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Symbiotic mycorrhizal types affect patterns of tree aboveground and belowground C allocation in Northeast China

Qinggui Wang^{1*} , Guoyong Yan¹, Xi Luo¹, Guancheng Liu¹, Honglin Wang¹ and Yajuan Xing^{1,2*}

Abstract

Background Given the ubiquitous nature of mycorrhizal symbioses, different symbiotic fungi have obvious differences in structure and function, which may affect associated tree aboveground and belowground C allocation dynamics. However, the mechanisms underlying tree aboveground and belowground C allocation and its response to symbiotic mycorrhizal types and other factors (e.g., resource availability) remain poorly understood.

Results We used forest inventory data to explore the potential mechanism of tree aboveground and belowground C allocation patterns in Northeast China. Our results showed that tree-fungal symbioses were related to the patterns of tree C allocation. The ratio of aboveground to belowground C pool was significantly higher in ectomycorrhizal (EM)-associated trees than that in arbuscular mycorrhizal (AM)-associated trees. Symbiotic mycorrhizal types were associated with the responses of tree aboveground and belowground C allocation to different factors, such as mean annual precipitation (MAP) and mean annual temperature (MAT). Almost all factors significantly increased aboveground C allocation in AM-associated trees but significantly decreased it in EM-associated trees. Moreover, after controlling the other factors, the effects of climate factors (MAT and MAP) on the C allocation of AM- and EM-associated trees were similar. Increases in MAT and MAP significantly increased belowground and aboveground C allocation, respectively.

Conclusions Our results demonstrate symbiotic mycorrhizal types play an important role in controlling tree aboveground and belowground C allocation and dynamics.

Keywords Symbiotic mycorrhizal type, Tree carbon allocation pattern, Forest carbon cycling, Plant-climate interaction, Temperate forest

Background

Tree aboveground and belowground carbon (C) allocation is an important issue in forest ecosystem C cycling and global C modeling (Chen et al. 2013; Rog et al. 2021). Tree C allocation depends partly on the capacity of

different components such as shoot and root tissues to metabolize, incorporate, and store C (Poorter et al. 2012; Yu et al. 2015). How the tree assimilated C is allocated and stored to above- and belowground components, affects the growth and nutrient absorption of trees and determines the residence time of C in ecosystems, which has a profound effect on the tree, soil and forest ecosystem C pool and flux (Chen et al. 2013; Herrera-Ramírez et al. 2020). For example, changes in tree aboveground and belowground C allocation affect litter decomposition and tree-atmosphere C exchange, as well as affect model estimates of the global woody C pool (Litton et al. 2007; Ise et al. 2010). Despite a long history of research on how trees coordinate above- and belowground C allocation,

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defining tree C allocation strategy is a complex process that remains not fully understood due to trees with different C allocation strategies co-occurring in the same ecosystem, which hampers the capacity to model forest ecosystem C cycling (Friedlingstein et al. 1999; Franklin et al. 2012; McMurtrie and Dewar 2013; Hartmann and Trumbore 2016; Dominguez et al. 2021).

Abiotic environmental factors (e.g., soil moisture and soil N availability) can affect the tree aboveground and belowground C allocation strategy (Poorter et al. 2012). According to the 'balanced growth hypothesis' and the 'optimal partitioning theory', trees allocate biomass in an optimal pattern that enhances the uptake of the most limiting factor (Gedroc et al. 1996; Shipley and Meziane 2002). Thus, if the limiting factor for growth is belowground resources (e.g., nutrients, water), trees will allocate relatively more C to roots; on the contrary, if the limiting factor is above ground (e.g., light), trees will allocate relatively more C to shoots (Poorter et al. 2012). For example, nitrogen (N) deposition alleviates soil N-limitation and can increase C allocation to aboveground parts (Li et al. 2020; Eastman et al. 2021). Climate changes also affect tree aboveground and belowground C allocation dynamics. For example, decreased precipitation can increase belowground C allocation by reducing soil water availability, and elevated temperature can enhance aboveground C allocation due to the increase in plant respiration (Way and Oren 2010; Hagedorn et al. 2016). However, at the current stage, most of our understanding of tree aboveground and belowground C allocation response to abiotic environmental factors is at the individual site and is based on manipulative experiments (local scale, Petit et al. 2011; Eastman et al. 2021). Tree aboveground and belowground C allocation responses to abiotic environmental factors at a large spatial scale (regional pattern) remain poorly understood, which hampers the prediction of future C sequestration by terrestrial ecosystems.

