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RESEARCH ARTICLE

Regenerated woody plants influence litter decomposition more than the dominant timber species present in a Chinese fir plantation

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Abstract

Background Plants can directly affect litter decomposition by producing litter materials of different qualities. However, whether living plants have indirect effects on litter decomposition by affecting changes in forest microenvironments is presently unclear in plantation forests.

Methods We addressed this issue by studying the decomposition of the leaf litter and fine roots of Chinese fir [*Cunninghamia lanceolata* (Lamb.) Hook.], a timber species widely planted in China, in 113 non-neighboring quadrats of varying basal area of the dominant plant species (i.e., Chinese fir) and distinct basal areas and species richness of regenerated woody plants (i.e., species other than Chinese fir) in a subtropical Chinese fir forest.

Results Our results showed that fine roots decomposed significantly more rapidly than leaf litter possibly because fine roots were easier access to mineralized nutrients and microbes compared with leaf litter. Further analyses showed that leaf litter and fine root decomposition rates were significantly controlled by the plant community attributes. The decomposition of both leaf litter and fine roots was mainly controlled by woody species regenerated during stand development rather than by Chinese fir. Specifically, leaf litter and fine root decomposition rates decreased with increasing basal area of regenerated woody plants, possibly due to nutrient competition and/or reduced photodegradation.

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Pan Yin and Kaiyan Zhai contributed equally to this work.

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Conclusions This study provides empirical evidence that woody species regenerated during stand development play a certain role in determining litter decomposition rates through plant-soil interactions in Chinese fir plantations. Regenerated woody plants should be considered in future studies on soil carbon and nutrient cycling in plantation forest.

Keywords Plant-soil interaction · Leaf litter decomposition · Fine root decomposition · Plantation forest · Plant community attributes · Regenerated woody plants

Introduction

Plant litter decomposition regulates carbon and nutrient recycling in terrestrial ecosystems (Handa et al. 2014), which is particularly important in a plantation forest because most of the nutrients needed for plant growth are derived from the release of elements during plant litter decomposition (Cao et al. 2020). Plants can directly affect litter decomposition by producing different litter materials that have different chemical traits. Generally, high litter decomposition rates are usually associated with high concentrations of initial nitrogen (N) and phosphorus (P), a low carbon to nitrogen ratio (C:N ratio) and a low carbon to phosphorus ratio (C:P ratio) (Aerts 1997; Sun et al. 2018; Zhang et al. 2016). In addition, living plants can also indirectly influence litter decomposition through the changing micro-environmental conditions and soil microbial activity (Ball et al. 2009). However, the direction and extent of these indirect effects have not been well evaluated.

The indirect effects of living plants on litter decomposition are generally considered to be associated with 'species energy theory' (Whittaker 2006). Plants with high abundance/biomass could input more substrates (plant litters and root exudate) into soils than other plants, which could improve soil microbial biomass and activity (Chen et al. 2020), accelerating plant litter decomposition (Lohbeck et al. 2015). In fact, Van Der Krift et al. (2002) reported that the presence of living plants tended to accelerate the decomposition rate of dead roots in a grassland ecosystem. A classic case from the 'Jena Biodiversity Experiment' also illustrated that increased plant diversity could presumably contribute to enhanced litter decomposition in a grassland ecosystem (Milcu et al. 2008). However, other studies have shown that living plants suppress litter decomposition due to strong nutrient competition between plants and soil decomposers through resource competition, which is termed 'Gadgil effect' (Averill et al. 2014; Gadgil and Gadgil 1971). For example, plant litter decomposition was reported to be high in root-trenched plots in some ecosystems (Brzostek et al. 2015), and this effect was particularly strong in nutrient-poor areas. Moreover, the suppressing effect of living plants on litter decomposition was also explained by the plant-induced changes in microclimate conditions (i.e., light transmittance, moisture, and temperature) on the forest floor (Hobbie et al. 2006). Previous studies showed that thinning (Trentini et al. 2017) and understory removal (Zhao et al. 2013) significantly enhanced soil temperature and decreased soil moisture, which resulted in higher plant litter decomposition rates. Consequently, our understanding of the complex response of plant litter decomposition to living plants is still limited in forest ecosystems, although this effect is thought to be stronger in forests than in other ecosystems due to the longevity of trees relative to other plants (Joly et al. 2017b).

In China, plantation area amounts to approximately 69.33 million hectares, which is one-third of the total plantation area in the world, ranking first globally (State Forestry Administration of China 2018). In such plantations, plant litter (such as aboveground leaf litter and belowground fine root litter) is mainly derived from the dominant species planted for timber production (i.e., timber species) or other commercial uses, and its decomposition might be affected by the abundance/biomass of the dominant planted species. According to 'species energy theory' (Whittaker 2006), a large abundance/biomass of dominant planted species may support the growth of decomposers and accelerate litter decomposition. In addition, native woody plants that regenerate in the understory strata during stand development (i.e., regenerated woody plants) may also play important roles in promoting biodiversity and the ecological functions of plantation ecosystems (Chen et al. 2019c; Rago et al. 2021). Regenerated woody plants maintain biodiversity in plantations (Rago et al. 2021); thus, a high richness of regenerated woody plants may promote fungi and fungal guild diversity, leading to increased litter decomposition (Xiao et al. 2019). However, we still lack empirical evidence about how regenerated woody plants influence litter decomposition.

Forests are mainly distributed in regions that have relatively complex topography, and plant litter decomposition might also be affected by abiotic environmental factors, such as topography (Scowcroft et al. 2000) and soil properties (Craine et al. 2007; Van Huysen et al. 2016) in such ecosystems. In fact, several studies have shown that various topographical landforms result in different environmental conditions, thereby altering litter decomposition by changing soil microbial activity (Scowcroft et al. 2000). For example, Sariyildiz (2015) found that that litter decomposed faster in areas with a south-facing aspect and bottom slope position than in those with a north-facing aspect and top slope position because the areas with a south-facing aspect and bottom slope position had higher soil temperatures, favoring decomposers. A positive effect of soil water content on litter decomposition was also reported in both laboratory incubation and field experiments (Lee et al. 2014; Zhong et al. 2017). In addition, field incubation experiments with P addition have illustrated that soil phosphorus influences litter decomposition, especially in P-limiting subtropical ecosystems (Van Huysen et al. 2016; Wieder et al. 2009). Therefore, it is essential to unravel these effects investigations of the relationships between living plants and litter decomposition.

Chinese fir (*Cunninghamia lanceolata* [Lamb.] Hook) is the most important planted species in subtropical China, and its plantation area has reached 9.9 million ha (State Forestry Administration of China 2018). In this study, we evaluated the role of living plants in regulating the spatial pattern of litter decomposition in a Chinese fir plantation. By using a litterbag technique, we measured the decomposition rates of leaf litter and fine root of Chinese fir in 113 quadrats containing varying numbers of Chinese fir and regenerated woody plants in a Chinese fir plantation. We hypothesized that (H1) the abundance/biomass of living plants, including dominant timber species (i.e., Chinese fir) and regenerated woody plants, can significantly accelerate litter decomposition, and this effect is mainly mediated by the dominant timber species due to the high abundance of Chinese fir (Whittaker 2006; Grime 1998); and (H2) regenerated woody plants can favor litter decomposition due to their high biodiversity (Milcu et al. 2008; Joly et al. 2017b).

Materials and methods

Study site

This study was carried out in a subtropical Chines fir plantation forest in the Yingzuijie National Nature Reserve (26°46’ N-26°59’ N, 109°49’E -109°58’ E), which is located in Huitong County, Hunan Province, China. The study area has a humid mid-subtropical monsoon climate. The mean annual temperature is 16.5 °C and the mean annual precipitation is 1,200 mm. The Yingzuijie Nature Reserve is one of the most biodiverse animal and plant biosphere reserves in subtropical China and covers an area of approximately 159 km^2, with elevations ranging from 270 to 938 m above sea level (asl) within Xuefeng Mountain in Hunan Province (Zeng et al. 2016).

In 2013, we followed the forest plot construction standard of the CTFS (Center for Tropical Forest Science) and established a 9-ha (300 × 300 m) long-term, stationary, dynamic monitoring plot (here after referred to as the HTF plot) in a Chinese fir plantation in the Yingzuijie National Nature Reserve in Huitong County. The HTF plot was divided into 225 quadrats (each 20 × 20 m). The Chinese firs in the HTF plot were planted at an initial planting density of 2 m × 2.3 m, and the age of this forest in 2021 was 30 years.

