A new approach to estimate fine root production, mortality, and decomposition using litter bag experiments and soil core techniques

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Abstract.

Aims: A new approach is proposed to estimate fine root production, mortality, and decomposition that occur simultaneously in terrestrial ecosystems utilizing sequential soil core sampling or ingrowth core techniques.

Methods: The calculation assumes knowledge of the decomposition rate of dead fine roots during a given time period from a litter bag experiment. A mass balance model of organic matter derived from live fine roots is applied with an assumption about fine root mortality and decomposition to estimate decomposed dead fine roots from variables that can be quantified.

Results: Comparison of the estimated fine root dynamics with the decision matrix method and three new methods (forward estimate, continuous inflow estimate, and backward estimate) in a ca. 80-year-old Chamaecyparis obtusa plantation in central Japan showed that the decision matrix nearly always underestimated production, mortality, and decomposition by underscoring the values of the forward estimate, which theoretically underestimates the true value. The fine root production and mortality obtained by the decision matrix were on average 14% and 38% lower than those calculated by the continuous inflow estimate method. In addition, the values by the continuous inflow estimate method were always between those calculated by the forward estimate and backward estimate methods. The latter is known to overestimate the true value.

Conclusions: Therefore, we consider that the continuous inflow estimate method provides the best estimates of fine root production, mortality, and decomposition among the four approaches compared.
Key words: continuous inflow estimate, decision matrix, decomposition, fine roots, litter bag, mortality, production

Introduction

Terrestrial ecosystems interact with the atmosphere by affecting its carbon dioxide concentration (Fung et al. 1983; Heimann et al. 1989). Therefore, good quantitative knowledge of terrestrial carbon dynamics is necessary to understand potential changes in the earth’s climate system (Cox et al. 2000; Melillo et al. 2002; Heimann and Reichstein 2008). Translocation of assimilates to belowground organs of plants in terrestrial ecosystems in order to grow fine roots and to support mycorrhizae is an important part of net primary production (NPP). In fact, the proportion of total annual NPP allocated to the belowground production may be more than 50% in some forests (Vogt et al. 1996) and even more in boreal ecosystems in cold climates (Osawa et al. 2010). However, the contribution of fine roots has not been fully incorporated into the estimates of NPP in natural ecosystems (Hendrick and Pregitzer 1993; Lopez et al. 2001) because of the difficulty of accurately measuring its pools and fluxes using available tools and approaches.

Various methods have been developed for estimating the dynamics of fine roots in natural ecosystems. Major methods include sequential soil core (Persson 1980; Ostonen et al. 2005), ingrowth core (Finér et al. 1997; Ostonen et al. 2005), minirhizotron (Hendrick and Pregitzer 1993; Majdi and Őhrvik 2004), nitrogen budget (Nadelhoffer et al. 1985), and ecosystem carbon balance (Ågren et al. 1980), among others. Sequential soil core and ingrowth core methods utilize several different approaches to calculate production, mortality, and decomposition using changes in the pools of live and/or dead fine roots (Vogt et al. 1998; Hendricks et al. 2006). Several in-depth comparisons (Neill 1992; Majdi 1996; Hertel and Leuschner 2002; Ostonen et al. 2005; Hendricks et al. 2006) and reviews (Vogt et al. 1996, 1998; Gill and Jackson 2000; Majdi et al. 2005; Noguchi et al. 2007) of these methods have been published. Despite these publications, there is still no consensus among belowground researchers on what methods most realistically reflect changing carbon pools in the belowground part of the ecosystem.

Currently, root scientists generally agree that simultaneous fine root growth and mortality cannot be measured directly with the sequential soil core and ingrowth core methods (Kurz and Kimmins 1987; Santantonio and Grace 1987; Majdi 1996; Majdi et al. 2005). The minirhizotron technique could allow measurement of production and mortality simultaneously (Hendrick and Pregitzer 1993; Steele et al. 1997; Ruess et al. 2003) but it has limitations (Majdi 1996; Dannoura et al. 2008). A method of
calculating fine root dynamics with the decision matrix was proposed for sequential soil
core and ingrowth core methods (McClaugherty et al. 1982; Fairley and Alexander 1985).  
Various versions exist and have been widely used (e.g. Hertel and Leuschner 2002;
Jiménez et al. 2009; Murach et al. 2009; Mei et al. 2010; Yang et al. 2010). The
decision matrix could estimate the changing values of fine root production, mortality, and
decomposition, but it has a serious disadvantage. The problem is summarized in the
following discussion.

The decision matrix provides a method to estimate fine root production, mortality,
and decomposition during a given period, as illustrated in Table 1 (Fairley and Alexander
1985). For example, if \( \Delta B \) and \( \Delta N \) are defined as changes in fine root biomass and
necromass between two observations, and if both of these quantities have positive values,
fine root production (g) during this period is \( \Delta B + \Delta N \). Mortality (m) is \( \Delta N \). Note that
decomposition (d) was assumed as zero. In contrast, if \( \Delta B \geq 0 \), but \( \Delta N < 0 \), then \( g = \Delta B \)
and \( d = -\Delta N \), under an assumption of \( m = 0 \). Values of \( g \), \( m \), and \( d \) for other
combinations of \( \Delta B \) and \( \Delta N \) values are calculated accordingly (Table 1). The decision
matrix has two notable characteristics. First, fine root production (g), mortality (m), and
decomposition (d) are calculated from knowledge of the changes in the pools of fine root
biomass (\( \Delta B \)) and necromass (\( \Delta N \)) but without knowledge of decomposition (d) or its
rate. Second, some assumptions used for the calculation of \( g \), \( m \), and \( d \) are intuitively
understandable; specifically that \( d = 0 \) for a condition of \( \Delta B \geq 0 \) and \( \Delta N \geq 0 \). However, it
is also clear that decomposition may or may not be zero in this case. Assumptions for
other conditions are also neither immediately clear nor acceptable. In reality, the mass
balance of \( \Delta B \) and \( \Delta N \) with mass flux of \( g \), \( m \), and \( d \) should lead to a relationship: \( g = \Delta B \)
+ \( \Delta N + d \) and \( m = \Delta N + d \) (explained fully in the next section) with non-negative values
of \( g \), \( m \), and \( d \). Therefore, the decision matrix only provides underestimates of the
variables of interest because production, mortality, or decomposition must be ignored in
specific calculations (Fairley and Alexander 1985). The discrepancy between the true
value and the calculation by the decision matrix is unknown due to lack of information
about concurrently occurring decomposition. Therefore, a more coherent approach is
desirable.

Santantonio and Grace (1987) proposed a modeling approach where the fine root
dynamics were evaluated by mass balance equations similar to those assumed in the
development of the decision matrix (McClaugherty et al. 1982; Fairley and Alexander
1985). The advantage of Santantonio and Grace’s (1987) approach is the evaluation of
mortality and decomposition through modeling of the decay coefficient for dead fine
roots as a function of soil temperature, temperature coefficient, and reference rate of fine
root decomposition (their Equation 11). However, this approach (Santantonio and Grace 1987) has not been readily utilized by researchers because it demanded additional measurement, estimation, and modeling of variables other than the decay coefficient itself (Vogt et al. 1998).