Besides abiotic factors, biological factors (e.g., tree species identity, tree-symbiotic mycorrhizae and species richness) can also affect the tree aboveground and belowground C allocation strategy (Poorter et al. 2012; Haselquist et al. 2016). It has been estimated that about 85% of all terrestrial plant species form associations with symbiotic mycorrhizal fungi to acquire nutrients from the soil (van der Heijden et al. 2015; Brundrett and Tedersoo 2018). Plant-fungal symbioses significantly regulate plant growth, shape the biogeochemistry of ecosystems, and modulate ecosystem C dynamics (Phillips et al. 2013; Terrer et al. 2016), which may affect plant aboveground and belowground C allocation patterns and their responses to environmental factors. Two main mycorrhizal types within trees are arbuscular mycorrhizal (AM) and

ectomycorrhizal (EM), which differ greatly in their environmental preferences, forms, and functions (Větrovský et al. 2019; Genre et al. 2020). For example, EM fungi can produce a wide range of enzymes that release N and other nutrients from organic matter, whereas AM fungi lack these enzymes (Read and Perez-Moreno 2003; Averill et al. 2014). Accordingly, EM-associated trees and AM-associated trees have different nutrient absorption and growth strategies (Phillips et al. 2013), suggesting that different mycorrhizal-associated trees may also have diverse aboveground and belowground C allocation patterns. Despite our increasing understanding of symbiotic mycorrhizal fungal functions, the patterns of aboveground and belowground C allocation between various mycorrhizal-associated trees are still unclear. Furthermore, tree species richness has been shown to positively affect tree productivity, aboveground C pool, soil C stock, and ecosystem C pool through niche complementarity, the insurance effect, and the selection effect (Reich et al. 2012; Poorter et al. 2015; Chen et al. 2018; Huang et al. 2018; Liu et al. 2018). Although species richness can increase the C pool of trees, it is unclear how the increased C of trees is distributed among different organs. Understanding how symbiotic mycorrhizal fungi and tree species richness affects tree aboveground and belowground C allocation is crucial to investigate the mechanism of tree aboveground and belowground C allocation and its feedback from climate change.

To fill the above knowledge gaps, we examined the effects of biological and abiotic factors on tree aboveground and belowground C allocation patterns based on data from 1910 field sites across large-scale ecological gradients in Northeast China obtained using standardized sampling methods. Here, we aimed to address three main questions: (1) Are tree C allocation patterns regulated by interactions between environmental and biological factors instead of just environmental factors? (2) Do tree species with different symbiotic mycorrhizal types (AM and EM) have different C allocation patterns? (3) Do trees symbiotic with different mycorrhizal fungi have different responses in C allocation to changing environmental factors? Based on previous experimental study results that environmental factor had a significant effect on tree aboveground and belowground C allocation (Petit et al. 2011; Zhang et al. 2015; Eastman et al. 2021), we hypothesized that tree aboveground and belowground C allocation was still related to biological and abiotic factors in a large-scale ecological gradient. Due to the different functions and structure between AM and EM symbiotic mycorrhizae (Větrovský et al. 2019; Genre et al. 2020) and the large amount of enzymes produced by EM fungi that consume a lot of organic matter, we further hypothesized that the ratio of aboveground to belowground C pool

was significantly higher in ectomycorrhizal (EM)-associated trees than that in arbuscular mycorrhizal (AM)-associated trees, and aboveground and belowground C allocation strategies of trees symbiotic with different mycorrhizal fungi have distinct responses to environmental factors.