Experimental design

We choose Chinese fir leaf litter and fine roots as substrates to test the effects of living plants on litter decomposition across 113 non-neighboring quadrats in the HTF plot (Fig. S1). Leaf litter and fine roots were collected in the forests near the HTF plot. For leaf litter, only fallen leaf litter with complete shapes were selected, whereas leaves with apparent signs of herbivory and fungal attacks or those that were still green were excluded. For fine roots, we collected them from 0–40 cm soil horizon. Only fine roots with diameters less than 0.8 mm were chosen because previous studies showed that Chinese fir fine roots with such diameters are mainly absorptive roots that have high turnover rates and play an important role in carbon cycling (Yin et al. 2020). All litter material and roots were air-dried at room temperature immediately after collection and then stored.

Nylon litterbags of 0.1 mm mesh-size were chosen to avoid the litter fragment loss that occurs when mesh bags of larger mesh sizes are used in the field (Coq et al. 2010). The litterbags were 15 × 15 cm and were filled with 5.0 g of air-dried leaf litter or 0.5 g of air-dried fine roots. Due to the challenges and heavy workload associated with fine root collection, we only used 0.5 g fine roots as our experimental materials. To overcome the high spatial heterogeneity that existed within each plot under field conditions, the litterbags of both leaf litter and fine root were replicated 10 times in each chosen quadrat. To better simulate the decomposition in nature, leaf litterbags were exposed on the surface soil, and the root litterbags were buried in the soil with a soil depth is under the surface of 10 cm. Thus, a total of 2, 260 litter bags (2 litter types × 113 quadrats × 10 replicates) were placed in 113 quadrats on September 25, 2019. All litterbags were retrieved after a total of 383 d of field exposure. The remaining litter was gently rinsed with tap water as soon as it was harvested to remove soil particles, dried at 60 °C to constant mass, and then weighed. The calculation of mass loss was based on the following equation:

$$mass\ loss(\%) = \left(M_0 - M_t\right)/M_0 \times 100$$

where M_t is the final dry mass at 60 °C, and M_0 is the initial mass of leaf litter or fine roots converted into the equivalent mass at 60 °C.

The mass loss values of each litter type within each plot were averaged, and the mean values were used for further analyses, leading to a total of 226 values (2 litter types × 113 quadrats).

Vegetation survey and plant attributes calculation

All living trees with a diameter at breast height (DBH) ≥ 1 cm were identified, labelled, measured, and mapped following the standard protocols of the CTFS in 2020. The results showed that the 34,364 tree individuals belonged to 133 species, 75 genera, and 40 families. In this study, we defined all these species except *C. lanceolata* as regenerated woody plants in each quadrat. Within the dynamic monitoring plot, 113 quadrats were selected to conduct the litter decomposition experiment, and these quadrats contained different combinations of Chinese fir and locally regenerated woody plants, with the richness of regenerated woody plants ranging from 1 to 37. The species numbers of regenerated woody plants in the specific quadrat were used to characterize the species richness of regenerated woody plants (i.e., regenerated woody plant richness; RR). The relative basal area of *C. lanceolata* (i.e., CBA) and regenerated woody plants (i.e., RBA) in each quadrat were used to characterize the abundance of Chinese fir and regenerated woody plants, respectively. Relative basal area means the basal area in each quadrat converted into the basal area per hectare, and it was calculated based on the following equation:

$$relative\ basal\ area = \sum\nolimits_0^m \sum_0^{n_j} \left(\pi \times \left(DBH_k * 0.01/2\right)^2\right)/(A * 0.0001)$$

where m is 1 (when calculating CBA) or the species number of regenerated woody plants in the specific quadrat, n_j is the tree numbers of the specific species m_i in each quadrat,DBH_k is the diameter at breast height (*DBH*; cm) of tree k. A is the area (400 m^2) of each quadrat.

Soil sampling and physicochemical analysis

In May 2019, 16 soil cores (0–10 cm in the topsoil layer) were randomly collected within each plot and then mixed as a composite sample. All soil samples were sieved through a 2.0-mm mesh and then used to measure soil physio-chemical properties. In total, we measured 6 indicators to characterize soil properties: soil water content (SWC), soil available nitrogen (AN; [$i.e., NH_4^+ + NO_3^-$]), soil available phosphorus (AP; [$i.e., PO_4^{3-}$]), soil organic carbon (SOC), total nitrogen (TN) and total phosphorus (TP). Determinations of soil water contents and soil nutrients were conducted as described by national standard methods (Liu 1996). Briefly, AN was extracted by 2 mol L^{-1} KCl solution and AP was extracted by 0.03 mol L^{-1} NH_4F-0.025 mol L^{-1} HCl solution, and then determined by a continuous-flow analyzer (AA3, SEAL Analytical, Australia). The concentrations of SOC and TN were determined by an elemental analyzer (Vario Macro Elementar, GmbH, Germany). TP concentrations were determined by inductively coupled plasma-mass spectrometry (ICP-Q, Thermo Scientific, America) after the samples were digested with HNO_3 and HF solution (at a volume ratio of 5:1).

Litter chemical analyses

Carbon (C), nitrogen (N) and phosphorus (P) contents for leaf litter and fine roots were measured using a subsample collected in the forests near the HTF plot. Leaf litter and fine roots were dried at 60 °C and ground before chemical determination. The concentrations of C and N were determined by an elemental analyzer (Vario Macro Elementar, GmbH, Germany). P concentrations were determined by a continuous-flow analyzer (AA3, SEAL Analytical, Australia) after the samples were digested with HNO_3 and $HClO_4$ solution (at a volume ratio of 5:1).

Topographic indicator determination and calculation

In 2013, the geographic coordinates and the elevation of each corner of the 225 plots within the HTF plot were measured by the electronic total station (KTS-442LLCN; KOLIDA, China). The elevation raster of each 20 × 20 m quadrat was obtained from the elevation at the four corners of each quadrat using kriging interpolation (Burrough 1986; McBratney and Webster 1986). The slope and aspect of each quadrat were calculated in ArcGIS 10.6 (ESRI 2018) based on the elevation raster. Then we extracted the mean values of elevation, slope, and aspect from each 20 × 20 m quadrat. Additionally, to better express aspect, we took the transformed values of $aspect_0$ derived from ArcGIS 10.6 as the aspect values in the data analyses and used the following transform formula:

$$aspect = sin(\pi \times aspect_0/360)$$

where $aspect_0$ (0–360°) identified the direction of the downhill slope faces, indicating the compass direction of the surface faces at the given location, and $aspect$(0 to 1; the higher the value is, the more southwards the aspect) was the transformation of the original values of $aspect_0$.

Data analyses

Paired Student's t-test was used to compare the difference in mass loss between leaf litter and fine roots. Then, we conducted correlation analyses to evaluate the relationships between the mass loss of litter (including leaf litter and fine roots) and potential explanatory variables. Given the strong connections and inter-correlations among the various factors (Fig. S4), partial correlation analysis was used to test whether the effect of living plants on mass loss was maintained when accounting for the individual factors of topography, soil properties, and other plant community attributes (Chen et al. 2019a). In addition, to disentangle the effects of these biotic and abiotic variables on the mass loss of leaf litter and fine roots, respectively, the individual variables were subjected to multiple regression model selection. Before multiple regression model analyses, mass loss was logit-transformed (Warton and Hui 2011) to ensure normal distribution and homoscedasticity of residuals. Predictors were standardized (average = 0 and SD = 1) to eliminate unit dimension effects. All models were performed following R syntax: (mass loss ~ $predictor_a$ + [...] + $predictor_n$). In all models, the variables showing variance inflation factor (VIF) values greater than 3 were removed from the models to avoid multicollinearity. The VIF values were calculated using the R package 'car'. Model selection was performed using the 'dredge' function of the 'MuMIn' package based on the corrected Akaike information criterion (AICc). For each explanatory variable, we estimated relative importance (Σwi) by summing AIC weights in overall models in which the explanatory variable appeared (Burnham and Anderson 2002). Then, we defined the important variables as those explanatory variables with Σwi > 0.4 following Burnham (2015) and reported the R^2 of the most parsimonious model including all important variables. Finally, we used the 'lavaan' package to construct structural equation models (SEM) to illustrate the relationship among all important variables and mass loss of leaf litter or fine roots. All data analyses were performed using R software, v.3.4.4 (R Core Team 2018).