The purpose of the present study is to propose a coherent and more practical approach for estimating fine root production, mortality, and decomposition that occur simultaneously. First, the fine root mass balance equations are solved mathematically with acceptable assumptions for the instantaneous rates of fine root mortality and decomposition. Then, fine root production, mortality, and decomposition are estimated from the changes in fine root biomass and necromass, and the decomposition ratio of dead fine roots during a measurement interval. The first two variables are provided by either sequential soil core measurements or ingrowth core experiments. An estimate of the third variable (decomposition ratio of dead fine roots) is also necessary. We show that the complex modeling of the decay coefficient in Santantonio and Grace’s (1987) method can be replaced by a simple fine root litter bag experiment. In the estimation of fine root mortality and decomposition with ordinary soil core techniques, none of the methods, except for Santantonio and Grace’s (1987) approach could take into account simultaneous changes of these variables during a sampling interval. The present study proposes a new equation that can be used to calculate these variables. We will compare the estimated values between the decision matrix and the new methods that we describe. In this study, fine root production is defined as the total amount of fine root ingrowth during a specified period. This is conceptually similar to NPP of aboveground organs and is approximately equivalent to what is often referred to as “belowground NPP.”

A mass balance model and rational for field measurement

Santantonio and Grace’s model (1987) suggests that if the sequential soil core or ingrowth core method is combined with an additional field experiment to assess fine root decomposition, we could estimate fine root production, mortality, and decomposition that occur simultaneously in a given ecosystem. As in Santantonio and Grace (1987), we assume a simple mass balance model with compartments and flow of organic matter of fine root origin during a discrete time interval. We then estimate the flow and change in stock of organic matter during this interval. Let us first consider a volume of soil in a natural ecosystem consisting of mineral soil, fine roots, and organic matter derived entirely from fine roots. The organic matter
originating from aboveground organs is ignored. This volume of soil contains a certain
amount of live fine roots at time i (denoted as $B_i$) and dead organic matter of fine root
origin ($N_i$). Hereafter, the former is called fine root biomass and the latter fine root
necromass. The fine root biomass and necromass change at time j (where $j > i$) to $B_j$ and
$N_j$ due to new growth of fine roots into the soil volume, their mortality, and their
decomposition. If $g_{ij}$ and $m_{ij}$ denote fine root production and mortality into or within the
soil volume between the times i and j (Fig. 1), the change in fine root biomass ($\Delta B$)
satisfies the following mass balance equation: $\Delta B = B_j - B_i = g_{ij} - m_{ij}$. Similarly, the
change in fine root necromass ($\Delta N$; Fig. 1) satisfies the following: $\Delta N =
N_j - N_i = m_{ij} - d_{ij}$, where $d_{ij}$ is decomposition of fine root necromass between i and j.

Therefore, these mass balance equations suggest that the fine root production and
mortality are calculated as,

$$g_{ij} = \Delta B + \Delta N + d_{ij} \quad (1)$$

$$m_{ij} = \Delta N + d_{ij} \quad (2)$$

where all terms have the dimension $g m^{-2} \Delta t d^{-1}$ and $\Delta t = j - i$ in the following
discussion. These relationships can be applied with periodic soil sampling and a root
litter bag experiment to estimate fine root production, mortality, and decomposition of a
given site simultaneously.

**Periodic soil sampling**

Soil cores of a specified diameter and volume are collected at different times, either by
harvesting natural soils or by recovering fine root ingrowth cores that were installed at the
beginning of the experiment at time 0. The first set of cores is collected at time i ($0 < i$;
Fig. 2) for measurement of fine root biomass and necromass in the soil volume. The
second set is collected later at time j ($i < j$; Fig. 2). The interval between the two
collections is generally several weeks to a few months. Fine root biomass and
necromass are also measured in the second set of soil cores. Here we assume that the
two sets of cores sampled at times i and j have the same initial condition and are left
under the same environment. Consequently, the patterns of fine root production,
mortality, and decomposition are considered identical between them. In other words, we
assume that fine root biomass and necromass at time i will be the same for the two sets.
In reality, there will be variations in the observed values among the cores of the same set.
However, we assume that the mean values are the same for the same variable at the same
time of observation when the growing conditions are identical.
**Root litter bag experiment**

Litter bags are used to evaluate the decomposition ratio of dead fine roots. The fine root litter bags containing a known amount of dead fine roots are set in the soil horizon at time \( t_i \). The fine root litter bags are recovered at time \( t_j \) for evaluating the decomposition ratio of fine root necromass. As there were no live fine roots in the litter bag when they were set in the soil, we also have condition \( B^C_i = 0 \). If fine root production between times \( t_i \) and \( t_j \) is zero, by artificially excluding fine root growth into the litter bag, the fine root biomass at time \( t_j \) will also be zero. Therefore, Equation 1 reduces to \( d_{ij} = N^C_i - N^C_j \) from which decomposition of fine root necromass can be estimated. Where \( \gamma_{ij} \) is the decomposition ratio (dimensionless) of fine root necromass between times \( t_i \) and \( t_j \), then

\[
\gamma_{ij} = \frac{d_{ij}^C}{N^C_i} = 1 - \frac{N^C_j}{N^C_i}
\]

(3).

Decomposition of naturally dead fine roots and artificially severed live fine root segments may represent different phenomena (Publicover and Vogt 1993). However, severed roots are often used in decomposition experiments, as is the case in the present study. Publicover and Vogt (1993) discuss possible variations and mechanisms of decomposition in roots of varying origins.

### Calculating decomposition of dead fine roots

A realistic estimate of fine root decomposition between times \( t_i \) and \( t_j \) may be obtained by assuming that the fine roots die continuously at a constant instantaneous mortality of \( \sigma \) (g m\(^{-2}\) d\(^{-1}\)) and disappear at an instantaneous decomposition of \( \gamma \cdot N \) (g m\(^{-2}\) d\(^{-1}\)) with a constant decomposition rate \( \gamma \) (d\(^{-1}\)), where \( \sigma \) and \( \gamma \) are formally defined as

\[
m_{ij} = \int_{t_i}^{t_j} \sigma \, dt \quad \text{and} \quad d_{ij} = \int_{t_i}^{t_j} \gamma \cdot N \, dt,
\]

and \( N \) is fine root necromass at time \( t \) (\( t_i \leq t \leq t_j \)).

