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Measurements of fine root decomposition rate: Method matters

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ABSTRACT

Fine root decomposition plays a major role in biogeochemical cycle in forests. Litterbags and intact cores are predominant methods for measuring fine root decomposition rate. However, their efficacies have not been critically reviewed. In this study, we identify six sources of error for both methods including use of unrepresentative substrates, changes in decomposer community composition, altered effects of living roots and mycorrhizal fungi, differences in experimental duration length and sampling regime, confounding of spatio-temporal resolution, and limited temporal resolution. We present an indirect method to quantify fine root decomposition rate by integrating soil core and minirhizotron measurements into a new equation. The indirect method requires measuring more fine root parameters but can generally overcome the weaknesses associated with litterbag and intact core methods. Directly measuring the decomposition rate inevitably disturbs interactions between roots, soil fauna and rhizosphere microbes, which could significantly undermine the credibility of the estimates. Indirect measurement based on fine root growth and death rates, biomass and necromass that can be assessed reliably should be the future choice.

1. Introduction

Fine roots are the most physiologically active component of the below-ground plant system (McCormack et al., 2015). Traditionally, fine roots are defined as distal roots with diameters <2 mm. Previous studies have shown that fine root system is composed of two functional pools: absorptive fine roots and transport fine roots (Pregitzer et al., 2002; McCormack et al., 2015). Absorptive fine roots represent the most distal roots and involve primarily in the absorption of soil resources, while transport fine roots occur higher in the branching hierarchy and function mainly as resource transportation and storage. Fine root mortality was estimated to account for around half of world forests' annual litter inputs (Jackson et al., 1997; Freschet et al., 2013) and the decomposition of the dead fine roots represents one of the largest annual carbon (C) fluxes and nutrient cycling in global terrestrial systems (Chen et al., 2019; See et al., 2019). In boreal forests, the plant and microbial byproducts of root decomposition make greater contributions to soil C stores relative to above-ground litter (Clemmensen et al., 2013). Faster decomposition indicates that more fine root litters are processed by soil microbes per unit time, which in turn could control storage of soil organic matter (Clemmensen et al., 2013; Cotrufo et al., 2013). Thus, accurate measurements of fine root decomposition rate (i. e. percent mass loss per year) are crucial to quantify fine root C fluxes (Li and Lange, 2015) and simulate soil C cycling in forests (Woodward and Osborne, 2000; Le Quéré et al., 2016).

Litterbags and intact cores are two direct methods for measuring fine root decomposition rate across ecosystems. Litterbags have been used in most fine root decomposition studies (Harmon et al., 2009; See et al., 2019). The intact core method was regarded as an improved alternative to litterbags (Dornbush et al., 2002). In this method, fine root decomposition rate is assessed based on cores sampled from the field soils; the cores covered by plastic sleeves are installed in the field and resampled periodically. However, the intact cores have been rarely applied because of its strict requirement on soil homogeneity and greater labor inputs (Sun et al., 2013). The reliability of litterbags has been challenged as litterbag preparation typically involves separation of fine roots from soil and rhizosphere communities and washing and drying live fine roots before field incubation (Dornbush et al., 2002; Beidler and Pritchard, 2017; Wang et al., 2019), whereas the intact cores' weaknesses are often ignored. In this paper, we review the sources of error for both methods, analyze how these errors may affect fine root decomposition rate estimates and then present an indirect approach which combines

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minirhizotron and sequential core measurements to derive absorptive fine root decay rates in forests (Table 1).

