Methodological Comparisons of Absorptive and Transport Fine Root Production, Mortality and Decomposition in A Loblolly Pine Plantation Forest

Xuefeng Li (lxf.victor@gmail.com)  
North Carolina State University  https://orcid.org/0000-0002-7783-9942

Xingbo Zheng  
Institute of Applied Ecology

Quanlai Zhou  
Institute of Applied Ecology

Michael Gavazzi  
Eastern Forest Environmental Threat Assessment Center

Yanlong Shan  
Beihua University

Steve McNulty  
Eastern Forest Environmental Threat Assessment Center

John S. King  
North Carolina State University

Research Article

**Keywords**: Fine root, production, mortality, decomposition, method, loblolly pine plantation

**DOI**: https://doi.org/10.21203/rs.3.rs-553243/v1

**License**: This work is licensed under a Creative Commons Attribution 4.0 International License. Read Full License
Methodological comparisons of absorptive and transport fine root production, mortality and decomposition
in a loblolly pine plantation forest

Xuefeng Li\textsuperscript{1,4*}, Xingbo Zheng\textsuperscript{1}, Quanlai Zhou\textsuperscript{1}, Michael Gavazzi\textsuperscript{2}, Yanlong Shan\textsuperscript{3}, Steven McNulty\textsuperscript{2}, John S. King\textsuperscript{4},

\textsuperscript{1}Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang City, 110016 China
\textsuperscript{2}USDA Forest Service, Eastern Forest Environmental Threat Assessment Center, Raleigh, NC, United States
\textsuperscript{3}Department of Forestry, Beihua University, Jilin City, 132013 China
\textsuperscript{4}Department of Forestry and Environmental Resources, North Carolina State University, Raleigh, NC, 27695, United States

\textsuperscript{*}Corresponding author: lxf.victor@gmail.com; Tel (919) 376-7856

Abstract

Background and aims Fine roots can be functionally classified into an absorptive fine root pool (AFR) and a transport fine root pool (TFR) and their production, mortality and decomposition play a critical role in forest soil carbon (C) cycling. Different methods give significant estimates. However, how methodological difference affects AFT and TFR production, mortality, and decomposition estimates remains unclear, impeding us to accurately construct soil C budgets.

Methods We used dynamic-flow model, a model combining measurements of litterbags and soil cores, and balanced-hybrid model, a model combining measurements of minirhizotrons and soil cores, to quantify these fine root estimates in a managed loblolly pine forest.

Results Temporal changes in production, mortality or decomposition estimates using both models were not different for both AFRs and TFRs. Annual production, mortality, and decomposition were comparable between AFRs and TFRs when measured using the dynamic-flow model but significantly higher for AFRs than for TFRs when measured using the balanced-hybrid model. Annual production, mortality and decomposition estimates using the balanced-hybrid model were 75\%, 71\% and 69\% higher than those using the dynamic-flow model ($P < 0.05$ for all), respectively, for AFRs, but 12\%, 6\% and 5\% higher than those using the dynamic-flow model ($P > 0.05$ for all), respectively, for TFRs. Model test showed that the balanced-hybrid model had greater estimation accuracy than the
dynamic-flow model. Lower AFR estimates using the dynamic-flow model appeared to result from the underestimated AFR mass loss rate induced by the litterbag method.

Conclusions Methodological difference had a more significant impact on AFR estimates than on TFR estimates. These results have important implications for better quantifying the most dynamic fraction of fine root system and understanding soil C cycling.

Key words Fine root · production · mortality · decomposition · method · loblolly pine plantation

Introduction

Fine roots are the most physiologically active component of the below-ground plant system (McCormack et al. 2015). Studies conducted at the ecosystem scale showed that fine root growth consumed up to 63% of forests’ net primary production (Vogt 1991; Litton et al. 2007). Fine root mortality and decomposition accounted for nearly half of organic carbon (C) input into the soil and around 10% of soil heterotrophic C emission, respectively (Ding et al. 2019; Li et al. 2020a). Thus, accurate measurements of fine root production, mortality and decomposition in forests are critical for quantifying forest C allocation and cycling and parameterizing climate change models (Woodward and Osborne 2000; Ghimire et al. 2016).