These assumptions are identical to those used by Santantonio and Grace (1987). The assumption of constant root mortality, \( \sigma \), must be introduced due to lack of sufficient knowledge about its behavior but it can vary for different observation intervals. Given these assumptions, the instantaneous necromass mass balance can be expressed as

\[
dN / dt = -\gamma \cdot N + \sigma \ .
\]

This is a linear first-order differential equation (Kreyszig 1972), and solving for \( N \) yields

\[
N = \frac{\sigma}{\gamma} + \left( N_i - \frac{\sigma}{\gamma} \right) e^{-\gamma(t-i)} .
\]

By applying this
relationship to the present situation, we obtain an expression for fine root decomposition between times $i$ and $j$ as (see Appendix for derivation)

$$d_{ij} = -\Delta N - (\Delta N / \gamma_{ij} + N_i) \cdot \ln(1 - \gamma_{ij})$$  \hspace{1cm} (4),

where, $\gamma_{ij}$ is as defined in Equation 3. Therefore, the amount of the decomposed dead fine roots can be estimated from three variables ($\Delta N$, $N_i$, and $\gamma_{ij}$) that can be measured by soil sampling and a relatively simple experiment. The modeling exercise (Santantonio and Grace 1987) is no longer required. The estimate of $d_{ij}$ from Equation 4 may be referred to as the continuous inflow estimate. Comparison of Equations 2 and 4 yields

$$m_{ij} = -(\Delta N / \gamma_{ij} + N_i) \cdot \ln(1 - \gamma_{ij})$$  \hspace{1cm} (5).

An estimate of fine root necromass at time $j$ ($N_j$) is known, but $N_i$, necromass at time $i$, is not known, fine root decomposition can also be estimated (backward estimate) as

$$d_{ij} = \gamma_{ij} \cdot N_j$$  \hspace{1cm} (6).

This expression (forward estimate) assumes that decomposition occurring between times $i$ and $j$ originates from the necromass present at time $i$ and that there is neither fine root mortality nor associated decomposition of the newly dead fine roots between $i$ and $j$ (in order to calculate the amount of decomposition). Therefore, the decomposition estimated with Equation 6 is an underestimate.

Alternatively, if $N_j$, necromass at time $j$ through decomposition of dead fine roots between times $i$ and $j$ with a decomposition ratio of $\gamma_{ij}$, is known, but $N_i$, necromass at time $i$, is not known, fine root decomposition can also be estimated (backward estimate) as

$$d_{ij} = \gamma_{ij} \cdot N_j / (1 - \gamma_{ij})$$  \hspace{1cm} (7).

This representation means that new dead fine roots may be added between times $i$ and $j$, all of which will occur as a pulse immediately after time $i$. However, in reality, fine root mortality can occur anytime between $i$ and $j$, which makes the residence time of these newly dead fine roots shorter than $j-i$. Therefore, the decomposition estimate from Equation 7 will be an overestimate. These considerations suggest that the true value of fine root decomposition lies between the values calculated by Equations 6 and 7 and the values will coincide only when there is no fine root mortality between times $i$ and $j$. 

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Therefore, the estimate of $d_{ij}$ from Equation 4 may be considered the most realistic theoretical value among the values calculated by Equations 4, 6, and 7. Fine root production ($g_{ij}$) and mortality ($m_{ij}$) are then calculated by Equations 1 and 2. Estimation using these relationships is practical. It is also expected to be applicable in many types of terrestrial ecosystems for varying amounts of production, mortality, and decomposition. The ability of the present approach to detect changes in fine root biomass and necromass pools is the same as that of the methods proposed earlier (e.g., decision matrix). However, the treatment of decomposition is different. The present approach takes into account decomposition directly, whereas the decision matrix in effect ignores decomposition, leading to underestimation when decomposition is not negligible.

Materials and methods

Study site

The proposed method of estimating fine root production, mortality, and decomposition was applied to a ca. 80-year-old plantation of Chamaecyparis obtusa Endl. (Hinoki cypress) at Ryukoku Forest, Ohtsu, Japan, at 34°58’N, 135°56’E. The elevation of the stand is 130 m above sea level. The soil of the study area is characterized by sand and small round gravel stones, and is classified as yellowish brown forest soil derived from lacustrine sediments of Cenozoic origin belonging to the Kobiwako Group (Ministry of Land, Infrastructure, Transportation and Tourism 1982). The Ryukoku Forest is a secondary forest of mainly canopy trees of Quercus serrata Thunb. and Pinus densiflora Sieb. et Zucc. that used to be managed communally. The forest supplied agricultural fertilizer and wood material for local farmers, but now the area is abandoned. The C. obtusa stand has not been managed for at least 40 years (Miyaura 2009) and shows signs of active self-thinning (Osawa and Allen 1993). The stand is about 800 m² with stem density, mean stem diameter at breast height, canopy tree height, and basal area of C. obtusa at 1175 ha⁻¹, 22 cm, 20 m, and 51 m²/ha, respectively (Tago J unpublished data). In addition, the stand also has some canopy and subcanopy trees of Q. serrata, P. densiflora, and Ilex pedunculosa Miq.
Ingrowth core experiment in 2007

To assess fine root dynamics, a cylindrical tube 32 mm in diameter and 21 cm in length was used as the fine root ingrowth core and the root litter bag. The cylindrical tube is made of plastic mesh with approximately 3 mm mesh openings and a mesh bottom made of the same material as the cylinder wall. This cylinder was filled with soil from the study site, but all live roots, dead roots, and decomposing organic matter (diameter $\phi > 0.5$ mm) were removed by washing the soil ten times with tap water in a container and sieving the supernatant fluid with suspended organic matter through a 0.5 mm mesh sieve after each washing. Fine particles ($\phi \leq 0.5$ mm) of mineral soil and particulate organic matter in the supernatant fluid were saved, dried at room temperature, broken into shatters, and mixed with the soil sediment in the container for use in the experiment.

Some of the soil-filled plastic mesh cylinders were covered with a ‘root-impermeable water-permeable (RIWP) sheet®’ (Toyobo Co., Osaka, Japan) to exclude fine roots that could grow into the cylinder. The RIWP sheet has a pore size of approximately 6μm and blocked practically all ingrowth of fine roots; however, fine particles of soil, rain water, and other microorganisms could penetrate through the sheet.

A known mass of dead fine roots of C. obtusa was added to each of the RIWP sheet-covered cylinders so that they acted as root litter bags. Severed live fine root segments were collected, dried at room temperature, and used as dead fine roots in the litter bags in this experiment (see Publicover and Vogt (1993) for caution). Soil was included in the litter bags to improve the physical contact of the soil particles with the inserted dead roots; however, use of ordinary litter bags without soil is a possible alternative. In total, 60 soil cylinders were prepared; 30 of which were covered with the RIWP sheet. The tops of all cylinders were covered with thin translucent fabric to exclude input of aboveground litter.

Six sampling lines, approximately 30 m long, were established in the stand. They were parallel to one another and about two-meters apart. The ground surface along the sampling lines was marked at one-meter intervals to indicate locations for the soil cylinders. The sampling points for the 30 soil cylinders (fine root ingrowth cores) and the 30 root litter bag cores were selected randomly. The 30 ingrowth cores were buried singly in early July 2007 after coring the ground with a stainless steel tube 38 mm in diameter and 45 cm in length by pounding it 20 cm into the ground. The narrow space between the ingrowth core and the inner wall of the cored hole was filled with the same soil as that used to fill the ingrowth core.

