datasets. Following the protocol by Qian and Jin (2016)⁴⁹, we used the function ‘S.PhyloMaker’ to produce the phylogeny. Species that had not been included in the supertree by Qian and Jin were added to the phylogeny using the approach implemented in Phylomatic and Branch Length Adjuster (BLADJ)⁴⁹. The phylogenetic trees were visualized with the R package ‘ggtree’⁵⁰ (Fig. 1a,b).

Statistical analyses

To explore the effect of mycorrhizal type on trees’ drought responses across the tropical and temperate zones, we adopted the phylogenetic generalized linear mixed model (PGLMM) that included mycorrhizal

type (AM vs. EM), climate zone (tropical vs. temperate) and their interaction as fixed factors. Study site and species nested within study site were selected as random factors, while species phylogeny was selected to define the covariance structure for random factors in these models. For the mortality dataset, each study represented one distinct study site. For the growth response dataset, we used the information in the “study name” provided by the ITRDB to assign studies to different sites. Because drought intensity significantly covaried with tree mortality, we additionally added SPEI and its interactions with mycorrhizal type and climate zone to the PGLMM for drought-induced mortality. All PGLMMs were conducted using the R package “phyr”⁵¹. Because mortality rate was zero-inflated, we added 0.0001 to the data and log-transformed the data before analyses. All continuous variables were scaled to and scaled to have a mean of 0 and standard deviation of 1 in order to increase data normality and decrease variance heterogeneity before analyses.

To compare the explanatory power of different traits on trees’ drought responses, we also adopted PGLMM analyses. Because there were different sample sizes for different traits, it is not possible to directly compare the explanatory power of all traits in one model. Thus, a separate PGLMM was conducted for each individual trait. In these analyses, because we were no longer interested in whether the pattern holds true across climate zones, we removed all terms concerning climate zone from the PGLMMs and substituted mycorrhizal type by one of the following traits (i.e., seed-bearing type, wood density, specific leaf area, maximum height, or rooting depth) in each separate model. The other model settings remained the same as those in previous analyses. To allow comparisons among traits, the two categorical variables, mycorrhizal type and seed-bearing type, were transformed to numeric variables, with “AM” and “gymnosperm” being assigned as “-1”, and “EM” and “angiosperm” being assigned as “1”. Similarly, mortality data was log-transformed, and all numeric variables, including mycorrhizal type and seed-bearing type, were scaled before analyses.

AM and EM biogeographic shift prediction

Steidinger et al. (2019) provided the global proportions of basal area for AM and EM trees at a 1 x 1 degree resolution as raster in CDF format²⁴. Thus, we directly obtained the data from Steidinger et al. (2019)²⁴ as a reference for the current AM and EM biogeography (i.e., in year 2020) using the package “RNetCDF”³⁷. Because the authors also included N-fixer in their dataset, we recalculated the relative proportion of AM and EM trees using the following equations:

$$\text{Prop}_{\text{AM}} = P_{\text{AM}} / (P_{\text{AM}} + P_{\text{EM}}) \quad (1)$$

$$\text{Prop}_{\text{EM}} = P_{\text{EM}} / (P_{\text{AM}} + P_{\text{EM}}) \quad (2)$$

Here, P_{AM} and P_{EM} are the proportions provided by Steidinger et al. (2019)²⁴, while Prop_{AM} and Prop_{EM} are the recalculated proportions of AM and EM trees in this study, respectively.

Without considering annual increases in the basal area of AM and EM trees, drought-induced biogeographic shift can be predicted by calculating the relative proportion of surviving AM and EM trees

within a certain time period. To do this, we need to first calculate annual mortality rate. After performing PGLMM analyses for the subset of mortality data in the tropical zone with mycorrhizal type and SPEI as fixed factors, we obtained the following equations for AM and EM mortality in the tropical zone:

$$\text{Mort}_{\text{AM}} = e^{-1.0542 \cdot \text{SPEI} - 4.7074} - 0.0001 \quad (3)$$

$$\text{Mort}_{\text{EM}} = e^{-2.2804 \cdot \text{SPEI} - 6.0871} - 0.0001 \quad (4)$$