The conventional ingrowth core and soil core methods, which are low cost and ready-to-use, had been extensively applied to assess fine root production and mortality (Vogt et al. 1998; Brunner et al. 2013; Addo-Danso et al. 2016). However, these methods are not reliable because the amount of fine roots died and decomposed during sampling intervals cannot be reasonably quantified (Osawa and Aizawa 2012). To overcome this weakness, several improved ingrowth core/soil core models have been developed in which fine root biomass and necromass dynamics and mass loss rate were integrated into mass balance equations (Osawa and Aizawa 2012; Li et al. 2013; Li and Lange 2015). Dynamic-flow model is a new improved soil core model (Li and Lange 2015). In theory, it has greater estimation accuracy than other modified soil coring methods because fine root decomposition rate is assumed to decrease over time rather than remain constant (Santantonio and Grace 1987; Osawa and Aizawa 2012). This assumption has been supported by the facts that the labile and recalcitrant components in fine roots have different mass loss rates, with the former being depleted much faster than the latter (Fan and Guo 2010; Lin et al. 2011). Minirhizotrons allow to monitor the growth and death of individual fine roots continuously while overcoming the
cofounding of spatiotemporal variation (McCormack et al. 2014, 2015). The balanced-hybrid model is an improved
minirhizotron-based model to quantify fine root production, mortality and decomposition by combining
measurements of soil cores and minirhizotrons with mass balance equations (Li et al. 2020a).

Fine roots have been traditionally defined as distal roots with diameters <2 mm. Recent studies have shown that
the hierarchical root system is morphologically, chemically and functionally heterogeneous and can be partitioned
into two pools: absorptive fine roots (AFRs) and transport fine roots (TFRs) (Pregitzer et al. 2002; McCormack et
al. 2015). AFRs represent the most distal roots with relatively higher N concentration and shorter lifespan and
involve primarily in the absorption of soil resources. In contrast, TFRs occur higher in the branching hierarchy with
relatively lower N concentration and longer lifespan and function mainly as resource transportation and storage.
Studying fine roots as two functional pools instead of a single diameter-based pool enables a more accurate
characterization of fine root processes (Sun et al. 2012). It has been recommended that multiple methods should be
used to yield more reliable fine root estimates (Hendricks et al. 2006; Addo-Danso et al. 2016). However, AFR and
TFR production, mortality and decomposition have not been jointly quantified using dynamic-flow and balanced-
hybrid models, leading to significant uncertainties in forest fine root C budgets. Loblolly pine (Pinus taeda L.)
plantation forests cover 11 million hectares, accounting for 50% of the standing pine volume in the southern USA
(Wear and Greis 2012). It has been estimated that over 1 billion seedlings are planted annually (Wear and Greis
2012). An improved understanding of AFR and TFR dynamics in loblolly pine plantation forests is critical for
developing silvicultural and rotation strategies to increase C sequestration capacity.

In this study, we used the soil core method, litterbags, and minirhizotrons to assess biomass and necromass
dynamics, mass loss pattern and growth and death rates of AFRs and TFRs in a managed loblolly pine forest. The
objectives were to 1) use both the dynamic-flow model and the balanced-hybrid model to quantify AFR and TFR
production, mortality, and decomposition in this forest, 2) assess to what extent methodological difference affects
AFR and TFR estimates and 3) determine which method is more reliable.

Materials and methods

Study site
The study was conducted in a commercially managed loblolly pine (*P. taeda* L.) forest (35°48'N 76°40'W) located in the lower coastal plain of Washington County, North Carolina, USA. Mean annual precipitation and temperature for the period 2011-2017 were 1320mm and 12.2 °C, respectively. The topography of the area is flat (<5m above sea level) and on a Belhaven series histosol soil (loamy mixed dysic thermic terric Haplosaprists). The study area was harvested of trees and ditched/drained in the late 19th to the early 20th century before being converted to a commercial pine plantation. The forest was fertilized with nitrogen and phosphorus at the time of planting and mid-rotation. The soil C and nitrogen concentrations at 20cm depth were 26% and 1.0%, respectively. The mean canopy height, diameter at the breast height, and stand age during the study period were approximately 24 m, 33cm, and 23 years, respectively. For a full site description, refer to Noormets et al. (2010). Three plots, about 5m ×9m for each and 100m to 800m apart, were established at random in the plantation in 2013. Only loblolly pine fine roots were studied as they accounted for over 90% of total fine root mass in this forest.