Results

Differences in the decomposition rate between leaf litter and fine root

The leaf litter and fine roots of Chinese fir used in our study exhibited a great difference in the initial litter chemistry properties. The C, N, and P concentrations of leaf litter were much higher than those of fine roots (Table 1). However, the C:N, C:P, and N:P ratios of leaf litter were significantly lower than those of fine roots (Table 1). After exposure for 383 days in the field, the

Table 1 Initial chemical properties of *Cunninghamia lanceolata* leaf litter and fine root

	C mg/g	N mg/g	P mg/g	C:N ratio	C:P ratio	N:P ratio
leaf litter	479.25 ± 0.15	8.06 ± 0.07	0.39 ± 0.01	59.45 ± 0.53	1238.02 ± 36.54	20.84 ± 0.72
fine root	454.01 ± 0.18	6.40 ± 0.04	0.27 ± 0.02	70.93 ± 0.38	1725.23 ± 124.69	24.35 ± 1.87

Table 1 shows the mean ± standard error of 5 samples

fine roots (42.28 ± 5.77%) decomposed significantly faster than leaf litters (40.56 ± 7.65%), and the mass loss variation of leaf litter (CV = 18.86%) was higher than that of fine roots (CV = 13.64%; Table 2) across the 113 quadrats. Additionally, the mass loss in leaf litter and fine roots were positively and significantly correlated ($R^2 = 0.3$; $p < 0.05$; Fig. 1b).

Effects of plant attributes on leaf litter and fine root decomposition

In this study, we evaluated the role of living plants in regulating plant litter (leaf litter and fine roots) decomposition in a Chinese fir plantation. The effect of living plants on plant litter decomposition varied between leaf litter and fine roots. Correlation analysis showed that the total basal area of living plants was significantly and negatively related to the decomposition of leaf litter ($R^2 = 0.09$, $P < 0.05$; Fig. 2a), but not to that of fine roots ($P = 0.3$; Fig. 2a). In addition, the decomposition of both leaf litter ($R^2 = 0$, $p = 0.8$; Fig. 2b) and fine roots ($R^2 = 0$, $p = 0.7$; Fig. 2b) was not affected by the basal area of Chinese fir. In contrast, we found that plant litter decomposition was mainly affected by regenerated woody plants. Leaf litter decomposed more slowly in quadrats with higher basal areas ($R^2 = 0.06$, $p < 0.05$; Fig. 2c) and richness ($R^2 = 0.08$, $p < 0.05$;

Table 2 Descriptive characteristics of topography, soil, plant and response variable in HTF plot

	Mean	SD	SE	C.V (%)	skewness	kurtosis	normtest.W	normtest.p
Topography								
Elevation (m)	420.03	19.42	1.83	4.62	0.10	-0.58	0.99	0.39
Slope (°)	30.29	8.49	0.80	28.02	-0.68	-0.18	0.95	< 0.001
Aspect	0.72	0.26	0.02	36.04	-0.90	-0.35	0.88	< 0.001
Soil properties								
SOC ($g{\cdot}kg^{-1}$)	65.63	17.89	1.68	27.26	0.71	0.46	0.96	< 0.001
TN ($g{\cdot}kg^{-1}$)	4.03	1.09	0.10	27.09	1.26	3.11	0.91	< 0.001
TP ($g{\cdot}kg^{-1}$)	3.64	1.13	0.11	31.12	0.99	0.46	0.92	< 0.001
AN ($mg{\cdot}kg^{-1}$)	26.35	5.86	0.55	22.25	0.42	0.35	0.98	0.18
AP ($mg{\cdot}kg^{-1}$)	10.53	5.53	0.52	52.51	2.03	4.33	0.77	< 0.001
SWC (%)	50.26	5.22	0.49	10.39	0.76	0.65	0.96	< 0.01
Plant attributes								
TBA ($m^2{\cdot}hm^{-2}$)	37.84	7.05	0.66	18.63	-0.75	1.82	0.97	< 0.01
CBA ($m^2{\cdot}hm^{-2}$)	29.11	9.95	0.94	34.19	-0.61	-0.03	0.97	< 0.01
RBA ($m^2{\cdot}hm^{-2}$)	8.73	7.32	0.69	83.85	0.80	-0.16	0.92	< 0.001
RR	19.90	7.93	0.75	40.00	-0.47	-0.59	0.96	< 0.001
Response variable								
Leaf mass loss (%)	40.56	7.65	0.72	18.86	0.45	-0.07	0.97	< 0.05
Root mass loss (%)	42.28	5.77	0.93	13.64	0.08	-0.35	0.99	0.60

TBA The basal area of total investigated plants; *CBA* The basal area of *C. lanceolata*; *RBA* The basal area of regenerated woody plants; *RR* The richness of regenerated woody plants; *SOC* Soil organic carbon; *TP* Total phosphorus; *AN* Available nitrogen; *AP* Available phosphorus; *SWC* Soil water content

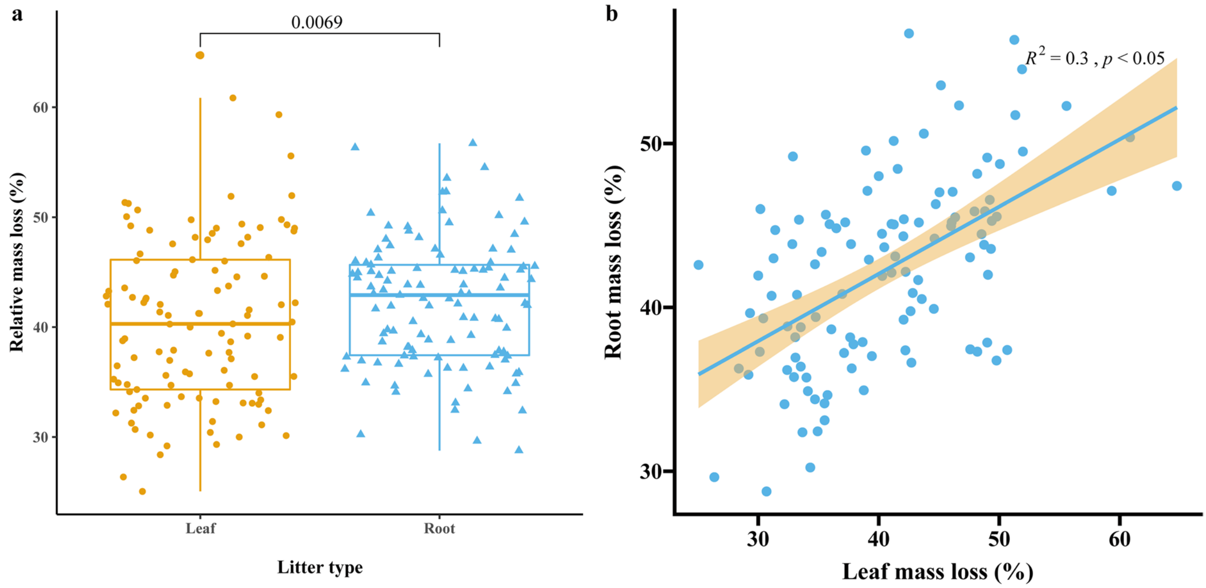

Fig. 1 (**a**) Relative mass loss of leaf (yellow box) and root (blue box) in a *C. lanceolata* forest. Student's t-test was performed to examine the significant difference in mass loss between different litter types (leaf and root). (**b**) Regression line showing the relation of leaf mass loss and root mass loss in a *C. lanceolata* forest

Fig. 2d) of regenerated woody plants, but this pattern was not found for fine root decomposition ($p > 0.05$; Fig. 2a, c, and d). Partial correlation analysis showed that leaf litter decomposition continued to be significantly correlated with the basal area and richness of regenerated woody plants in most cases after controlling for the topography and soil effects (Fig. 3a), and fine root decomposition was still not affected by plant community attributes.

Effects of topography and soil properties on leaf litter and fine roots decomposition

The decomposition of leaf litter and fine roots was also affected to some extent by topography and soil properties. The leaf litter decomposition rate significantly decreased with elevation ($R^2 = 0.17$, $p < 0.05$; Fig. S2a) and slope ($R^2 = 0.04$, $p < 0.05$; Fig. S2b) and increased from the north-facing to south-facing aspect ($R^2 = 0.06$, $p < 0.05$; Fig. S2c) across all quadrats; fine root decomposition increased from the north-facing to south-facing aspect ($R^2 = 0.04$, $p < 0.05$; Fig. S2c) but was not affected by the elevation and slope ($P > 0.05$, Figs. S2a and S2b). We also found that leaf litter decomposed much faster in quadrats with high concentrations of soil TP ($R^2 = 0.06$, $p < 0.05$; Fig. S2f), AN ($R^2 = 0.06$, $p < 0.05$; Fig. S2g), and AP ($R^2 = 0.08$, $p < 0.05$; Fig. S2h), but those patterns were not found for fine root decomposition. It should be noted that the concentrations of SOC, TN, and SWC had little effect on the decomposition of leaf litter and fine roots in the studied Chinese fir plantation (all $p > 0.05$, Fig. S2). Partial correlation analysis showed that the effects of topography and soil properties on leaf litter decomposition were still significant in most cases, even after filtering the effect of living plants (Fig. 3a). These results implied that the decomposition of leaf litter and fine roots might be independently influenced by living plants and abiotic factors.

