Warming effects on biomass allocation are jointly regulated by precipitation and mycorrhizal association in terrestrial plants

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Article

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Abstract

Biomass allocation in plants is fundamental for understanding and predicting terrestrial carbon storage. Recent studies suggest that climate warming can differentially affect root and shoot biomass, and subsequently alter root: shoot ratio. However, warming effects on root: shoot ratio and their underlying drivers at a global scale remain unclear. Using a global synthesis of >300 studies, we here show that warming significantly increases biomass allocation to roots (by 13.1%), and two factors drive this response: mean annual precipitation of the site, and the type of mycorrhizal fungi associated with a plant. Warming-induced allocation to roots is greater in relatively drier habitats compared to shoots (by 15.1%), but lower in wetter sites (by 4.9%), especially for plants associated with arbuscular mycorrhizal fungi compared to ectomycorrhizal fungi. Root-biomass responses to warming predominantly determine the biomass allocation in terrestrial plants suggesting that warming can reinforce the importance of belowground resource uptake. Our study highlights that the wetness or dryness of a site and plants’ mycorrhizal associations strongly regulate terrestrial carbon cycle by altering biomass allocation strategies in a warmer world.

Introduction

Root: shoot ratio (R/S) or the ratio between below- and aboveground plant biomass (BGB and AGB) is a key parameter for estimating terrestrial ecosystem carbon (C) storage, which is regulated by plant development in relation to the availability of above- and belowground resources. Global change-induced alteration of resource supply may cause a disproportional allocation of dry matter between roots and shoots of terrestrial plants. For example, drought and elevated CO\textsubscript{2} generally enhance the allocation of root biomass over shoot biomass for acquiring both water and nutrients, whereas increased precipitation and nitrogen deposition usually elevate shoot biomass allocation for increased competition for light. Climate warming has also been shown to affect net primary production in terrestrial ecosystem, such as by increasing biomass production, which is further shown to trigger higher demands for resources by plants. Accordingly, warming effects on R/S may depend on temperature effects on resource supply, which makes it challenging to predict warming effects on plant’s biomass allocations, particularly at a global scale.

Given the coupled hydro-thermal processes and dependence of belowground resource availability on soil water content for plant growth, antecedent precipitation and temperature are key factors for predicting R/S’ response to on-going climate warming. However, whether the long-term natural patterns between R/S and climatic factors (e.g., temperature or precipitation) conform to immediate R/S’ response to a warmed environment remain unknown. Apart from local climate, belowground properties of ecosystem (e.g., nutrients, root traits, and root-soil interface) can further influence the response of R/S to warming. For instance, the mutualistic symbiosis between root and mycorrhizal fungi (MF), which are universally present in terrestrial ecosystems, might affect patterns of plant carbon allocation depending on different nutrient foraging strategies of mycorrhizal root systems. Plants with the same
mycorrhizal association generally act in ecologically similar ways in the face of changing environments, especially to alteration of resource availability in soils\textsuperscript{21}. As two major types of mycorrhizas, arbuscular mycorrhizal fungi (AMF)’s hyphae penetrate the cell wall and invaginate the cell membrane within the host plant root, while ectomycorrhizal fungi (EMF)’s hyphae do not penetrate individual cell. AMF increase host-plant’s uptake of inorganic nutrients, while EMF provide greater access to organic nutrient pools in the soil\textsuperscript{22,23}. Biomes with different dominance of mycorrhizal fungal types (MFTs) could therefore differ in biomass allocation belowground, which could potentially determine warming-induced shifts in R/S in different biomes\textsuperscript{20,24,25}.