Methods

This study included a network of 1910 plots (30 m × 30 m) across temperate forests of Northeast China with a wide latitudinal and longitudinal range (latitude 39°54'–53°19'N, longitude 118°51'–133°52'E; Supporting Information Fig. 1 and Additional file 1: Table S1). In this study, all artificial forest sites were excluded. The climate of the study area was characterized as a temperate continental climate: average annual precipitation ranged from 110 mm to 1108 mm and average annual temperature varied from – 6.8 °C to 9.2 °C across the study plots. Elevation varied from 0 to 1936 m a.s.l. Annual nitrogen deposition ranged from 12.80 kg/ha to 16.80 kg/ha (Wen et al. 2020). More background information is presented in Additional file 1: Table S1.

Tree C pool and C allocation patterns

For each plot, all trees with DBH (diameter at breast height = 1.3 m) ≥ 3 cm were identified, recorded, and measured (including DBH and height). The Flora of China (<http://foc.eflora.cn/>) and Catalogue of Life China

(Checklist 2015, <http://www.sp2000.org.cn/>) were used to determine the names of all species. All measurements were completed between 2011 and 2013 according to the sampling method outlined by the Technical Manual Writing Group of the Ecosystem Carbon Sequestration Project (2015). Meanwhile, the number of tree species was recorded within each plot and used as the measure of species richness. In total, more than 500,000 trees from 1910 plots were recorded and measured in the study. Each tree's dry biomass was calculated using the relevant allometric equation with tree height and DBH as predictors (Ecosystem Carbon Sequestration Project 2015; Tang et al. 2018). For each part of the tree (stem, branch, leaf, and root) a specific allometric equation was used (Additional file 1: Table S2). The aboveground C pool, belowground C pool and total tree C pool were the aboveground biomass, belowground biomass and total tree biomass multiplied by conversion coefficient (0.5), respectively. Tree species richness was assessed as the number of species per plot with at least one tree individual DBH ≥ 10 cm.

Estimation of AM- and EM-associated tree C pool and C allocation patterns

The symbiotic mycorrhizal type of each tree was identified according to the global online database of plant mycorrhizal associations and the symbiotic fungi website (<http://mycorrhizas.info/index.html>; Soudzilovskaia et al.

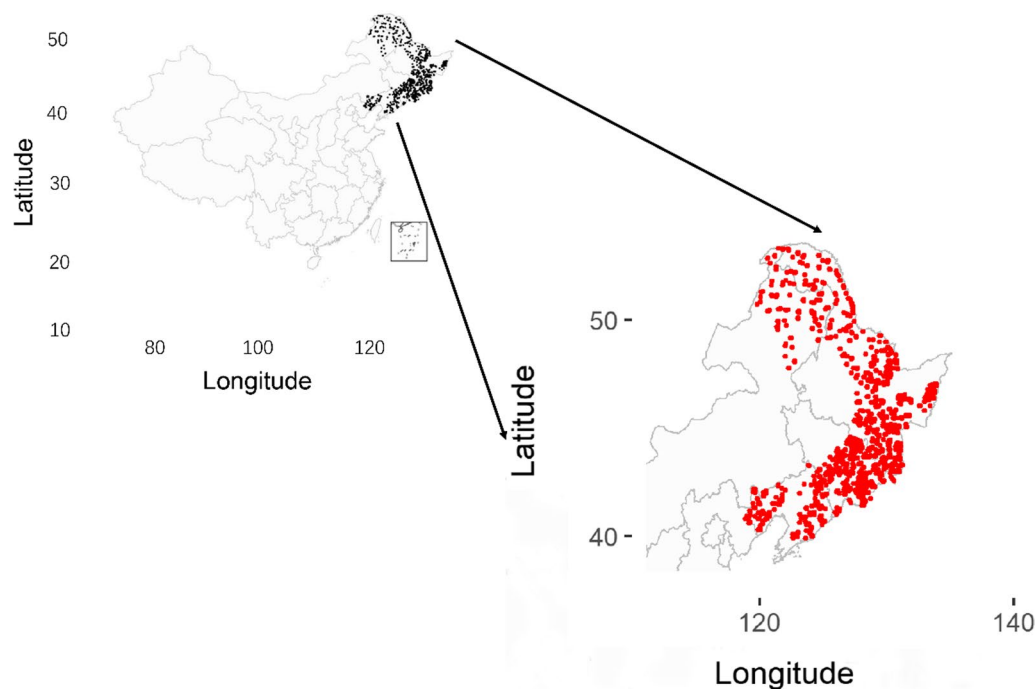


Fig. 1 The map of sampling sites. A total of 1910 plots were included and collected