Similarly, we obtained the following equations for AM and EM mortality in the temperate zone:

$$\text{Mort}_{\text{AM}} = e^{-0.7662 \cdot \text{SPEI} - 5.7542} - 0.0001 \quad (5)$$

$$\text{Mort}_{\text{EM}} = e^{-1.9825 \cdot \text{SPEI} - 5.1985} - 0.0001 \quad (6)$$

To use the above equations, information on annual drought intensity under future climate changes was also needed. Cook et al. (2014) provided the past and future global SPEI from 1900 to 2099 based on 15 general circulation models ensembled by Coupled Model Intercomparison Project Phase 5 (CMIP5)⁵. For convenience, we only downloaded the predicted SPEI based on the CCSM4 model (<http://kage.ldeo.columbia.edu:81/SOURCES/.LDEO/.ClimateGroup/.PROJECTS/.IPCC/.CMIP5/.pdsi-spei/.spei/.CCSM4/>), which was shown to have the greatest capacity to capture both precipitation and evaporation signals among all models⁵. The SPEIs across 6 replicated simulations by the CCSM4 model were averaged for each 1 x 1 degree grid before we calculated the proportions of surviving AM and EM trees at each 1 x 1 degree grid in 2021 basing on the following equations:

$$\text{Prop}'_{\text{AM}2021} = \text{Prop}_{\text{AM}2020} * (1 - \text{Mort}_{\text{AM}2021}) \quad (9)$$

$$\text{Prop}'_{\text{EM}2021} = \text{Prop}_{\text{EM}2020} * (1 - \text{Mort}_{\text{EM}2021}) \quad (10)$$

Similarly, for each year afterwards, the proportions of surviving AM and EM trees could be calculated using the proportions of the previous year and the mortality rates of the focal year. Following this approach, we calculated the proportions of surviving AM and EM trees from 2021 to 2070. It is important to note that because we did not consider annual increase in the basal area of AM and EM trees, the sum of AM and EM proportions continually reduced along the timeline. To fix this issue, the relative proportions of AM and EM trees in each year were adjusted using the following equations:

$$\text{Prop}_{\text{AM}} = \text{Prop}'_{\text{AM}} / (\text{Prop}'_{\text{AM}} + \text{Prop}'_{\text{EM}}) \quad (11)$$

$$\text{Prop}_{\text{EM}} = \text{Prop}'_{\text{EM}} / (\text{Prop}'_{\text{AM}} + \text{Prop}'_{\text{EM}}) \quad (12)$$

The R package “ggplot2” was used to visualize the global biogeographic shift in AM vs. EM dominance⁵¹.

Results

Effect of mycorrhizal type on drought-induced tree mortality

There were significant effects of mycorrhizal type ($Z = 2.20$, $P = 0.027$), interaction between mycorrhizal type and SPEI ($Z = -2.61$, $P = 0.009$), and interaction between mycorrhizal type and climate zone ($Z = -2.11$, $P = 0.035$) on drought-induced mortality (Table S1), indicating that AM and EM trees responded differently to increased drought intensity in different climate zones. Specifically, a significantly positive correlation between mortality and drought intensity (i.e., reverse of SPEI) was observed in both AM and EM trees in the tropical zone, the strength of which did not differ between mycorrhizal types (Fig. 2a; Table S2). However, in the temperate zone, the significantly positive correlation between mortality and drought intensity was only observed in EM trees, resulting in a lack of overall drought intensity effect and a significant interactive effect between mycorrhizal type and drought intensity (Fig. 2b; Table S2).

Effect of mycorrhizal type on growth responses to drought

For drought sensitivity, there were significant effects of mycorrhizal type ($Z = -4.62$, $P < 0.001$), climate zone ($Z = -5.31$, $P < 0.001$) and their interaction ($Z = 3.68$, $P < 0.001$) (Table S3), indicating opposite effects of mycorrhizal type in the tropical and temperate zones. Specifically, EM trees have stronger drought sensitivity compared to AM trees in the tropical zone, whereas the opposite was true in the temperate zone (Fig. 3a; Table S4). Because trees in the temperate zone showed much stronger drought sensitivity compared to those in the tropical zone, and the effect of mycorrhizal type was much stronger in the temperate compared to the tropical zone, we observed a significantly stronger drought sensitivity in AM compared to EM trees across climate zones (Fig. 3a; Table S4).