2. Sources of error

2.1. Use of unrepresentative fine root materials

Root litter quality, defined by chemical and morphological traits, is a primary controller of fine root decomposition (Zhang and Wang, 2015; See et al., 2019; Jiang et al., 2021). In litterbag decomposition experiments, living roots rather than naturally senesced roots are used as decomposing materials because it is very difficult to assess the decomposition state of dead fine roots (Sun et al., 2018; Jiang et al., 2021). It is particularly true for the order-based or function-based fine root decomposition studies (Fan and Guo, 2010; Goebel et al., 2011; Lin et al., 2011; Minerovic et al., 2018), where dead, low order roots are easily separated from high order root branches, making it hard to ascertain their hierarchical positions in root system. In these studies, living fine root materials were collected to ensure that fine roots can be separated into order classes or functional categories. Living and senescing roots form a continuum in forests (Hobbie et al., 2010). A previous study showed that nitrogen (N) level decreased, while starch and soluble carbohydrate levels increased during the senescence of fine roots, leading to significant differences in N and starch and soluble carbohydrate concentrations between living and dead fine roots (Zadworny et al., 2015; Wojciechowska et al., 2020). Also, living fine roots are different from senescing fine roots in morphological characteristics as they have intact stele and periderm structures (Hertel and Leuschner, 2002; Enstone et al., 2003). Starch and soluble carbohydrates are more decomposable than other carbon constituents and soil decomposers may take longer to break down and process the intact structures of living roots (Fan and Guo, 2010; Zhuang et al., 2018). As a result, living fine root tissues might have a lower mass loss rate but a greater N mineralization rate than senescing fine root tissues, at least at the early decomposition stage. In intact core studies, soil cores used for measuring the decomposition rate are directly sampled from forest soil (Dornbush et al., 2002; Sun et al., 2013). Therefore, fine roots in these intact soil cores are composed of both living and partly decomposed fine roots, representing a significant departure from naturally senesced fine roots.

Table 1
Strengths and weaknesses of litterbags, intact cores and the indirect method for measuring fine root decomposition rate.

Method	Strengths	Weaknesses	Comments
Litterbags	· Easy and cheap · Can assess the decomposition rate of individual species · Can be applied in all forest types	· Use of unrepresentative substrates · Altered decomposer community composition · Reduced living root effect · May amplify hyphal effect · Affected by differences in experimental duration length and sampling regime · Subject to confounding of spatiotemporal resolution · Limited temporal resolution	Suitable for making comparisons among species and treatments
Intact cores	· Can maintain rhizosphere integrity	· Use of unrepresentative substrates · Altered decomposer community composition · No living root and hyphal effect · Affected by differences in experimental duration length and sampling regime · Subject to confounding of spatiotemporal resolution · Limited temporal resolution · Labor intensive · Limited to mono-dominant plantation forests	Should be used for reciprocal exchange of substrates from one location to another
Indirect method	· Can preserve interactions between roots, soil fauna and rhizosphere microbes · Better assessment of the temporal change · Estimation accuracy can be tested · Not affected by the study's length and timing	· Labor intensive · Unable to measure the decomposition rate of each species in the mixed natural forests · Fine roots growing at the tube-soil interface may not well represent those living in the bulk soil. · Subject to confounding of spatiotemporal resolution	Perform well in mono-dominant forests

2.2. Changes in decomposer community composition

Altered soil microbial community composition due to litterbag related disturbances could significantly affect fine root decomposition processes (Hopkins and Gregorich, 2005; Li et al., 2010; Luo et al., 2017). In litterbag studies, fine root materials are often washed and then air-dried to constant weights before field incubation (Minerovic et al., 2018; Jiang et al., 2021). This process could greatly change the original microbial communities on fine roots, which causes soil microbes to take an extra time to recolonize the fine root materials (Wang et al., 2019). Moreover, to assess decomposition rates of different functional groups, fine roots occurring at different branching hierarchy were manually separated from each other and those belonging to the same functional group were input into the litterbags (Fan and Guo, 2010; Goebel et al., 2011; Lin et al., 2011; Xiong et al., 2013; Minerovic et al., 2018; Jiang et al., 2021), creating a great distortion in the measurements. Li et al. (2015) found that fungal communities were considerably different in decaying fine roots between litterbags and intact cores. Such differences made fine roots decompose about twice as fast overall for intact cores than litterbags. Compared with litterbags, the intact cores can reduce this source of error by maintaining rhizosphere associations. However, soil microbial community composition in intact cores could be still different from those in bulk soil as plastic sleeves and small mesh size nets exclude living roots and therefore changes rhizosphere microbial communities (Dornbush et al., 2002). Also, soil fauna communities could be altered by both litterbags and intact cores. Small mesh-size litterbags (<0.5 mm) keep earthworms, macro-arthropods, and large soil animals away from fine root materials (Bokhorst and Wardle, 2013), while the intact cores completely block soil animal exchange between soil and the intact cores (Dornbush et al., 2002; Beidler and Pritchard, 2017). Soil animals consume or fragment fine roots, leading to a great change in fine root shape. A field study showed that the morphological traits could have a stronger control over fine root decay than the chemical traits (Minerovic et al., 2018). Fragmentation increases the surface area of fine roots and facilitates the access of soil microbes to the dead roots. To what extent changes in decomposer communities affect fine root decomposition is unclear. But one thing for sure is that fine

roots in litterbags and intact cores were processed by many decomposers that are different from those in the bulk soil (Bokhorst and Wardle, 2013; Li et al., 2015; Beidler and Pritchard, 2017).

