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REGULAR ARTICLE

Fine root biomass, production and turnover rates in plantations versus natural forests: effects of stand characteristics and soil properties

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Abstract
Aims Fine roots play a significant role in regulating the biogeochemical cycles of forest ecosystems, but how fine root biomass (FRB), production (FRP) and turnover rates (FRT) vary with forest origins remains not well understood.
Methods The meta-analysis approach was used to examine the differences in FRB, FRP and FRT between plantations and their adjacent natural forests based on 238 cases reported in 45 published studies.
Results FRB and FRP were 36.5% and 36.0% lower, respectively, in plantations than in natural forests. FRT was 22.4% higher in plantations relative to natural forests. The decrease in FRB in plantations relative to natural forests varied among plantations with different plant genera and root diameter classes. The general patterns for FRP and FRT in relation to various factors (biogeographic zone, leaf form, leaf seasonality, plant genus in plantations, and root diameter class) did not differ among the groups. The difference in FRB between plantations and natural forests was positively correlated with stand age but negatively related with soil total nitrogen concentration, the difference in FRP was positively affected by diameter at breast height (DBH) and soil pH, and the difference in FRT was positively affected by DBH, tree height, soil bulk density and soil pH and negatively affected by soil organic carbon and total nitrogen concentration.
Conclusions FRB, FRP and FRT exhibit significant differences between plantations and natural forests and that these differences are partially caused by shifts in stand characteristics and variations in soil properties.

Keywords Fine roots · Forest origins · Planted forests · Stand structure · Soil nutrient

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Introduction

Fine roots, i.e., small-diameter, short-lived roots, are functionally the most important component of the overall root systems of plants (Leuschner and Hertel 2003). Forest ecosystems allocate up to 75% of their annual total net primary production to fine roots, which in turn are the primary pathways for water and nutrient uptake for trees (Jackson et al. 1997; Schenk and Jackson 2002). Thus, fine roots have important effects on nutrient and carbon (C) cycling of forest ecosystems (Waisel et al. 2002; Campos et al. 2017).

Similar to other belowground processes, parameters of fine roots, such as fine root biomass (FRB), fine root production (FRP) and fine root turnover rate (FRT) may be altered by changes in land-use type. As a consequence of ongoing reforestation and afforestation efforts, planted forests (plantations) around the world play a great role in timber production and atmospheric CO_2 sequestration (van Dijk and Keenan 2007). However, compared with adjacent natural forests, plantations can potentially alter the biogeochemical cycles of forest ecosystems as a consequence of changes in tree species composition (Liao et al. 2012; Hu et al. 2018) and intervention by silvicultural activities (Zheng et al. 2008; Mujuru et al. 2014). Therefore, examining whether and to what extent FRB, FRP and FRT differ between plantations and natural forests is essential for predicting plant growth under projected global land-use changes, forecasts of which serve as the basis for improving and refining ecosystem models (Jackson et al. 2000).

The number of field studies of the differences in fine root parameters between plantations and natural forests remain limited. This is probably due to methodological limitations, the labor-intensive nature of this type of study and the relative inaccessibility of root systems (Vogt et al. 1998). The results obtained from the limited number of studies that have been conducted are highly variable. For example, FRB as well as FRP are lower (Kotowska et al. 2015a; Cai et al. 2016; Pransiska et al. 2016) and FRT is higher (An et al. 2017) in plantations than in natural forests. However, other studies have reported that FRB and FRP increase (Lin et al. 2015; Silva et al. 2011; Chia et al. 2017) and FRT decreases (Yang et al. 2004) in plantations compared with natural forests. The mixed results of these field studies prevent us from fully understanding the changes in FRB, FRP and FRT that occur in forests of these two origins, especially for a broad study scale.

The inconsistent results might stem from the fact that the difference in FRB, FRP, and FRT between plantations and natural forests are influenced by a number of factors, such as leaf form, leaf seasonality of the trees in plantations, and the geographic environment in the study region. The FRB is higher in broadleaved plantations with *Euxylophora paraensis*, but lower in coniferous plantations with *Pinus caribaea* than in natural forests (Smith et al. 2002). Moreover, FRB is greater in evergreen plantations with *Pinus koraiensis* but lower in deciduous plantations with *Larix gmelinii* relative to natural forests (Quan et al. 2010). FRP decreases in plantations in temperate regions (Yang et al. 2004) but increases in tropical regions (Silva et al. 2011) in comparison with natural forests. Root diameters and tree species of plantations may also influence the differences in FRB, FRP and FRT between plantations and natural forests (Chen et al. 2013; Kooch et al. 2016). However, individual field studies cannot take all these factors into account, precluding broad generalization of their results.

Earlier studies have noted that the stand characteristics and soil properties of plantations and natural forests differ significantly (Guo and Ren 2014; Liao et al. 2012; Wall and Hytönen 2005), and this may also greatly affect the differences in FRB, FRP and FRT between forests with different origins. Compared to natural forests, plantations are often located in defined areas (e.g., clear-cut or burned areas) in which the environmental conditions are relatively homogeneous. The species (often only one) and tree densities in plantations are usually carefully manipulated for high productivity (Guo and Ren 2014). However, natural forests naturally regenerate with higher habitat heterogeneity, species diversity and structural stability (Ren et al. 2017). Tree species origin (native or exotic) and site preparation for planted forests could also result in differences in soil properties between plantations and natural forests. Liao et al. (2012) used data from all continents except Antarctica and reported that soil moisture and soil C, nitrogen, phosphorus and potassium concentrations were all lower in plantations than in natural forests. Nevertheless, how these factors regulate differences in FRB, FRP and FRT between forests of the two origins remains unknown.

