



Biomass carbon stock and allocation of planted and natural forests in the Loess Plateau of China

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ABSTRACT

Establishing planted forests (PF) by afforestation and naturally regenerating forests (NF) are important measures of enhance carbon (C) sequestration in terrestrial ecosystems. However, the difference of biomass C stocks and allocation between NF and PF and their determinants in water-limited areas remain unclear. To address this gap, we conducted a synthesis of above-ground biomass C (AGBC), below-ground biomass C (BGBC) stocks and root to shoot ratios (R:S) of PF and NF in the Chinese Loess Plateau. The changes in biomass C stock and R:S along a climate gradient were investigated, and the relationships between R:S and soil properties were also quantified. We found that PF exhibited lower AGBC and BGBC stocks compared to NF, but the average R:S in PF was significantly higher than that of NF (0.48 ± 0.27 vs. 0.30 ± 0.11 , $p < 0.05$). Turning points existed in biomass C allocation along climatic gradient for both PF and NF. More biomass C was allocated to AGBC in PF and NF when mean annual precipitation exceeded 494 mm and 588 mm, respectively. Higher mean annual temperature promoted larger C allocations to BGBC in PF compared to NF. Soil properties had a stronger effect on the biomass C allocation patterns after afforestation, but to a lesser extent on NF. This study indicates that afforestation promotes a larger allocation of biomass C into the below-ground compared to naturally regenerated forests, and using the default R:S estimates may result in a severe underestimation of below-ground C stocks in water-limited areas. The biomass C stocks and allocation are collectively determined by climate conditions and soil properties, and accumulated below-ground biomass C stock induced by dryland afforestation may be an important C sink at a broad geographic scale.

1. Introduction

Forests account for 92 % of all terrestrial biomass (Pan et al., 2013), holding about 80 % of the global total above-ground biomass carbon (AGBC) stock and 40 % of below-ground biomass C (BGBC) stock (Dixon et al., 1994). Therefore, forests play a key role in regulating global climate (Qubaja et al., 2020; Le Noë et al., 2021). These and other statistics indicate that tree species on average disproportionately allocate more biomass to their above-ground body parts (i.e., leaves, stems, and reproductive organs) compared to their below-ground body parts (i.e., root systems) (Niklas, 2004, 2005; Reich et al., 2014). This biomass is

often used as a proxy for C content, although the actual C content can vary between above- and below-ground biomass. This tendency is subjected to various intrinsic and extrinsic factors influencing C allocation (Levy et al., 2004; Yang and Luo, 2011; Liu et al., 2014), i.e., forest species composition, climate, and soil properties. The general lack of knowledge on forest biomass C allocation is critical to the accuracy of global C cycle modeling and predicting (Spawn et al., 2020).

Primarily because of The Bonn Challenge (www.bonnchallenge.org), the interest in C accounting has been focused on planted forests (PF) and naturally regenerated forests (NF) (Pugh et al., 2019; Yu et al., 2019). Establishing plantations on abandoned or degraded agricultural lands

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has been recommended as an effective measure to reduce atmospheric CO₂ globally or regionally (Cao and Chen, 2017). However, recent studies have challenged the effectiveness of PF in this respect (Hua et al., 2022; Lewis et al., 2019), by emphasizing that NF exhibit higher C sequestration than PF, such that expanding NF to store C, instead of planting more trees, may be a more effective way to mitigate climate warming (Lewis et al., 2019). One of the reasons for this controversy is that the differences in the biomass C changes and its allocation between PF and NF are not well documented, particularly in water-limited areas. Yet, the data show that more than one-fifth of global drylands are covered by forests (1.1 billion hectares, about 27 % of the world's forest area) (Patriarca et al., 2019), indicating that forest biomass C and its allocation patterns in water-limited areas may have a significant effect on global C assessment or C cycling.

Root to shoot ratios (R:S) have been used as one effective method to gain a greater understanding of biomass allocation and to explore the relationship of C allocation between roots and shoots (Cairns et al., 1997; Mokany et al., 2006; Ye et al., 2021). As forests play an increasingly important role in reducing CO₂ due to increasing global warming, R:S has become a key metric for accurately assessing forest C sequestration (Ye et al., 2021; Guo et al., 2022). Up to now, studies on forest R:S have been conducted at the stand scale, watershed, regional, and global scales (Cairns et al., 1997; Huang et al., 2021; Luo et al., 2012; Marziliano et al., 2015; Ma et al., 2021). However, debate continues about whether R:S varies with intrinsic (e.g., forest type) or extrinsic factors (e.g., climate or soil properties) (Levy et al., 2004; Wang et al., 2008; Yang and Luo, 2011; Liu et al., 2014). For example, the Isometric Partitioning Theory (IPT) proposes that the logarithm of above-ground biomass (AGB) scales one-to-one with the logarithm of below-ground biomass (BGB) across a diverse range of forest types and tree species (Enquist and Niklas, 2002; Niklas, 2005, 2006; Zhang et al., 2016). In contrast, Optimal Partitioning Theory (OPT) proposes that biomass allocation is flexible, allowing plants to optimize resource acquisition, depending on which resource is most limiting at given point in time (Chave et al., 2014). OPT has been supported by evidence from several empirical studies (Ledo et al., 2017; Reich et al., 2014). These theories are not mutually exclusive because the magnitude and direction of forest biomass allocation are affected by multiple factors at different regions, because intraspecific scaling relationships may have different scaling exponents, and because scaling relationships with the same scaling exponents can have different normalization constants (Niklas, 2004). To the best of our knowledge, no systematic study has investigated the dynamics of forest biomass C allocation (PF and NF) in water-limited areas. This knowledge gap engages current debates on whether forests in water-limited areas have the potential to effectively mitigate climate change (Rohatyn et al., 2022; Hanan et al., 2021).

In the arid and semi-arid Chinese Loess Plateau, long-term agricultural exploitation has led to intense ecological degradation, and it is one of the most severely eroded regions in the world due to human activities (Zhang et al., 2021). In 1999, China launched the “Grain for Green” project (converting croplands into grasslands, planted shrubs, or planted forests), one of the world's most ambitious conservation set-aside projects (Li et al., 2021a), and the nation's largest ecological restoration project (Deng et al., 2014). It is reported that the total area of forest increased in the Loess Plateau from 8.19 % to 15.82 % with an increment of 48,786 km² during 2001–2016 (Wang et al., 2018). This large-scale land-use change has profoundly altered forest C stocks and allocation patterns over a large region. However, there have been few comprehensive investigations of the changes in forest biomass C stocks and allocation over this large region despite many observations made at the local level (Cao and Chen, 2017; Gao et al., 2014; Li and Liu, 2014; Wang et al., 2016; Yang et al., 2019; Zhang et al., 2018). Several studies compared the differences in biomass C stocks and allocation between PF and NF at the plot scale (Cao and Chen, 2017; Gao et al., 2014; Song et al., 2016). However, it is also necessary to understand how the C allocation pattern in PF and NF respond to climate factors and soil

properties at the regional scale. Such understanding can provide valuable insights into the long-term impacts of the “Grain for Green” project on forest C sequestration in the Loess Plateau and guide future conservation and restoration efforts.