Similarly, for growth reduction by and growth recovery from severe drought, there were significant effects of mycorrhizal type ($Z_{\text{reduction}} = 5.42$, $P < 0.001$; $Z_{\text{recovery}} = -2.70$, $P = 0.007$) and climate zone ($Z_{\text{reduction}} = 3.02$, $P = 0.003$; $Z_{\text{recovery}} = -3.06$, $P = 0.007$), as well as a marginally significant effect of interaction between mycorrhizal type and climate zone ($Z_{\text{reduction}} = -1.75$, $P = 0.080$; $Z_{\text{recovery}} = 1.82$, $P = 0.068$) (Table S3), indicating opposite effects of mycorrhizal type in the tropical and temperate zones. Specifically, EM trees suffered from greater growth reduction and less growth recovery compared to AM trees after severe drought events, which was only significant in the temperate zone (Fig. 3b,c; Table S4).

Shifts in relative proportion of AM vs. EM trees at the global scale

Based on model prediction, the dominance of EM trees at the temperate sites around 40° N and 40° S, such as those in central USA, southern Europe and Chile, will be greatly challenged by AM trees in 2070 (Fig. 4). Although the dominance of EM trees was predicted to be reduced at some sites in the tropical zone, the in relative proportion of AM vs. EM trees between 30° N and 30° S would remain largely unchanged (Fig. 4).

The explanatory power of mycorrhizal type on drought responses of trees

Regardless of climate zone, mycorrhizal type could explain all aspects of trees' growth responses to drought (Fig. 5b-d; Table S5). Specifically, mycorrhizal type had a strong explanatory power on growth reduction by severe drought ($Z = 4.83$, $P < 0.001$), which was only weaker than maximum height among all study traits ($Z = -7.49$, $P < 0.001$) (Fig. 5c; Table S5). Its explanatory effect on drought sensitivity ($Z = -2.75$, $P = 0.006$) and growth recovery from severe drought ($Z_{\text{recovery}} = -1.74$, $P = 0.083$) were also weaker than wood density ($Z_{\text{sensitivity}} = -4.40$, $P < 0.001$; $Z_{\text{recovery}} = -1.99$, $P = 0.046$) and maximum height ($Z_{\text{sensitivity}} = 14.12$, $P < 0.001$; $Z_{\text{recovery}} = 7.64$, $P < 0.001$) (Fig. 5b,d). Mycorrhizal type could also explain the correlation between mortality and SPEI ($Z = -1.99$, $P = 0.047$), but not mortality *per se* ($Z = 0.81$, $P = 0.418$) (Fig. 5a; Table S5).

Discussion

Differential drought responses between AM and EM trees

According to our analyses, AM and EM trees significantly differed in their responses to drought, and such differences were more prominent in the temperate compared to the tropical zone. Specifically, in the tropical zone, we had only detected a significantly lower drought sensitivity in AM vs. EM trees (Fig. 3a), indicating that the growth of AM trees was less affected by varying drought intensity compared to EM trees in the tropical zone. In the temperate zone, however, we detected an exactly opposite pattern: AM trees may be more sensitive to varying drought intensity compared to EM trees (Fig. 3a). In addition, there were lower mortality rate, weaker mortality-drought intensity correlation, less growth reduction by severe drought and more growth recovery from severe drought in AM vs. EM trees in the temperate zone (Fig. 2,3), indicating that when drought stress became intense, both growth and survival of EM trees would be impacted to a greater extent compared to AM trees in the temperate zone. To our knowledge, this study is the first to reveal differences in the drought responses between AM vs. EM trees at the global scale.

Mycorrhizal fungi are frequently reported to mitigate drought stress on trees through various mechanisms¹⁷⁻²². However, EM fungi may be less beneficial for drought stress mitigation compared to AM fungi. Firstly, although both types of fungi have been reported to enhance host performance under drought stress, many studies detected prominent eco-physiological changes corresponding with improved drought responses in AM-inoculated individuals^{19,20,53}, whereas quite a few studies failed to detect such changes in EM-inoculated individuals²⁹⁻³¹. Secondly, EM fungi may be more vulnerable to drought stress compared to AM fungi in soil^{27,28}, suggesting that EM hosts may have less access to their symbiotic partners, and thus have a harder time in maintaining mutualistic symbiosis under drought stress than AM hosts. The above evidence may help explain our finding of worse drought responses of EM trees under severe drought compared to AM trees, suggesting that mycorrhizal type may be an important predictor of trees' drought responses.