In this study, published studies on FRB, FRP and FRT that utilized paired-site design across temperate and tropical regions were synthesized (boreal forests were excluded from the analysis because of the small amount of available data). Specifically, this study aimed (1) to quantify the overall direction and magnitude of the differences in FRB, FRP and FRT between plantations and natural forests; and (2) to identify the factors that contributed to the differences. We hypothesize that FRB and FRP are lower and that FRT is higher in plantations than in natural forests, because natural forests generally have higher species diversity and stand structure diversity than plantations, and both of these characteristics have positive effects on below-ground productivity (Brassard et al. 2013; Ma and Chen 2016).

Methods

Data sources

An extensive literature survey of peer-reviewed publications was conducted through the Web of Science (http://apps.webofknowledge.com), Google Scholar and China National Knowledge Infrastructure (http://www.cnki.net/) databases. The keywords used in the literature search included “fine root” AND “biomass OR production OR turnover rate” AND “natural forest AND plantation”. To minimize potential uncertainties in the data analysis, the following criteria were applied to select appropriate studies. (1) The reference systems relative to plantations were primary and secondary forests that were naturally generated forests (i.e., natural forests). (2) The trees in plantations were arbor species, plantations consisting of bamboo, shrubs or fruit trees were excluded. (3) All plantations were used in the analysis of the effect of stand age, but only plantations larger than 25 years old were included in the analysis of other effects to minimize the influence of stand age. The threshold value of 25 years was determined by the common practice that mature plantation stands with fast growth rate are generally considered to be of less than 25 years in age (Liao et al. 2010). (4) Data were collected from samples at the same soil depths between plantations and natural forests in each study, and there was no significant effect of soil depth among studies on the difference in FRB, FRP and FRT between plantations and natural forests (Appendix S3). Roots of all species were included. (5) If a manipulated experiment was employed, only data from the control or untreated plots were included. (6) If multiple measurements across several years were reported for a study or multiple samplings were conducted within a single year, the mean value was used to provide a single estimate. (7) If studies utilized a chronosequence design for plantations compared with natural forests, the data obtained from the oldest plantation were used. (8) If more than one root diameter class was reported, the diameter class ≤2 mm was preferred. To avoid autocorrelation between root diameters, other root diameter classes were used only in the analysis of the effect of root diameter but not in the analysis of other effects. (9) Only studies in which sampling was conducted using corer or by the monolith technique were used. FRP data obtained by the sequential coring method or the ingrowth cores method were selected. If more than one method was used, the sequential coring method was preferred, since the ingrowth cores method has been observed to underestimate the value (Vogt et al. 1998). (10) The FRT was either directly extracted from the original publication or calculated as the ratio of FRP to FRB when both parameters were recorded in the same publication. A total of 45 papers published from 1982 to July 2018 were included in this synthesis (the relevant information is shown in Appendix S1 and a list of the data sources can be found in the Appendix S2 in the Supporting Information).

The compiled dataset included the following variables: (1) stand characteristics variables: stand age (yr), stand density (stems/ha), diameter at breast height (DBH) (cm), tree height (m) and basal area (m^2/ha); (2) soil properties: soil bulk density (g/cm^3), soil pH, and soil organic carbon (SOC) and soil total nitrogen concentrations (g/kg). For each variable, the mean, standard deviation (SD), and sample size (*n*) in plantations and natural forests were extracted from the original publications. If the standard error (SE) was reported, the SD was calculated as $SD = SE\sqrt{n}$.

In cases in which no SE or SD was reported, the SD was assigned a value of 1/10 of the mean (Luo et al. 2006). When the original study reported results graphically, we used Origin 7.0 (OriginLab Ltd., USA) to digitally extract data from the figures.

Given that tree species of the genera *Abies*, *Larix*, *Pinus* and *Cunninghamia* are widely used to establish plantations, the planted tree species of these genera were used to determine the differences in FRB, FRP and FRT between plantations and natural forests. In addition, plantations were categorized into two groups in relation to leaf form (broadleaved versus coniferous) and leaf seasonality (deciduous versus evergreen). The biogeographic zones of the study regions were classified into temperate and tropical, with the tropical zone situated between 23.5°S and 23.5°N and the boreal zone situated >46°N; the temperate zone included all the zones between the tropical and boreal zones. Fine root diameter classes were categorized as ≤2 mm, ≤ 5 mm and 2–5 mm.