2.3. Altered effects of living roots and mycorrhizal fungi on decaying roots

Living roots and their rhizo-deposits affect microbial activities and soil C and N mineralization, inducing a rhizosphere priming effect (Kuzyakov, 2010). The ongoing supply of root-derived rhizo-deposit C and N can increase, decrease or have no effect on the decomposition of soil organic carbon. Measured rhizosphere priming effect ranged from −70% to +380% (Zhu and Cheng, 2011; Cheng et al., 2014). A most recent study also proved that living roots stimulate the decomposition of complex plant substrates by increasing soil microbial growth and enzyme production (Moore et al., 2020). Fine roots die where they live and dead fine roots are close to living ones. Therefore, it can be deduced that the rhizosphere priming effect could affect fine root decomposition. Mycorrhizal fungal hyphae and root exudates could pass through the litterbag mesh to affect the decomposition of fine root materials. However, the existence of litterbags excludes living roots and therefore greatly reduces the rhizosphere priming effect. Moreover, the only inclusion of hyphae may potentially amplify hyphosphere priming effect, which could affect soil organic matter decomposition by suppressing saprotrophic microbial activities (Gadgil and Gadgil, 1971; Bending, 2003) or stimulating activities of microbial decomposers (Bunn et al., 2019). Recent studies showed that both living roots and mycorrhizal fungi could promote or inhibit fresh organic matter decomposition and that the direction of living root and mycorrhizal fungal effects on the decomposition depends on tree speciessoil nutrient conditions and the chemical properties of the litter itself (Meier et al., 2015; Bunn et al., 2019; Lin et al., 2019; Smith and Wan, 2019). The intact cores completely keep hyphae and living roots from fine root materials, greatly increasing saprotrophic microbial activities (Moore et al., 2015, 2020).

2.4. Differences in length of experimental duration and sampling regime

The labile components in fine roots are degraded first, while the recalcitrant ones take longer to decompose (Fan and Guo, 2010; Li et al., 2010; Lin et al., 2011). As the proportion of the former decreases and the proportion of the latter increases, the decomposition rate declines. As a result, short-term studies could give greater decomposition rate estimates than long-term experiments. We compiled data on fine root mass remaining values of 19 tree species in subtropical and temperate forests (Fan and Guo, 2010; Li et al., 2010; Goebel et al., 2011; Xiong et al., 2013; Kou et al., 2018) and used a single exponential negative model described in Goebel et al. (2011) to calculate the decomposition rate across species. The mean decomposition rate after around one-half year, one year and two years of field incubation was 0.25 $year^{-1}$, 0.22 $year^{-1}$ and 0.15 $year^{-1}$, respectively, for absorptive fine roots and 0.32 $year^{-1}$, 0.30 $year^{-1}$ and 0.24 $year^{-1}$, respectively, for transport fine roots. In addition, litterbag sampling regime affects the decomposition rate estimates. Suppose the number of sampling occasions and length of experiment duration are constant. The decomposition rate estimates would be higher if more sampling occasions occurred in the fast decomposition phase than in the slow decomposition phase. By excluding the percent mass remaining values in the first year, the decomposition rates in those studies were reduced by −0.03% to +39%. Since there are no unified protocols for the length of experimental duration and sampling regime, the decomposition rates measured in different studies are not comparable (Zhang and Wang, 2015; See et al., 2019). Long-term studies showed that fine root percent mass remaining values did not decrease appreciably over time at the later slow decomposition stage (Harmon et al., 2009; Sun et al., 2018). For this reason, the decomposition experiments should continue till the later slow decay stage. However, the measured values reflect the results of excluding living roots and altering soil microbial and fauna communities rather than real situations. Thus, the simple and dual negative exponential equations with or without an asymptote could not reliably model fine root mass loss patterns even though they significantly fit the measured percent mass remaining values (Harmon et al., 2009).