Here, we propose two potential hypotheses for a better understanding of how biomass allocation in response to warming would alter the distribution of terrestrial carbon at a global scale\textsuperscript{26}. First, biomass allocation between above- and belowground compartments of plants may differ due to warming. Using a quantitative global synthesis, we test this hypothesis by examining how the intercept between R/S at warmed temperature and R/S at ambient temperature deviates from 0- we refer this to as a shift in vertical biomass allocation in terrestrial plants (Figs. 1a and b). For instance, when this intercept >0, it would imply greater biomass is allocated downwards (i.e., vertically), meaning that there will be a greater R/S under warming than that at ambient temperature (Figs. 1a and b). Second, warming can homogenize R/S across the biomes. To test this, we examine how the slope between R/S at warmed temperature and R/S at ambient temperature (as a proxy of biomes) deviates from 1 - we refer this to as a shift in horizontal variability of R/S in terrestrial plants across biomes (Figs. 1c and d). For instance, when this slope < 1, it would imply that warming decreases the horizontal variability of R/S, and indicate homogenization of R/S among diverse biomes due to warming (Fig. 1c and d). To test these hypotheses, we collected 322 warming experiments with 93 pairs of observations to explore the effect of warming on R/S (Figs. S1 and S2). Our results show that warming increases R/S (intercept >0) and decreases the variability of R/S among biomes (slope<1, Fig. 1e). We further show how climatic context and mycorrhizal associations explain these patterns of R/S in terrestrial plants at the global scale.

**Results**

On average, warming significantly increased root: shoot ratio (R/S) by 6.7% with the confidence interval (CI) of intercept of 0.044-0.107 (Fig. 1e), which was significantly larger than 0 (\(p<0.05\)), agreeing with the assumption of more biomass allocation to roots in vertical dimension in warmed environments. Meanwhile, the variability of R/S among diverse biomes decreased with the CI of slope of 0.908-0.997 (Fig. 1e), which was significantly lower than 1 (\(p<0.05\)), conforming to the assumption of horizontal homogenization of R/S under warmer condition. Overall, warming also enhanced total biomass (TB, +10.0%) mainly by increasing belowground biomass (BGB, +13.1%), but not the aboveground biomass of plants (AGB, -8.9%, \(p>0.05\), Fig. S2).

At the global scale, mean annual precipitation (MAP) was the most important factor in determining the warming effects on R/S [i.e., response ratio (\(RR\) of R/S, \(RR(R/S)\)] relative to all other predictors (Fig. 2).
We found that MAP was negatively correlated with $RR(R/S)$ ($R^2=0.104$, Figs. 2 and 3). Moreover, the weighted $RR(R/S)$ reversed from positive to negative in sites higher than 900 mm MAP (Figs. 3 and 4). However, the sensitivity of $RR(R/S)$ to MAP (i.e., the slopes in Fig. 3b, c) in biomes with ecto-mycorrhizal fungi (EMF) was smaller than those with arbuscular mycorrhizal fungi (AMF).

Mycorrhizal fungal types (MFT) was the second most important factor for explaining the warming effects on plant's R/S (Fig. 2). Warming did not change both TB and BGB of plants associated with AMF but decreased their AGB by 13.8% and subsequently increased R/S by 9.9%. Warming stimulated TB, AGB, and BGB in biomes with both EMF and AMF-EMF dominance, but only enhanced R/S for EMF (Figs. S4 and S5). In our path model, we also found that mycorrhizal fungal types (i.e., AMF, EMF, and AMF-EMF) contributed significantly in explaining 22.9% variation of AGB's response to warming, whereas plant functional types (PFT, i.e., herbs and woody plants) and MAP were the main significant pathways contributing to 25.4% of variation of BGB's response (Fig. S8). Both AGB and BGB responses to warming directly contributed (AGB negatively and BGB positively) to shifts in $RR(R/S)$ under warming with our path model explaining a total of 46.3% variation in $RR(R/S)$ at the global scale (Fig. S8). Moreover, across all studies, $RR(R/S)$ was correlated linearly with root biomass responses [$RR(BGB)$] ($R^2=0.31$, $p<0.001$, Fig. S12), but not with AGB responses ($R^2=0.01$, $p=0.392$, Fig. S12). The importance of PFTs on $RR(R/S)$ was only true in studies with a warming-induced inhibition of TB (Fig. S6).