Combined effects of abiotic and biotic factors on the decomposition of leaf litter and fine root

The combined effect of plant attributes (i.e., CBA and RBA), topography (i.e., elevation and aspect) and soil properties (i.e., AN) in the global model explained a total of 32% of the variance in leaf litter decomposition (Table 3). CBA, RBA, and elevation had negative effects, while aspect and soil AN had a positive effect on leaf litter decomposition (Table 3).

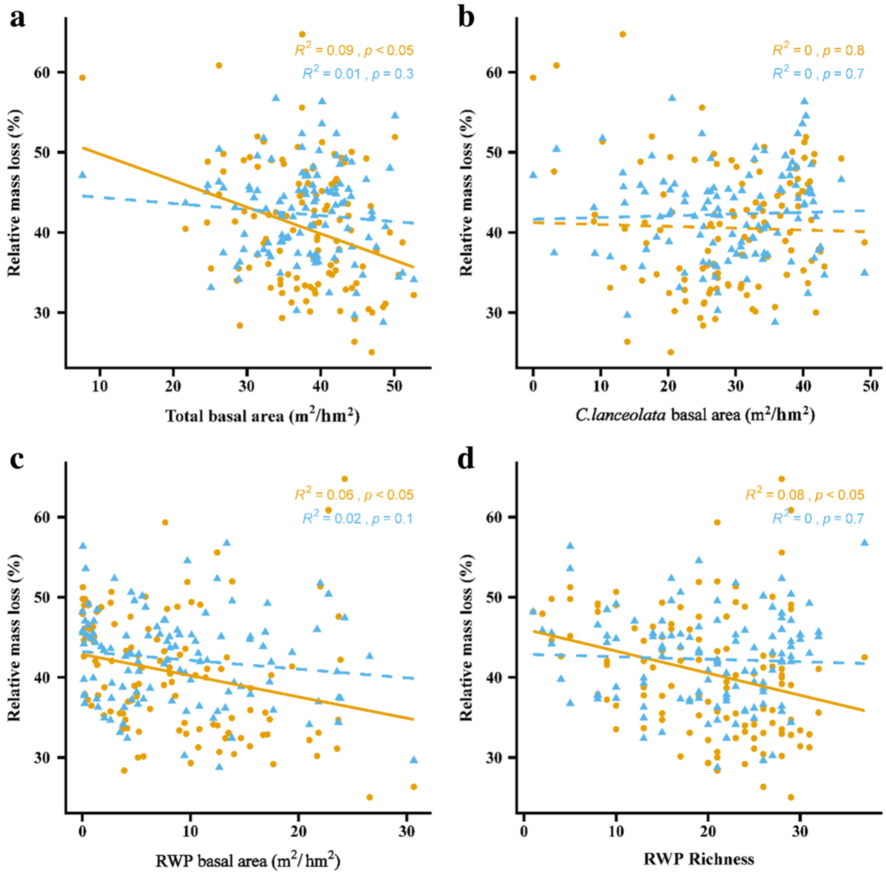

Fig. 2 Regression lines showing the effects of plant attributes on leaf (yellow circle) and root (blue triangle) mass loss in a *C. lanceolata* forest. Plant attributes: (**a**) total basal area, (**b**) basal area of *C. lanceolata*, (**c**) basal area of regenerated woody plants, (**d**) richness of regenerated woody plants. The solid and dashed lines indicate significant and no significant effects, respectively

After assessing the relative importance of each predictor in the optimal models, RBA (Σwi = 0.55; Table 3) was more important for the regulation of leaf litter decomposition than CBA (Σwi = 0.42; Table 3). The most important predictors of leaf litter decomposition were elevation, aspect, and soil nitrogen availability (all Σwi = 1; Table 3). In addition, fine root decomposition was best explained by RBA, RR, elevation, slope, aspect, and AN, which explained 16% of the variance (Table 3). RBA, elevation, and slope showed similar negative effects on fine root decomposition as that on leaf litter decomposition (Table 3). RR, aspect, and AN all showed positive effects on the decomposition of fine roots (Table 3). Both RBA (Σwi = 0.74) and RR (Σwi = 0.83) had important influence on fine root decomposition, while CBA did not (Σwi = 0.14 < 0.4; Table 3). The most important predictor of fine root decomposition was soil nitrogen availability (Σwi = 1; Table 3).

Structural equation modelling analysis revealed that the combined effect of plant attributes, soil properties, and topography explained 32% and 16% of the variance in the mass loss of leaf litter and fine roots (Fig. 4a-b), respectively. Of the tested variables in the SEMs, elevation had the largest standardized effect on leaf litter decomposition (r = -0.40); elevation not only had a significant direct negative effect (r = -0.32) on leaf litter decomposition but also had a significant indirect negative effect (r = -0.08) by increasing the RBA. RBA not only had a direct negative effect (r = -0.28) on leaf litter decomposition but also had an indirect negative effect (r = -0.10) by decreasing AN. Aspect (r = 0.26) and AN (r = 0.20) only had direct positive effects on leaf litter decomposition. CBA had the least standardized effect (r = -0.05) and only indirectly affected leaf litter decomposition by decreasing AN (Fig. 4a and c). With regard to fine root decomposition, RR had the largest standardized effect and only had a direct positive effect on fine

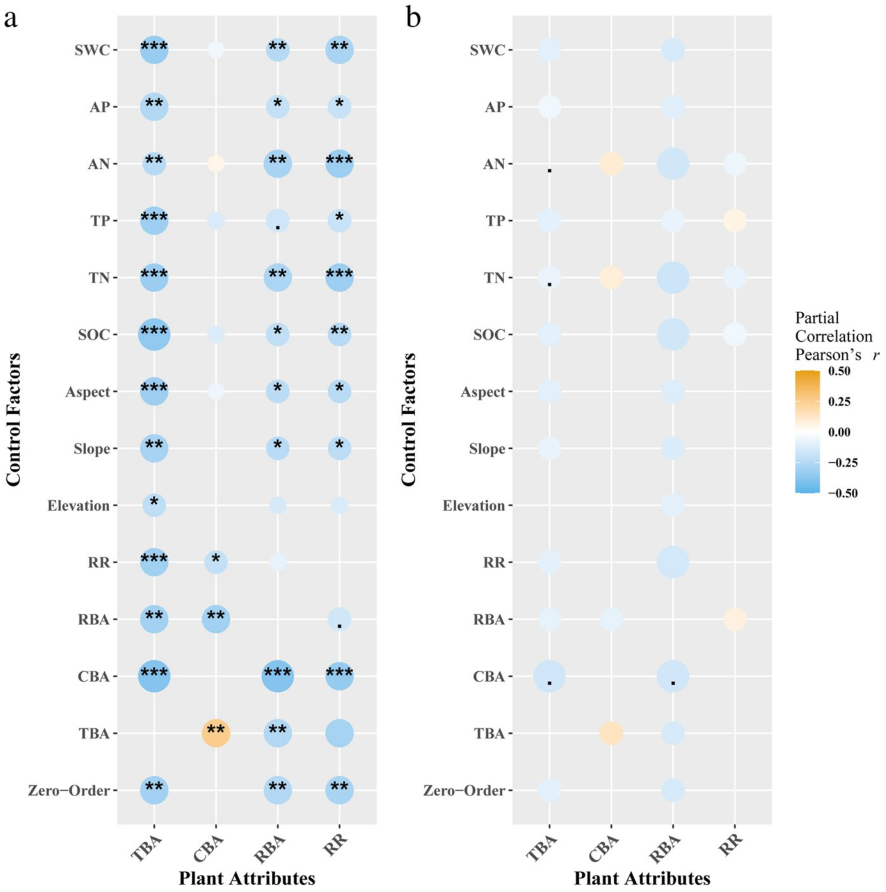

Fig. 3 Partial correlations between plant attributes and (**a**) the leaf relative mass loss, (**b**) the root relative mass loss after controlling topography, soil properties and other plant attributes. The x-axis shows the plants attributes of which the correlations with the mass loss are examined. The y-axis shows the zero-order (without controlling any factors) and the factors being controlled. The size and color of the circles indicate the strength and sign of the correlation. Differences in circle size and color between the zero-order and controlled factors indicate the level of dependency of the correlation between the mass loss and the examined factor on the controlled variable (no change in circle size and color between the controlled factor and zero-order = no dependency; a decrease/increase in circle size and color intensity = loss /gain of correlation). Abbreviation and unit for each given variable is explained in Table 2. Note: (.$p < 0.1$; *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$)

root decomposition ($r = 0.36$). RBA had a direct negative effect ($r = -0.29$), while AN had a direct positive effect ($r = 0.19$) on fine root decomposition. Elevation had a direct negative effect ($r = -0.20$), an indirect negative effect through increasing RBA ($r = -0.10$), and an indirect positive effect through increasing RR ($r = 0.15$) on fine root decomposition. Aspect not only had a direct positive effect ($r = 0.19$) on fine root decomposition but also had an indirect negative effect (r = -0.06) by decreasing the RR. Slope not only directly decreased fine root decomposition ($r = -0.21$) but also indirectly increased fine root decomposition ($r = 0.11$) by increasing the RR (Fig. 4b and d).