**Fine root biomass and necromass measurements**

Fine root biomass and necromass were determined using the soil coring method. The number of soil cores required at both plot and stand-level was calculated using the methods in Bartlett et al. (2001) and Dornbush et al. (2002). In each plot, 8 cylindrical soil cores (3.0 cm diameter, 30 cm depth) were randomly collected on 6 sampling occasions from April 2016 to April 2017, forming 5 soil sampling intervals (Li et al. 2020a). Previous study showed that over 90% of fine roots were distributed in 0 – 30 cm soil layer. Collected soil cores were rinsed with clean tap water through a 0.5mm mesh sieve to isolate roots. We only studied loblolly pine fine roots as they accounted for over 95% of total fine root mass. Loblolly pine fine roots with light color and intact stele and periderm were regarded as live roots, while those with dark color and damaged stele and periderm were dead ones. In this study, AFRs represented the first and second-order roots, while TFRs were third-order roots and higher with diameter <2mm. Live and dead AFRs and TFRs were separated according to the procedures described in Li et al. (2020b). All fine roots were dried at 50 °C to a constant weight and weighed. The measurements of biomass and necromass in the soil cores were scaled to g m⁻² over a 0-0.30 m soil layer.
Litterbag measurements

AFR and TFR mass loss rates were assessed using litterbags. To provide input parameters for dynamic-flow model, we used four types of fine roots including live and dead AFRs and TFRs as the decomposing substrate in in situ decomposition experiments. Each litterbag (20 cm × 3.5 cm, 0.05 mm mesh) was evenly filled with about 0.15 g fine root materials and inserted vertically into a 0-20 cm of soil. This experimental design intended to have fine root materials distributed evenly in different soil layers. The decomposition experiment began on 8 August 2016. The litterbags were collected after 65, 105 and 310 days of incubation. On each sampling occasion, three litterbags of each of the four root types were retrieved from each plot. Roots from the litterbags were rinsed with clear tap water, carefully sorted, dried at 50 °C to a constant weight and then weighed.

Dynamic-flow model

AFR and TFR production, mortality and decomposition were determined using the dynamic-flow model (Li and Lange 2015; Li et al. 2020b). Interval \( i \) was any given soil coring interval (1 ≤ \( i \) (year)). \( G_{I,i} \) and \( G_{II,i} \) were the fine roots that died before the start of interval \( i \) and in interval \( i \), respectively. The mass loss patterns of \( G_{I,i} \) and \( G_{II,i} \) were simulated by the litterbag method with dead and live roots used as decomposing substrates, respectively.

Fine root mass loss pattern was simulated using an exponential equation with only two parameters:

\[
y(t) = y_0 e^{-\lambda t / k} (1 - e^{-kt}) \quad (1)
\]

where \( y(t) \) and \( y_0 \) are root mass at time \( t \) (year) and the start, respectively. The two parameters \( \lambda \) (year\(^{-1}\)) and \( k \) (year\(^{-1}\)) were calculated based on the fine root mass remaining in litterbags collected on all sampling occasions using nonlinear regression. \( e^{-kt} \) is fine root decomposition rate which is time-dependent. It is the highest at the beginning and decreases over time.

The fine root mortality rate in interval \( i \) (\( \mu_i \)) was assumed to be constant. The total production (\( g_i \)), mortality (\( m_i \)) and decomposition (\( d_i \)) in interval \( i \) were calculated by the following equations,

\[
g_i = B_i (0) - B_i + m_i \quad (2)
\]

\[
d_i = m_i - (N_i - N_i (0)) \quad (3)
\]
\[ N_{i+1} = N_i (0) e^{(\lambda_{i-1}/k_{i-1}) \left[ 1 - e^{-k_{i-1}T} \right]} \]  \hspace{1cm} (4)

where \( B_i(0) \) and \( B_i \) represented the fine root biomass in soil cores sampled at the start and the end of interval \( i \), respectively, \( N_i(0) \) and \( N_i \) represented the fine root necromass at the start and the end of interval \( I \), and \( N_{II,i} \) and \( N_{I,i} \) were the mass remaining of \( G_{II,i} \) and \( G_{I,i} \) at end of interval \( i \), respectively. \( T \) was time length of interval \( i \).