In this study, the Loess Plateau was selected as a representative research area to investigate and compare changes in biomass C stock and allocation patterns in NF and PF in water-limited areas. The objectives of this study were to (1) quantify the differences of biomass C stocks and R:S between NF and PF; (2) explore the general patterns of biomass C stocks and allocation along a climatic gradient; and (3) determine the relationships between R:S and climate and soil factors. We also compared the data drawn from the Loess Plateau with the global mean data (for example, Ma et al., 2021) to discuss the effects of afforestation on biomass C stock and allocation among different regions. By focusing on the Loess Plateau as a case study, we aimed to contribute valuable insights into the dynamics of forest biomass C stock changes and allocation in water-limited areas and its implications for global C sequestration and climate change mitigation.

2. Materials and methods

2.1. Study area

The Loess Plateau is situated in the arid and semi-arid regions of North China (Fig. 1), covering an area of 640,000 km², and sustaining a population over 108 million people. Recognized as one of the largest and thickest loess plateaus globally (Kapp et al., 2015), the Loess Plateau has an average thickness of 105.7 m (Zhu et al., 2018). Its distinctive features include severe soil erosion and water scarcity due to limited rainfall, the high erodibility of loess soils, low vegetation cover, and significant human intervention (Jiang et al., 2017; Lu and Stocking, 2000). Consequently, the Loess Plateau is ecologically vulnerable, facing mounting challenges from climate change and human activities. Ongoing efforts on enhancing ecological functions were achieved through the implementation of the “Grain for Green” project and “Natural Forest Protection” within the Loess Plateau. Over the past few decades, extensive areas of degraded croplands have been transformed to PF, leading to substantial changes in ecosystem structure and the C stocks. Presently, the forested area in the Loess Plateau has expanded by approximately 50,000 km², with the existing forest area reaching about 123,700 km², accounting for 20 % of the total area. The proportion of PF and NF stands at around 60 % and 40 %, respectively (Wang et al., 2018). Consequently, the Loess Plateau offers an ideal platform to investigate the alterations in biomass C stocks and allocation between dryland NF and PF under long-term anthropogenic perturbations, ranging from degradation to restoration.

In the Loess Plateau, NF mainly consists of deciduous broadleaf forests, with the climax vegetation being the *Quercus liaotungensis* forest (Deng et al., 2013). Regarding PF, the restoration of the degraded land involves the native and exotic species. Native species utilized for afforestation include *Pinus tabulaeformis*, *Platycladus orientalis*, *Prunus armeniaca*, *Larix principis-rupprechtii*, *Ulmus pumila*, and *Prunus davidiana*. Additionally, exotic species such as *Robinia pseudoacacia*, *Populus simonii* and *Populus bolleana* were also used in afforestation efforts (Peng and Coster, 2007). Among all these tree species, *Robinia pseudoacacia* is extensively distributed in the region due to its exceptional drought resistance and rapid growth characteristics (Liang et al., 2018).

2.2. Data collection

An extensive literature search was conducted to gather data on forest biomass C stocks in the Loess Plateau. Specifically, we utilized two prominent databases, the Clarivate Web of Science (www.webofscience.com) and China National Knowledge Infrastructure (www.cnki.net), with the keywords, “afforestation” or “forest”, “carbon”, and “Loess Plateau” between 1988–2021. We followed the PRISMA standards to

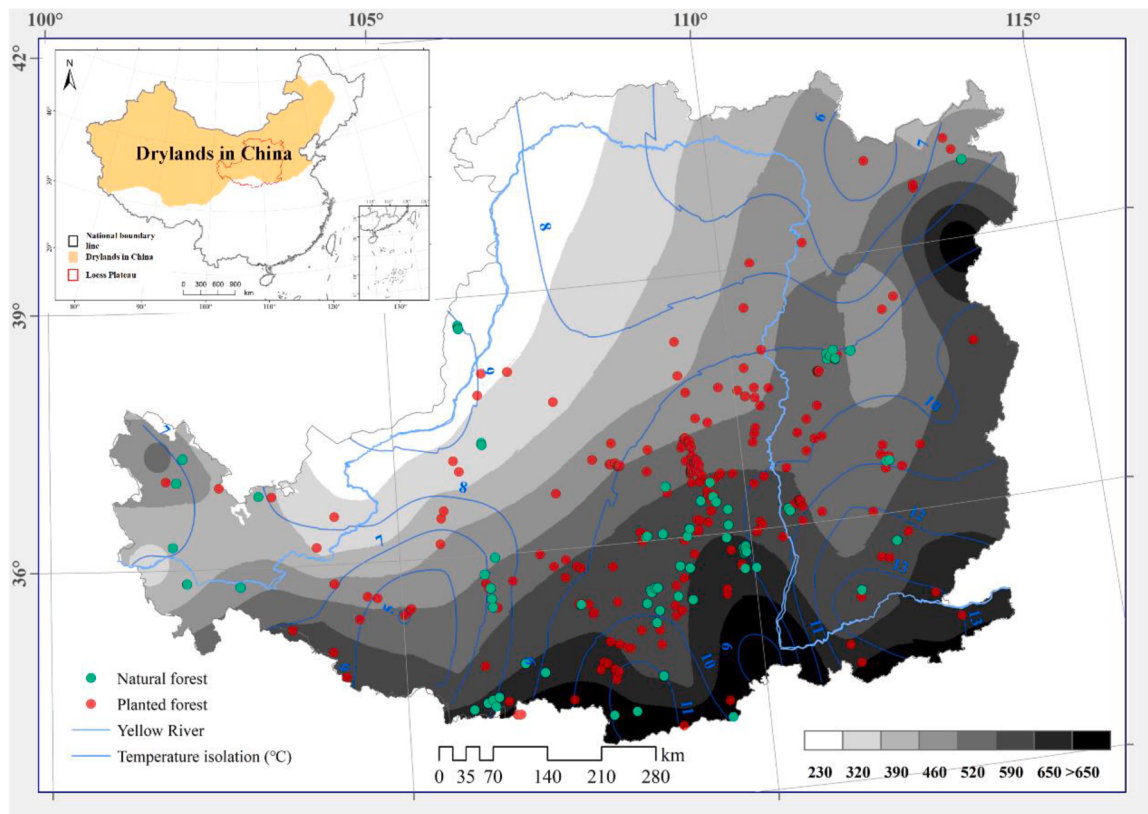


Fig. 1. The spatial distribution of sampling points for planted forest and natural forest in the Loess Plateau.