The potential role of mycorrhizal-type-dependent drought responses in shaping global tree biogeography

Recent evidence showed that there is a clear global biogeographic pattern of plant-mycorrhizal symbiosis³⁶: AM trees dominate the tropical zone, whereas EM trees dominate the temperate zone. These global patterns were proposed to be driven by the preference of AM trees for fast litter decomposition in warm and wet regions, and the preference of EM trees for slow litter decomposition rate in cold and dry regions²⁴, indicating a potentially stronger drought adaptation, if not drought tolerance, of EM vs. AM trees at the global scale. Interestingly, we found that AM trees exhibited lower sensitivity to minor and moderate droughts in the tropical zone compared to EM trees, where they also happened to be the dominating group. Likewise, a lower drought sensitivity and a higher dominance of EM vs. AM trees were found in the temperate zone. These mycorrhizal-type-dependent drought sensitivity may provide additional explanation for the global biogeographic patterns of tree-mycorrhizal symbioses besides the previously identified mycorrhizal-type-dependent preference for litter decomposition rate.

However, a review on EM fungi and water relations of trees argued that although EM trees mostly dominate the temperate zone, they are more common in wet compared to dry temperate habitats³⁰, suggesting a weaker drought tolerance of EM vs. AM trees^{27,28}. Our analyses also provided partial supports for this argument: under severe drought stress, EM trees showed significantly weaker tolerance compared to AM trees in the temperate zone. Thus, we would argue that the effects of mycorrhizal type on trees' drought responses depend on both climate zone and drought intensity. By incorporating future drought scenarios, we did predict loss of EM dominance in some temperate regions in the future 50 years (Fig. 4), indicating that the weaker tolerance of EM vs. AM trees to severe drought may result in prominent shifts in the global biogeographic pattern of plant-mycorrhizal symbiosis under climate drying.

The importance of mycorrhizal type in understanding trees' drought responses

By comparing the explanatory power of a suite of traits on trees' drought responses, we found that different aspects of drought responses could be best explained by different traits. Overall, species wood density and maximum height seemed to be the best predictors of species drought responses. Species with denser wood and smaller maximum height may be less sensitive to drought intensity variation and have lower mortality rates under drought stress (Fig. 5 a,b), which is consistent with the results from previous studies^{4,9}. However, they may also suffer from stronger growth reduction and weaker growth recovery under severe drought (Fig. 5 c,d).

Although mycorrhizal type was not the best predictor for drought responses, it still had a greater explanatory power than seed-bearing type, specific leaf area and rooting depths in most cases (Fig. 5), highlighting the importance of mycorrhizal type in understanding trees' drought responses across species (Fig. 2, 3). In fact, mycorrhizal type is a complex trait that may be associated with many eco-physiological processes contributing to trees' drought responses. In particular, drought avoidance involves processes that maintain the hydraulic and photosynthetic efficiencies of trees under drought stress⁸. AM fungi may play a more prominent role in osmoregulation and increasing photosynthetic rate under drought than EM fungi³¹, which may explain why we observed a smaller growth reduction by severe drought and a lower drought-induced mortality rate in AM vs. EM trees (Fig. 2b, 3b). Meanwhile, drought recovery involves

processes that compensate drought-induced losses or repair drought-induced damages⁸. Oxidative damage is a common form of damage to plant tissue after drought. Evidence showed that both AM and EM fungi could increase antioxidant enzyme activity in inoculated vs. non-inoculated trees^{53,54}, which may explain why we observed less difference in growth recovery from severe drought in AM vs. EM trees (Fig. 3c). As to the opposite mycorrhizal-type-dependent patterns of drought sensitivity in the tropical and temperate zones, the underlying mechanism remains to be explored.