In mid-August 2007, six ingrowth cores were chosen randomly, taken out of the ground by creating 20-cm deep incisions around the core with a knife and the ingrowth
core was pulled out by hand. These six ingrowth cores correspond to Core A in Fig. 2.

At the same time, six root litter bag cores were established at randomly selected locations among the remaining sampling points (corresponding to Litter bag C in Fig. 2). Six weeks later, these six litter bag cores and another set of six randomly selected regular ingrowth cores (Core B in Fig. 2) were recovered on the same day by a method similar to the one described above. The collected soil cylinders were brought to the laboratory. The contained soil was washed using the same method applied in preparation of the soil material. Then the recovered organic material was sorted into live fine roots, dead fine roots, and other organic matter. The live and dead fine roots were differentiated by their color and resilience (Hishi and Takeda 2005; Konôpka et al. 2006) because more exact methods were not practical in field studies. The roots of different tree species were not distinguished in the present study; however, most were from C. obtusa. They were dried in a forced air oven at 80°C for 48 hours, and biomass and necromass were measured separately. The mass of the live fine roots was considered fine root biomass, and the mass of the dead fine roots combined with other organic matter (ϕ > 0.5 mm) was regarded as necromass.

Each time the soil cylinders corresponding to Core B and Litter bag C were recovered, another set of six root litter bag cores was buried at randomly selected sampling points. They were taken out of the ground on the next sampling occasion (new Litter bag C; generally six weeks later) along with a set of six randomly selected fine root ingrowth cores (new Core B). Core B from the previous sampling time becomes the new Core A. Analysis of these cores gave the biomass and necromass values at the experiment’s next time step. By repeating this process, fine root production, mortality, and decomposition were estimated until December 2007, generally at six-week intervals.

In addition, six root litter bags were set, using a method similar to that employed initially, and were recovered in mid-August so that the fine root decomposition ratio during the first period could also be estimated.

**Sequential soil core sampling in 2010**

Soil cores were sampled sequentially with the same stainless steel tube at randomly selected points, generally at nine-week intervals between June 22 and December 16, 2010. The potential sampling points were located at one-meter intervals along the sampling lines in the same C. obtusa stand. Usually three cores were collected at each sampling. Root litter bags of the same construction as the 2007 experiment were prepared and buried each time soil samples were collected. The root litter bag cores recovered at each sampling was generally three. The collected soil cylinders and
contents of the root litter bag cores were washed in tap water applying the same method used in the 2007 experiment. Then, after oven-drying at 80°C for 48 hours, live fine roots, dead fine roots, and other organic matter ($\phi > 0.5$ mm) were quantified. Only the mass of dead fine roots was regarded as necromass in the 2010 study because the origin of decomposing organic matter was generally unknown. The stand was thinned to reduce the tree density and stem volume of *C. obtusa* by 47% and 36%, respectively, in March 2010 (Tago *personal communication*) for a separate study of forest growth prior to the start of the present soil core sampling, which commenced on June 22, 2010.

**Mass flux calculation and statistical analysis**

The measured values of fine root biomass and necromass in each soil core, ingrowth core, and root litter bag were divided by the area of the inner cross-section of the stainless steel pipe (0.00101 m$^2$ for soil core) or of the ingrowth core and root litter bag (0.000706 m$^2$) to obtain the mass per square meter of the ground. Then, they were divided by the duration of each experiment in days ($\Delta t = j - i$) to calculate the mass flux in g m$^{-2}$ d$^{-1}$. The 95% confidence limits of the estimated means were calculated by the bootstrap method with bias-corrected percentile approach by randomly sampling a set of mass data n times with replacement (when sample size is n) to obtain the means, then repeating the process 1,000 times to generate the 95% confidence interval (CI) (Efron 1979; Efron and Gong 1983). Decomposition is calculated from a relatively complex equation (Equation 4), making use of traditional statistical inference inappropriate. Therefore, significant differences in the means of biomass or necromass (Hendricks et al. 2006) were not applied to calculate production, mortality, and decomposition in the present study, except for comparisons in Table 2.

The following is an example of the mass flux calculation. Data collected on October 11 and November 10, 2007 (55 days apart) are used. The fine root necromass in the root litter bag core was 0.739 g on October 11. On November 10, it was 0.482 g. Therefore, the root decomposition ratio during this period ($\gamma_{ij}$) was 0.347 (Equation 3). The mean values of fine root biomass and necromass per core were 0.0101 g and 0.0259 g, respectively, on October 11. These values changed to 0.165 g and 0.0439 g, respectively, on November 10. Therefore, $\Delta B = 0.165 - 0.0101 = 0.154$ g and $\Delta N = 0.0439 - 0.0259 = 0.0180$ g per core. Fine root decomposition during this period will be calculated by Equation 4 as $d_{ij} = -0.018 - (0.018/0.347 + 0.0259)\ln(1-0.347) = 0.015$ (g per core per 55 days). Then fine root mortality ($m$) and production ($g$) become $m = 0.018 + 0.015 = 0.033$ and $g = 0.154 + 0.018 + 0.015 = 0.187$ (g per core per 55 days);
Equations 2 and 1). The results of calculation can be translated to $d = 0.392$, $m = 0.855$, and $g = 4.849$ (g m$^{-2}$ d$^{-1}$).

### Results

**Ingrowth core experiment in 2007**

Based on the continuous inflow estimate (Equation 4), the observed decomposition, $d_{ij}$, ranged between 0.14 and 0.76 g m$^{-2}$ d$^{-1}$ and showed little seasonal variation (black pattern in Figs. 3a-3d). Values of fine root mortality, $m_{ij}$, ranged between 0.85 and 1.57 g m$^{-2}$ d$^{-1}$. The mortality was relatively low during summer and fall, and increased during winter between November and December (black pattern in Figs. 3e-3h).

Seasonal dynamics of fine root production, $g_{ij}$, showed a different pattern. It was low in the summer (August value was 1.42 g m$^{-2}$ d$^{-1}$), peaked in October at 4.84 g m$^{-2}$ d$^{-1}$, and became nearly zero through November and December in the continuous inflow model (black pattern in Figs. 3i-3l). The bootstrap 95% CI of the estimated fine root production was large, mostly due to the small sample size (generally six) and propagation of errors associated with the measurement of $m_{ij}$ and $d_{ij}$ (see Equations 1, 2, 4, and 5).

Due to the large 95% CI, fine root production was not distinguishable from zero in November and December (Figs. 3k and 3l).

The calculated values of fine root production, mortality, and decomposition by the forward estimate (Equation 6) were lower than those estimated by the continuous inflow assumption (Equation 4). On average, the values were 47% lower for decomposition (Figs. 3a-3d), 15% lower for mortality (Figs. 3e-3h), and 7% lower for production (Figs. 3i-3l). On the other hand, the values calculated by the backward estimate (Equation 7) were always higher than the continuous inflow estimate. They were higher on average by 59% for decomposition (Figs. 3a-3d), 18% for mortality (Figs. 3e-3h), and 8% for production (Figs. 3i-3l). The fine root production calculated by the forward estimate and the continuous inflow assumption were negative during the fourth period (ending on December 21; Fig. 3l); however, because negative values are ecologically unacceptable, we assigned zero to them. The reason for the negative production is the non-closure of mass balance with all non-negative terms in Equation 1.