2020; Bueno et al. 2021). The plots together contained 202 tree species, including 116 species of AM trees, 75 species of EM tree species and 11 species (5.4% of all species) with other mycorrhizal associations. These 11 species were not included in our analyses because of the low overall contribution to the whole species collection. The C pools of AM-associated trees and EM-associated trees per plot were calculated by summing tree C pools with the same mycorrhizal type. The aboveground and belowground C pools of AM-associated trees and EM-associated trees per plot were determined by summing the tree aboveground and belowground C pools within the same mycorrhizal type. Species richness of the AM-associated trees or the EM-associated trees per plot was assessed as the number of the same mycorrhizal type species with at least one individual DBH ≥ 10 cm.

Climate and other environmental factors

The data for nitrogen deposition (ND) was collected from the Nationwide Nitrogen Deposition Monitoring Network (NNDMN, Wen et al. 2020). Mean annual precipitation (MAP) and mean annual temperature (MAT) were retrieved from a resolution of 30 arc seconds WorldClim database (Hijmans et al. 2005).

Statistical analyses

The Shapiro–Wilk test was performed to examine the statistical distribution of data normality before statistical analyses in this study. One-way ANOVA followed by the Fisher LSD (least-significant difference) was used to detect the significance of the differences in the ratios of the aboveground C pool to the belowground C pool between different mycorrhizal-related trees at $p < 0.05$. The partial correlations analysis method was performed to explore the relationship of aboveground-belowground C pool ratio with six factors (including MAP, MAT, ND, AM-associated tree species richness (AMSR), EM-associated tree species richness (EMSR), species richness (SR) in the packages ‘Hmisc’ and ‘ppcor’ in R 4.0.0 (R Development Core, 2020). After that, we conducted the partial least squares path model (PLS-PM) to infer potential direct and indirect effects of climate factors (including MAT and MAP), ND, and species richness (including TSR, AMSR, and EMSR) on the ratio of aboveground C storage to belowground C storage. We used the 95% bootstrap confidence interval to judge whether the estimated path coefficients were significant. Path coefficient represents the direction and strength of the direct effect. The PLS-PM was performed using the package ‘plsmpm’ in R 4.0.0 (R Development Core, 2020). All figures were drawn using the package ‘ggplot2’ and all statistical analyses were conducted in the R 4.0.0.

Results

Tree C storage in Northeast China

In the study area, the average tree C pool, AM-associated tree C pool, and EM-associated tree C pool were 64.26 ± 1.85 , 8.52 ± 0.40 , and 52.10 ± 1.76 Mg C/ha, respectively (Additional file 1: Table S1). Total EM-associated tree C pool was higher than the AM-associated tree C pool. Likewise, the aboveground C pool (39.76 ± 1.47 Mg C/ha) and belowground C pool (12.34 ± 0.39 Mg C/ha) of EM-associated trees also were higher than that of AM-associated trees (the aboveground C pool was 6.54 ± 0.30 Mg C/ha and the belowground C pool was 1.97 ± 0.09 Mg C/ha). The ratio of aboveground C storage to belowground C (RAB) storage was higher in EM-associated trees than that in AM-associated trees at the plot level and individual level (Fig. 2; Additional file 1: Fig. S1), indicating that AM-associated trees allocated more C to belowground components.