Conclusion

Based on global datasets of four aspects of trees' drought responses, we found evidence of lower sensitivity to minor to moderate drought stress by AM and EM trees in the tropical and temperate zone, respectively, indicating that mycorrhizal-type-dependent drought sensitivity may be a potential mechanism shaping the current global biogeographic pattern of plant-mycorrhizal symbiosis. More importantly, we found evidence for greater impacts of severe drought stress on EM vs. AM trees in the temperate zone, and predicted shifts from EM to AM dominance in some temperate regions under climate drying scenarios. This study is the first to reveal the importance of mycorrhizal type in understanding drought-driven biogeography of plant-symbiosis at the global scale. Based on these findings, we may increase drought adaptation of our forest ecosystems and reduce the potential ecological and economic losses by paying more conservation efforts on EM-dominated forests in the temperate zone. Cultivating more EM tree species and EM fungi varieties that have stronger drought tolerance may be a good solution to prevent the die-off of EM trees and maintain the valuable ecological services of forest ecosystems in the temperate zone under future climate changes.

Declarations

Data Availability

The data that supported the findings in this manuscript can be found in Supplementary Data (Table 1-3).

Code Availability

No customized codes were used in this work.

Competing Interests statement

The authors declare no competing interests.

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Figures

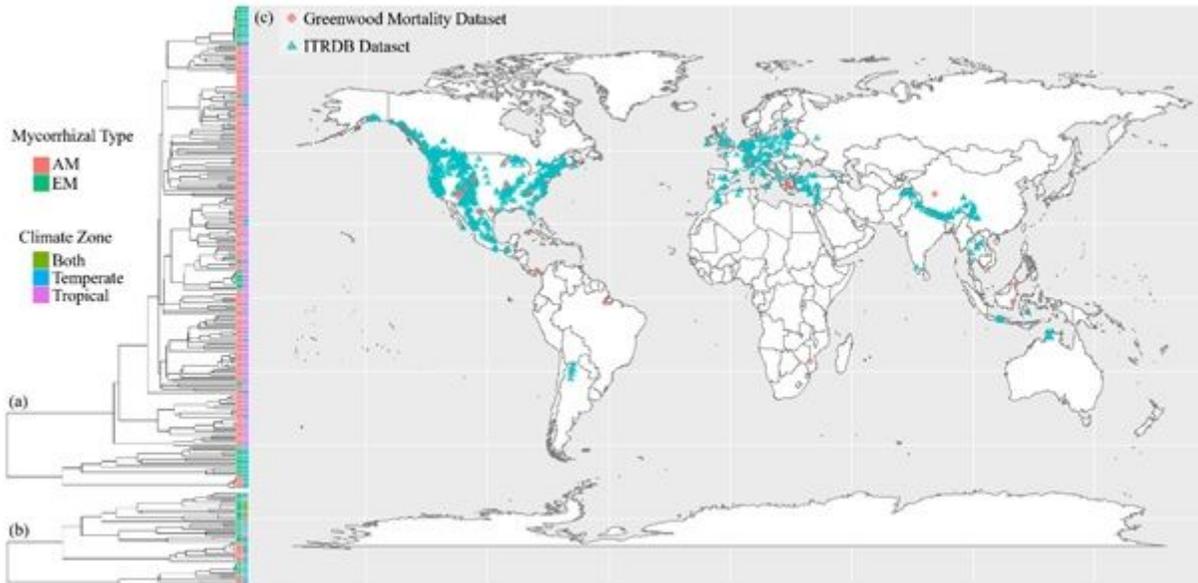


Figure 1

Mycorrhizal type and climate zone for the compiled global datasets based on Greenwood et al. (2017) (a) and the International Tree-Ring Data Bank (ITRDB) (b), as well as the locations of all study sites for these two datasets (c). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