sort through papers and identify studies. Initially, we conducted a preliminary search using keywords, resulting in 357 identified literatures, including journal paper and dissertation. Following this, we performed a preliminary screening based on titles and abstracts, resulting in 208 relevant literatures. Among these studies, some authors employed the “soil pit” method to estimate root biomass, where several soil pits were excavated within the plot to measure root biomass, and the biomass in the plot was estimated based on the plot’s area and the soil pits. However, it was observed that in most studies using the “soil pit” method, the root crown was not included during root sampling (Wang et al., 2008), leading to a significant underestimation of root biomass (Mokany et al., 2006). As a result, all root biomass data using the “soil pit” method were excluded. Additionally, we excluded studies derived from plot culture experiments or model simulations to ensure a consistent dataset. Therefore, we conducted a full-text review and further filtered the literatures, ultimately retaining 108 literatures conducted at the plot or slope scale that provided clear and relevant information on the two forest types (PF and NF). The detailed PRISMA flow diagram for sorting through literature was shown in Figure S1. The detailed information of the 108 literatures was listed in Table S1. The sampling points of these literatures were widely distributed in the Loess Plateau (Fig. 1). For these selected studies, raw data were obtained either directly from tables or by extracting data points from graphs using the GetData Graph Digitizer (version 2.24). This approach ensured the accuracy and reliability of the data used in our analysis.

For each paper, a comprehensive dataset was compiled, encompassing various aspects of the research. This dataset included publication details such as authorship and journal, geographic location specified by longitude and latitude coordinates, mean annual precipitation (MAP), mean annual temperature (MAT), forest types (PF or NF), forest age, mean tree diameter at breast height (DBH) and tree height, stand density, AGBC, BGBC, as well as soil organic carbon (SOC), soil total nitrogen (TN), soil moisture (SM), soil total phosphorus (TP), and

soil microbial biomass C (MBC). The data for SOC, TN, TP, and MBC were collected down to a maximum depth of 100 cm in the soil. In this study, the MBC was utilized as an indicator to describe the potential nutrient availability (Cai et al., 2018). Considering that SM in the deep soil layer significantly influences vegetation productivity in the Loess Plateau (Huang and Shao, 2019), we extended the data collection for SM beyond the upper 100 cm to a maximum depth of 500 cm, with a primary focus on SM variations in PF and NF. Detailed information regarding the data collection of SM is described in a previous study (Li et al., 2021b).

To enhance the reliability of the comparison between PF and NF, we have also screened the paired data of PF and NF from the database. During the selection process, studies were included if they contained data for both PF and NF within the same study area. For studies that provided data for either PF or NF alone, we considered their geographic locations. Specifically, studies were included if the distance between the locations of PF and NF plots did not exceed 10 km. This 10 km criterion was established to ensure that the paired locations share similar climatic and soil conditions, thus providing a robust basis for comparative analysis. Seven paired data of PF and NF were identified in the Loess Plateau (Figure S2).

2.3. Calculation of biomass C stock and allocation

We recorded all estimates of dry biomass (Mg ha^{-1}) or C stored per unit area (Mg C ha^{-1}) in total AGB, or BGB of both PF and NF. Notably, it has been reported that the C stocks in understory vegetation in the Loess Plateau only account for 0.06–3.45 % of the C stocks in the whole ecosystem (Cao and Chen, 2017). Therefore, the C stocks in understory vegetation were not considered in this study. In cases where studies did not report dry biomass per unit area, the above-ground biomass (including stem, branch, leaf, and bark) and below-ground (including root) were estimated using the DBH (and tree height) with the biomass

allometric growth models (BAGM) in the Loess Plateau. These site and species-specific BAGMs at different climate zones were developed by previous studies in the region (Li and Liu, 2014; Wang, 2006; Yang et al., 2019). Since most of the BAGM results are on a per plant biomass (g or kg) basis, the stand density (plants per ha) was used to convert the results into unit biomass (Mg ha^{-1}). For studies that only reported dry biomass per unit area, the AGBC stock and BGBC stock were obtained by multiplying AGB and BGB with C fraction, respectively. To improve accuracy, we estimated the C fraction based on the coefficient related to the C content in stems, branches, leaves, bark, or roots, rather than using a common constant, e.g., 0.45 (Song et al., 2020). Specifically, the root to shoot ratio (R:S) was calculated as $R:S = \text{BGB}/\text{AGB}$, where BGB is the below-ground biomass (Mg ha^{-1}) and AGB is the above-ground biomass (Mg ha^{-1}).

2.4. Data analysis

Before data analysis, we examined the spatial autocorrelation among the sample points using the spatial autocorrelation (Moran I) analysis within the ArcToolbox. To test for differences in AGBC, BGBC stock and R:S between PF and NF, we employed the Kruskal-Wallis rank sum test, performed using the *kruskal.test* function in R (De Mendiburu, 2014). Differences were considered significant at $p < 0.05$. The Kruskal-Wallis test is analogous to a one-way ANOVA but is applicable when one or more samples have a limited number of observations and the data are not normally distributed.

To examine the possible nonlinear relationships of biomass C stock and allocation (AGBC, BGBC, and R:S) with climatic factors (MAP and MAT) and soil properties, a piecewise regression model was selected. Piecewise regression models can elucidate the relationships between the response variable and one or more explanatory variables using two or more straight lines connected at unknown values, often referred to as turning points, change points, or join points (Toms and Lesperance, 2003).

3. Results

3.1. Biomass C stock and allocation of planted and natural forests

In total, the final database comprised 2009 observations for AGBC, 1992 observations for BGBC, and 1987 observations for R:S at the plot scale. The Moran I index for the PF and NF sampling points had a p -value of 0.17 and 0.47, respectively, indicating that the spatial autocorrelation among the sample points is relatively low. Additionally, there were 1295 observations for SOC, 980 for TN, 647 for TP, and 428 for MBC within a depth of 100 cm, which corresponded to forest biomass C data. Furthermore, a total of 1800 observations for SM within the 500 cm soil profile were collected, distributed as follows: 513 observations for the 0–100 cm layer, 433 for 100–200 cm layer, 358 for 200–300 cm layer, 320 for 300–400 cm layer, and 306 for 400–500 cm layer.

Based on this database, NF had overall higher C stocks in both AGB and BGB compared to PF (Figs. 2a and b; $p < 0.05$). Specifically, the AGBC stocks of NF and PF were 49.5 ± 36.0 and $22.0 \pm 23.3 \text{ Mg C ha}^{-1}$ (means $\pm$ standard deviations), respectively (Fig. 2a), whereas the BGBC stocks were 12.1 ± 6.8 and $7.7 \pm 7.7 \text{ Mg C ha}^{-1}$, respectively (Fig. 2b). Nevertheless, the proportion of BGBC stocks in PF (25.8 %) was higher than that in NF (19.6 %) (Figure 2b; $p < 0.05$), which was consistent with the R:S values, i.e., the R:S in PF (0.48 ± 0.27) was about 1.6 times higher than that in NF (0.30 ± 0.11) (Fig. 2c).