The estimates of fine root decomposition by the decision matrix were zero for the first three periods until November 10 (Figs. 3a-3c). In contrast, the decomposition estimates by the forward, continuous inflow, and backward models were generally positive. The pattern differed in the fourth period (ending on December 21) where the decision matrix decomposition estimate was greater than both the forward and continuous inflow
estimates (Fig. 3d). On average, fine root decomposition estimated by the decision matrix was 69% lower than that calculated by the continuous inflow assumption.

Relationships among the mortality values calculated by the decision matrix and by the forward, continuous inflow, and backward models (Figs. 3e-3h) are similar to those observed for fine root decomposition. The mortality values estimated by the decision matrix were on average 31% lower than those calculated by the continuous inflow assumption. The decision matrix also returned the lowest fine root production values when the four approaches were compared (Figs. 3i-3l). The decision matrix production estimates were on average 18% lower than the continuous inflow estimates.

Sequential soil core sampling in 2010

Patterns of the calculated fine root decomposition, mortality, and production by the four methods (decision matrix, forward estimate, continuous inflow, and backward estimate) in the sequential soil core sampling for 2010 (Fig. 4) were generally similar to those observed in the 2007 ingrowth core experiment (Fig. 3). The decision matrix gave the lowest estimates. The values calculated by the continuous inflow model were also between those predicted by the forward and backward estimates.

The continuous inflow model (Equation 4) returned decomposition values, $d_{ij}$, ranging between 0.27 and 0.42 g m$^{-2}$ d$^{-1}$. It showed little seasonal variation, as evidenced in the 2007 data (black pattern in Figs. 4a-4c). Fine root mortality, $m_{ij}$, ranged between 0.38 and 1.60 g m$^{-2}$ d$^{-1}$. The mortality was somewhat high in summer but decreased after August (black pattern in Figs. 4d-4f). The greatest value of fine root mortality was observed during the first period (ending on August 24) at 1.60 g m$^{-2}$ d$^{-1}$ (Fig. 4d). Seasonal dynamics of fine root production, $g_{ij}$, was relatively stable, and varied only between 2.07 and 2.38 g m$^{-2}$ d$^{-1}$ (black pattern in Figs. 4g-4i). This may reflect the low fine root production at Ryukoku Forest in 2010 (Hattori 2011). The bootstrap 95% CI of the estimated fine root production was large—a pattern similar to the observation in 2007 (Figs. 3i-3l).

The fine root decomposition estimated by the decision matrix were all zero, but other methods predicted positive values (Figs. 4a-4c). Mortality estimated by the decision matrix were on average 47% lower than that calculated by the continuous inflow assumption. The decision matrix also led to the lowest fine root production estimates when the four approaches were compared (Figs. 4g-4i). The production estimates from the decision matrix were on average 15% lower than the continuous inflow estimates.
Some previous studies reported that simultaneously varying fine root production, mortality, and decomposition cannot be measured directly with sequential soil core or ingrowth core methods (Kurz and Kimmins 1987; Santantonio and Grace 1987; Majdi 1996; Majdi et al. 2005); however, such measurement is possible with the addition of litter bags as we have described in the present study.

Our results showed that the decision matrix nearly always gave values lower than those calculated by the forward estimate (Figs. 3 and 4), which in itself is an underestimate. This was because increments of both fine root biomass and necromass were positive at nearly all periods, which forced the calculation of fine root decomposition by the decision matrix to zero (Fairley and Alexander 1985), although there were appreciable amounts of decomposition according to the other methods. In one case, the decision matrix estimates were greater than those of other methods (Figs. 3d and 3h). However, this is an anomaly created by non-closure of mass balance in fine root dynamics due to the measurement error. Theoretically, the calculations by the decision matrix are nearly always underestimates, and consequently cannot be regarded as the best method.

The forward estimate is also bound to be an underestimate, because it only takes into account decomposition of dead fine roots present at the beginning of the period considered. It ignores decomposition of new roots that died during the measurement period. On the other hand, the backward estimate will be an overestimate because it assumes that death of new roots during the period occurs at one time immediately following the start of the period under consideration. Therefore, the true value of decomposition must lie between the values calculated by the forward and backward estimates. The continuous inflow estimate consistently satisfies this condition (Figs. 3 and 4).

Another characteristic of the present examples of continuous inflow estimates is that the magnitude of 95% CI tends to be large for fine root production (Figs. 3 and 4). This is mainly due to the propagation of measurement errors in the calculation which involves several variables (Equations 1 and 4) each of which contain variations. Propagation of measurement error is a problem that cannot be avoided when several measurements are added to derive a production estimate. There are mainly two sources of error. One is addition of increments in biomass and necromass and decomposition during a single measurement period (Equation 1). Each of these terms has its own variation, which must be added to obtain that of production. The other source of error comes from addition of production values for different measurement periods. Use of only the significant differences will reduce the propagated error by omitting variation in non-
significant data; however, it cannot be free of error propagation as long as addition of terms is involved. A relatively large sample size will be necessary to improve accuracy substantially and the necessary sample size is likely to vary depending on plant species and site conditions.

However, if the purpose of the study is to assess the magnitude of NPP or the contribution of fine root production in total NPP, a continuous inflow estimate will be more desirable. The estimate of fine root production by the decision matrix (as compared to continuous inflow model) was 14% lower on average, and 38% lower in an extreme case, in the present study of the *C. obtusa* stand in 2007 and 2010. Therefore, use of the decision matrix is likely to lead to substantial underestimation of NPP of the ecosystem. The degree of error was even greater for fine root mortality. When calculated by the decision matrix fine root mortality was 38% lower on average than the value estimated by the continuous inflow assumption. In an extreme case, the decision matrix estimate was 80% lower.

The effect of the use of different methods of calculation on fine root production over a longer measurement period is also of interest. When only the significant differences of biomass and necromass between measurement periods (ΔB and ΔN) were added, decision matrix led to an estimate of 256 g m$^{-2}$ 166d$^{-1}$ for the 2007 experiment. In contrast, the decision matrix suggested 333 g m$^{-2}$ 166d$^{-1}$ when all ΔB and ΔN values were used for calculation regardless of their significance (Table 2). We also obtained production of 304 g m$^{-2}$ 166d$^{-1}$ when only the first and last sampling data were used to calculate ΔB+ΔN (Table 2). The last calculation is identical to the estimate by the decision matrix using the same two observations (Table 2), and is clearly an underestimate since decomposition is ignored (Equation 1). When we use the same observations, but take into account decomposition calculated using the mean decomposition rate (the parameter $\gamma$ in Equation A2) for all periods and the continuous inflow estimate, the fine root production (Equation 1) becomes 392 g m$^{-2}$ per 166 d (Table 2). Use of only significant differences has been the method to avoid overestimation; however, it resulted in substantial underestimation (256 g m$^{-2}$ 166d$^{-1}$) when combined with the decision matrix. This value was 15% smaller than the known underestimate of 304 g m$^{-2}$ 166d$^{-1}$. It was also 34% smaller than the continuous inflow estimate (392 g m$^{-2}$ 166d$^{-1}$) calculated with the first and last sampling data (Table 2).

