Effects of Methodological Difference on Fine Root Production, Mortality and Decomposition Estimates Differ Between Functional Groups in A Planted Loblolly Pine Forest

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Effects of methodological difference on fine root production, mortality and decomposition estimates differ between functional groups in a planted loblolly pine forest

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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 significantly different estimates. However, how methodological difference affects AFT and TFR production, mortality, and decomposition estimates remains unclear, impeding us to accurately construct fine root C budgets.

Methods We used dynamic-flow model, a model based on measurements of litterbags and soil cores, and balanced-hybrid model, a model based on measurements of minirhizotrons and soil

cores, to quantify AFT and TFR production, mortality, and decomposition in a planted loblolly pine forest.

Results Temporal changes in AFR and TFR production, mortality and decomposition estimates were generally the same between the two models. 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, respectively, for AFRs, but 12%, 6% and 5% higher than those using the dynamic-flow model, respectively, for TFRs. Model test showed that the balanced-hybrid model had greater accuracy than the dynamic-flow model in estimating AFR and TFR production, mortality and decomposition. Lower AFR estimates using the dynamic-flow model than using the balanced-hybrid model appeared to result from the underestimated AFR mass loss rate induced by the litterbag method.

Conclusions The balanced-hybrid model is more reliable than the dynamics-flow model. Methodological difference has greater effects on AFR estimates than TFR estimates. Effects of methodological difference must be taken into consideration when quantifying fine root production, mortality and decomposition by functional groups.

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

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

production consumed up to 63% of forests' net primary production (Vogt 1991; Litton et al. 2007). Fine root mortality accounted for nearly half of organic carbon (C) input into the soil (Ding et al. 2019), while fine root decomposition (i.e. amount of dead fine roots decomposed) represented around 10% of soil heterotrophic C emission in planted loblolly pine forests (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).

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 miss fine root dying and decomposing processes during sampling intervals, resulting in great uncertainties in the estimates (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 (Santantonio and Grace 1987; Osawa and Aizawa 2012; Li et al. 2013). Dynamic-flow model is a new improved soil core model (Li and Lange 2015) and the model structure is the same as that in Osawa and Aizawa (2012) except that fine root decomposition rate is assumed to decrease over time. In theory, the dynamic-flow model has greater estimation accuracy than other modified soil coring methods. This is because fine root decomposition rate has been found to decline with time rather than remain constant due to 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).

Minirhizotron technique is a visual method of studying roots in which clear tubes are inserted into the ground and miniature cameras are used to capture the photographic images of roots

growing on the tube surface (Hendrick and Pregitzer 1993). It allows to monitor the growth and death of individual fine roots continuously while overcoming the confounding of spatiotemporal variation (McCormack et al. 2014, 2015). Combining minirhizotrons and soil cores enables to quantify fine root production and mortality but fails to assess fine root decomposition, an important component in soil C fluxes (Hendricks et al. 2006; Addo-Danso et al. 2016). The balanced-hybrid model is an improved minirhizotron-based model in which measurements of soil cores and minirhizotrons are integrated into mass balance equations (Li et al. 2020a). It can be used to quantify not only fine root production and mortality but also fine root decomposition.

Fine roots have been traditionally defined as distal roots with diameters <2mm. 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) (McCormack et al. 2015; Kou et al. 2018). AFRs represent the most distal roots and involve primarily in the absorption of soil resources, while TFRs occur higher in the branching hierarchy and function mainly as resource transportation and storage. AFRs have relatively higher N concentration and shorter lifespan when compared with TRFs (McCormack et al. 2015). 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 C budgets. Planted loblolly pine (*Pinus taeda* L.) forests cover 11 million hectares in the US, 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 planted loblolly pine forests is critical for developing silvicultural and rotation strategies to increase C sequestration capacity, in particular the large soil pools.

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 planted 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 and farmed for about a decade before being converted to a commercial pine plantation forest. The usual rotation period is around 30 years. 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, 100m to 800m apart, were established at random in the planted forest in 2013. Each plot was about 6 m ×9 m in size. Only loblolly pine fine roots were studied.