Data analysis

The method of meta-analysis used in this study was the same as that used in previous studies (e.g., Hedges et al. 1999; Luo et al. 2006). Plantations were regarded as treatment relative to natural forests. The difference in each variable between plantations and natural forests was estimated as the natural logarithm transformed response ratio (*RR*), which improves its statistical behavior in meta-analyses (Hedges et al. 1999):

$$RR = \ln(\bar{X}_t/\bar{X}_c) = \ln(\bar{X}_t) - \ln(\bar{X}_c)$$

where $\bar{X}_t$ and $\bar{X}_c$ are the means of the concerned variable in plantations and natural forests, respectively. The variance (v) was estimated as

$$v = \frac{s_t^2}{n_t\bar{X}_t^2} + \frac{s_c^2}{n_c\bar{X}_c^2}$$

where n_t and n_c are the sample sizes of the concerned variable in plantations and natural forests, respectively, and s_t and s_c are the SDs of the variable in plantations and natural forests, respectively. The inverse of the variance ($w = \frac{1}{v}$) was used as the weight of each *RR*, assuming that *RR* with a lower variance should be weighted more highly. To summarize the results from independent studies, the weighted mean response ratio (RR_{++}) was calculated from *RR* to increase the precision of the combined estimate and the power of the tests, as follows:

$$RR_{++} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij}RR_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij}}$$

where m is the number of groups (e.g., biogeographic zones) and k is the number of comparisons in the ith group.

We used a bootstrapping method with 5000 iterations to generate 95% confidence intervals (CIs) of RR_{++} (Adams et al. 1997). If the 95% bootstrap CIs of RR_{++} for a concerned variable overlapped with zero, the variable was not considered significantly different between plantations and natural forests. Otherwise, it was considered significantly different. The percentage change in the variable was estimated as Effect size (%) = [exp (RR_{++}) − 1] × 100%. To examine whether the *RR*s differed among diverse biogeographic zones, leaf forms, leaf seasonalities, plant genera and fine root diameters, the total heterogeneity among groups was partitioned into within-group heterogeneity and between-group heterogeneity. Significant between-group heterogeneity suggests that the *RR*s differ among the categorical groups (Hedges et al. 1999). Meta-analysis was conducted with MetaWin 2.1 software (Sinauer Associates, Inc., Sunderland, MA, USA).

The interaction among different factors on differences in FRB, FRP and FRT between plantations and natural forests were examined by analysis of variance (ANOVA) and regression analysis (Appendix S4 and S5). The correlations of *RR* among different variables were examined by correlation analysis. An α value of 0.05 was chosen to indicate statistical significance. All statistical analyses were performed in R 3.3.2.

Results

Differences in stand characteristics and soil properties between plantations and natural forests

A total of 238 observations from 45 studies were collected in this study (Table 1, Appendix S1 and S2 in Supporting Information). Across all studies, stand density decreased significantly by 23.0%, and DBH and tree height increased significantly by 15.4% and 36.5%, respectively, in plantations relative to natural forests (Table 2). The basal area did not differ significantly between plantations and natural forests. With respect to soil properties, soil bulk density was 11.9% higher, and SOC and soil total nitrogen were 24.1% and 23.4% lower, respectively, in plantations than in natural forests (Table 2). The soil pH in plantations and natural forests did not differ (Table 2).

Differences in FRB, FRP and FRT between plantations and natural forests

Across all individual studies, FRB, FRP and FRT differed significantly between plantations and natural forests (Fig. 1). FRB and FRP were 36.5% and 36.0% higher, respectively, in natural forests than in plantations. However, plantations showed significantly higher

Table 1 Fine root biomass (FRB), fine root production (FRP) and fine root turnover rate (FRT) showing the number of cases with negative (decrease) and positive (increase) differences for plantations relative to natural forests in this meta-analysis

	Number of cases			
Variables	Total	Decrease	Increase	Unchanged
FRB	138	119	19	0
FRP	50	40	9	1
FRT	50	21	29	0

Table 2 Differences in stand characteristics and soil properties between plantations and natural forests

Variables	Sample size	Response ratio	Bootstrap CIs
Stand density	89	−0.262	−0.428, −0.098
DBH	68	0.143	0.008, 0.277
Tree height	62	0.311	0.185, 0.437
Basal area	35	−0.044	−0.144, 0.053
Soil bulk density	57	0.112	0.049, 0.172
Soil pH	39	−0.010	−0.043, 0.020
Soil organic carbon	101	−0.276	−0.419, −0.132
Soil total nitrogen	56	−0.267	−0.399, −0.134

FRT (22.4%) than natural forests (Fig. 1). Significantly decreased patterns of FRB for different biogeographic zones, leaf forms and leaf seasonalities were found in plantations relative to natural forests (Fig. 1). Plant genus in plantations significantly affected the *RR* of FRB (Table 3). For planted tree species of the genera *Larix*, *Pinus* and *Cunninghamia*, the difference in FRB between plantations and natural forests was significant. However, no significant difference was found for the genus *Abies* (Fig. 2). Differences in the *RR* of FRB were also significant among root diameter classes (Table 3). Leaf seasonality and root diameter had interactive effect on the *RR* of FRB (Appendix S4).

Significantly decreased patterns of FRP in plantations relative to natural forests were found across almost all categories except tropical zone, planted tree species of the genera *Abies*, and 2–5 mm root diameter (Figs. 1 and 2). However, the *RR* of FRP did not differ significantly among the categories (Table 3).

FRT consistently increased in plantations relative to natural forests depending on biogeographic zones, leaf forms and leaf seasonality except in broadleaved plantations (Fig. 1). Among the four plant genera of plantations we considered, only plantations with the genera *Larix* and *Pinus* had significant higher FRT than natural forests (Fig. 2). FRT increased by 28.1% for ≤5 mm root diameter in plantations relative to natural forests, but no significant differences were found for ≤2 mm root diameter (Fig. 2). However, none of the factors considered in our analysis significantly affected the *RR* of FRT (Table 3).