3.2. Biomass C stock and allocation along climatic gradient

Along precipitation gradients, the AGBC stocks of PF initially decreased at a rate of $-0.12 \text{ Mg C ha}^{-1} \text{ mm}^{-1}$ ($p < 0.05$) and subsequently increased at a rate of $0.13 \text{ Mg C ha}^{-1} \text{ mm}^{-1}$ ($p < 0.001$), with a turning point at 460 mm, whereas that of NF initially decreased at a rate of

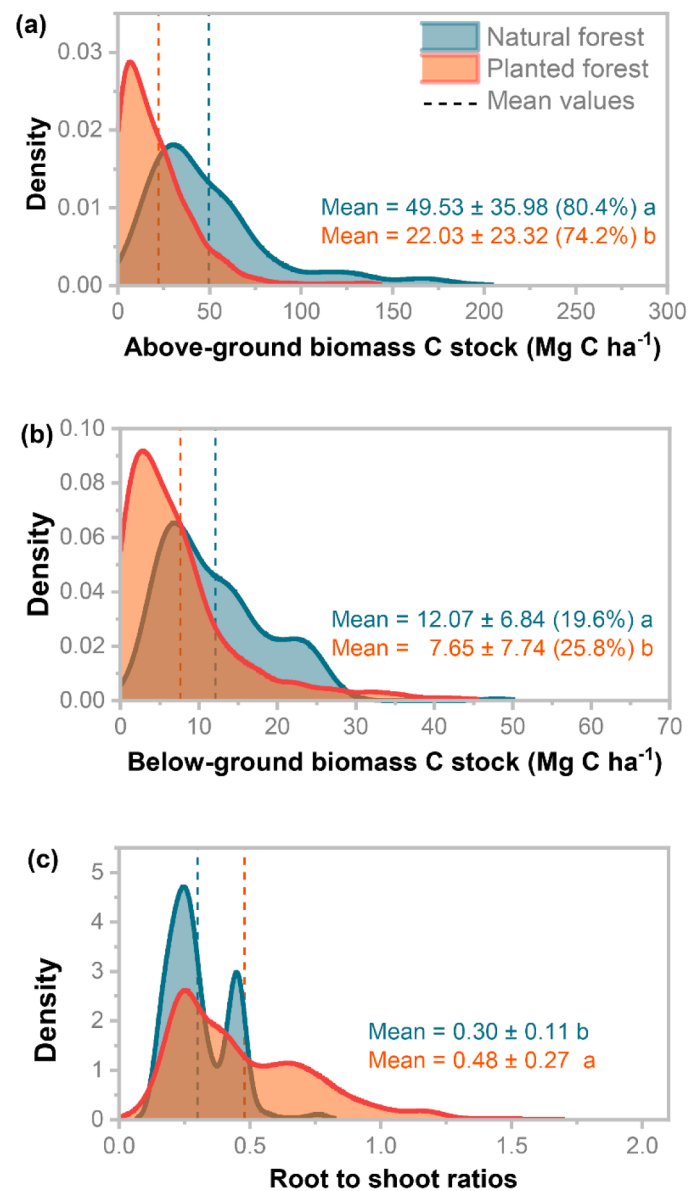


Fig. 2. The density distribution of (a) above-ground biomass C stock, (b) below-ground biomass C stock, and (c) root to shoot ratios of planted forests and natural forests in the Loess Plateau. Numbers indicate represents the mean $\pm$ standard deviation; The percentages in parentheses represent the proportion of C stocks in above-ground biomass and below-ground biomass of planted forests and natural forests with respect to their respective total C stocks. Different lower-case letters denote the significant difference ($p < 0.05$) between planted forests and natural forests.

$-0.10 \text{ Mg C ha}^{-1} \text{ mm}^{-1}$ ($p < 0.05$) and subsequently increased at a rate of $0.23 \text{ Mg C ha}^{-1} \text{ mm}^{-1}$ ($p > 0.05$), with a turning point at 676 mm (Fig. 3a). In addition, the BGBC stocks of PF showed similar trends with that of AGBC but with different rates and turning points. The changes of BGBC stocks in NF were insensitive to MAP (Fig. 3b). The R:S of both PF and NF initially increased and subsequently decreased along precipitation gradients, with turning points at 494 mm and 588 mm, respectively (Fig. 3c). When exceeding the turning points, the sensitivity of R:S to MAP in PF was about 2.33 times that in NF (-0.0014 mm^{-1} vs. -0.0006 mm^{-1}) (Fig. 3c).

Along temperature gradients, the C stocks in AGB and BGB of PF increased linearly at the rates of $2.41 \text{ Mg C ha}^{-1} \text{ }^{\circ}\text{C}^{-1}$ ($p < 0.001$) and $1.58 \text{ Mg C ha}^{-1} \text{ }^{\circ}\text{C}^{-1}$ ($p < 0.001$), respectively (Fig. 3d and e). The AGBC stock in NF initially decreased at rate of $-6.33 \text{ Mg C ha}^{-1} \text{ }^{\circ}\text{C}^{-1}$ ($p < 0.001$) with