Fine root biomass and necromass measurements

Fine root biomass and necromass were measured 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) (Table 1). Previous study showed that over 90% of fine roots were distributed in 0 - 30 cm soil layer in this forest (Noormets et al. 2010; Li et al. 2020a). Collected soil cores were rinsed with clean tap water through a 0.5 mm mesh sieve to isolate roots. We only studied loblolly pine fine roots as they accounted for over 95% of total fine root mass in 0 - 30 cm soil layer. 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 (Pregitzer et al. 2002; McCormack et al. 2015). 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.

133

134 Litterbag measurements

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

146

147 Dynamic-flow model

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

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

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

where $y(t)$ and y_0 are root mass at time t (year) and the start, respectively. The two parameters λ (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. $e^{-k t}$ 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 (μ_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,

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

$$d_i = m_i - (N_i - N_i(0)) \quad (3)$$

$$N_{I-i} = N_i(0) e^{(-\lambda_{I-i}/k_{I-i})(1-e^{-k_{I-i} T})} \quad (4)$$

$$N_{II-i} = N_i - N_{I-i} \quad (5)$$

$$m_i = \mu_i T \quad (6)$$

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 .

$$\mu_i = k_{II-i} N_{II-i} \frac{e^{-(\lambda_{II-i}/k_{II-i})e^{-k_{II-i} T}}}{E_1((\lambda_{II-i}/k_{II-i})e^{-k_{II-i} T}) - E_1(\lambda_{II-i}/k_{II-i})} \quad (7)$$

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

where

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

$B_i(0)$, B_i , N_i , $N_i(0)$, N_{II-i} , and N_{I-i} had the unit $\text{g}\cdot\text{m}^{-2}$. g_i , m_i and d_i have the unit $\text{g}\cdot\text{m}^{-2}\text{year}^{-1}$. λ_{I-i} , k_{I-i} , λ_{II-i} , and k_{II-i} were decomposition parameters for G_{I-i} and G_{II-i} , respectively, which can be calculated using Eq. 1. $B_i(0)$, B_i , N_i and $N_i(0)$ were measured using 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.

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). Root scanning began one year after tube installation to allow the soil around the tubes to stabilize. Only root images taken between late April 2016 to late April 2017 were used as these images co-occurred with soil coring (Li et al. 2020a) (Table 1). There were 17 image-capturing occasions during the study period. 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. Note that AFRs and TFRs included both mycorrhizal and non-mycorrhizal fine roots. 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).

192

193 Balanced-hybrid model

194 Fine root length production (LP_i , $m\ m^{-2}$ image) and mortality (LM_i , $m\ m^{-2}$ image) in a given soil
195 coring interval i were estimated from minirhizotron image analysis. LP_i and LM_i were calculated
196 as the length of fine roots that were produced and died in interval i , respectively (Kou et al.
197 2018).

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

199 $TR_i = LP_i / SL_i$ (8)

200 $DR_i = LM_i / SL_i$ (9)

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

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

205 $g_i = B_i(0) \times TR_i$ (10)

206 $m_i = B_i(0) \times DR_i$ (11)

207 $B_i(0)$ is fine root biomass at the start of interval i .

208 Resorting to Eq. 3, d_i can be calculated (Li et al. 2020a).

209

210 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. The reason was that temperature and precipitation in April to July were comparable to those in July to September. In dynamic-flow model testing, the interval April to July and the interval July to September were combined into one and fine root production and mortality rates in the new interval were assumed to be constant. AFR and TFR biomass and necromass in April and September and AFR and TFR mass loss patterns were employed to calculate AFR and TFR production, mortality and decomposition in April to September. The balance-hybrid model testing was the same as that in Li et al. (2020a). The predicted AFR and TFR biomass in July were calculated according to the procedures described in Hendrick and Pregitzer (1993), Hendricks et al. (2006) and Li et al. (2020a). Smaller differences between predicted and measured biomass values mean greater estimation accuracy.