Patterns of the estimated production were similar for the 2010 experiment. Decision matrix with data from all periods resulted in underestimation of 493 g m$^{-2}$ 177d$^{-1}$ since this value was equal to the estimate of ΔB+ΔN calculated by using only the first and last sampling data without decomposition (Table 2). Another characteristic of the 2010 data is that the estimates calculated only with the significant differences resulted in unusually
low values. This was because all differences in fine root biomass and necromass were not significantly different between the measurement periods.

These observations and results of Table 2 suggest that use of only the significant differences tends to substantially underestimate fine root production, particularly when the decision matrix was used for calculation. Forward estimate also led to values lower than the known underestimate of $ΔB + ΔN$ in the majority of cases. On the other hand, the continuous inflow estimate suggested stable production values regardless of the number of measurement periods applied.

The decomposition rates of fine root necromass that we observed in the present study are probably reasonable. The decomposition rates ($\gamma$; evaluated with Equation A2) were 0.0071±0.0014 (d$^{-1}$) for a series of ca. six-week-long experiments in 2007. They are equivalent to annual rates of 2.61±0.53 (y$^{-1}$; Table 3). These are also translated as monthly values of the decomposition ratio ($\gamma_{ij}$) at 0.19±0.03 (dimensionless), or annual values of 0.87±0.07 (dimensionless; Table 3) for a hypothetical condition that assumes the rate does not change for an entire year (e.g., Equation A2). Similarly, the decomposition rates ($\gamma$) for the 2010 sequential soil cores were 0.0035±0.0007 (d$^{-1}$) for ca. two-month observation periods. They are equivalent to annual rates of 1.30±0.28 (y$^{-1}$). They correspond to monthly rates $\gamma_{ij}$ of 0.10±0.01 (dimensionless), or annual values of 0.65±0.05. Therefore, the decomposition rates of dead fine roots observed in the present study are generally of similar magnitude to those assumed by Publicover and Vogt (1993) in their simulation: monthly $\gamma_{ij}$ of 0.15 or annual $\gamma_{ij}$ of 0.85 (Table 3).

Comparison of annual decomposition rates ($\gamma$) among various ecosystems, presented in Table 3 indicates that the estimates for the C. obtusa forest in the present study are somewhat higher than those reported for other ecosystems. It is also noted that the various ranges of decomposition rates are similar regardless of the methods used for estimation. For example, when the method used in the present study was applied, the annual $\gamma$ was 0.16 for an old jack pine stand in Canada. This value is nearly equal to the global mean for a conifer forest when regular envelope-type litter bags are used (Table 3). Therefore, variation in observed decomposition rates is likely to have originated primarily from differences in the characteristics of ecosystems, and not from the methods used for analysis. In the present study, the annual decomposition rates were extrapolated from data from field experiments that lasted 30—91 days during non-winter seasons. True annual decomposition rates will be lower than those reported.

In summary, both sequential soil cores and ingrowth cores could be used with root litter bag experiments to estimate fine root production, mortality, and decomposition occurring simultaneously, and could provide those parameters with mass-based flux variables (e.g., g m$^{-2}$ d$^{-1}$). Generalized relationships were derived that allow calculation
of production, mortality, and decomposition from changes between observations in fine root biomass and necromass, and from the decomposition ratio of dead fine roots (Equations 1, 2, and 4). The decomposition estimate calculated with the continuous inflow assumption (Equation 4) is considered the best among the four approaches compared because it may closely represent the reality of the process of fine root mortality. Accordingly, the continuous inflow approach would also be the best choice for calculating fine root mortality and production (Equations 1 and 2). A large sample size is necessary to reduce the 95% CI of the estimated production by the continuous inflow estimate; however, it would be theoretically more appropriate than the decision matrix which could not realistically take into account decomposition. Development of the continuous inflow approach is significant not necessarily because it suggests values different from those calculated by the decision matrix, but because it is applicable to general situations regardless of the magnitude of decomposition of dead roots, root mortality, and production. The decision matrix will give theoretically realistic values only for situations where decomposition, mortality, or production is negligible. The ability of the continuous inflow approach to estimate fine root dynamics with a simple litter bag experiment is also a significant improvement over the method of Santantonio and Grace (1987), in which decomposition must be estimated through relatively complex modeling with additional environmental data.

**Acknowledgments**

We thank T. Miyaura and the Open Research Center for Satoyama Studies at Ryukoku University for supporting the present study in the *C. obtusa* stand at Ryukoku Forest, N. Kurachi and A. Kawamura for helping to calculate the bootstrap 95% CI, and M. Dannoura, D. Epron, K. Noguchi, S. Sugita, and two anonymous reviewers for commenting on the manuscript.

**References**


global warming due to carbon-cycle feedbacks in a coupled climate model.

Cusack D F, Chou W W, Yang W H, Harmon M E, Silver W L, and the LIDET team
(2009) Controls on long-term root and leaf litter decomposition in neotropical

optical scanner method for observation of plant root dynamics. Plant Root 2: 14-
18.

1-26.

Efron B and Gong G (1983) A leisurely look at the bootstrap, the jackknife, and cross-

Fairley R I, and Alexander I J (1985) Methods of calculating fine root production in
forests. In Ecological Interactions in Soil: Plants, Microbes and Animals. Eds. A
H Fitter, D Atkinson and D J Read. pp 37-42. Blackwell Scientific Publications,
Oxford.

conifer- broad-leaved forest stands at different successional stages after fire. Can.

tracer model study of atmospheric CO₂: Response to seasonal exchanges with the

of Chamaecyparis obtusa Endl.: A field experiment using root ingrowth cores.
Plant Soil 266: 325-332.

Gaudinski J B, Trumbore S E, Davidson A, Cook A C, Markewitz D, and Richter D D
(2001) The age of fine-root carbon in three forests of the eastern United States


Hattori K (2011) The pipe-model and quantitative relationships of leaf biomass and fine
root biomass in forest communities. M.S. thesis. Graduate School of
Agriculture, Kyoto University, Kyoto, Japan (in Japanese).

Heimann M, Keeling C D, and Tucker C (1989) A three dimensional model of
atmospheric CO₂ transport based on observed winds, 3, Seasonal cycle and
synoptic time scale variations, in Aspects of Climate Variability in the Pacific and
the Western Americas, Geophys. Monogr. Ser., vol. 55, edited by D.H. Peterson,
pp. 277-303, AGU, Washington, D. C.