Discussion

To the best of our knowledge, this study represents the first attempt to assess the effects of living plants on plant litter decomposition in plantation forests. Through a field incubation involving leaf litter and fine roots, our empirical study clearly showed that plant litter decomposition was significantly regulated by living plants, and this regulation was mainly mediated by the native woody plants regenerated during stand development (i.e., regenerated woody plants). Various statistical methods, including partial correlation analysis, multiple linear regression analysis,

Table 3 Output of multiple linear models testing the combined effects of aboveground plant attributes, topography and soil fertility retained variables on leaf litter and fine root mass loss rates

	Leaf litter mass loss					Fine root mass loss			
	Slope (±SE)	Σwi	R^2	AICw		Slope (±SE)	Σwi	R^2	AICw
CBA	**-0.21 (±0.12)$^{\#}$**	**0.42**	**0.32**	**0.09**	CBA		0.14	**0.16**	**0.12**
RBA	**-0.28 (±0.13)***	**0.55**			RBA	**-0.29 (±0.13)***	**0.74**		
RR					RR	**0.36 (±0.15)***	**0.83**		
Elevation	**-0.32 (±0.09)*****	**1.00**			Elevation	**-0.20 (±0.10)$^{\#}$**	**0.63**		
Slope		0.18			Slope	**-0.21 (±0.11)***	**0.54**		
Aspect	**0.26 (±0.08)****	**1.00**			Aspect	**0.19 (±0.10)$^{\#}$**	**0.95**		
SOC		0.38			SOC				
TP		0.03			TP		0.09		
AN	**0.20 (±0.09)***	**1.00**			**AN**	**0.19 (±0.09)***	**1.00**		
AP		0.32			AP		0.38		
SWC		0.23			SWC		0.09		

For each group of variables, we report the slope (±SE) of each variable and its relative importance (sum of Akaike information criterion (AIC) weights (Σwi) over all models including the explanatory variable bound between 0 (not important) and 1 (relevant)). We also report the R^2 and its AIC weight (AICw) of the most parsimonious model. The variables retained in the most parsimonious models are in bold and the variables with different significant level were note as following: (#$p<0.1$; *$p<0.05$; **$p<0.01$; ***$p<0.001$). Abbreviation and unit for each given variable is explained in Table 2

and structural equation modelling analysis, provided robust results to demonstrate the effects of living plants on litter decomposition. These findings provide complementary evidence for understanding the importance of plant–soil interactions in driving litter decomposition and emphasize the urgent need to investigate the role of regenerated woody plants in soil carbon and nutrient cycling in plantation forests.

Differential response of decomposition of leaf litter and fine roots to biotic factors

In the current study, we found that the fine root of Chinese fir decomposed more rapidly than the leaf litter (Fig. 1 and Table 1) across the studied Chinese fir plantation. This is unlikely to be caused by the difference in their initial qualities since both the N and P concentrations in leaf litter were much higher than those in the fine root. In contrast, this difference in decomposition rate between fine root and leaf litter might be related to their incubation depths during decomposition. To better simulate the natural decomposition environment, fine roots were buried in the soil, while leaf litter was left on the surface soil. The fine roots thus had easier access to mineralized nutrients and microbes in the soil (Fujii and Takeda 2012; Ostertag and Hobbie 1999), which in part may explain the higher mass loss compared to leaf litter. Similar results were also found in previous studies (Fujii and Takeda 2012; Jacobs et al. 2018).

Before starting the experiment, based on the 'species energy theory' (Whittaker 2006), we hypothesized that (H1) plants that have higher abundance/biomass might contribute more nutrients and energy to the soil, stimulating soil microbial biomass and activity and accelerating plant litter decomposition. However, we found that plant abundance/biomass, expressed as tree basal area, had a significant inhibitory effect on leaf litter decomposition in the studied Chinese fir plantation (Figs. 2 and 3). This effect might be attributed to the following two reasons. One is related to the competition for nutrients between plants and soil decomposers. Plants in the quadrats with higher basal areas need to take up more inorganic nutrients from the soil to support their growth and thus decrease leaf litter decomposition by suppressing soil microbial biomass and activities (Kuzyakov and Xu 2013; Zhu et al. 2016). Our SEM showed that both increases in the abundance of Chinese fir and regenerated woody plants retarded leaf litter decomposition by decreasing available nitrogen (Fig. 4a), which may also imply that competition for available nitrogen between plants and decomposers

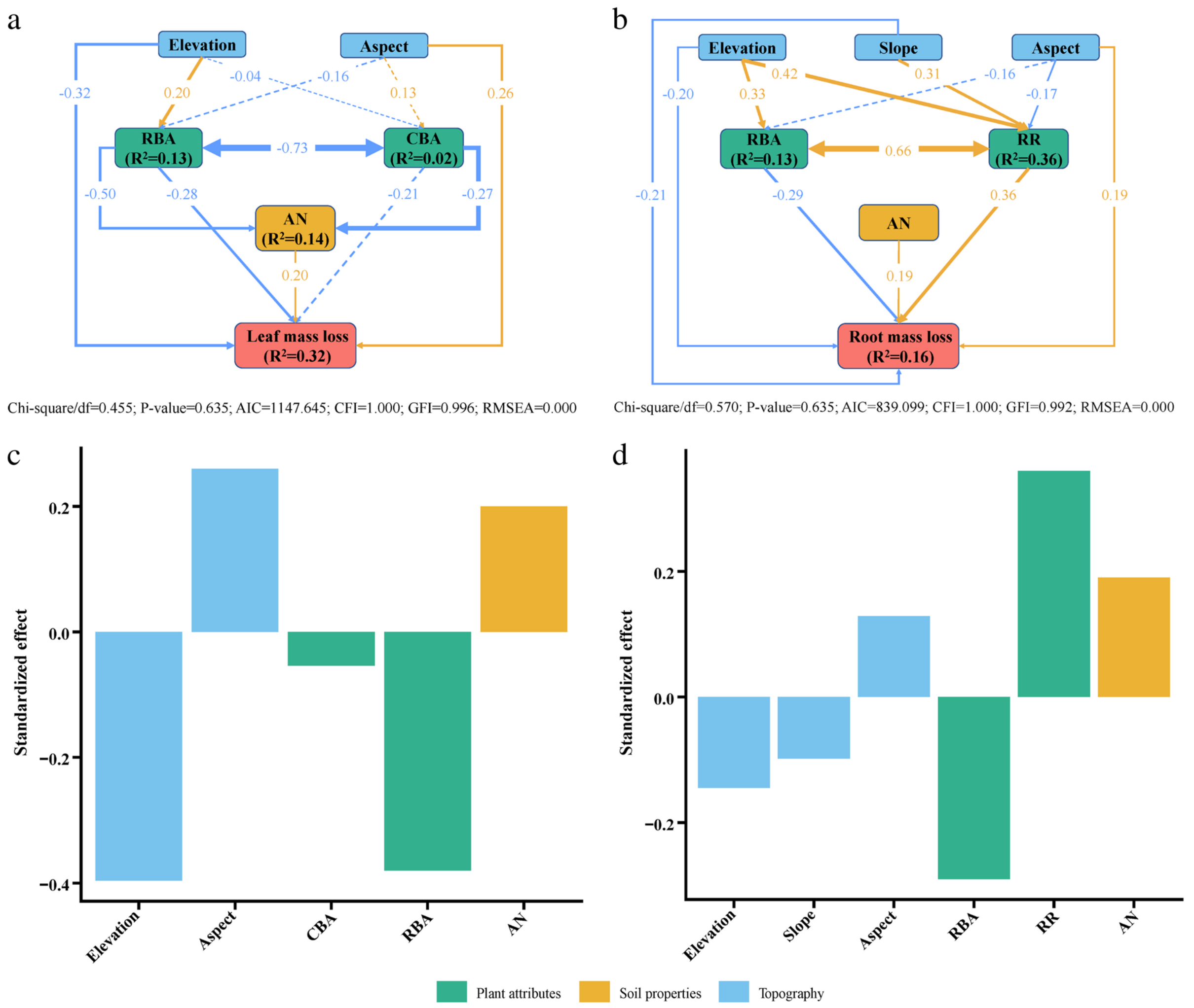

Fig. 4 Direct and indirect effects of plant attributes, soil properties and topography on the litter decomposition. The structural equation modelling was conducted for mass loss of two litter tissue: (**a**) leaf mass loss; (**b**) root mass loss. Single-headed arrows indicate the hypothesized direction of causation. Gold and blue arrows indicate positive and negative relationships, respectively. Solid and dotted arrows indicate significant and insignificant relationship, respectively. The arrow width is proportional to the strength of the relationship. The numbers adjacent to the arrows are the standardized path coefficients. We also reported the total standardized effect of each predictor on (**c**) leaf mass loss; (**d**) root mass loss. Abbreviation and unit for each given variable is explained in Table 2