**Discussion**

Our global synthesis show that climate warming enhances belowground biomass allocation in plants but mainly so in relatively drier habitats. Such a plant strategy can have important implications for soil carbon dynamics, due to the lower turnover rate of root-associated carbon (i.e., carbon in hyphae and root per se) in comparison with that of shoot$^{27,28}$. Specifically, our results suggest that, in areas receiving mean annual precipitation (MAP) lower than ~900 mm, warmer air and soil surface temperature could induce greater biomass allocation into roots potentially to exploit deeper soil layers, where water is more readily available and temperature is cooler (Figs. 4a and S12)$^{29}$. The long-term adaptation of plants to water deficiency, e.g., a higher water use efficiency, ensures more biomass accumulation under warmed conditions, improving an up-regulation of R/S (Fig. 4a), thereby prolonging the residence time for plant C$^{30}$. Among the sites with MAP > ~900 mm, adequate soil moisture could enable warming's positive effect on nutrient turnover and availability, e.g., soil $NH_4^+$ and $NO_3^-$ for AMF and EMF, respectively, due to their differential nutrient economy and nitrate leaching losses (Fig. 4b)$^{31}$. The belowground biomass allocation in these areas declined consequently$^{32}$, but only so for terrestrial plants associated with AMF as revealed by our synthesis (Fig. 4b).

The regulation of MAP on R/S under warmer condition was mainly through the adjustment of belowground biomass accumulation, which responded to warming-induced changes of soil moisture differently among PFTs (Fig. S3 and S8)$^{33,34}$. Woody plants, being characterized with deeper and evolutionarily mature roots$^{35}$, can redistribute soil water by process of hydraulic lift, supporting an
averaged increment in BGB under warmer condition (Fig. S8)\textsuperscript{36}. Herbaceous plants, which are characterized with evolutionarily younger roots relative to woody plants, can adjust root traits (e.g., specific root length) compared to biomass\textsuperscript{33,34}, which may have contributed to their non-significant responses in terms of BGB under warmer condition (Figs. S4 and S5). In addition to MAP, due to interaction between temperature and soil moisture, antecedent MAT was another important background climatic factor influencing the response of R/S in our global synthesis\textsuperscript{37}. For instance, MAT displayed a negative relationship with R/S due to warming-induced significant increment of AGB in most of the biomes with MAT < 13\textdegree C and ecto-mycorrhizal fungi (EMF) (Table S2)\textsuperscript{25}.

Mycorrhizal fungi also regulated biomass allocation patterns of terrestrial plants in our global synthesis. Although both AMF- and EMF- plants exhibited an average increase in R/S in total, the underlying mechanisms were different (Figs. 4 and S4). Benefiting from hydrolytic and oxidative extracellular enzymes produced by the hyphae of ecto-mycorrhizal fungi\textsuperscript{38}, EMF are capable for growing better under nutrient-deficient conditions relative to AMF\textsuperscript{9,25}. EMF associated plants showing an increasing trend of AGB, BGB and R/S under warming (Fig. S5), due to hypha-facilitated soil organic matter (SOM) degradation and root nutrient absorption\textsuperscript{39}, confirms this assumption. Contrastingly, AMF are often more abundant in warmer sites (e.g., in temperate grasslands and deciduous forests) with drier soils\textsuperscript{40-42}. Although AMF enhanced the total water use efficiency under warmed conditions (WUE, Figs. S9-S11), AMF slowed down shoot biomass accumulation due to warming-induced soil water deficiency (mainly so in grasses, Fig. S3)\textsuperscript{43}. Interestingly, the regulation of MFTs on R/S responses to warming were mainly related with shoot growth but not root (Fig. S8), implying important roles of mycorrhizal associations on aboveground biomass allocation in terrestrial plants in a warmer world\textsuperscript{20,44}.