Appendix

Continuous inflow estimate of $d_{ij}$ (Equation 4): First, let us consider the decomposition process of dead fine roots occurring in a root litter bag treated with the ‘root-impermeable water-permeable (RIWP) sheet’ (see Materials and methods). The amount $N$ of dead fine root is assumed to decompose with instantaneous decomposition of $\gamma \cdot N$ where $\gamma$ is the decomposition rate. This process can be described by a differential equation,

$$\frac{dN}{dt} = -\gamma \cdot N.$$  

With a boundary condition, $N = N_i$ at $t = i$, this differential equation is solved as

$$N = N_i \cdot e^{-\gamma(t-i)} \quad (A1).$$

If $N = N_j$ at $t = j$, and $\Delta t = j - i$, Equation A1 gives, $N_j = N_i \cdot e^{-\gamma \Delta t}$.

This relationship and Equation 3 in the text yield an expression for the decomposition ratio of fine root necromass between times $i$ and $j$, $\gamma_{ij}$, as

$$\gamma_{ij} = 1 - e^{-\gamma \Delta t} \quad (A2).$$

Note that $\gamma$ and $\gamma_{ij}$ in Equation A2 are different parameters.

Next, let us consider the decomposition process of dead fine roots in an ingrowth core where there is both instantaneous fine root decomposition of $\gamma \cdot N$ and instantaneous fine root mortality (addition of new dead roots) at a constant level of $\sigma$. Here, the process can be described by a differential equation:

$$\frac{dN}{dt} = \sigma - \gamma \cdot N \quad (A3).$$

It is well known that the linear first-order differential equation of a form $dy/dx + P(x) \cdot y = Q(x)$ with two variables $x$ and $y$ has a solution (Kreyszig 1972):

$$y = e^{-\int P(x)dx} \left[ \int_0^x Q(x) e^{\int P(x)dx} dx + C \right],$$

where $C$ is any constant. Therefore, Equation (A3) can be solved with a boundary condition, $N = N_i$ at $t = i$, as,

$$N = (\sigma / \gamma) + (N_i - \sigma / \gamma) e^{-\gamma(t-i)} \quad (A5).$$
By calculating $N_j$ with Equation A5 for $t = j$, then inserting Equation (A2), we obtain the relationship, $\sigma / \gamma = \Delta N / \gamma_j + N_j$, where $\Delta N = N_j - N_i$. Applying this relationship in Equation A5 yields,

$$N = \Delta N \cdot (1 - e^{-\gamma(t-i)}) / \gamma_j + N_i$$  \hspace{1cm} (A6).

Then, by noting $\gamma \cdot \Delta t = -\ln(1 - \gamma_j)$ from Equation A2, the amount of decomposed dead fine roots between times i and j could be obtained from Equation A6 as,

$$d_{ij} = \int_{i}^{j} \gamma \cdot N dt = -\Delta N - (\Delta N / \gamma_j + N_j) \cdot \ln(1 - \gamma_j)$$  \hspace{1cm} (A7).
Table 1  A version of the decision matrix by Fairley and Alexander (1985) for calculating production \((g)\) and mortality \((m)\) of fine roots and decomposition \((d)\) of dead fine roots during a measurement interval.  \(\Delta B\) and \(\Delta N\) represent change during a measurement interval in the pools of live fine root mass and dead fine root mass, respectively.  Inequalities in the top two rows and those in the first column from the left indicate conditions on the values of \(\Delta B\) and \(\Delta N\).  Suggested equations for calculation of \(g\), \(m\), and \(d\) are given in the Table for specific combination of the values of \(\Delta B\) and \(\Delta N\).  The equations in parentheses are assumptions under specific conditions.

<table>
<thead>
<tr>
<th>(\Delta B \geq 0)</th>
<th>(\Delta B &lt; 0)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\Delta N &gt;</td>
<td>\Delta B</td>
</tr>
<tr>
<td>(\Delta N \geq 0)</td>
<td>(\Delta N &lt; 0)</td>
</tr>
<tr>
<td>(g = \Delta B + \Delta N)</td>
<td>(g = \Delta B)</td>
</tr>
<tr>
<td>(m = \Delta N)</td>
<td>(m = \Delta N)</td>
</tr>
<tr>
<td>((d = 0))</td>
<td>((d = 0))</td>
</tr>
<tr>
<td>(\Delta N &lt; 0)</td>
<td>(\Delta N &gt; 0)</td>
</tr>
<tr>
<td>(g = \Delta B)</td>
<td>((g = 0))</td>
</tr>
<tr>
<td>((m = 0))</td>
<td>(m = -\Delta B)</td>
</tr>
<tr>
<td>(d = -\Delta N)</td>
<td>(d = -\Delta B - \Delta N)</td>
</tr>
</tbody>
</table>
Table 2  Comparison of fine root production in dry mass during the entire period of experiment estimated by various methods of calculation for the Chamaecyparis obtusa forest at Ryukoku Forest in 2007 and 2010. The 2007 experiment started on July 6, ended on December 21, and lasted for 166 days with four measurement periods. The 2010 experiment started on June 22, ended on December 16, and lasted for 177 days with three measurement periods. Fine root ingrowth core was used in 2007 while sequential soil cores were taken in 2010, both with accompanying root decomposition experiment. Production was calculated for three groups of data that differed in characteristics. First group includes only significant differences in $\Delta B$ and $\Delta N$; second group consists of data of all measurement periods regardless of significance of difference; third includes only data of the first and last soil cores sampled during the experiment.

<table>
<thead>
<tr>
<th>Method used for calculation</th>
<th>2007 study</th>
<th>2010 study</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(g m$^{-2}$ 166d$^{-1}$)</td>
<td>(g m$^{-2}$ 177d$^{-1}$)</td>
</tr>
</tbody>
</table>

**Using only significant differences**

| Decision matrix | 256$^\dagger$ | 0$^\dagger$ |
| Forward estimate | 304$^\dagger$ | 56$^\dagger$ |
| Continuous inflow estimate | 330 | 89$^\dagger$ |
| Backward estimate | 365 | 130$^\dagger$ |

**Using data from all periods**

| Decision matrix | 333 | 493$^\dagger$ |
| Forward estimate | 243$^\dagger$ | 538 |
| Continuous inflow estimate | 391 | 574 |
| Backward estimate | 408 | 622 |

**Using only first and last sampling data**

| $\Delta B + \Delta N$ | 304$^\dagger$ | 493$^\dagger$ |
| Decision matrix | 304$^\dagger$ | 493$^\dagger$ |
| Forward estimate | 304$^\dagger$ | 505 |
| Continuous inflow estimate | 392 | 588 |
| Backward estimate | 619 | 744 |

$^\dagger$ Decomposition was calculated by forward, continuous inflow, or backward estimate, then significant values of $\Delta B$ and $\Delta N$ (Equation 1) were added. $^\ddagger$ Conservative estimate of production in boldface numerals by ignoring decomposition in Equation 1.
Italic numerals indicate values smaller than or equal to the estimate shown with boldface numerals for each year.