Factors regulating differences in FRB, FRP and FRT between plantations and natural forests

Stand characteristics

The *RR* of FRB was positively correlated with the *RR* of stand age ($P = 0.049$; Fig. 3a), and the *RR* of FRP was

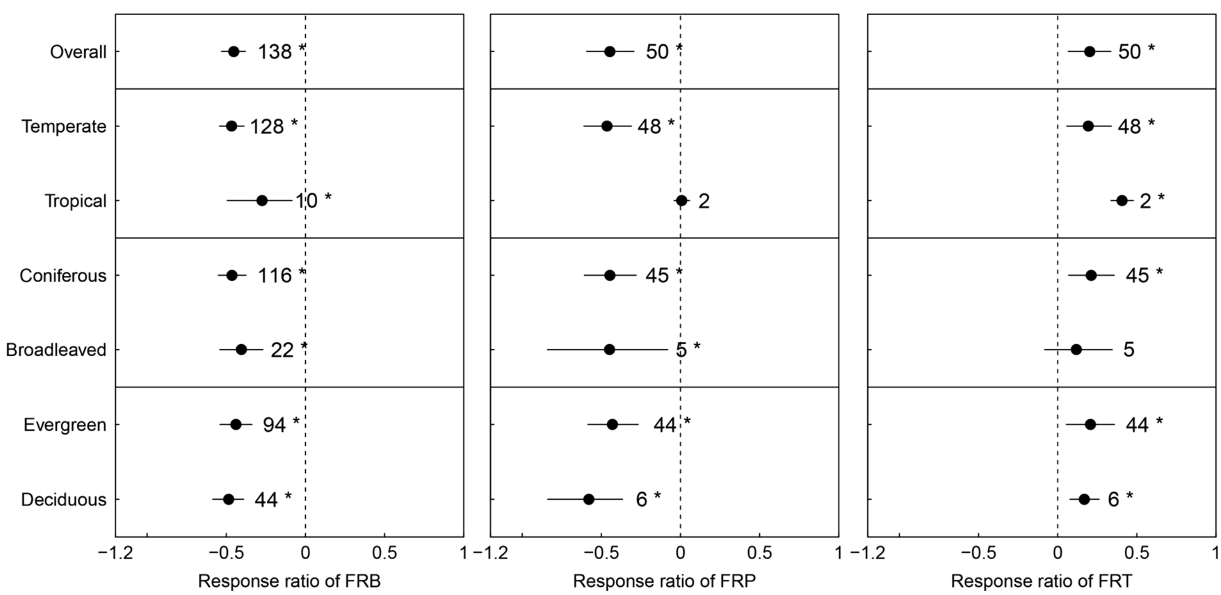

Fig. 1 Comparison of fine root biomass (FRB), fine root production (FRP) and fine root turnover rate (FRT) between plantations and natural forests in different biogeographic zones, and for different leaf forms and leaf seasonalities. The black circles with error bars indicate the mean response ratios with 95% bootstrap confidence intervals (CIs). The vertical dashed lines are the reference of a response ratio of zero. The numbers adjacent to the CI bars are sample sizes, and the asterisks indicate significant differences

Table 3 Between-group heterogeneity (Q_b) of the observed differences in fine root biomass (FRB), fine root production (FRP) and fine root turnover rate (FRT) between plantations and natural forests

Category	FRB		FRP		FRT	
	Q_b	*P* value	Q_b	*P* value	Q_b	*P* value
Biogeographic zone	1.875	0.171	1.175	0.278	0.261	0.610
Leaf form	0.360	0.548	0.001	0.992	0.121	0.728
Leaf seasonality	0.378	0.539	0.326	0.568	0.024	0.878
Plant genera	11.007	**0.012**	5.430	0.143	0.996	0.062
Root diameter	6.549	**0.038**	4.914	0.086	0.407	0.524

Biogeographic zone includes temperate and tropical. Leaf form is classified as coniferous forests and broadleaved forests. Leaf seasonality is classified as evergreen forests and deciduous forests. Plant genera include *Abies*, *Larix*, *Pinus* and *Cunninghamia*. Root diameter is classified as ≤ 2 mm, 2–5 mm and ≤ 5 mm. Significant between-group heterogeneity was marked in bold.

positively correlated with the *RR* of DBH ($P = 0.050$; Fig. 4f). However, no significant relationship was found for *RR* of FRB and *RR* of FRT with any other factor related to stand characteristics (Fig. 4). The *RR* of FRT was positively correlated with the *RR* of DBH ($P = 0.006$; Fig. 4j) and *RR* of tree height ($P = 0.012$; Fig. 4k), but showed no correlation with the *RR* of stand density or basal area (Fig. 4i and l).

Soil properties

Among the four soil factors we considered, only the *RR* of soil total nitrogen had a negative effect on the *RR* of FRB ($P = 0.025$; Fig. 5d), and only the *RR* of soil pH had a positive effect on the *RR* of FRP ($P < 0.001$; Fig. 5f). However, the *RR* of FRT was significantly correlated with all four soil factors, it was positively correlated with the *RR* of soil bulk density ($P = 0.003$; Fig. 5i) and soil pH ($P = 0.010$; Fig. 5j) but negatively correlated with the *RR* of SOC ($P = 0.026$; Fig. 5k) and soil total nitrogen ($P = 0.014$; Fig. 5l).