\[ m_i = \mu_i T \]  \hspace{1cm} (6)

\[ \mu_i = k_{II,i} N_{II,i} \frac{e^{-\left(\lambda_{II,i}/k_{II,i}\right) e^{-k_{II,i}T}}}{E_1\left(\lambda_{II,i}/k_{II,i}\right) - E_1\left(\lambda_{II,i}/k_{II,i}\right)} \]  \hspace{1cm} (7)

where \( E_1(z) = \int_z^{\infty} \frac{e^{-x}}{x} \, dx \)

was an exponential integral function (Abramowitz and Stegun, 1964, ch. 6).

\[ B_i(0), B_i, N_i, N_i(0), N_{II,i}, \text{ and } N_{I,i} \] had the unit g·m\(^{-2}\). \( \lambda_{I,i}, k_{I,i}, \lambda_{II,i}, \text{ and } k_{II,i} \) were decomposition parameters for \( G_{I,i} \) and \( G_{II,i} \), respectively, calculated using Eq.1. \( B_i(0), B_i, N_i \) and \( N_i(0) \) were measured in the soil cores, \( N_{II,i} \) was calculated by Eq. (4) and \( m_i = \mu_i T \). Thus, \( g_i \) and \( d_i \) were calculated by Eqs. 2 and 3, respectively. \( g_i, m_i \) and \( d_i \) have the unit g·m\(^{-1}\)·year\(^{-1}\).

Minirhizotron measurements

A total of 18 acrylic tubes (80 cm long, 6cm outer diameter) were installed in 2013 at a 45° angle to a vertical soil depth of 50cm in the three plots (5 to 8 tubes per plot). We took root images on 17 sampling dates from late April 2016 through late April 2017, which co-occurred with soil coring (Li et al. 2020a). Images were collected using a Bartz digital camera with the image capture software BTC I-CAP (Bartz Technology Corp., Carpinteria, CA, USA). Fine root length and diameter were quantified by analyzing the images with WinRHIZO software (Regents Instruments Inc., Quebec, Canada). AFR and TFR length production, mortality and standing length density (mean root length per unit root image area) were calculated based on the image analysis. An AFR or TFR was counted as dead if its diameter shriveled to half the original diameter, it showed signs of deterioration including fragmenting...
and ectomycorrhizal fungal mantle detachment, or it was consumed by soil animals; otherwise, roots were considered as living (McCormack et al. 2014; Kou et al. 2018).

Balanced-hybrid model

Fine root length production ($LP_i$, m m$^{-2}$ image) and mortality ($LM_i$, m m$^{-2}$ image) in a given soil coring interval $i$ were estimated from minirhizotron image analysis. LP$_i$ and LM$_i$ were calculated as the length of fine roots that were produced and died in interval $i$, respectively (Kou et al. 2018).

Fine root turnover ($TR_i$) and death rates ($DR_i$) in the interval were calculated as

$$TR_i = \frac{LP_i}{SL_i} \quad (8)$$
$$DR_i = \frac{LM_i}{SL_i} \quad (9)$$

where SL$_i$ is the mean standing live fine root length of minirhizotron images captured at the start of interval $i$ (m m$^{-2}$ image).

$g_i$ and $m_i$ are assessed by combining measurements of minirhizotrons and soil cores (Hendricks et al. 2006; Li et al. 2020a).

$$g_i = B_i(0) \times TR_i \quad (10)$$
$$m_i = B_i(0) \times DR_i \quad (11)$$

$B_i(0)$ is fine root biomass at the start of interval $i$.

Resorting to Eq. 2, $d_i$ can be calculated (Li et al. 2020a).

Model test

The efficacy of the models for estimating the production, mortality, and decomposition was tested by comparing the predicted with the measured AFR and TFR biomass in July using a subset of data not used for model parameterization. Smaller differences between predicted and measured biomass values mean greater estimation.
accuracy. The predicted AFR and TFR biomass in July were calculated according to the procedures described in Hendrick and Pregitzer (1993) and Hendricks et al. (2006).

Statistical analysis

The plots were considered as replicates (n = 3), and data collected (sub-replicates) within the same plot were averaged before performing statistical analysis. One-way ANOVA or paired t-test was used to assess the differences in means of measured fine root variables. The data were log-transformed to normalize variances among the estimates of the two models before analysis when necessary. All data were analyzed using the SPSS statistical software (version 17.0; IBM Corporation, Somers, NY 10589, USA).