Table 3  Comparison of annual decomposition rate $\gamma$ ($y^{-1}$) and annual decomposition ratio $\gamma_{ij}$ of dead fine roots reported in various forest ecosystems. Equation A2 was used for the necessary conversion between $\gamma$ and $\gamma_{ij}$. Mean±SE are indicated where appropriate. Data are categorized into four groups depending on the method used for estimation: Litter bags (loose soil contact) is ordinary envelope-type litter bags made of mesh cloth, Litter bags (close soil contact) is the root-impermeable water-permeable sheet-covered and soil-filled ingrowth core—a construction identical to that used in the present study, Trench-plot is a trenched soil block in which root decay is monitored, and Simulation indicates a value derived hypothetically for use in a simulation study.

Superscripts indicate references where decomposition rates or ratios were reported: Interrupted superscript letters are not meaningful. In the tables, superscript letter $a$ is Silver and Miya (2001), $b$ Cusack et al. (2009), $c$ Osawa A. (unpublished data), $d$ Publicover (1992), $e$ Silver and Vogt (1993), $f$ calculated from monthly $\gamma_{ij}$ of 0.15 in Publicover and Vogt (1993), and $g$ sample size not applicable due to simulation.

<table>
<thead>
<tr>
<th>Site</th>
<th>$\gamma$ $(y^{-1})$</th>
<th>annual $\gamma_{ij}$ (dimensionless)</th>
<th>Number of estimated $\gamma$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Litter bags (loose soil contact)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Global mean, broadleaf</td>
<td>0.44±0.06</td>
<td>0.35</td>
<td>40</td>
</tr>
<tr>
<td>Global mean, conifer</td>
<td>0.17±0.02</td>
<td>0.15</td>
<td>10</td>
</tr>
<tr>
<td>LUQ†, Puerto Rico</td>
<td>1.06±0.28</td>
<td>0.65</td>
<td>4</td>
</tr>
<tr>
<td>GSF†, Puerto Rico</td>
<td>0.42±0.07</td>
<td>0.34</td>
<td>4</td>
</tr>
<tr>
<td><strong>Litter bags (close soil contact)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>this study at RKF†, 2007</td>
<td>2.61±0.53</td>
<td>0.87±0.07</td>
<td>5</td>
</tr>
<tr>
<td>this study at RKF†, 2010</td>
<td>1.30±0.28</td>
<td>0.65±0.05</td>
<td>4</td>
</tr>
<tr>
<td>WBNP†, young jack pine</td>
<td>0.24±0.03</td>
<td>0.21±0.02</td>
<td>2</td>
</tr>
<tr>
<td>WBNP†, mid-age jack pine</td>
<td>0.30±0.05</td>
<td>0.26±0.03</td>
<td>5</td>
</tr>
<tr>
<td>WBNP†, old jack pine</td>
<td>0.16±0.04</td>
<td>0.14±0.04</td>
<td>5</td>
</tr>
<tr>
<td><strong>Trench-plot</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>NJPB†, pine</td>
<td>0.58</td>
<td>0.44</td>
<td>1</td>
</tr>
<tr>
<td>NJPB†, oak</td>
<td>0.56</td>
<td>0.42</td>
<td>1</td>
</tr>
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</table>
Simulation

<table>
<thead>
<tr>
<th></th>
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<th>1</th>
</tr>
</thead>
<tbody>
<tr>
<td>NJPB†, Ericaceous</td>
<td>0.78 (d)</td>
<td>0.54</td>
<td></td>
</tr>
<tr>
<td>LUQ†, lower plot</td>
<td>0.8 (e)</td>
<td>0.55</td>
<td>1</td>
</tr>
<tr>
<td>LUQ†, upper plot</td>
<td>0.9 (e)</td>
<td>0.59</td>
<td>1</td>
</tr>
<tr>
<td>LUQ†, control forest</td>
<td>0.4 (e)</td>
<td>0.32</td>
<td>1</td>
</tr>
</tbody>
</table>

†Abbreviations of names of places (locations): LUQ: Luquillo Experimental Forest, Puerto Rico (18°N, 5°W); GSF: Guanica State Forest, Puerto Rico (17°N, 65°W); RKF: Ryukoku Forest, Japan (34°N, 135°E); WBNP: Wood Buffalo National Park, Canada (68°N, 113°W); NJPB: New Jersey Pine Barrens, USA (39°N, 74°W).

\(^{\S}\)Calculation was based on field data from experiments each consisting of several periods that lasted 30—92 days during non-winter seasons.

**Figure captions**

Fig. 1  A compartment model representing the mass balance of organic matter that is derived from live fine roots in the soil volume. The boxes express the stock: \(B\) is live fine roots and \(N\) is dead fine roots and organic matter of fine root origin. The arrows indicate mass flow into, between, or out of the compartments: \(g_{ij}\) is fine root ingrowth; \(m_{ij}\) is fine root mortality; and \(d_{ij}\) is decomposition of dead organic matter between the times \(i\) and \(j\). The amounts of live fine roots at times \(i\) and \(j\) are expressed as \(B_i\) and \(B_j\), respectively, in the text. \(N_i\) and \(N_j\) express the amounts of necromass at times \(i\) and \(j\), respectively. \(\Delta B\) and \(\Delta N\) represent changes in fine root biomass and necromass between times \(i\) and \(j\).

Fig. 2  A sequence of soil core installations into the soil horizon (open circles) and recovery or soil core sampling to measure fine root biomass and necromass (filled circles) of a set of three soil cylinders used to evaluate fine root ingrowth, mortality, and decomposition simultaneously between times \(i\) and \(j\), where \(0 < i < j\). For ingrowth cores, the cores A and B are installed at the same time (time zero) but are recovered at different times. For sequential soil sampling, soil cores A and B are collected at times \(i\) and \(j\), respectively. Litter bag C is the 'root-impermeable water-permeable (RIWP)
sheet'-covered core installed with known mass of dead fine roots added at time i, and recovered at time j with core B.

**Fig. 3** Estimated values of fine root decomposition ($d_{ij}$), mortality ($m_{ij}$), and production ($g_{ij}$) for the ingrowth core experiment of 2007. The estimates are compared to those calculated by the decision matrix (DM, cross pattern), forward estimate (F, left-slanting pattern), continuous inflow estimate (C, black), and backward estimate (B, right-slanting pattern). Vertical bars indicate the upper 95% confidence limits based on the bootstrap method. For the decision matrix method, all decomposition estimates are zero except for the fourth period that ended on December 21. Note that the vertical scale is different for fine root production, $g_{ij}$.

*The values of fine root production were set at zero due to the negative values obtained. See text for further explanation.

**Fig. 4** Estimated values of fine root decomposition ($d_{ij}$), mortality ($m_{ij}$), and production ($g_{ij}$) for the sequential soil core sampling of 2010. The estimates are compared to those calculated by the decision matrix (DM, cross pattern), forward estimate (F, left-slanting pattern), continuous inflow estimate (C, black), and backward estimate (B, right-slanting pattern). Vertical bars indicate the upper 95% confidence limits based on the bootstrap method. For the decision matrix method, all decomposition estimates are zero. Note that the vertical scale is different for fine root decomposition, $d_{ij}$.
Figures

Fig. 1

$\Delta B = B_j - B_i$

$\Delta N = N_j - N_i$

Fig. 2

Course of time, $t$
Fig. 3
Fig. 4

1003
1004