Discussion

Significant differences in FRB, FRP, and FRT between plantations and natural forests

Based on all data collected from field studies with paired-site designs, our analysis demonstrated that FRB and FRP were lower and FRT was higher in plantations than in natural forests (Fig. 1). This result supports our hypothesis and is consistent with the results of previous studies (Ma and Chen 2016; Pransiska et al. 2016). Several possible mechanisms may underlie these results. First, natural forests with higher species diversity and

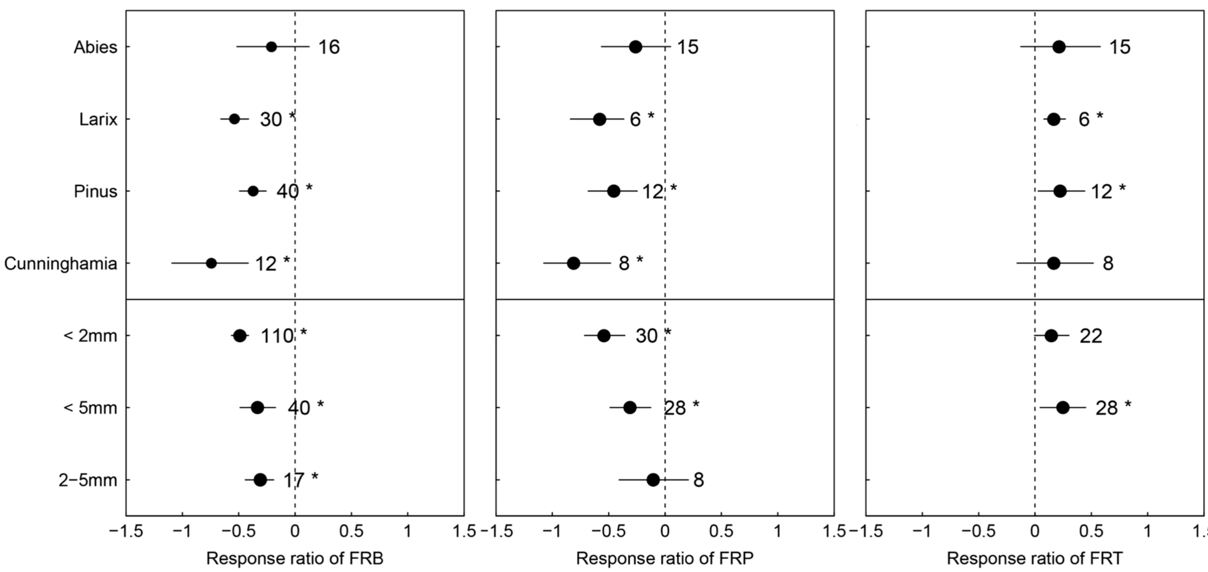

Fig. 2 Comparison of fine root biomass (FRB), fine root production (FRP) and fine root turnover rate (FRT) between plantations and natural forests for different plant genera of plantations and root diameter classes. The black circles with error bars indicate the mean response ratios with 95% bootstrap confidence intervals (CIs). The vertical dashed lines are the reference of a response ratio of zero. The numbers adjacent to the CI bars are sample sizes, and the asterisks indicate significant differences

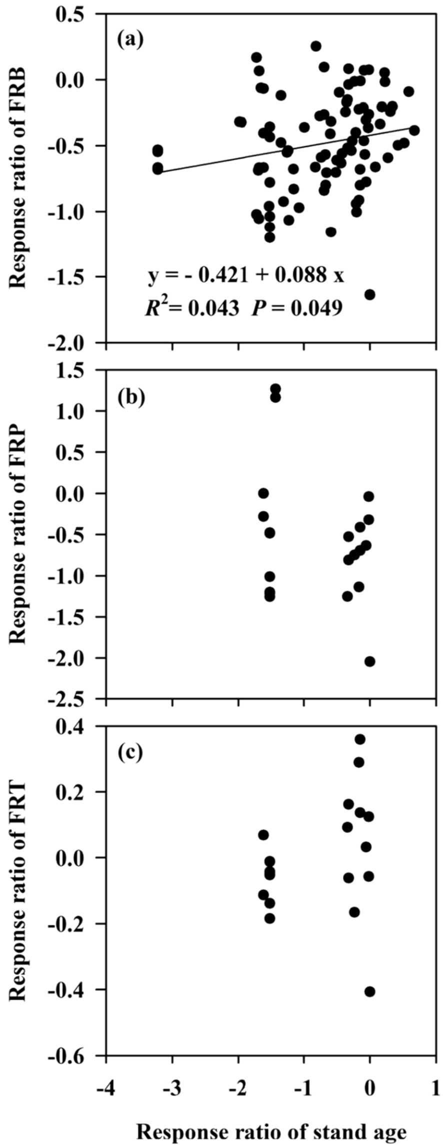

Fig. 3 Relationship of the response ratio of fine root biomass (FRB) (**a**), fine root production (FRP) (**b**) and fine root turnover rate (FRT) (**c**) to the response ratio of stand age

stand structure diversity display a greater variety of traits in rooting depth and root morphology and can thus exploit diverse below-ground niches and better utilize available resources, thereby resulting in larger FRB and greater FRP than are found in plantations with very few tree species (Mueller et al. 2013; Zhang et al. 2012). Second, plantations afforested in croplands, grasslands and shrublands decreased stream flow, and climate feedbacks are unlikely to offset the soil water loss (Jackson et al. 2005). Thus, soil moisture was lower in plantations relative to natural forests (Liao et al. 2012), and the decreased soil moisture may limit root growth in plantations. Third, lower nutrient availability (i.e., SOC and soil total nitrogen) due to reduced litter input, which can be expected in plantations (Kotowska et al. 2015b), leads to a lower rate of uptake of soil nutrients and lower metabolic activity (Bai et al. 2008). Therefore, roots located in nutrient-poor soil in plantations may have shorter life spans and higher turnover rates (Burton et al. 2000).