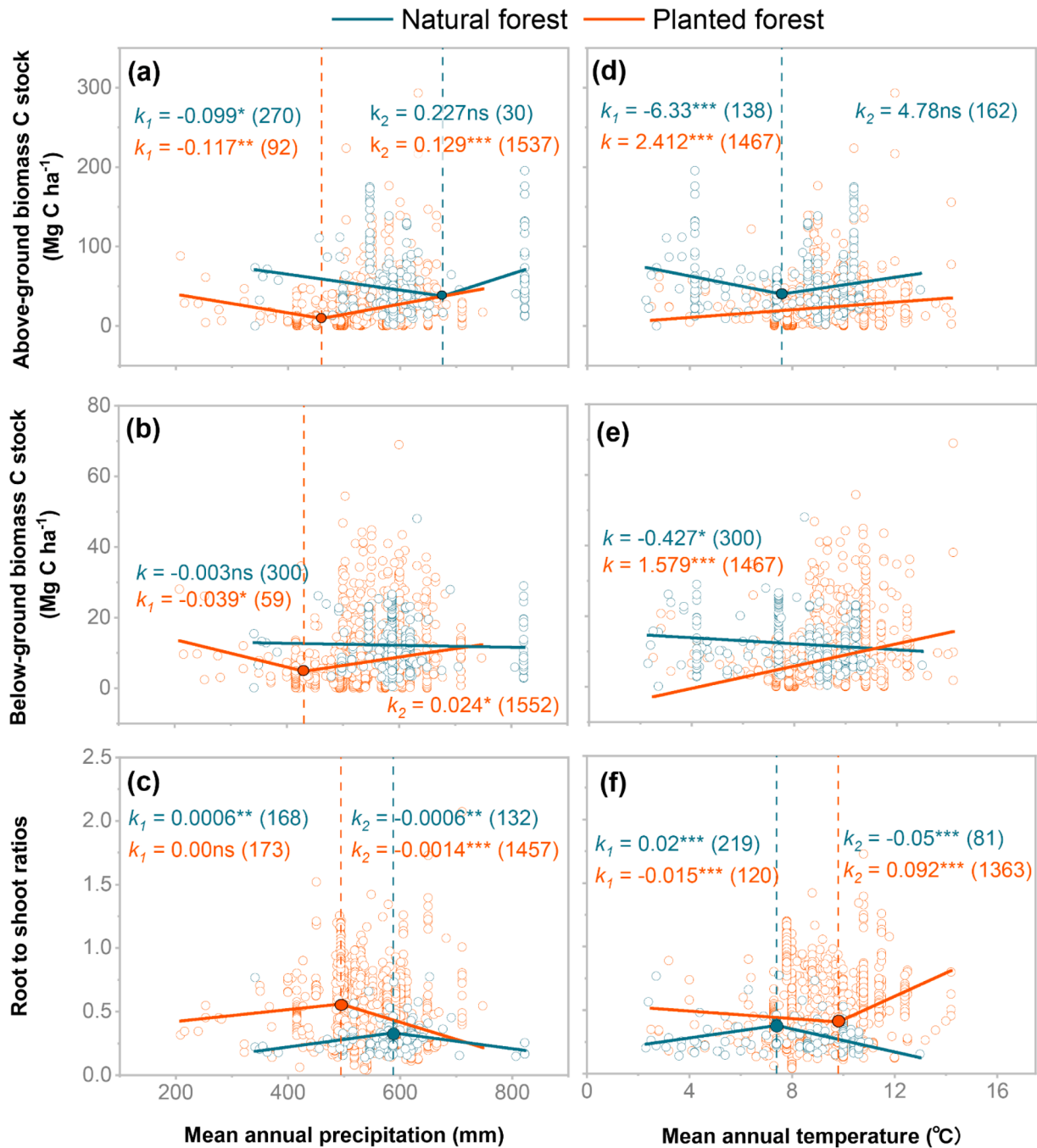


Fig. 3. Changes of biomass C stocks and allocation in response to mean annual precipitation (a-c) and temperature (d-f) under planted forests and natural forests. k_1 and k_2 indicate the regression slopes before and after the turning point. “***”, “**”, “*”, and “ns” indicate significance at $p < 0.001$, $p < 0.01$, $p < 0.05$ and $p > 0.05$, respectively. The number of observations is indicated in parentheses.

a turning point (7.58 °C) and subsequently increased at rate of 4.78 Mg C ha⁻¹ °C⁻¹ ($p > 0.05$), whereas the BGBC stock linearly decreased, albeit in a statistically insignificant way (Fig. 3e). The R:S of PF and NF showed opposite trends in response to MAT (Fig. 3f), i.e., the R:S of PF initially decreased and then increased with MAT increasing, whereas the R:S of NF showed an initial increase and then decreased. In addition, after the turning point, the increasing rate of R:S reached 0.10 °C⁻¹ for PF, indicating a higher sensitivity to warming (Fig. 3f).

3.3. Relationship between root to shoot ratio and soil properties

Distinct differences in the relationships between R:S and soil

properties were observed between PF and NF (Fig. 4). SM, SOC, and TN were negatively correlated with R:S in PF ($p < 0.001$), whereas the correlation in NF was not significant (Fig. 4a-c). In contrast, TP was positively and significantly correlated with R:S in the case of PF (Fig. 4d), whereas only TP showed a significant negative relationship ($p < 0.01$) with R:S in the case of NF (Fig. 4d). Thus, the R:S of PF was much more sensitive to soil properties compared to NF.

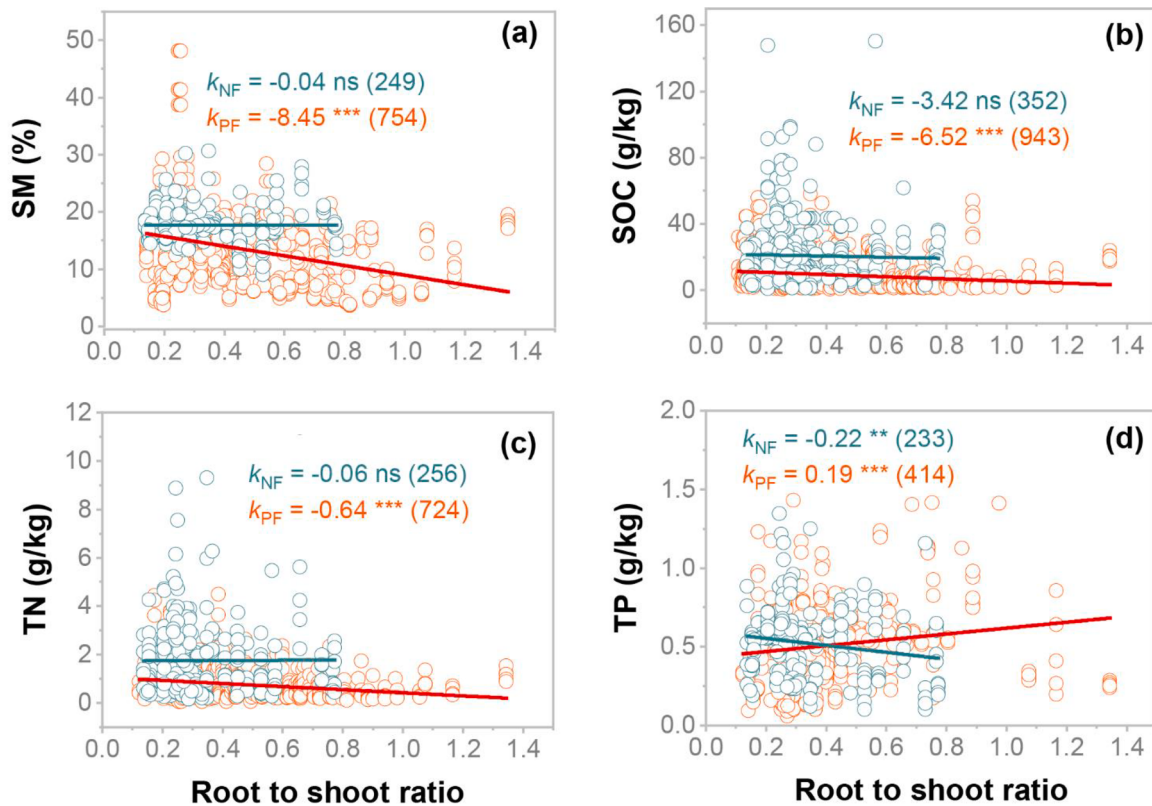


Fig. 4. Relationships between root to shoot ratios and soil properties for planted and natural forests (SM: soil moisture, SOC: soil organic carbon, TN: soil total nitrogen, TP: soil total phosphorus). Note: k indicates the regression slopes; *****, ***, **, and ns indicate significant at $p < 0.001$, $p < 0.01$, $p < 0.05$ and $p > 0.05$, respectively; The number of observations is indicated in parentheses.