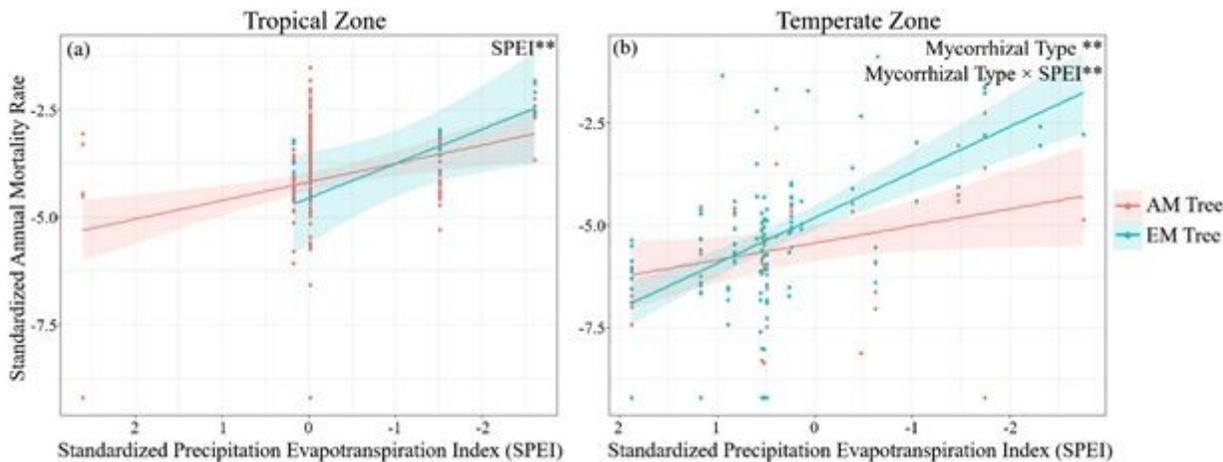


Figure 2

Effects of mycorrhizal type, drought intensity and climate zone on drought-induced tree mortality in the tropical zone (a) and the temperate zone (b) based on the phylogenetic generalized linear mixed model (PGLMM) for 220 species from 20 different locations ($n = 359$). Annual mortality rate was standardized by scaling $\log(\text{data} + 0.0001)$. Because a more negative SPEI corresponds with a more severe drought intensity, standardized drought intensity was quantified by scaling the Standardized Precipitation

Evapotranspiration Index (SPEI) and reversing the direction of the axis. Factors with significant effects on drought-induced mortality are indicated (** $p < 0.01$). Refer to statistics in Table S1 and S2.