The plant genera within plantations significantly influenced the differences in FRB between plantations and natural forests (Table 3), and these results were associated with species-specific traits. For example, early-successional species such as those in the genera *Larix* and *Cunninghamia* have a greater capacity to explore soil volume and thus have deeper root systems, whereas late-successional species such as those in the genus *Abies* usually have shallower root systems but higher soil resource exploitation efficiency (Yuan and Chen 2010; Xiang et al. 2015). Therefore, variations in the soil resource exploitation patterns of fine roots among tree species may greatly affect the FRB. In addition, fine root dynamics are highly dependent on root diameter, and roots of small diameter are physiologically more active than larger ones (McCormack et al. 2015). Therefore, the use of different root diameter classes might result in inconsistent results for *RR* of FRB (Table 3, Fig. 2).

Differences in FRB, FRP, and FRT between plantations and natural forests associated with stand characteristics and soil properties

Stand age had a positive effect on the *RR* of FRB, this pattern appears to be a result of aboveground and belowground biomass accumulation associated with stand development. However, this finding is in contrast to the widespread results that the FRB generally increases at young stages of forest development, and then remains stable or decreases when the forests reach maturity (Claus and George 2005; Børja et al. 2008). The contrasting pattern could be due to the few data from old plantations in our dataset, which may limit the potential to capture the decreasing phase of FRB-age relationship. In addition, soil total nitrogen concentration was found to regulate the difference in FRB between plantations and natural forests (Fig. 5d). This is consistent with previous studies in which it was reported that nutrient availability is an important factor accounting for differences in FRB among sites with varying nutrient resources (Vogt et al. 1987; Lee et al. 2007). According to the optimal