3. Results

Biomass and necromass

AFR and TFR biomass showed the same temporal pattern, with the highest values in July and the lowest values in January, while AFR and TFR necromass did not show evident peak and trough values during the whole study period (Fig. 1). AFRs had significantly lower mean biomass than TFRs (67.8 ±5.3 vs. 88.7±2.9 g m⁻²) (P<0.05). The mean necromass of AFRs was lower than that of TFRs (41.2 ±2.8 vs. 50.4 ±5.2 g m⁻²), but the difference was not significant (P>0.05).

Mass loss rate

Live AFR substrates had significantly higher percent mass remaining than live TFR substrates at the late decomposing stage, but dead AFR and TFR substrates had comparable percent mass remaining during the whole study period (Fig. 2). All live root substrates decomposed significantly faster than dead root substrates (Fig. 2).

Temporal changes in fine root estimates
Temporal changes in fine root production, mortality and decomposition rates were generally the same between the two models, with greater production in warmer months and greater mortality and decomposition occurring in cooler months (Fig. 3). Production, mortality, and decomposition rates using dynamic-flow model were comparable between AFRs and TFRs at all intervals. In contrast, production, mortality, and decomposition rates using the balanced-hybrid model were significantly higher for AFRs than for TFRs in most intervals (Fig. 3). AFR production, mortality and decomposition rates using the dynamic-flow model were significantly lower than those using the balanced-hybrid model in most intervals, while TFR production, mortality and decomposition rates were not significantly different between the two models in all intervals (Fig. 3).

Annual fine root estimates

Annual production, mortality, and decomposition were comparable between AFRs and TFRs in dynamic-flow model estimation but significantly higher for AFRs than for TFRs in balanced-hybrid model estimation (Fig. 4). Annual AFR production, mortality, and decomposition estimates using the balanced-hybrid model were 75%, 71%, and 69% higher than those using the dynamic-flow model ($P < 0.05$ for all), respectively (Fig. 4). By contrast, annual TFR production, mortality, and decomposition estimates using the balanced-hybrid model were 12%, 6%, and 5% higher than those using the dynamic-flow model ($P > 0.1$ for all), respectively (Fig. 4). Annual fine root (i.e. AFR + TFR) production, mortality, and decomposition were $119 \pm 9, 133 \pm 7$, and $124 \pm 11$ g m$^{-2}$, respectively, when using the dynamic-flow model and $172 \pm 11, 185 \pm 12$, and $171 \pm 14$ g m$^{-2}$, respectively, when measured using the balanced-hybrid model.

Model Test

The measured AFR biomass in July was 28% and 15% higher than that estimated by the dynamic-flow model and the balanced-hybrid model, respectively, while the measured TFR biomass in July was 19% and 11% higher than that estimated by the dynamic-flow model and the balanced-hybrid model, respectively, indicating that the balanced-hybrid model is more accurate than the dynamic-flow model.

Discussion
Fine root dynamics in forests have been increasingly studied by functional groups. However, most of the existing studies were two-dimensional minirhizotron analysis (McCormack et al. 2015; Kou et al. 2018) and did not include measurements of AFR and TFR biomass and necromass dynamics due to great labor and time input (Li et al. 2020b). Failing to assess the biomass and necromass dynamics impedes us to characterize soil C flux dynamics through AFR and TFR growth, death and decay. In this managed loblolly pine forest, AFRs had significantly lower biomass than TFRs but made comparable or even significantly greater contributions to total fine root production, mortality and decomposition than TFRs did, demonstrating that three-dimensional, function-based study is essential to accurately quantify fine root C budget.

Different methods yielded divergent fine root estimates, but all these methodological comparisons were diameter-based rather than function-based estimates (Hendricks et al. 2006; Osawa and Aizawa 2012; Li and Lange 2015). This knowledge gap has hindered us to better identify the strengths and weaknesses of each method and characterize the C allocation pattern within the root system. Our study for the first time used two types of models, a litterbag-based model and a minirhizotron-based model, to assess AFR and TFR production, mortality, and decomposition. AFR estimates were significantly more responsive to methodological difference than TFR estimates. Thus, methodological difference impact must be taken into account when assessing AFR and TFR dynamics.