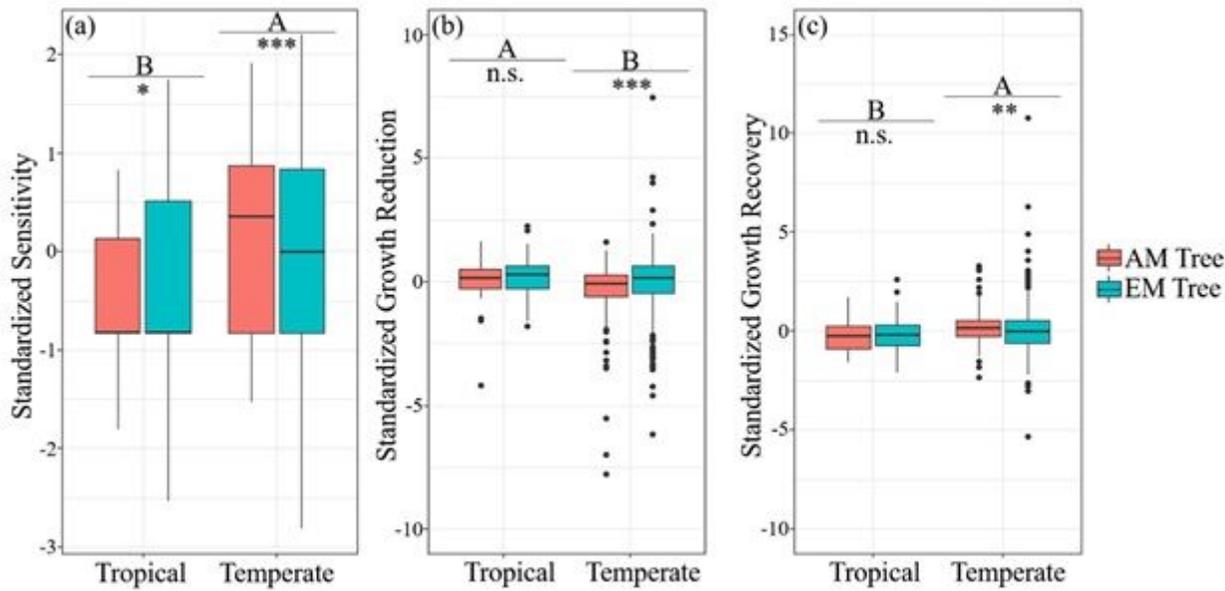


Figure 3

Effects of mycorrhizal type, drought intensity and climate zone on sensitivity to drought (a), growth reduction by severe drought (b) and growth recovery from severe drought (c) based on the phylogenetic generalized linear mixed model (PGLMM) for 48 species from 1186 different studies ($n = 1186$). Severe drought refers to the drought event during which SPEI was smaller than -1.5. All continuous variables were scaled before analyses. Boxplots show the 5th, 25th, 50th, 75th and 95th percentiles; outliers are represented by black points. Significant effects of mycorrhizal type are indicated by asterisks (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Significant effects of climate zone are indicated by different upper-case letters. Refer to statistics in Table S3 and S4.

Relative Proportion of AM vs. EM Trees (%)