Effects of different factors on tree C pool

The EM-RAB was negatively associated with the SR, AMSR, ND, MAT, and MAP (Fig. 3). The EM-RAB was significantly positively correlated with EMSR. After controlling the role of AMSR and SR, the positive relationship between EM-RAB and EMSR was strengthened (Fig. 3). Moreover, excluding the effect of MAT,

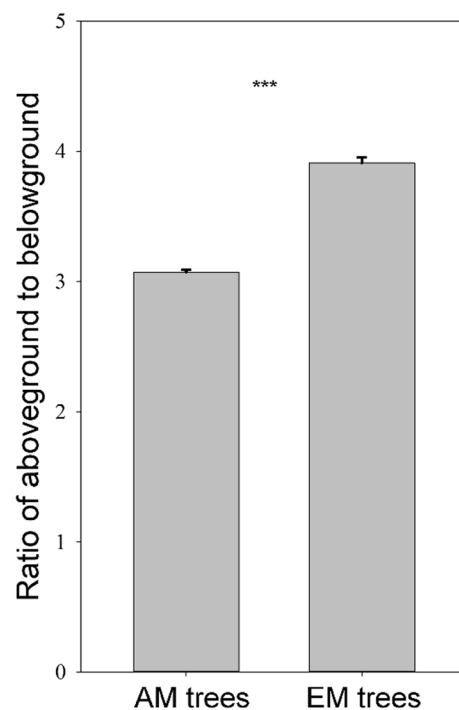


Fig. 2 Ratio of aboveground C to belowground C of EM-associated trees and AM-associated trees in each plot. ***indicates a significant difference within the group ($p < 0.001$)

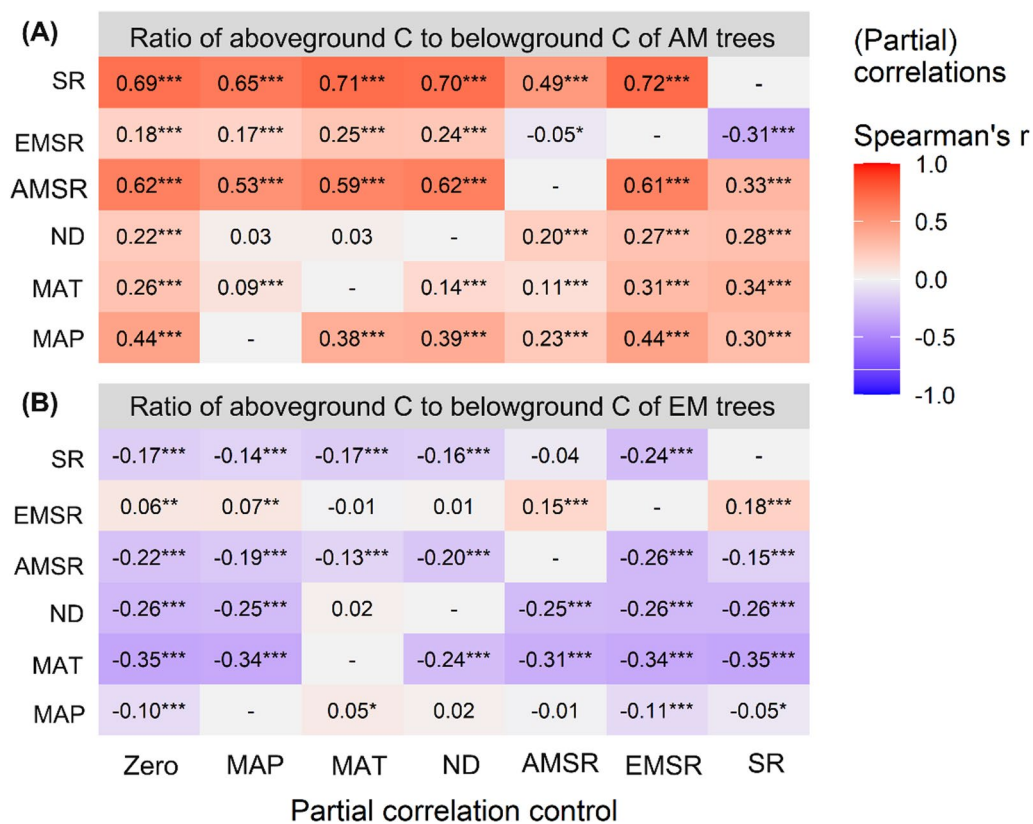


Fig. 3 Partial correlations between the ratio of AM-associated tree aboveground C storage to belowground C storage (A) and the ratio of EM-associated tree aboveground C storage to belowground C storage (B), and different factors in the partial Least Squares Path Modeling. The intensity of colors and numbers indicates the strength of the correlation. Significant levels are: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$. *MAP* annual average precipitation, *MAT* annual average temperature, *ND* nitrogen deposition, *AMSR* AM-associated tree species richness, *EMSR* EM-associated tree species richness, *SR* total species richness

EM-RAB was positively associated with ND and MAP (Fig. 3). The AM-RAB was significantly positively correlated with MAT, MAP, SR, and AMSR, even after controlling the role of other factors (Fig. 3). However, after controlling the roles of SR and AMSR, AM-RAB was significantly negatively associated with EMSR (Fig. 3).