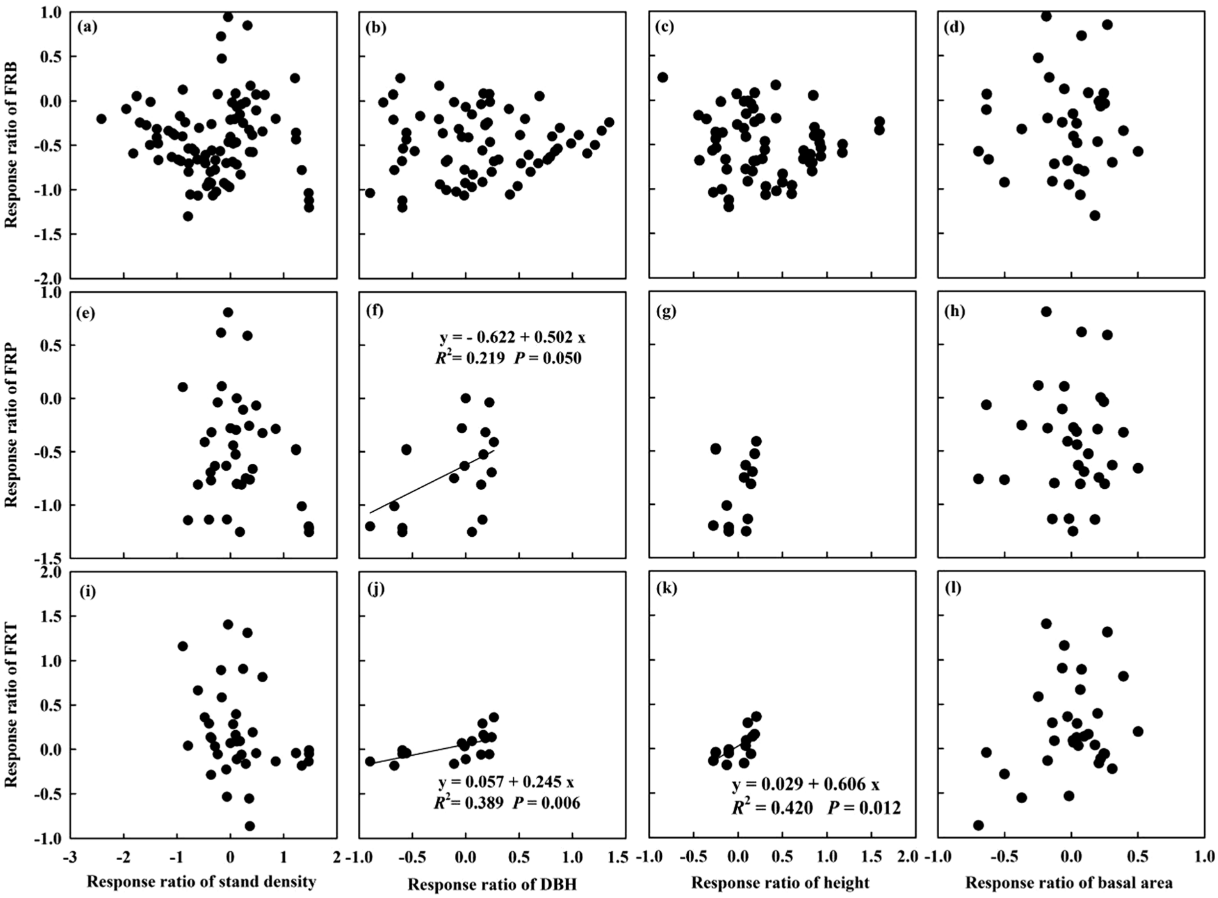

Fig. 4 Relationship of the response ratio of fine root biomass (FRB) (**a**-**d**), fine root production (FRP) (**e**-**h**) and fine root turnover rate (FRT) (**i**-**l**) to the response ratio of stand density, diameter at breast height (DBH), tree height and basal area

partitioning theory (Bloom et al. 1985), which predict that plants preferentially allocate additional biomass to roots when resources are limited, and increasing soil nutrient supply could reduce C allocation to fine roots. Thus, changes in soil nitrogen availability will have a negative effect on FRB. A number of studies have also indicated that FRB is closely correlated with basal area (Finér et al. 2011a; Helmisaari et al. 2007), this was not observed in our analysis, possibly due to the smaller dataset on basal area.

Both stand characteristics and soil properties drive the difference in FRP between plantations and natural forests. The DBH had a positive effect on the *RR* of FRP (Fig. 4f), this pattern can be attributed to the synchronism of growth between aboveground and belowground (Li et al. 2003). In addition, soil pH is also an important factor affecting the *RR* of FRP (Fig. 5e). In acidic soils, microbial growth and activity are inhibited (Zhou et al. 2017); thus, soils with a higher pH can potentially stimulate root growth (Yuan and Chen 2010). The levels of exchangeable aluminum have been found to be high in acidic soils, and this can inhibit root elongation and reduce the resource exploitation capacity of roots (Valle et al. 2009). Previous studies have reported that soil resource availability also greatly affects FRP (Nadelhoffer 2000; Yuan and Chen 2012), but no significant relationships were observed in our results (Fig. 5g and h). This could partly result from the small dataset and the different FRP estimation methods used in the studies. Although earlier study indicates that FRP estimates are significantly affected by the method used (Finér et al. 2011b), we did not limit ourselves to one method only, because that would have resulted in a very limited dataset.

Soil properties greatly affected the difference in FRT between plantations and natural forests. Soil bulk density had a positive effect on the *RR* of FRT (Fig. 5i). Higher soil bulk density (i.e., soil compaction) in plantations may impede the access of roots to water and