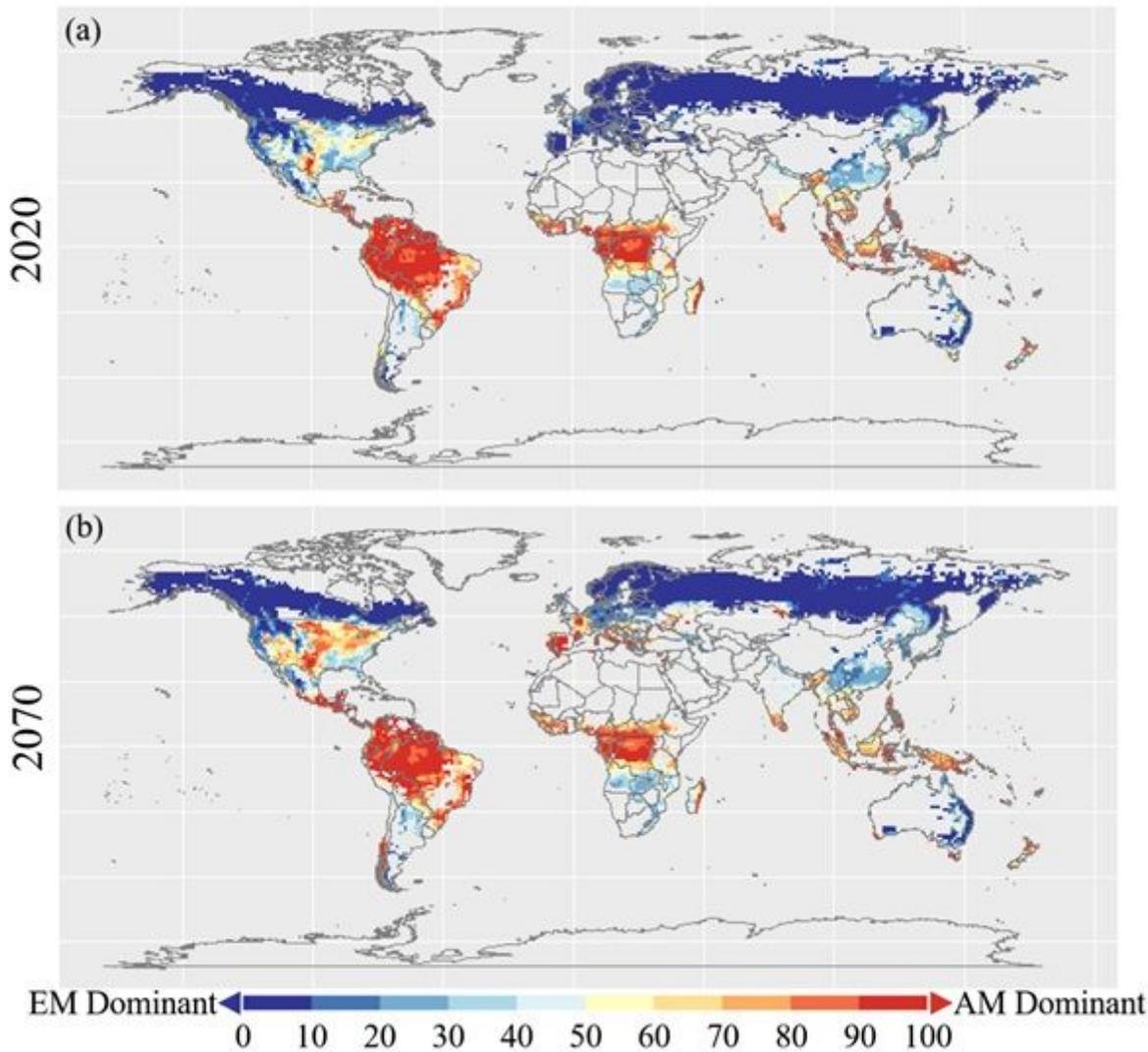


Figure 4

Relative proportions of AM vs. EM trees in 2020 (a) and 2070 (b). AM and EM proportions in 2020 were calculated using data from Steidinger et al. (2019)⁴, while those in 2070 were predicted using the annual mortality rates of AM and EM trees based on the phylogenetic generalized linear mixed model (PGLMM). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

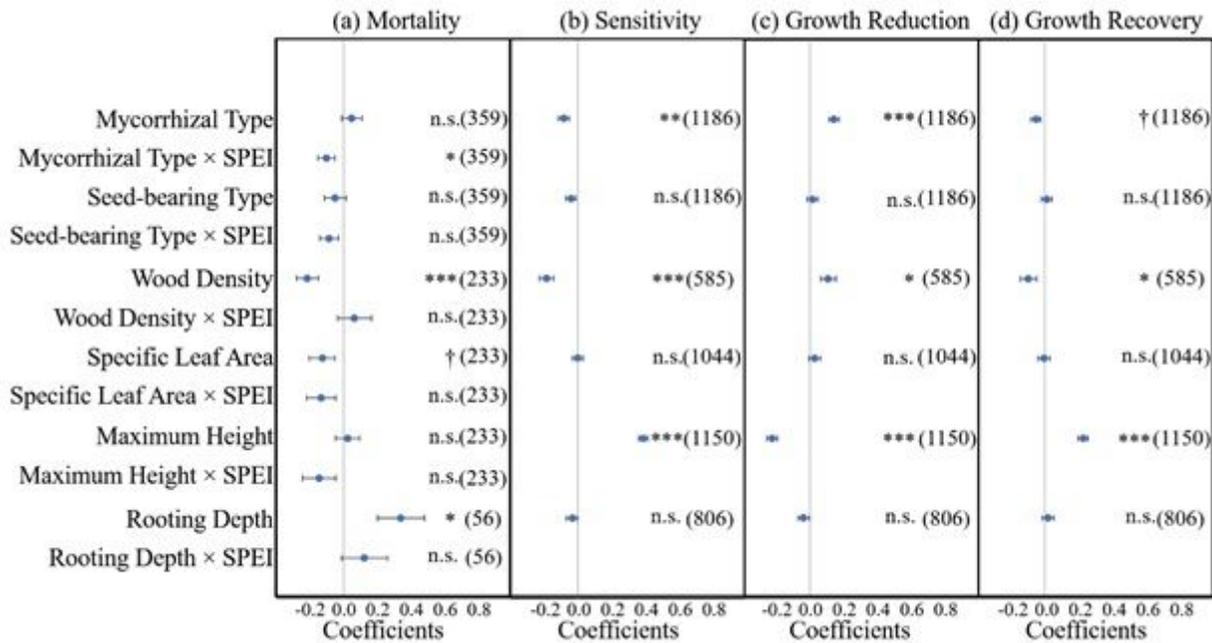


Figure 5

Coefficient estimates of different traits on mortality (a), drought sensitivity (b), growth reduction by severe drought (c) and growth recovery from severe drought (d) based on the phylogenetic generalized linear mixed model (PGLMM). Coefficient estimates and standard errors are shown. Sample sizes are shown in brackets. For drought-induced mortality, because different drought events had experienced different levels of drought intensity, which strongly affected tree mortality, the effect of drought intensity (i.e., Standardized Precipitation Evapotranspiration Index, SPEI) was included in the PGLMM when looking at trait effects. Significant estimates are indicated by asterisks († $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Refer to statistics in Table S5.

Supplementary Files

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