Consistently, the structural equation models (SEM) analysis revealed that MAP and MAT had a significant positive effect on species richness, while the ND had a significant negative effect on species richness. Species richness and MAT exerted positive effects on AM-RAB, while MAP and ND were less responsible for the variations of AM-associated tree C allocation (Fig. 4, Additional file 1: Table S3). MAT, ND, and species richness had a negative relationship with the EM-RAB but MAP had a positive effect on EM-RAB (Fig. 4).

Discussion

Hypotheses were supported by our results. We found AM-associated trees invested relatively more C in belowground components and relatively less C in aboveground

components than EM-associated trees (Fig. 2), indicating that tree C allocation pattern is related to changes in community mycorrhizal composition. These results also explicitly show that changes in tree symbiotic mycorrhizal types may be important drivers influencing tree C allocation strategies in natural ecosystems.

Based on the concept of functional equilibrium between the capture of above- and below-ground resources by shoots and roots, shoot C allocation increases when aboveground resources (e.g., light and CO_2) become more limiting, whereas root C allocation increases when soil resources (e.g., nutrients and water) become more limiting (Hilbert and Reynolds 1991; McMurtrie and Dewar 2013). Diverse symbiotic mycorrhizae strongly affected the capacity of associated tree roots to take up different nutrients, leading to the spatial and temporal changes in the main limiting factors for diverse associated trees and then causing the alteration of its aboveground and belowground C allocation pattern (Poorter et al. 2012; Hasselquist et al. 2016). In Northeast China, boreal and temperate forests are

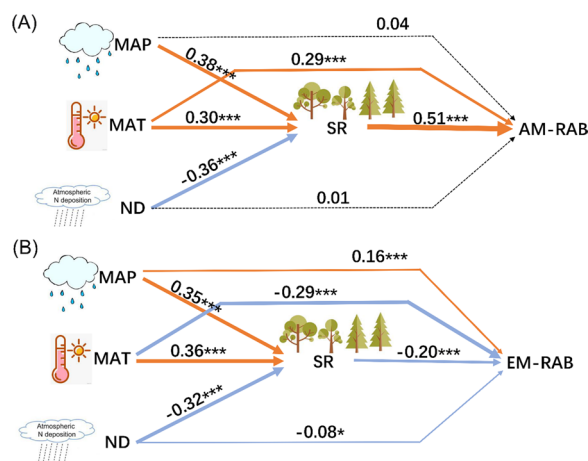


Fig. 4 Structure equation models (SEM) showing the effects of MAP, MAT, species richness (including AM-associated tree species richness, EM-associated tree species richness, and total species richness), and nitrogen deposition on the ratio of aboveground C storage to belowground C storage. **A** AM-RAB, the ratio of AM-associated tree aboveground C storage to belowground C storage; **B** EM-RAB, the ratio of EM-associated tree aboveground C storage to belowground C storage. The yellow line indicates a significant positive correlation, the blue line indicates a significant negative correlation, and the dotted line indicates a non-significant correlation. Arrow width is proportional to the strength of the relationship. Numbers adjacent to arrows denote standardized path coefficients. Significant levels are: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

typically associated with N limitations (Gao et al. 2020). Trees should allocate more C below ground to enhance N absorption and assimilation. However, AM fungi are unable to liberate their N and thus more reliant on the availability of soil mineral N than their EM counterparts (Terrer et al. 2016). EM-associated trees acquire substantially more organic N from the soil than AM-associated trees (Read and Perez-Moreno 2003; Averill et al. 2014), suggesting that AM-associated trees might be subject to relatively stronger N limitations in the study area. This might explain why AM-associated trees allocated relatively more C to belowground components, resulting in a relatively lower ratio of aboveground C pool to belowground C pool.