4. Discussion

4.1. Differences of biomass C stock and allocation between planted and natural forests

Our results show that naturally regenerated forests stored more C than planted forests, both in above- and below-ground biomass (Fig. 2a and b), which coincides with what is found at a global scale (Hua et al., 2022; Lewis et al., 2019). However, planted forests invest more biomass C to their root systems (25.8 %) compared to natural forests (19.6 %) in the arid and semi-arid Loess Plateau (Fig. 2). The average R:S of the PF and NF paired-sample data across the Loess Plateau (Figure S2) were 0.30 ± 0.11 and 0.19 ± 0.06 , respectively, suggesting that PF allocate more biomass to belowground compared to NF, which supports the observation at the regional scale. Some local studies such as Sun et al. (2020) reported that the proportion of below-ground biomass C stock in a *Robinia pseudoacacia* planted forest was 5.9 % higher than that in *Quercus liaotungensis* natural forests. The carbon allocation disparities between PF and NF are intricately linked to soil conditions (Mokany et al., 2006; Wang et al., 2008). In many regions of China, PF were commonly established in soils characterized by higher productivity, with enhanced fertility and moisture levels (Luo et al., 2012). This phenomenon may result in a reduced allocation of biomass to the root system. However, in arid areas such as the Loess Plateau, PF were frequently situated on degraded sloping croplands with poor soil conditions for land restoration efforts (Peng et al., 2007). Thus, PF tend to allocate more biomass to their root systems to enhance deep root growth and acquire more soil water and nutrients (Mokany et al., 2006; Ye et al., 2021). In contrast, NF usually grew in relatively fertile soil conditions after long-term succession, and less biomass is allocated to root systems in NF (Wang et al., 2015), and more specifically trees will only naturally establish in conditions that are favorable for their growth, which are

typically less arid.

Our results show that the average R:S in planted forests (0.48) is significantly higher than that of natural forests (0.30), and is about 1.8–2.2 times that of the average R:S in China and globe. Specifically, in China, R:S for natural forests and planted forests are 0.26 and 0.22, respectively. At the global level, R:S for natural forests and planted forests are 0.27 and 0.24, respectively (Luo et al. 2012; Mokany et al. 2006; Ledo et al. 2017) (Fig. 5; Text S1). The latest research findings indicated that the average global forest R:S was 0.37 which did not distinguish between NF and PF (Ma et al., 2021). Furthermore, the forest sites in the Loess Plateau used by Ma et al. (2021) were primarily situated within the natural forest distribution area, while our study encompassed a broader geographic scope. Additionally, the average forest R:S (0.28 ± 0.13) in the Loess Plateau reported by Ma et al. (2021) was close to that of NF (0.30 ± 0.11) in this study, but much lower than the that of PF (0.48 ± 0.27) (Figure S3). This reinforces the significance of highlighting the biomass carbon allocation differentiation between NF and PF. The ratio of below- and aboveground biomass of forests in water-limited areas is often assigned a small value in several popular biomass simulation models (Hanan et al., 2021; Penman et al., 2003; Spawn et al., 2020), which likely result in an underestimation of belowground C stocks. Consequently, using the average R:S at the global level or other regions will result in substantial underestimation of belowground C stock in water-limited areas.

During the last decades, there have been several efforts to promote global afforestation, with those in water-limited areas estimated to account for 36 %–42 % of the potential restoration area (Bastin et al., 2019; Liu et al., 2022). Previously, it was a common practice to estimate belowground biomass using aboveground biomass or to predict changes in R:S using aboveground biomass, aiming to assess large-scale biomass C stocks. However, we also found that there were significant differences in the relationships between biomass (either aboveground biomass or

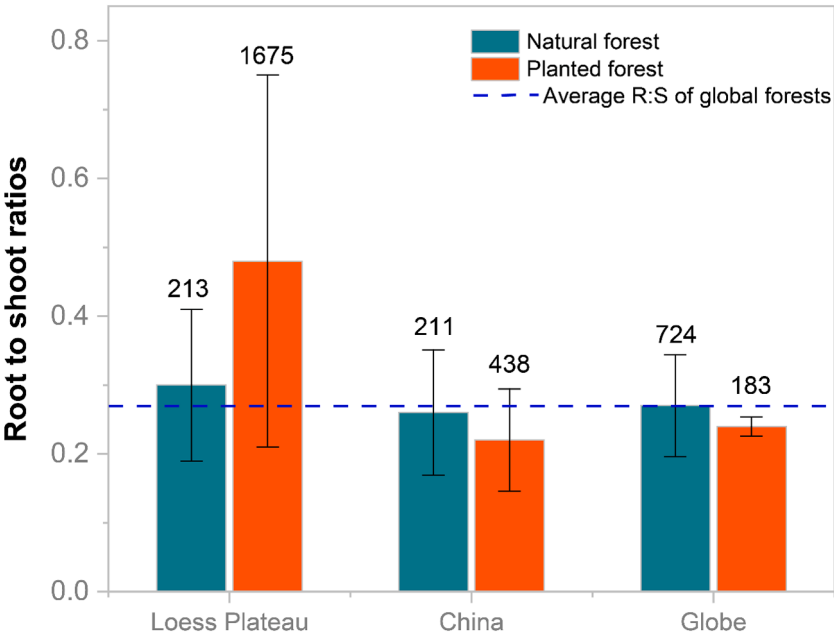


Fig. 5. Comparison of root to shoot ratios of planted and natural forests in the Loess Plateau, China, and globally. The average R:S of NF and PF in China was synthesized from Luo et al. (2012), whereas the global value is the mean value reported by Luo et al. (2012), Mokany et al. (2006), and Ledo et al. (2017). The average R:S of forests globally is that reported by Cairns et al. (1997).