Our results provide a compelling support of the idea that MAP and MFTs together determine the shifts in R/S in warmer conditions (Fig. 3 and Fig. 4). These result provide insights for the importance of how mycorrhizal-mediated belowground resource allocation in plants could depend on soil water availability in warmer environments\textsuperscript{45}. As for biomes with both AMF and EMF (AM-EMF, Figs. 4 and S7), the complementarity of resource use (e.g., water and nutrients) between plants with arbuscular and ecto-mycorrhizal fungi provides a plausible explanation for this stability of R/S and increasing productivity in response to warming (Fig. S4)\textsuperscript{24,46}. We suspect that such differential warming effects on biomass allocation caused by local climate and mycorrhizal associations could potentially lead to a redistribution of R/S in horizontal dimension with more homogenization and lower variability of biomass allocation patterns among diverse biomes (Fig. 1)\textsuperscript{47}. Future studies are required to understand the implication of such shifts on terrestrial carbon balance.

In summary, climate warming can enhance belowground biomass allocation but mainly so in relatively drier habitats. Moreover, habitat dryness (or wetness) and types of mycorrhizal association jointly determine how R/S vary across biomes, and subsequently such variation determine R/S responses to warmer environments. We conclude that shifts in biomass allocation strategy in response to warming in
vascular plants across biomes depend on the dryness of a site and their mycorrhizal symbiosis, both of which will therefore play a central role in understanding terrestrial carbon dynamics in a warmer world.

References


**Figures**
Figure 1

Hypotheses of warming effects on root: shoot ratio (R/S, a, b, c, d) and the actual relationship between log 10- transformed R/S with experimental warming and that at ambient temperature (e). Across studies used in our global synthesis, the intercept in e was larger than 0, implying greater biomass is allocated (vertically) downwards, i.e., greater R/S under warming than that at ambient temperature (a and e); the opposite scenario of downward allocation (i.e., upward allocation, intercept smaller than zero) is illustrated in b. When the slope is smaller than 1, it would imply that warming decreased the horizontal variability of R/S, which indicate homogenization of R/S among diverse biomes due to warming as found in our synthesis (c and e); the opposite scenario of homogenization (differentiation, slope greater than 1) is illustrated in d. The size of each dot indicate relative weight of the individual response ratio of R/S.
Figure 2

Model-averaged importance of various predictor variables for warming effects on root: shoot ratio [RR (R/S)]. The variables with importance value >0.8 were considered as essential predictors. The importance value of predictor is based on the sum of Akaike weights derived from model selection using corrected Akaike's information criteria. MFT, mycorrhizal fungal types; PFT, plant functional types; MAP, mean annual precipitation; MAT, mean annual temperature; LAT, latitude; CLAY, the proportion of clay in soil; BD, bulk density; SOC, soil organic carbon; WM, warming magnitude; DUR, warming duration.
Figure 3

Correlations of mean annual precipitation (MAP, mm) with (log) response ratio (RR) of root: shoot ratio (R/S). The correlation in plot a and b are based on total studies (a), and biomes with dominant root symbiosis of arbuscular mycorrhizal and ecto-mycorrhizal fungi (AMF and EMF, b), respectively. The size of the data points indicate relative weights in each plots.
Figure 4

Illustration of our main finding of warming effects on total biomass (TB), above- and belowground biomass (AGB and BGB), and root: shoot ratio (R/S). The plot a and b reflects biomes with low mean annual precipitation (MAP) irrespective of mycorrhizal association (a), and those with high MAP and arbuscular mycorrhizal (AMF) or ecto-mycorrhizal fungi (EMF) (b). MB, microbial biomass; MB C/N, microbial biomass C/N; SIN, soil inorganic nitrogen; WUE, water use efficiency; the up- and down-ward arrows indicated significant increment and decrement of a variable at $P < 0.05$, while “ns” indicated non-significant changes under warming condition. “~” corresponds to no change, and “?” indicates not known.

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