Model test showed that the balanced-hybrid model had greater estimation accuracy than the dynamic-flow model. This can be explained by the inherent differences between them. In the balanced-hybrid model, the relative production and mortality rates at the tube-soil interface are assumed to be representative of those in bulk soil. This assumption has been proved to be very likely in previous studies (Hendrick and Pregitzer 1993; Hendricks et al. 2006; Li et al. 2020a). By contrast, in the dynamic-flow model, the estimation is based on the assumptions that fine root mortality rate remains constant in a certain interval and fine root mass loss pattern in litterbags is the same as that in bulk soil. Both are unrealistic as the mortality rate has been found to vary greatly among seasons (McCormack et al. 2014; Kou et al. 2018) and the decomposer community compositions in litterbags are different from those in natural soil (Bokhorst and Wardle 2013; Li et al. 2015; Beidler and Pritchard 2017). As a result, there would be greater errors in fine root estimates using the dynamic-flow model than using the balanced-hybrid model.

The significantly smaller AFR estimates of the dynamic-flow model compared to the balanced-hybrid model can be ascribed to the underestimated AFR mass loss rate by litterbags. In existing litterbag-based models including the...
dynamics-flow model (Osawa and Aizawa 2012; Li and Lange 2015), mortality is positively related to the production and decomposition and fine root mass loss rate is the dominant determinant in mortality estimation. Higher fine root mass loss rate results in greater mortality estimate and therefore greater production and decomposition estimates. Since both models used the same biomass and necromass data, lower mass loss rate was the only cause for the smaller AFR estimates in the dynamic-flow model estimation. Whether litterbags significantly underestimate TFR mass loss rate is still unclear. But one thing is certain: litterbag studies misrepresent fine root mass loss rate by using unrepresentative root materials (Kunkle et al. 2009; Fan and Guo 2010; Sun et al. 2018) and disrupting the interactions between roots, soil fauna and soil microbes (Koide et al. 2011; Li et al. 2015; Beidler and Pritchard 2017; Moore et al. 2020).

The balanced-hybrid model can continuously track the growth and death of individual AFRs and TFRs while maintaining the rhizosphere associations (McCormack et al. 2015; Beidler and Pritchard 2017), which makes it effective in comparing fine root estimates between functional groups. By contrast, the capacity of the dynamic-flow model in distinguishing AFR and TFR estimates has been severely undermined by its inherent weaknesses. First, hyphal connections with AFRs and TFRs were cut off when processing the root samples in the decomposition experiment, representing a major departure from in situ conditions (Koide et al. 2011; Sun et al. 2018). Second, AFR and TFR litterbags were placed at different locations in forest soils, which results in a cofounding of spatiotemporal variation (i.e. the effect of variances in soil environmental conditions on the mass loss rate could cover the inherent difference in decomposability between AFRs and TFRs). For this reason, the higher estimates for AFRs than for TFRs in the balanced-hybrid estimation generally reflected the real situation, while the comparable estimates between AFRs and TFRs in the dynamic-flow model estimation was most likely an error of the model.

Conclusion

The balanced-hybrid has a greater estimation accuracy than the dynamic-flow model and differences between the two models did not significantly affect TFR estimates but significantly affected AFR estimates. Thus, the methodological difference must be considered to accurately characterize AFR and TFR dynamics and to quantify fine root C fluxes in forests.
Acknowledgments We thank Jordan Luff, Wen Lin, and Yuan Fang for their help with analyzing the minirhizotron images and processing the samples. Primary supports were provided by USDA NIFA (Multi-agency A.5 Carbon Cycle Science Program) award 2014-67003-22068 and National Natural Science Foundation of China.

Declaration of Competing Interest

The authors declare that they have no conflict of interest.

References

Addo-Danso SD, Presscott CE, Smith AR (2016) Methods for estimating root biomass and production in forest and woodland ecosystem carbon studies: A review. For Ecol Manage 359: 332–351.

Bartlett JE, Kotrlic JW, Higgins CC (2001) Organizational Research: Determining the Appropriate Sample Size in Survey Research. ITLPJ 19: 43-50.