involved in leaf litter decomposition may exist in our study plantation. Previous studies also indicated that plant presence possibly retarded litter decomposition by reducing the availability of nitrogen for microbial immobilization to support decomposition (Moorhead et al. 1998; Brzostek et al 2015), while girdling increased the litter decomposition rate by reducing nutrient competition between rhizosphere microbes and enzyme-producing saprotrophs (Brzostek et al 2015). The second reason for this pattern is related to the modification of the microclimate driven by living plants (Kaye and Hone 2016). For example, Wang et al. (2021) reported that photodegradation is an important driver of decomposition in the mesic forest ecosystem. The high abundance/biomass of regenerated woody plants in our study was likely to result in more canopy cover and cause less light transmittance to the forest floor (Barbier et al. 2008), which could also reduce the photodegradation of leaf litter to some extent (Fig. 4a) and lower the soil temperature (Zhao et al. 2012), leading to the lower levels of biodegradation (Li et al. 2021) of leaf litter and fine roots observed in our study.

Moreover, we found that the inhibitory effect of plant abundance/biomass on leaf litter decomposition is mainly mediated by native woody plants regenerated during stand development (i.e., regenerated woody plants) and not by Chinese fir (Fig. 4a). This is consistent with a prior result that showed that understory removal significantly affected litter decomposition in the plantation ecosystems (Chen et al. 2019c). This observation might be explained by the difference in nutrient requirements between Chinese fir and regenerated woody plants. The studied plantation was in the late stages of stand development, and nutrient acquisition in Chinese fir declines at low growth rates; in contrast, the regenerated woody plants are generally young and in a fast-growing stage and have higher requirements for nutrients compared to Chinese fir. This may therefore result in different abilities of competition in Chinese fir and regenerated woody plants for nutrients with soil decomposers, resulting in contrasting effects on plant litter decomposition (Fig. 4a).

Although the effect of regenerated woody plants on fine root decomposition was not significant in the correlation analysis (Fig. 2c and d), we found that the decomposition of fine roots decreased with an increasing basal area of regenerated woody plants and increased with the richness of regenerated woody plants after accounting for other confounding factors (Table 3). This pattern partly supported our second hypothesis that (H2) regenerated woody plants can favor litter decomposition due to their high biodiversity. Generally, the diverse root exudates released by different regenerated woody plants are considered to stimulate soil microbial biomass (Eisenhauer et al. 2017) and enzyme activity (Barbe et al. 2017; Spohn et al. 2013), resulting in a higher fine root decomposition in our study.

Non-negligible effects of abiotic factors on litter decomposition

Although our results showed that plant attributes can explain certain variations in the decomposition of both leaf litter and fine roots across the Chinese fir plantation, it seems that other predictors, such as topography and soil properties, can play an even more important role in regulating the decomposition process (Table 3). We found that both leaf litter and fine roots decomposed faster in quadrats with lower elevation and south-facing aspects (Fig. S2 and Fig. S3; Table 3). Similar results have also been found in previous studies showing that decomposition is accelerated in areas with low elevations and/or south-facing aspects than in areas at higher elevations and/or north-facing aspects (Bohara et al. 2020; Sariyildiz 2015; Wang et al. 2009). These effects that are driven by topography might mainly relate to the alteration of temperature induced by topographic conditions. Although soil temperature was not measured in the current study, the different topographic conditions generally made a difference in soil temperature (Jasińska et al. 2019; Sariyildiz 2015). For instance, south-facing slopes generally receive more solar radiation, resulting in higher soil temperatures than north-facing slopes in the Northern Hemisphere (Jasińska et al. 2019; Sariyildiz 2015), which in turn facilitates decomposers and promotes litter decomposition (Sariyildiz 2015). The litter decomposition rate (expressed as mass loss or decay parameter *k*) declined with increasing elevation because decreasing temperature has also been reported in tropical and subtropical regions with elevation gradients greater than 1000 m (Salinas et al. 2011; Wang et al. 2009). In principle, it is unexpected that both leaf and root mass loss declined with increasing elevation in the subtropical study area, which had an elevation difference of only 100 m. However, a translocation experiment in a model subtropical forest also showed that only a 0.85 °C difference existed in soil temperature between low-elevation sites (30 m) and high-elevation sites (300 m); nonetheless, the effects of the soil temperature increase induced by altitudinal transplant on litter decomposition were still significant (Liu et al. 2017). These results implied that the microorganisms and enzymes involved in decomposition remained sensitive to the alterations in temperature induced by topographic conditions in subtropical areas with small elevation differences. Similarly, Bokhorst et al. (2010) noted that increasing temperature may stimulate litter decomposition as long as microbial activity is not limited by moisture and substrate levels. As precipitation is relatively abundant in subtropical areas and high soil water content in our studied plantation (Fig. S2i), soil decomposer activity in these areas may not be limited by soil moisture (Joly et al. 2017a) but may increase with increasing temperature, which may also be the reason why soil water content did not affect both leaf and root decomposition. In addition, we found that slope only played a negligible role in fine root decomposition (Table 3 and Fig. 4), although previous studies reported that slope had significant effects on litter decomposition rates through nutrient and energy redistribution (Hu et al. 2020).

Phosphorus is considered to be an important driver of litter decomposition in tropical and subtropical areas since the soils are generally highly weathered, and carbon and nutrient cycling in these areas may be limited by P availability (Wieder et al. 2009). However, we used correlation analysis to reveal that soil P availability only had a marginally significant effect on plant litter decomposition (both leaf litter and fine roots) and was not included in the most parsimonious model when other plant attribute-related variables were considered (Fig. S2h and Table 3). In contrast, we found that soil N availability was an important indicator in explaining the variation in the decomposition of both leaf litters and fine roots (Fig. S2g and Table 3), which is in line with previous results obtained from N addition experiments. For example, Zhong et al. (2017) and Xia et al. (2018) both found that enhanced soil N availability resulting from N addition significantly increased soil microbial activity and the decomposition of plant litter. These results indicate that decomposition processes might be constrained by soil N availability in subtropical Chinese fir plantations.

We found that the variance in leaf litter decomposition can be better explained by living plants and other environmental factors than that in fine root decomposition (Table 3; Fig. 4a and b). Similar to the difference in the decomposition rate between leaf litter and fine roots, this phenomenon is possibly related to the difference in incubation depths. Firstly, living plant mainly mediate soil ecological processes by producing litter materials of different quantities and qualities. However, dissolved organic materials leached from decomposing litters have difficulty reaching mineral soils and cause a dramatic change in soil microbial activity (Cotrufo et al. 2015; Zhang et al. 2019). For example, Chen et al. (2019b) reported that aboveground trees had significant influences on the soil microbial communities of the top layer of organic soil but did not affect deep mineral soils in subtropical forest ecosystems. Second, the environmental gradient (such as soil temperature) induced by elevation and aspect is larger at the surface than in the mineral layer of soil (Gong et al. 2016). Lastly, photodegradation might not be as important for buried fine roots. All of the abovementioned mechanisms can make it difficult to predict the spatial variance in fine root decomposition.

Conclusion

In the current study, we present clear evidence demonstrating the indirect effects of living plants on litter decomposition in a subtropical Chinese fir plantation forest. The decomposition of leaf litter and fine roots was inhibited by living plants, possibly due to nutrient competition and reduced photodegradation. In addition, we found that Chinese fir litter decomposition was mainly mediated by woody plants that were regenerated during stand development but not by Chinese fir. Thus, we should take regenerated woody plants into consideration in future studies on soil carbon and nutrient cycling, especially in plantation forest ecosystems.