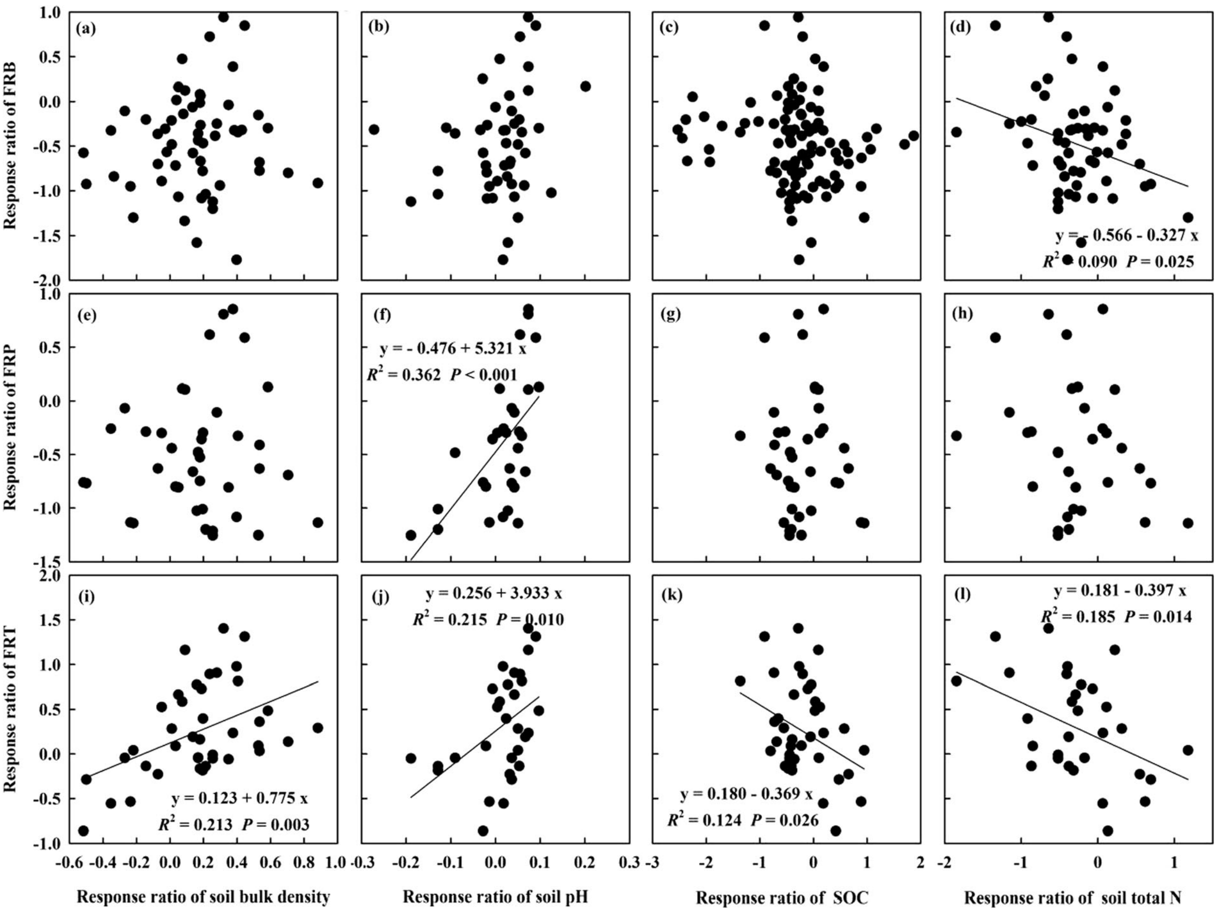

Fig. 5 Relationship of the response ratio of fine root biomass (FRB) (**a**-**d**), fine root production (FRP) (**e**-**h**) and fine root turnover rate (FRT) (i-l) to the response ratio of soil bulk density, soil pH, soil organic carbon (SOC) and soil total nitrogen (N)

nutrients and reduce root respiration rates, leading to shorter life spans and higher turnover rates. In addition, the *RR* of FRT showed a pattern similar to that of *RR* of FRP with respect to soil pH (Fig. 5f, j), probably because acidic sites result in reduced root growth and higher mortality and turnover. The *RR* of FRT was negatively related to the concentration of soil nutrients such as C and nitrogen (Fig. 5k, l). This may be best explained by the cost-benefit hypothesis (Eissenstat and Yanai 2002), which holds that increasing the availability of soil nutrients generally leads to a higher rate of uptake and greater metabolic activity (Peng et al. 2017). Root growth in nutrient-rich environments might have a longer lifespan (lower turnover rate), and in nutrient-poor environments it should have a shorter lifespan (higher turnover rate). Therefore, the lower soil nutrient availability may be responsible for the increased FRT in plantations relative to natural forests. In addition, the *RR* of FRT was positively correlated with the difference in DBH and tree height (Fig. 4j and k). One possible explanation is that root lifespan (the inverse of FRT) was negatively related to tree growth rate (McCormack et al. 2012), and the tree growth rate increases continuously with tree size (Stephenson et al. 2014), which is closely linked to DBH and tree height. However, due to the limited data in our analysis, we cannot conclude that this relationship represents a general pattern, further studies are needed when new data become available.

Methodological considerations

This study used a synthesis of 238 observations from 45 studies to describe differences in FRB, FRP and FRT between plantations and natural forests across temperate and tropical regions. While we can draw important conclusions from such empirical datasets, they also have limitations. An important limitation of the current study is that the forest ages of the plantations and natural forests in the individual studies were not exactly the same. This could affect the evaluation of the differences in FRB, FRP and FRT between plantations and natural forests despite the fact that plantations <25 years old were excluded from our analysis to minimize the influence of forest age. Moreover, the study regions are not randomly distributed, and the datasets we analyzed may come from regions in which ecologists have conducted extensive studies, such as in China, whereas many other plantation regions have not attracted much attention from ecologists. This could bias our results. In addition, the number of cases for some variables, such as basal area, was relatively small (Table 2), and the effects of these variables on the *RR* of FRB, FRP and FRT might be sensitive to the addition and deletion of new data. However, it is difficult to evaluate these uncertainties. Different methodological approaches, such as the use of soil cores versus ingrowth cores, have an effect on the quantification of FRB, FRP and FRT (Eissenstat and Yanai 2002). The use of different sampling depths in individual studies could also lead to uncertainties (Jackson et al. 1996). Therefore, the present results showing a difference in FRB, FRP and FRT between plantations and natural forests at large spatial scales still remain highly uncertain. Increasing the geographical coverage and reporting the corresponding stand characteristics and soil properties, in particular including more data on fine roots based on a unified measurement framework, will furnish greater potential for more robust conclusions.

Implications for belowground C dynamics

The current analysis attempts to comprehensively evaluate differences in FRB, FRP and FRT between plantations and natural forests across temperate and tropical forest ecosystems. Our results demonstrated that plantations had lower FRB and FRP but higher FRT compared with their adjacent natural forests, and these differences were partially explained by differences in stand characteristics and soil properties. These findings have important implications for understanding belowground C dynamics. First, the significant differences in FRB, FRP and FRT between plantations and natural forests indicate that plantations do not have the same belowground ecosystem functions as natural forests. Second, the variation in the difference in FRB between plantations and natural forests among plant genera and among roots of different diameters should be considered in future modeling to gain a better understanding of root dynamics under projected global land-use changes. Third, the relationship of stand characteristics and soil properties to the differences in FRB, FRP and FRT between plantations and natural forests can be incorporated into ecosystem models to improve the prediction of belowground C dynamics. Overall, the differences in fine root parameters between plantations and natural forests and their correlations with stand characteristics and soil properties, as revealed in this study, provide valuable insights into the understanding of belowground C dynamics that should not be overlooked when predicting the response of forest ecosystems to changes in land-use type.

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