Beidler KV, Pritchard SG (2017) Maintaining connectivity: Understanding the role of root order and mycelial networks in fine root decomposition of woody plants. Plant Soil 420: 19-36.

Brunner I, Bakker MR, Bjork RG, Hirano Y, Lukac M, Aranda X et al. (2013) Fine-root turnover rates of European forests revisited: an analysis of data from sequential coring and ingrowth cores. Plant and Soil 362: 357–372.

Ding Y, Leppälammi-Kujansuu J, Helmisaari H (2019) Fine root longevity and below-and aboveground litter production in a boreal Betula pendula forest. For Ecol Manage 431: 17–25.

Dornbush ME, Isenhart TM, Raich JW (2002) Quantifying fine root decomposition: an alternative to buried litterbags. Ecology 83: 2985-2990.

Fan P, Guo D (2010) Slow decomposition of lower order roots: a key mechanism of root carbon and
nutrient retention in the soil. Oecologia 163: 509-515.

Ghimire B, Riley WJ, Koven CD, Mu M, Randerson JT (2016) Representing leaf and root physiological
traits in CLM improves global carbon and nitrogen cycling predictions. J Adv Model Earth Syst 8: 598–613.

Hendrick RL, Pregitzer KS (1993) The dynamics of fine root length, biomass, and nitrogen content in two northern
hardwood ecosystems. Can J For Res 23: 2507–2520.

Hendricks JJ, Hendrick RL, Wilson CA, Mitchell RJ, Pecot SD, Guo DL (2006) Assessing the patterns
and controls of fine root dynamics: an empirical test and methodological review. J Ecol 94: 40–57.

Hertel D, Leuschner C (2002) A comparison of four different fine root production estimates with
ecosystem carbon balance data in a Fagus–Quercus mixed forest. Plant Soil 239: 237-251.

Koide RT, Fernandez CW, Peoples MS (2011) Can ectomycorrhizal colonization of Pinus resinosa roots affect
their decomposition? New Phytol 191: 508–514.

Kou L, Jiang L, Fu X, Dai X, Wang H, Li S (2018) Nitrogen deposition increases root production and
turnover but slows root decomposition in Pinus elliottii plantations. New Phytol 218: 1450-1461.

Kunkle JM, Walters MB, Kobe RK (2009) Senescence-related changes in nitrogen in fine roots:
mass loss affects estimation. Tree Physiol 29: 715-723.

Li A, Fahey TJ, Pawlowska TE, Fisk MC, Burris J (2015) Fine root decomposition, nutrient mobilization and fungal
communities in a pine forest ecosystem. Soil Biol. Biochem 83:76-83.

Li X, Lange H (2015) A modified soil coring method for measuring fine root production, mortality and
decomposition in forests. Soil Biol Biochem 91: 192-199.

Li X, Minick KJ, Li T, Williamson JC, Gavazzi M, McNulty S, King JS (2020a) An improved method
for measuring total fine root decomposition in plantation forests combing minirhizotrons with soil coring.

Tree Physiol. 40: 1466-1473.

Li X, Minick KJ, Luff J, Noormets A, Miao G, Mitra B, Domec J-C, Sun G, McNulty S, King JS (2020b) Effects
of microtopography on absorptive and transport fine root biomass, necromass, production, mortality and decomposition in a coastal freshwater forested wetland, southeastern USA. Ecosystems 23: 1294-1308.

Li X, Zhu J, Lange H, Han S (2013) A modified ingrowth core method for measuring fine root production, mortality and decomposition in forests. Tree Physiol 33: 18-25.

Li X, Yang Y, Guo J, Chen G, Xie J (2011) Fine root decomposition of evergreen broadleaved and coniferous tree species in mid-subtropical China: dynamics of dry mass, nutrient and organic fractions. Plant Soil 338: 311–327.

Litton CM, Raich JW, Ryan MG (2007) Carbon allocation in forest ecosystems. Glob Chang Biol 13: 2089–2109.

McCormack ML, Adams TS, Smithwick EAH, Eissenstat DM (2014) Variability in root production, phenology, and turnover rate among 12 temperate tree species. Ecology 95: 2224–2235.

McCormack LM, Dickie IA, Eissenstat DM et al. (2015) Redefining fine roots improves understanding of belowground contributions to terrestrial biosphere processes. New Phytol 207: 505-518.