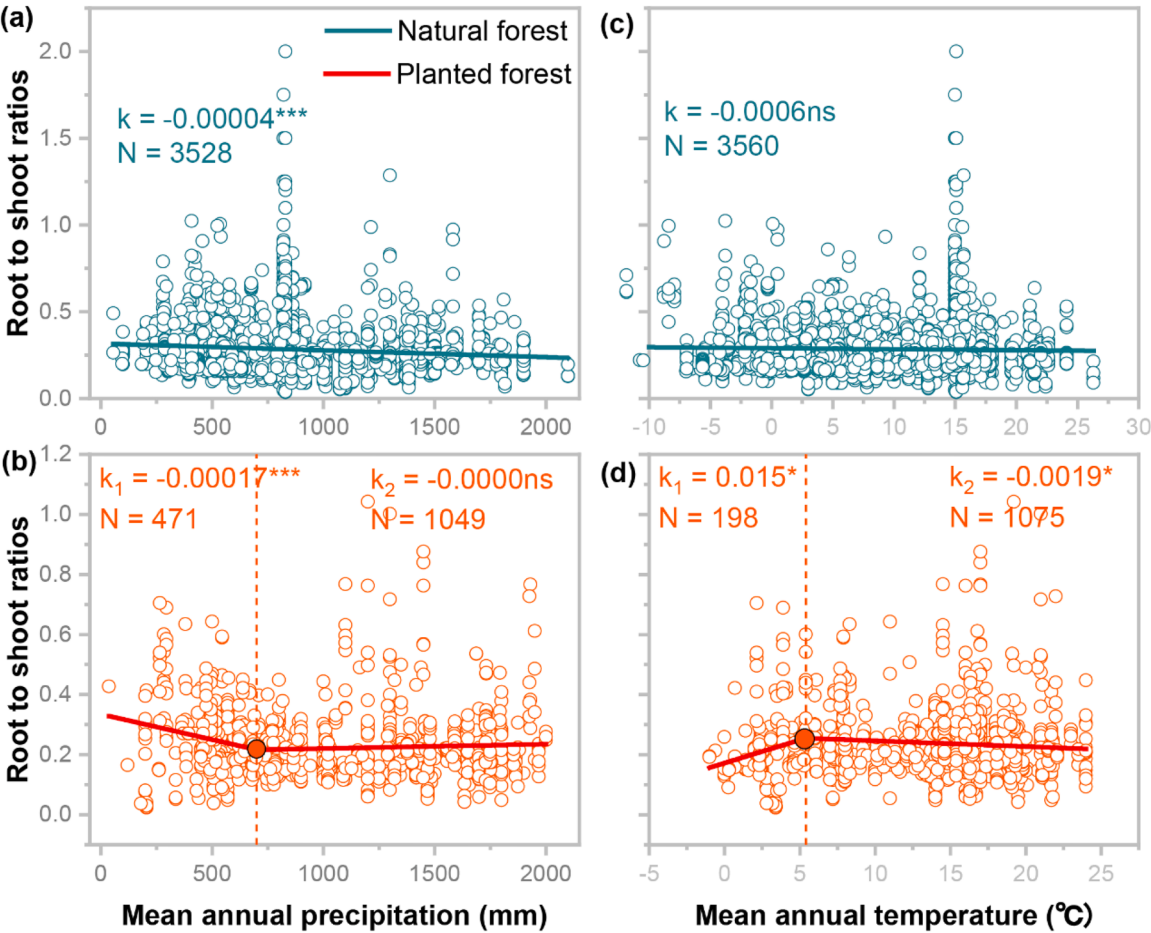


Fig. 6. Relationship between global root to shoot ratios and climatic gradients in planted and natural forests. k_1 and k_2 are the regression slopes before and after the turning point, respectively. “***”, “**”, “*”, and “ns” indicate significance at $p(0.001, p < 0.01, p < 0.05$ and $p) 0.05$, respectively.

total biomass) and R:S among PF and NF (Figure S4). PF exhibited a faster rate of decrease in R:S with increasing biomass compared to NF, and reached a higher stable R:S value (about 0.35) than NF (about 0.20). Therefore, assigning the R:S for these two forest types based on the same method cannot be straightforwardly applied. In summary, when assessing forest C sequestration effects in arid and semi-arid regions, it is crucial to differentiate between planted and natural forests, and adopting differentiated methods to obtain R:S and assess the respective C stocks of belowground biomass, thereby avoiding significant biases in assessing large-scale biomass C stocks.

4.2. Effects of climatic conditions on biomass C stock and allocation in planted and natural forests

In this study, the R:S of both planted and natural forests in the Loess Plateau at first increased with increasing mean annual precipitation and then decreased rapidly (Fig. 3c). Previous studies along the precipitation gradients report that forest R:S can (1) decrease and then increase (Luo et al., 2012), (2) decrease (Mokany et al., 2006; Qi et al., 2019), (3) do not change (Cairns et al., 1997), (4) increase (Luo et al., 2012; Ni et al., 2022), or (5) increase and then decrease (Qi et al., 2019). Therefore, there appears to be no single canonical trend. Luo et al. (2012) concluded that the responses of forest R:S to mean annual precipitation can be classified into three types according to precipitation, with a negative relationship in areas with low mean annual precipitation (less than 1200 mm), a U-shaped relationship in areas with a wide range of mean annual precipitation, and no significant relationship in areas with high mean annual precipitation, suggesting that the effect of precipitation on forest R:S is nonlinear and complex. The non-linear variation of R:S with mean annual precipitation may be related to soil moisture changes. In addition, R:S in planted and natural forests exhibits different trends to precipitation gradients at the global scale (Fig. 6) as well as in our study (Fig. 3c). In general, as mean annual precipitation increases, soil moisture increases (Deng et al., 2016; Liang et al., 2018), resulting in a lower R:S. However, in water-limited areas such as the Loess Plateau, soil moisture is inherently low, a small increase in mean annual precipitation can not satisfy the water requirement of forest and may even stimulate water consumption leading to more soil moisture deficit (Figure S5), thus forest tends to allocate more biomass to their root systems to acquire more soil water and nutrients, which results in increasing R:S (Li et al., 2021b). Soil moisture further increases and will be enough for forest growth until the mean annual precipitation is sufficient (Figure S5), and less biomass is allocated to root systems, resulting in the decreasing R:S with precipitation (Fig. 3c).

In the Loess Plateau, soil moisture following afforestation changed nonlinearly with mean annual precipitation, and there was a moisture deficit in the deep soil layer (>300 cm) (Li et al., 2021b). Afforestation in this region must consider the rainfall being a particularly significant limiting factor. Our previous study suggested that planting trees becomes practical only when mean annual precipitation is greater than 480 mm (Li et al., 2023). Interestingly, the turning points of R:S in the planted forests evaluated in this study occurs at 494 mm (Fig. 3c), which is close to 480 mm. This observation may provide valuable considerations for forest management and climate change mitigation strategies. Specifically, our findings suggest that afforestation efforts may not face severe water stress when mean annual precipitation exceeds 494 mm in the Loess Plateau. Moreover, these insights imply a potential mitigation of adverse effects on both shallow and deep soil moisture dynamics. By emphasizing these practical implications, our research highlights the significance of understanding and incorporating such turning points into forest management practices and broader climate change adaptation strategies.