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Author contributions Pan Yin: Investigation, Formal analysis, Data Curation, Visualization, Writing- Original draft. Kaiyan Zhai: Investigation, Data curation, Writing- Reviewing and Editing. Weidong Zhang, Silong Wang: Funding acquisition, Supervision, Project administration, Conceptualization, Methodology, Writing- Reviewing and Editing. Qingpeng Yang: Funding acquisition, Writing- Reviewing and Editing. Longchi Chen, Xin Yu, Qingkui Wang, Björn Berg: Writing- Reviewing and Editing. Xin Guan, Zhangquan Zeng, Munan Zhu: Investigation, Data curation.

Data availability The datasets analysed during the current study are available from the first and corresponding author on reasonable request.

Code availability The code analysed during the current study are available from the first and corresponding author on reasonable request.

Declarations

Competing interests The authors declare they have no relevant financial or non-financial interests to disclose.

References

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79(3):439–449. https://doi.org/10.2307/3546886

Averill C, Turner BL, Finzi AC (2014) Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. Nature 505:543–545. https://doi.org/10.1038/nature12901

Ball BA, Bradford MA, Coleman DC, Hunter MD (2009) Linkages between below and aboveground communities: decomposer responses to simulated tree species loss are largely additive. Soil Biol Biochem 41:1155–1163. https://doi.org/10.1016/j.soilbio.2009.02.025

Barbe L, Jung V, Prinzing A, Bittebiere AK, Butenschoen O, Mony C (2017) Functionally dissimilar neighbors accelerate litter decomposition in two grass species. New Phytol 214:1092–1102. https://doi.org/10.1111/nph.14473

Barbier S, Gosselin F, Balandier P (2008) Influence of tree species on understory vegetation diversity and mechanisms involved—a critical review for temperate and boreal forests. For Ecol Manage 254:1–15. https://doi.org/10.1016/j.foreco.2007.09.038

Bohara M, Acharya K, Perveen S, Manevski K, Hu C, Yadav RKP, Shrestha K, Li X (2020) In situ litter decomposition and nutrient release from forest trees along an elevation gradient in Central Himalaya. Catena 194. https://doi.org/10.1016/j.catena.2020.104698

Bokhorst S, Bjerke JW, Melillo J (2010) Impacts of extreme winter warming events on litter decomposition in a sub-Arctic heathland. Soil Biol Biochem 42:611–617. https://doi.org/10.1016/j.soilbio.2009.12.011

Brzostek ER, Dragoni D, Brown ZA, Phillips RP (2015) Mycorrhizal type determines the magnitude and direction of root-induced changes in decomposition in a temperate forest. New Phytol 206:1274–1282. https://doi.org/10.1111/nph.13303

Burnham KP (2015) Multimodel Inference: Understanding AIC relative variable importance values. [WWW document] URL https://sites.warnercnr.colostate.edu/kenburnham/wp-content/uploads/sites/25/2016/08/VARIMP.pdf. Accessed 1 June 2021

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Burrough PA (1986) Principles of Geographical Information Systems for Land Resources Assessment. Oxford University Press, New York

Cao J, He X, Chen Y, Chen Y, Zhang Y, Yu S, Zhou L, Liu Z, Zhang C, Fu S (2020) Leaf litter contributes more to soil organic carbon than fine roots in two 10-year-old subtropical plantations. Sci Total Environ 704:135341. https://doi.org/10.1016/j.scitotenv.2019.135341

Chen C, Chen HYH, Chen X (2020) Functional diversity enhances, but exploitative traits reduce tree mixture effects on microbial biomass. Funct Ecol 34:276–286. https://doi.org/10.1111/1365-2435.13459

Chen L, Liu L, Qin S, Yang G, Fang K, Zhu B, Kuzyakov Y, Chen P, Xu Y, Yang Y (2019a) Regulation of priming effect by soil organic matter stability over a broad geographic scale. Nat Commun 10:5112. https://doi.org/10.1038/s41467-019-13119-z

Chen L, Xiang W, Wu H, Ouyang S, Zhou B, Zeng Y, Chen Y, Kuzyakov Y (2019b) Tree species identity surpasses richness in affecting soil microbial richness and community composition in subtropical forests. Soil Biol Biochem 130:113–121. https://doi.org/10.1016/j.soilbio.2018.12.008

Chen Y, Zhang Y, Cao J, Fu S, Hu S, Wu J, Zhao J, Liu Z (2019c) Stand age and species traits alter the effects of understory removal on litter decomposition and nutrient dynamics in subtropical Eucalyptus plantations. Glob Ecol Conserv 20. https://doi.org/10.1016/j.gecco.2019.e00693

Coq S, Souquet JM, Meudec E, Cheynier V, Hattenschwiler S (2010) Interspecific variation in leaf litter tannins drives decomposition in a tropical rain forest of French Guiana. Ecology 91:2080–2091. https://doi.org/10.2307/25680461

Cotrufo MF, Soong JL, Horton AJ, Campbell EE, Haddix Michelle L, Wall DH, Parton WJ (2015) Formation of soil organic matter via biochemical and physical pathways of litter mass loss. Nat Geosci 8:776–779. https://doi.org/10.1038/ngeo2520

Craine JM, Morrow C, Fierer N (2007) Microbial nitrogen limitation increases decomposition. Ecology 88:2105–2113. https://doi.org/10.1890/06-1847.1

Eisenhauer N, Lanoue A, Strecker T, Scheu S, Steinauer K, Thakur MP, Mommer L (2017) Root biomass and exudates link plant diversity with soil bacterial and fungal biomass. Sci Rep 7:44641. https://doi.org/10.1038/srep44641

ESRI (2018) ArcGIS desktop: release 10.6. Environmental Systems Research Institute, Redlands, California, USA

Fujii S, Takeda H (2012) Succession of collembolan communities during decomposition of leaf and root litter: effects of litter type and position. Soil Biol Biochem 54:77–85. https://doi.org/10.1016/j.soilbio.2012.04.021

Gadgil RL, Gadgil PD (1971) Mycorrhiza and litter decomposition. Nature 233:133–133. https://doi.org/10.1038/233133a0

Gong XY, Giese M, Dittert K (2016) Topographic influences on shoot litter and root decomposition in semiarid hilly grasslands. Geoderma 282:112–119. https://doi.org/10.1016/j.geoderma.2016.07.017

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86:902–910. https://doi.org/10.1046/j.1365-2745.1998.00306.x

Handa IT, Aerts R, Berendse F (2014) Consequences of biodiversity loss for litter decomposition across biomes. Nature 509:218–221. https://doi.org/10.1038/nature13247

Hobbie SE, Reich PB, Oleksyn J (2006) Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87:2288–2297. https://doi.org/10.1890/0012-9658(2006)87[2288:tseoda]2.0.co;2

Hu A, Angerer J, Duan Y, Xu L, Chang S, Chen X, Hou F (2020) Effects of terrain on litter decomposition and nutrient release in typical steppe of Eastern Gansu Loess Plateau. Rangel Ecol Manage 73:611–618. https://doi.org/10.1016/j.rama.2020.06.004

Jacobs LM, Sulman BN, Brzostek ER, Feighery JJ, Phillips RP (2018) Interactions among decaying leaf litter, root litter and soil organic matter vary with mycorrhizal type. J Ecol 106:502–513. https://doi.org/10.1111/1365-2745.12921

Jasińska J, Sewerniak P, Markiewicz M (2019) Links between slope aspect and rate of litter decomposition on inland dunes. Catena 172:501–508. https://doi.org/10.1016/j.catena.2018.09.025

Joly FX, Kurupas KL, Throop HL (2017a) Pulse frequency and soil-litter mixing alter the control of cumulative precipitation over litter decomposition. Ecology 98:2255–2260. https://doi.org/10.1002/ecy.1931

Joly FX, Milcu A, Scherer-Lorenzen M, Jean LK, Bussotti F, Dawud SM, Muller S, Pollastrini M, Raulund-Rasmussen K, Vesterdal L, Hattenschwiler S (2017b) Tree species diversity affects decomposition through modified microenvironmental conditions across European forests. New Phytol 214:1281–1293. https://doi.org/10.1111/nph.14452

Kaye MW, Hone CM (2016) Removal of invasive shrubs alters light but not leaf litter inputs in a deciduous forest understory. Restor Ecol 24:617–625. https://doi.org/10.1111/rec.12363