We also found that biological and abiotic factors were correlated to tree aboveground and belowground C allocation and correlations varied with mycorrhizal type, suggesting that mycorrhizal fungal types could influence tree abilities to adapt to future environmental change. Previous studies confirmed that AM fungi could alleviate the negative consequences of rainfall variability via increased water use efficiency (Mohan et al. 2014; Delavaux et al. 2017). Increased water uptake in AM-associated trees can be accomplished by using AM fungal

structure and function (Maurel et al. 2015; Bennett and Classen 2020). MAP ranged from 110 to 1108 mm in the study area, and the maximum annual precipitation should be still less than the maximum water demand of trees (Knapp et al. 2017). Thus, MAP should have a positive relationship with tree growth and C accumulation. Based on the optimal partitioning theory (Gedroc et al. 1996; Shipley and Meziane 2002), due to AM fungi improving tree water uptake, trees can allocate relatively more C to aboveground components rather than belowground components, which can explain why the AM-RAB was positively associated with MAP. Meanwhile, AM fungi have a wider temperature tolerance, which can promote host root tolerance to warming (Antunes et al. 2011). In high-latitude forest types, warming can promote tree growth (García-Valdés et al. 2020). AM fungal temperature tolerance could promote host root nutrient absorption, thus AM-associated trees can allocate relatively more C to aboveground components rather than belowground components with warming, which can explain why AM-RAB is positively associated with MAT. Nevertheless, EM fungi have a narrower climate niche than AM fungi, including lower temperature valence and narrower precipitation valence (Větrovský et al. 2019). The narrower climate niche of EM fungi indicates that its associated trees might have to respond to climate change challenges by shifting their physiology (Větrovský et al. 2019), which might lead to a negative relationship between EM-RAB and MAT and MAP. However, due to the different adaptability of AM-associated trees and EM-associated trees to climate change, AM-associated trees may partially replace EM-associated trees in future climate change scenarios (e.g., warming, Jo et al. 2019), which will lead to less aboveground C allocation, more belowground C allocation and change the C cycle of the entire forest ecosystem. Our results also showed that C allocation of AM-associated trees is more strongly tied to climate factors than C allocation of EM-associated trees, suggesting that C allocation in AM trees may be more affected by global change than EM trees (Jo et al. 2019; Steidinger et al. 2019). Moreover, nitrogen (N) deposition is rapidly and profoundly altering and increasing soil N availability (IPCC 2013). It is generally believed that EM-associated trees responded to N enrichment by decreasing their investment in N-acquisition enzymes (Midgley and Phillips 2016). However, in fact, fungal biomass and functional responses to N inputs probably depend on ecosystem phosphorus status (Lilleskov et al. 2019). According to 'optimal partitioning theory' (Gedroc et al. 1996; Shipley and Meziane 2002), N deposition-induced P limitation may increase the belowground C allocation of EM-associated trees that enhances the uptake of the

limiting factor, which can partly explain the negative relationship between N deposition and the ratio of aboveground C to belowground C of EM trees. AM fungi can better access immobile soil phosphorus and transfer large quantities of phosphorus to the host than EM species (Soudzilovskaia et al. 2019). Thus, AM symbiosis could better facilitate tree aboveground growth under N deposition that increases soil N availability, which can partly explain the positive relationship between N deposition and the ratio of aboveground C to belowground C of AM trees. As mentioned above, an increase in MAT and MAP might increase AM-RAB and reduce EM-RAB. In general, AM-associated trees or EM-associated trees aboveground and belowground C allocation pattern responses to these abiotic factors were through the specific function of different symbiotic fungi. Further work is necessary to evaluate the immediacy of the different mutualistic tree symbiont's C allocation patterns response to these abiotic factors.