2.5. Confounding of spatiotemporal variation

Estimates of fine root decomposition rate have relied on removing litterbags or intact cores to assess the percent mass loss. Individual litterbags or intact cores cannot be replicated in time, as the sampled materials are destroyed. Fine root traits and soil environments are variable both in time and space and changes between adjacent sampling points over distances of a few meters could be as large as between sample periods (Burke et al., 2009; Defrenne et al., 2019a; b). Thus, spatial and temporal variation cannot be separated using both methods. Field studies showed that litterbags retrieved at later time points had higher percent fine root mass remaining values than those retrieved previously (Harmon et al., 2009; Goebel et al., 2011; Xiong et al., 2013), indicating that spatial variation can confound temporal variation. Additionally, the intact core method is subject to another sampling error. The initial mass of fine roots within each intact core was unknown as the intact cores were maintained as intact units until being resampled. To overcome this obstacle, it was assumed to equal the mean fine root mass measured from different soil cores. The measured mean of these soil cores differs from the field's actual values and the intact cores, introducing an error to the estimates. Moreover, this kind of error could be doubled by adding each sampling occasion.

2.6. Limited temporal resolution

In forests, fine root death and decomposition occur simultaneously. Fine roots dying in different seasons may have different mass loss patterns because of variances in temperature and precipitation. Most fine root decomposition experiments were initiated at one or two time points in a year (Harmon et al., 2009; Sun et al., 2018; Li et al., 2020b), failing to reflect this natural process. A study conducted in wetland forests indicated that the decomposition experiments starting in growing and non-growing seasons had quite different fine root mass loss patterns (Li et al., 2020b). Similarly, fine root decomposition rates in the same larch plantation forest measured in different years showed over 90% of the difference (Fan and Guo, 2010; Xiong et al., 2013). Seasonal effects on fine root decomposition rate can be partly reconciled by using the established relationship between percent fine root mass remaining values and cumulative soil temperature to infer fine root decomposition rates in various seasons (Li et al., 2020b). Unfortunately, this approach was based on the assumption that fine root mass loss patterns measured by the litterbags or intact cores represented those in bulk soils, which has been suggested to be very unlikely.

2.7. Indirect measurement

Li et al. (2020a) developed a new method for measuring absolute or total fine root decomposition (i.e. amount of fine roots decomposed per year) by integrating measurements of soil cores and minirhizotrons into a mass balance model. Their method overcomes several disadvantages associated with the litterbag-based methods (Li et al., 2020b) but cannot assess fine root decomposition rate. To assess fine root decomposition rate, we modified Li et al. (2020)'s approach by integrating the measurements of soil cores and minirhizotrons into a new equation. Instead of assessing temporal changes in fine root mass in litterbags or intact cores, fine root decomposition rate is calculated as fine root mortality (i.e. the amount of dead fine roots returning to soil) divided by mean fine root necromass. Fine root vitality was judged using the standards in Hertel and Leuschner (2002), Hendricks et al. (2006) and Li et al. (2020b). Fine root mortality can be measured using the two models in Li

et al. (2020a). The input parameters are listed in Table 2. In any given time interval, fine root decomposition rate (DR) is

$$DR = \frac{Mo}{\frac{1}{2}(N_0 + N_t)} \quad (1)$$

where Mo is fine root mortality (g m^{-2} $year^{-1}$), N_0 and N_t are fine root necromass at the start and end of the interval (g m^{-2}), respectively.

In Model 1,

$$Mo = Pr - (B_t - B_0) \quad (2)$$

$$Pr = B_0 \times TR_{live} \quad (3)$$

where Pr is fine root production (g m^{-2} $year^{-1}$), TR_{live} is fine root turnover rate ($year^{-1}$), and B_0 and B_t (g m^{-2}) are fine root biomass at the start and the end of the interval, respectively.

$$TR_{live} = Pr_L / SL_{mean} \quad (4)$$

where Pr_L and SL_{mean} are fine root length production (m m^{-2} $year^{-1}$) and the mean standing live fine root length (m m^{-2}), respectively.

In model 2,

$$Mo = B_0 \times DR_{dead} \quad (5)$$

$$DR_{dead} = Mo_L / SL_{mean} \quad (6)$$

where DR_{dead} is fine root death rate ($year^{-1}$) and Mo_L is the length of fine roots that died in the interval (m m^{-2}).

The model test showed that Model 1 and 2 had comparable accuracy (Li et al., 2020a). Compared with Model 2, Model 1 can avoid the technical difficulty of deciding the dead time of individual fine roots but requires accurate fine root biomass dynamics measurements. Because each one has strengths and weaknesses, Mo should be assessed using both models. In this study, the Mo estimates of the two models were averaged when calculating the decomposition rate.