Kuzyakov Y, Xu X (2013) Competition between roots and microorganisms for nitrogen: mechanisms and ecological relevance. New Phytol 198:656–669. https://doi.org/10.1111/nph.12235

Lee H, Fitzgerald J, Hewins DB, McCulley RL, Archer SR, Rahn T, Throop HL (2014) Soil moisture and soil-litter mixing effects on surface litter decomposition: a controlled environment assessment. Soil Biol Biochem 72:123–132. https://doi.org/10.1016/j.soilbio.2014.01.027

Li R, Guan X, Han J, Zhang Y, Zhang W, Wang J, Huang Y, Xu M, Chen L, Wang S, Yang Q (2021) Litter decomposition was retarded by understory removal but was unaffected by thinning in a Chinese fir [*Cunninghamia lanceolata* (Lamb.) Hook] plantation. Appl Soil Ecol 163. https://doi.org/10.1016/j.apsoil.2021.103968

Liu G (1996) Soil physical and chemical analysis and description of soil profiles (in Chinese). Standards press of China, Beijing

Liu J, Liu S, Li Y, Liu S, Yin G, Huang J, Xu Y, Zhou G (2017) Warming effects on the decomposition of two litter species in model subtropical forests. Plant Soil 420:277–287. https://doi.org/10.1007/s11104-017-3392-9

Lohbeck M, Poorter L, Martinez-Ramos M, Bongers F (2015) Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. Ecology 96:1242–1252. https://doi.org/10.1890/14-0472.1

McBratney AB, Webster R (1986) Choosing functions for semi-variograms of soil properties and fitting them to sampling estimates. J Soil Sci 37:617–639. https://doi.org/10.1111/j.1365-2389.1986.tb00392.x

Milcu A, Partsch S, Scherber C, Weisser WW, Scheu S (2008) Earthworms and legumes control litter decomposition in a plant diversity gradient. Ecology 89:1872–1882. https://doi.org/10.1890/07-1377.1

Moorhead DL, Westerfield MM, Zak JC (1998) Plants retard litter decay in a nutrient-limited soil: a case of exploitative competition? Oecologia 113(4):530–536. https://doi.org/10.1007/s004420050406

Ostertag R, Hobbie SE (1999) Early stages of root and leaf decomposition in Hawaiian forests: effects of nutrient availability. Oecologia 121:564–573. https://doi.org/10.1007/s004420050963

Rago MM, Urretavizcaya MF, Defossé GE (2021) Relationships among forest structure, solar radiation, and plant community in ponderosa pine plantations in the Patagonian steppe. For Ecol Manag 502. https://doi.org/10.1016/j.foreco.2021.119749

R Core Team (2018) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Salinas N, Malhi Y, Meir P, Silman M, Roman Cuesta R, Huaman J, Salinas D, Huaman V, Gibaja A, Mamani M, Farfan F (2011) The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests. New Phytol 189:967–977. https://doi.org/10.1111/j.1469-8137.2010.03521.x

Sariyildiz T (2015) Effects of tree species and topography on fine and small root decomposition rates of three common tree species (*Alnus glutinosa*, *Picea orientalis* and *Pinus sylvestris*) in Turkey. For Ecol Manag 335:71–86. https://doi.org/10.1016/j.foreco.2014.09.030

Scowcroft PG, Turner DR, Vitousek PM (2000) Decomposition of *Metrosideros polymorpha* leaf litter along elevational gradients in Hawaii. Glob Chang Biol 6:73–85. https://doi.org/10.1046/j.1365-2486.2000.00282.x

Spohn M, Ermak A, Kuzyakov Y (2013) Microbial gross organic phosphorus mineralization can be stimulated by root exudates – A ^{33}P isotopic dilution study. Soil Biol Biochem 65:254–263. https://doi.org/10.1016/j.soilbio.2013.05.028

State Forestry Administration of China (2018) Forestry resource statistics for China in 2014–2018 (in Chinese). Chinese Forestry Press, Beijing

Sun T, Hobbie SE, Berg B, Zhang H, Wang Q, Wang Z, Hättenschwiler S (2018) Contrasting dynamics and trait controls in first-order root compared with leaf litter decomposition. Proc Natl Acad Sci U S A 115:10392–10397. https://doi.org/10.1073/pnas.1716595115

Trentini CP, Campanello PI, Villagra M, Ritter L, Ares A, Goldstein G (2017) Thinning of loblolly pine plantations in subtropical Argentina: impact on microclimate and understory vegetation. For Ecol Manage 384:236–247. https://doi.org/10.1016/j.foreco.2016.10.040

Van Der Krift TAJ, Kuikman PJ, Berendse F (2002) The effect of living plants on root decomposition of four grass species. Oikos 96:36–45. https://doi.org/10.1034/j.1600-0706.2002.10978.x

Van Huysen TL, Perakis SS, Harmon ME (2016) Decomposition drives convergence of forest litter nutrient stoichiometry following phosphorus addition. Plant Soil 406:1–14. https://doi.org/10.1007/s11104-016-2857-6

Wang QW, Pieriste M, Liu C, Kenta T, Robson TM, Kurokawa H (2021) The contribution of photodegradation to litter decomposition in a temperate forest gap and understorey. New Phytol 229:2625–2636. https://doi.org/10.1111/nph.17022

Wang S, Ruan H, Wang B (2009) Effects of soil microarthropods on plant litter decomposition across an elevation gradient in the Wuyi Mountains. Soil Biol Biochem 41:891–897. https://doi.org/10.1016/j.soilbio.2008.12.016

Warton DI, Hui FKC (2011) The arcsine is asinine: the analysis of proportions in ecology. Ecology 92:3–10. https://doi.org/10.1890/10-0340.1

Whittaker RJ (2006) Island species-energy theory. J Biogeogr 33:11–12. https://doi.org/10.1111/j.1365-2699.2005.01442.x

Wieder WR, Cleveland CC, Townsend AR (2009) Controls over leaf litter decomposition in wet tropical forests. Ecology 90:3333–3341. https://doi.org/10.1890/08-2294.1

Xia M, Talhelm AF, Pregitzer KS (2018) Long-Term Simulated Atmospheric Nitrogen Deposition Alters Leaf and Fine Root Decomposition. Ecosystems 21:1–14. https://doi.org/10.1007/s10021-017-0130-3

Xiao W, Chen HYH, Kumar P, Chen C, Guan Q (2019) Multiple interactions between tree composition and diversity and microbial diversity underly litter decomposition. Geoderma 341:161–171. https://doi.org/10.1016/j.geoderma.2019.01.045

Yin L, Xiao W, Dijkstra FA, Zhu B, Wang P, Cheng W (2020) Linking absorptive roots and their functional traits with rhizosphere priming of tree species. Soil Biol Biochem 150. https://doi.org/10.1016/j.soilbio.2020.107997

Zeng Z, Wang S, Zhang C, Tang H, Wu Z, Li X (2016) Biomass and activity of soil microbes in evergreen broad-leaf forests at different succession stages in Yingzuijie. J Northwest A&F University (Nat Sci Ed) 44(7):115–121 (in Chinese)

Zhang P, Li B, Wu J, Hu S (2019) Invasive plants differentially affect soil biota through litter and rhizosphere pathways: a meta-analysis. Ecol Lett 22:200–210. https://doi.org/10.1111/ele.13181

Zhang W, Chao L, Yang Q, Wang Q, Fang Y, Wang S (2016) Litter quality mediated nitrogen effect on plant litter decomposition regardless of soil fauna presence. Ecology 97:2834–2843. https://doi.org/10.1002/ecy.1515

Zhao J, Wan S, Fu S (2013) Effects of understory removal and nitrogen fertilization on soil microbial communities in *Eucalyptus* plantations. For Ecol Manag 310:80–86. https://doi.org/10.1016/j.foreco.2013.08.013

Zhao J, Wan S, Li Z (2012) *Dicranopteris*-dominated understory as major driver of intensive forest ecosystem in humid subtropical and tropical region. Soil Biol Biochem 49:78–87. https://doi.org/10.1016/j.soilbio.2012.02.020

Zhong Y, Yan W, Wang R, Shangguan Z (2017) Differential responses of litter decomposition to nutrient addition and soil water availability with long-term vegetation recovery. Biol Fertil Soils 53:939–949. https://doi.org/10.1007/s00374-017-1242-9

Zhu Q, Riley WJ, Tang J, Koven CD (2016) Multiple soil nutrient competition between plants, microbes, and mineral surfaces: model development, parameterization, and example applications in several tropical forests. Biogeosciences 13:341–363. https://doi.org/10.5194/bg-13-341-2016