Generally speaking, as the mean annual temperature increases, the availability of soil nutrients increases, and the biomass allocated to roots decreases, resulting in a lower R:S (Luo et al., 2012). However, in this study, in R:S of planted forests initially decreased and subsequently

increased with increasing mean annual temperature, whereas natural forests initially increased and subsequently decreased (Fig. 3f), perhaps indicating that changes in nutrient availability induced by mean annual temperature were not sufficient to explain changes in forest R:S in water-limited areas, although there may be other critical factors, such as soil moisture or stand density. Mokany et al. (2006), Wang et al. (2008), and Cairns et al. (1997) all reported that temperature did not explain changes in forest R:S, suggesting that the responses of R:S to temperature may be very complex. Our synthesized global R:S data in part supports this conclusion because the R:S in natural forests as opposed to planted forests is comparatively insensitive to mean annual temperature (Figs. 6c and d). In water-limited areas, the initial decrease in R:S of planted forests may be attributed to an increase in nutrient availability induced by warming (Figure S6) thereby reducing competition among individuals, whereas the increase of R:S after the turning point may be due to a soil moisture deficit as a consequence of increasing mean annual temperature and nutrient availability. Warming may also intensify evapotranspiration that may encourage planted forests to invest in deeper roots to access water. For example, with increasing mean annual temperature, either nutrient availability (described as microbial biomass carbon) (Figure S6) or stand density (Figure S7) in natural forests increased significantly, which may have to some extent intensified interspecific competition causing the R:S to increase when the effect of interspecific competition exceeds the effect of increasing nutrient availability. With a continued increase of mean annual temperature, increasing nutrient availability may alleviate the effects of interspecific competition caused by an increase in stand density, resulting in a decrease of R:S. In contrast, changes in nutrient availability in planted forests resulting from increasing mean annual temperature appears to be less than that of natural forests, perhaps due to relatively shallow substrates (Cao and Chen, 2017).

4.3. Effects of soil properties on biomass C stock and allocation in planted and natural forests

In this study, significant relationships between R:S and soil properties were observed (including soil moisture, soil organic carbon, total nitrogen, and total phosphorus) in planted forests rather than in naturally regenerating forests (Fig. 4). Specifically, the negative relationship between R:S and soil moisture in planted forests (Fig. 4a) is consistent with the general observation that R:S decreases with increasing soil moisture (Mokany et al., 2006). We identified a negative correlation between SOC in the top soil and R:S. This phenomenon may be attributed to the following factors. (1) As the R:S increases, forests allocate a higher proportion of carbon to belowground, which implies a potential decrease in aboveground carbon inputs, such as the accumulation of litter, which is a crucial source of SOC in top soils (Lafleur et al., 2015). (2) The reduction in aboveground C input may lead to decreased canopy closure, potentially increasing shallow soil erosion and accelerating the loss of SOC. However, the significant and positive relationship between R:S and total phosphorus (Fig. 4d) may have important implications to understanding forest growth and biomass allocation in phosphorus-limited soils. Previous studies have suggested that soil phosphorus limitation commonly occurs in tropical forests (Mori et al., 2018; Waring et al., 2014). However, Cui et al. (2022) reported a widespread soil phosphorus limitation across Chinese forests, from boreal to tropical forests as ecosystems become wetter, warmer, and more productive. More data are need to be gathered and analyzed to explore whether these trends and speculations are valid.

4.4. Implications and further scopes

Using a large database gathered from the arid and semiarid Loess Plateau, we found that the natural forests store more C in their above- and belowground organs, but afforestation drives more biomass C into root systems, resulting in higher R:S, such that belowground biomass C

stocks are underestimated in planted forests when using the average forest R:S. Furthermore, the planted forests may be subjected to more severe environmental stresses, such as soil moisture deficits, which in turn may change biomass C allocation strategies. Specifically, based on the relationship between the forest R:S and climatic factors, it appears that planting trees can be promoted in areas with mean annual precipitation exceeding 494 mm in the Loess Plateau, which will contribute to C sequestration sustainability. In addition, an increase in mean annual temperature may drive dryland forests to allocate more biomass into root systems when exceeding the threshold, which may be a considerable C sink at a very large scale. Moreover, changes in forest R:S are closely related to key soil ecological processes, such as soil carbon, nitrogen, phosphorus, and water. Therefore, additional analyses of forest biomass allocation patterns in water-limited areas would be extremely beneficial for improving our understanding of ecosystem stability.

Although this study integrated a large amount of data to compare the differences in biomass carbon stock and allocation between planted and natural forests, several issues still need further study. There are some confounding variables (i.e., location, forest species and age) that complicate the comparison at the regional scale. In this study, we have used several paired sampling data to do fair comparison, as detailed in the supplementary information (Figure S2). This includes some general checks to ensure the robustness of our results. Nonetheless, more detailed data should be collected and more complex modeling (i.e., multiple linear regression) that controls for different levels of environmental variables can be used to do further analysis. Furthermore, this study can be extended to other areas in the world to get the spatial patterns about the changes of biomass C sequestration and allocation between planted and natural forests across different regions. The observation and model simulation can be combined to reveal the underlying mechanisms and predict the carbon dynamics over a long period.

5. Conclusions

Our study reveals that NF has significantly higher biomass C stocks in both above- and below-ground parts compared to PF in the Loess Plateau. However, the proportion of below-ground C stocks is much higher in PF, resulting in a higher R:S. This shows that using the default R:S to estimate the C stocks in below-ground biomass of PF may result in a severe underestimation in water-limited areas. Furthermore, turning points existed in biomass C allocation along climatic gradient for both PF and NF. Specifically, more biomass C was allocated to AGB in PF and NF when mean annual precipitation exceeded 494 mm and 588 mm, respectively. An increase of mean annual temperature may promote a greater allocation of C to root systems in PF compared to NF. In addition, forest biomass C allocation in water-limited areas is also influenced significantly by soil properties in both top- and deep soil layers. Our study indicates that the below-ground biomass C stock in dryland afforestation may be an important C sink over a broad spatial scale. These findings further inform our understanding of C stocks in planted and naturally regenerating forests, and can improve future attempts to model the effects of climate change on forest dynamics.

CRedit authorship contribution statement

Binbin Li: Writing – original draft, Investigation, Formal analysis, Data curation. **Guangyao Gao:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Karl J. Niklas:** Writing – review & editing, Supervision. **Yiqi Luo:** Writing – review & editing, Supervision. **Mingxiang Xu:** Writing – review & editing, Supervision. **Guobin Liu:** Writing – review & editing, Supervision. **Bojie Fu:** Writing – review & editing, Supervision.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Supplementary materials

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