We assessed seasonal and mean annual decomposition rates of absorptive fine roots based on the published data on Mo, N_t, and N_0 of a managed loblolly pine forest (Li et al., 2020a). Absorptive fine root decomposition rates varied over three-fold among different seasons (Fig. 1). Mean decomposition rate measured by the indirect method was 1.60 ± 0.28 $year^{-1}$, which was 2 times higher than the decomposition rate calculated by the single negative exponential equation based on the litterbag measurements in the same type of forest (King et al., 1997). The higher decomposition rate estimates using the indirect method may be due to the enhanced access of soil fauna to the senescing fine roots and intact decomposer communities (Beidler and Pritchard, 2017; Lin et al., 2019).

Table 2
Parameters required in the indirect method for estimating absorptive fine root (AR) decomposition rate in a certain interval (year) and the methods used for measuring these parameters.

Symbol	Description	Unit	Method	Sampling frequency
B_0	AR biomass at the start of the interval	g m^{-2} m^{-1} soil depth	Soil cores	Bimonthly
B_t	AR biomass at the end of the interval	g m^{-2} m^{-1} soil depth	Soil cores	Bimonthly
N_0	AR necromass at the start of the interval	g m^{-2} m^{-1} soil depth	Soil cores	Bimonthly
N_t	AR necromass at the end of the interval	g m^{-2} m^{-1} soil depth	Soil cores	Bimonthly
SL_{mean}	Mean standing live AR length	m m^{-2} image	Minirhizotrons	Weekly
Pr_L	AR length production	m m^{-2} image $year^{-1}$	Minirhizotrons	Weekly
Mo_L	AR length mortality	m m^{-2} image $year^{-1}$	Minirhizotrons	Weekly
TR_{live}	AR turnover rate	times $year^{-1}$	Minirhizotrons	Weekly
DR_{dead}	AR death rate	times $year^{-1}$	Minirhizotrons	Weekly

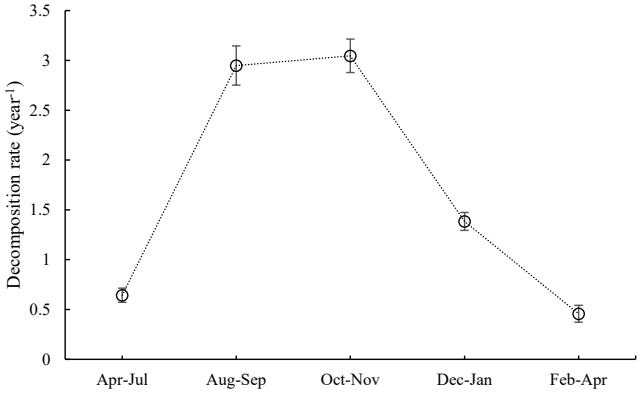

Fig. 1. Temporal changes in absorptive fine root decomposition rate measured using the indirect new method in a managed loblolly pine forest (n = 3; mean ± SE).

Compared with litterbags and intact cores, the indirect method involves greater labor and time efforts. In addition, its reliability depends on how well the relative fine root growth and death rates measured at the tube-soil interface represent those in bulk soil. To test the representativeness, Hendrick and Pregitzer (1993) and Hendricks et al. (2006) used measurements of minirhizotrons and soil cores to predict fine root biomass at a certain time point and compared it with the measured biomass. The mean differences ranged from 8.1 to 34.4%. Smaller differences mean better representativeness. Li et al. (2020a) used the same method to assess the mean differences in this managed loblolly pine forest and found an 11% of mean difference.

Despite these weaknesses, the indirect method has several advantages over litterbags and intact cores (Dornbush et al., 2002; Beidler and Pritchard, 2017): maintaining mycorrhizae's integrity by avoiding the disruption of rhizosphere associations (Moore et al., 2015), free soil animals' access to both naturally senesced and living roots, no need to use living roots or a mixture of living and dead roots as decomposing materials, better assessment of the temporal change in the decomposition rate, allowing to independently test the estimation accuracy (Hendrick and Pregitzer, 1993; Hendricks et al., 2006) and independent of effects of the study's length and timing on the decomposition rate estimate.

3. Conclusions

The inherent weaknesses associated with litterbag and intact core methods could substantially undermine the accuracy of fine root decomposition rate estimates. The indirect method should be considered as an improved alternative rather than a compromise as it maintains the interactions between roots, soil fauna, and rhizosphere microbes. Direct measurement of the decomposition rate inevitably disrupts rhizosphere environments, which could introduce uncontrollable errors. Future studies aiming to accurately quantify fine root decomposition rate should consider the use of more reliable measurements of fine root growth and death rates, as well as quantification of fine root biomass and necromass.

Declaration of competing interest

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

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