We further found that the relationship between tree aboveground and belowground C allocation and species richness also varied with mycorrhizal association. Species richness and AM-associated tree species richness strongly positively correlated with AM-RAB and negatively correlated with EM-RAB, suggesting that increases in species richness and AM-associated tree species richness could promote AM-associated trees to allocate relatively more C to aboveground parts and EM-associated trees to allocate relatively more C to belowground parts. Previous studies found that AM tree species showed a stronger conspecific inhibition effect than EM tree species at multiple spatial scales (Bennett et al. 2017). Thus, an increase in AM-associated tree species richness with crown complementarity and crown plasticity increase might enhance AM-associated tree aboveground growth (Bachelot et al. 2017; Kunz et al. 2019), which might explain the positive relationship between AM-RAB and AM-associated tree species richness. In the same area, high AM-associated tree species richness enhances AM fungal diversity and belowground hyphal networks, providing AM species-specific benefits and suppressing superior competitors (e.g., EM-associated tree species) (Tedersoo et al. 2020). To improve the competitiveness of soil resources, EM-associated trees might allocate relatively more C to the belowground parts with the increase in AM-associated tree species richness, which could partly explain the negative relationship between EM-RAB and AM-associated tree species richness. These results demonstrate that mycorrhizal-associated species richness can mediate shifts in tree aboveground

and belowground C allocation patterns, while the relevant mechanism is still unclear and needs to be further studied.

However, there are still several imperfections in this study. First, the belowground allocation from the allometric equations is likely assessing coarse root biomass, not fine (absorptive) root biomass. Thus, it is uncertain if the relationships discussed between RAB and nutrient acquisition truly hold. Second, the use of a single set of allometric equations for each species at all sites where they occur also possibly confounds the effects of MAT and MAP. Since the same allometric equation is used for a species wherever it occurs, the results cannot show within-species effects. Third, a large number of previous studies have shown that N deposition affects plant C allocation (Schulte-Uebbing and de Vries 2018), which is consistent with our findings. But, for many of the larger, older trees, much of the biomass that is currently contributing to their RAB may have been formed when N deposition was much lower. To accurately estimate the effects of N deposition on tree RAB, it may be necessary to construct specific allometric equations for trees under different levels of N deposition (Ibanez et al. 2016).

Conclusions

To summarize, our results provide evidence that the tree aboveground and belowground C allocation pattern was correlated with mycorrhizal associations. AM fungi promoted the associated trees to invest relatively more C in belowground parts, while EM fungi had the opposite effect, suggesting that variation in mycorrhizal fungal type might cascade aboveground and belowground to alter tree-species-specific C allocation patterns and affect forest ecosystem C cycling. Meanwhile, environmental factors were correlated with tree aboveground and belowground C allocation, and the correlations varied with mycorrhizal type, suggesting that symbiotic mycorrhizal fungi could influence associated tree species abilities to adapt to future environmental change. However, although we identified symbiotic mycorrhizal fungi-mediated tree C allocation patterns, the mechanisms of mycorrhizal fungi causing different tree C allocation remain poorly understood. Given our results and the important role of mycorrhizal fungi in forest ecosystems, additional experimental and field studies targeting the factors that affect the exchange of nutrients and C in trees-mycorrhizal symbioses are needed to better understand the mechanisms underlying trees C allocation and forest ecosystem C cycling.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s13717-023-00440-1>.

Additional file 1: Table S1. Range of values for all parameters, and all the time of data measurements and a number of sampling plots were shown. **Table S2.** Main allometric equations for tree biomass estimation in this study. Allometric equations were established for different organs of each tree species. The applicable DBH range of each equation is shown. **Table S3.** Total effects, direct effects, and indirect effects of different factors in the ratio of aboveground C storage to belowground C storage. **Fig. S1.** Ratio of aboveground C to belowground C of EM-associated tree and AM-associated tree at an individual level. *** indicates a significant difference within the group.

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Author contributions

QW and YX designed the study, got grants from the foundation, supervised data collection and edited the manuscript. QW, GY and YX contributed to the whole manuscript preparation and design and wrote the main manuscript text. GY, QW and YX prepared all figures, GY, QW, YX, XL, GL and HW prepared field experiments, prepared tables and collected literatures. All authors read and approved the final manuscript.

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Availability of data and materials

Data are available from the corresponding author upon reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no conflict of interest.

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