Moore JAM, Sulman BN, Mayes MA, Patterson CM, Classen AT (2020) Plant roots stimulate the decomposition of complex, but not simple, soil carbon. Funct Ecol 34:899-910.

Noormets A, Gavazzi MJ, McNulty SG, Domec J-C, Sun G, King JS, Chen J (2010) Response of carbon fluxes to drought in a coastal plain loblolly pine forest. Glob Chang Biol 16: 272-287.

Osawa A, Aizawa R (2012) A new approach to estimate fine root production, mortality, and decomposition using litter bag experiments and soil core techniques. Plant Soil 355: 167-181.

Pregitzer KS, DeForest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL (2002) Fine root architecture of nine North American trees. Ecol Monog 72:293–309.

Santantonio D, Grace JC (1987) Estimating fine-root production and turnover from biomass and decomposition data: a compartment-flow model. Can J For Res 17(8): 900-908.
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. PNAS 115: 10392-10397.

Sun JJ, Gu J, Wang Z (2012) Discrepancy in fine root turnover estimates between diameter-based and
branch-order-based approaches: a case study in two temperate tree species. J For Res 23: 575–581.

Vogt KA (1991) Carbon budgets of temperate forest ecosystems. Tree Physiol 9: 69–86.

Vogt KA, Vogt DJ, Bloomfield J (1998) Analysis of some direct and indirect methods for estimating root biomass
and production of forests at an ecosystem level. Plant Soil 200: 71–89.

Wear DN, Greis JG, The Southern Forest Futures Project: Summary Report; USDA Forest Service Southern
Research Station: Washington, DC, USA, 2012; p. 54.

Woodward FI, Osborne CP (2000) The representation of root processes in models addressing the responses of
vegetation to global change. New Phytol 147: 223-232.
Fig. 1 Absorptive (AFR) and transport (TFR) fine root biomass and necromass dynamics (g m$^{-2}$ for the 0-0.30 m soil depth; n= 3; mean ± SE).

Note: AFR biomass and necromass have been reported. We use these values for the purpose of comparison.

Fig. 2 Mass loss patterns of live and dead absorptive (AFR) and transport (TFR) fine root substrates measured using litterbags in a managed loblolly pine forest (n= 3; mean ± SE; different letters stand for significant difference in means, $P<$0.05).

Fig. 3 Temporal changes in production, mortality and decomposition estimates of absorptive (AFR) and transport (TFR) fine roots using balanced-hybrid model (BH) and dynamic-flow model (DF) in a managed loblolly pine plantation forest (n= 3; mean ± SE). Different letters stand for significant difference in means ($P<$0.05).

Note: AFR production, mortality and decomposition estimates using balanced-hybrid model have been reported. We use these values for the purpose of comparison.

Fig. 4 Annual absorptive (AFR) and transport (TFR) fine root production, mortality and decomposition measured using balanced-hybrid model (BH) and dynamic-flow model (DF) in a managed loblolly pine plantation forest (n= 3; mean ± SE). Different letters stand for significant difference in means ($P<$0.05).
Figures

Figure 1

Absorptive (AFR) and transport (TFR) fine root biomass and necromass dynamics (g m$^{-2}$ for the 0-0.30 m soil depth; $n= 3$; mean ± SE). Note: AFR biomass and necromass have been reported. We use these values for the purpose of comparison.
Figure 2

Mass loss patterns of live and dead absorptive (AFR) and transport (TFR) fine root substrates measured using litterbags in a managed loblolly pine forest (n=3; mean ± SE; different letters stand for significant difference in means, P<0.05).
Figure 3

Temporal changes in production, mortality and decomposition estimates of absorptive (AFR) and transport (TFR) fine roots using balanced-hybrid model (BH) and dynamic-flow model (DF) in a managed loblolly pine plantation forest (n= 3; mean ± SE). Different letters stand for significant difference in means (P<0.05). Note: AFR production, mortality and decomposition estimates using balanced-hybrid model have been reported. We use these values for the purpose of comparison.
Figure 4

Annual absorptive (AFR) and transport (TFR) fine root production, mortality and decomposition measured using balanced-hybrid model (BH) and dynamic-flow model (DF) in a managed loblolly pine plantation forest (n= 3; mean ± SE). Different letters stand for significant difference in means (P<0.05).