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 was used to assess the difference in means of measured fine root mass loss rates. Within each model, paired-t test was performed to test the differences in the production, mortality and decomposition between AFRs and TFRs. The data were log-transformed to normalize variances before analysis when necessary. All data were analyzed using the SPSS statistical software (version 17.0; IBM Corporation, Somers, NY 10589, USA).

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; mean $\pm$ SE) ($P < 0.05$). The mean necromass of AFRs was lower than that of TFRs (41.2 ± 2.8 vs. 50.4 ± 5.2 g m⁻²; mean $\pm$ SE), 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 end of the experiment, 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 February to July and greater mortality and decomposition occurring in October to November (Fig. 3). Production, mortality, and decomposition estimates using dynamic-flow model were comparable between AFRs and TFRs at all intervals. In contrast, production, mortality, and decomposition estimates using the balanced-hybrid model were significantly higher for AFRs than for TFRs in most intervals (Fig.

3). AFR production, mortality and decomposition estimates using the dynamic-flow model were lower than those using the balanced-hybrid model in most intervals, while TFR production, mortality and decomposition estimates using the two models were between comparable in most intervals (Fig. 3).

Annual fine root estimates

Annual production, mortality, and decomposition were not significantly different between AFRs and TFRs when estimated using the dynamic-flow model, but significantly higher for AFRs than for TFRs when estimated using the balanced-hybrid model (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, 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, respectively (Fig. 4). Annual fine root (i. e. AFR + TFR) production, mortality, and decomposition were 119 ± 9 , 133 ± 7 , and $124 \pm 11 \text{ g m}^{-2}$ (mean $\pm$ SE), respectively, when measured using the dynamic-flow model and 172 ± 11 , 185 ± 12 , and $171 \pm 14 \text{ g m}^{-2}$ (mean $\pm$ SE), 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 29% 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 reliable 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 planted 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. These results demonstrated that two-dimensional minirhizotron analysis cannot reflect the contributions of AFRs and TFRs to total fine root production, mortality and decomposition, while three-dimensional, function-based study is essential to accurately quantify fine root C budget and understand fine root dynamics.

Different methods had been found to yield 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 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, indicating that choice of method matters when assessing AFR and TFR contributions to fine root C fluxes.

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 confounding 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. AFR estimates are more sensitive to the differences between the two models than TFR estimates. Thus, the methodological difference must be considered to accurately characterize AFR and TFR dynamics and to quantify fine root C fluxes in forests.

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Declaration of Competing Interest

The authors declare that they have no conflict of interest.

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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 $\pm$ SE).

Note: AFR biomass and necromass have been reported in Li et al. (2020a). 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 $\pm$ SE; different letters stand for significant difference in means, $P<0.05$). The lines are the simulated values using Eq. 1.

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 planted loblolly pine forest ($n=3$; mean $\pm$ SE). * stands for significant difference between AFR and TFR estimates using BH, while # represents significant difference between AFR and TFR estimates using DF ($P<0.05$).

Note: AFR production, mortality and decomposition estimates using balanced-hybrid model have been reported in Li et al. (2020a). 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 planted loblolly pine forest ($n=3$; mean $\pm$ SE). * stands for significant difference between AFR

and TFR estimates using BH, while # represents significant difference between AFR and TFR estimates using DF ($P<0.05$).

Table 1 Minirhizotron-image capturing and soil core sampling dates from 2016 to 2017

Dates	Minirhizotrons	Soil core
25-Apr	†	†
10-May	†	
28-May	†	
30-Jun	†	
12-Jul	†	
28-Jul	†	†
12-Aug	†	
25-Aug	†	
10-Sep	†	
29-Sep	†	†
18-Oct	†	
25-Nov	†	†
5-Dec	†	
25-Jan	†	†
15-Feb	†	
16-Mar	†	
26-Apr	†	†

Figure 1

Figure 2

475 Figure 3

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