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Reconcilable differences: a joint calibration of fine-root turnover times with radiocarbon and minirhizotrons

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Summary

- We used bomb-radiocarbon and raw minirhizotron lifetimes of fine roots (< 0.5 mm in diameter) in the organic layer of Norway spruce (*Picea abies*) forests in southern Sweden to test if different models are able to reconcile the apparently contradicting turnover time estimates from both techniques.
- We present a framework based on survival functions that is able to jointly model bomb-radiocarbon and minirhizotron data. At the same time we integrate prior knowledge about biases of both techniques – the classification of dead roots in minirhizotrons and the use of carbon reserves to grow new roots.
- *Two-pool* models, either in parallel or in serial setting, were able to reconcile the bomb-radiocarbon and minirhizotron data. These models yielded a mean residence time of 3.80 ± 0.16 yr (mean ± SD). On average 60 ± 2% of fine roots turned over within 0.75 ± 0.10 yr, while the rest was turning over within 8.4 ± 0.2 yr. Bomb-radiocarbon and minirhizotron data alone give a biased estimate of fine-root turnover.
- The *two-pool* models allow a mechanistic interpretation for the coexistence of fast- and slow-cycling roots – suberization and branching for the *serial-two-pool* model and branching due to ectomycorrhizal fungi–root interactions for the *parallel-two-pool* model.

Introduction

The turnover of fine roots is a crucial part of the terrestrial carbon cycle. In addition to litterfall from leaves, needles, twigs and fruits, root litter constitutes a major addition of carbon and nutrients to the soil organic matter pool. Contrary to aboveground litterfall, the flux of root litter has eluded quantification, partly because roots – the 'hidden half' of the terrestrial biosphere – are more difficult to observe and study. In addition, different techniques used to quantify fine-root turnover – ranging from ^{13}C labeling, tracing the ^{14}C bomb peak, sequential soil coring and ingrowth cores to root cameras (minirhizotrons) – have yielded widely contradictory estimates of root turnover (Trumbore & Gaudinski, 2003; Pritchard & Strand, 2008; Strand *et al.*, 2008; Lukac, 2012).

The largest differences in inferred root turnover times are between isotopic techniques (here we use bomb-radiocarbon) and direct observations of root growth and persistence (minirhizotron methods) (Trumbore & Gaudinski, 2003; Guo *et al.*, 2008). For a given standing stock of fine roots in a forest stand, the root litter input estimated from common minirhizotron turnover times (*c.* 2 yr, Strand *et al.* (2008); Hansson *et al.* (2013)) is *a priori* 75% higher than the root litter input based on bomb-radiocarbon derived turnover times (*c.* 8 yr; Gaudinski *et al.*, 2001; Gaul *et al.*, 2009; Fröberg, 2012).

The *Radix* model (Gaudinski *et al.*, 2009, 2010; Riley *et al.*, 2009) has been a recent attempt to model complete fine-root dynamics with five different pools – a storage pool with carbon reserves that can be used to grow new roots, two live-root pools and two dead-root pools. Gaudinski *et al.* (2010) made use of both bomb-radiocarbon and minirhizotron data to parameterize the turnover times of the two parallel, independent live-root pools. In their parameterization, however, Gaudinski *et al.* (2010) solely used the median longevity from minirhizotrons for the turnover time of the short-lived root pool. They then estimated the turnover time of the long-lived root pool using the ^{14}C content of fine roots given the turnover time of the short-lived root pool. However, the *separate* parameterization of the short-lived and the long-lived root pool does not fully reconcile minirhizotron observations with the ^{14}C in fine roots because this would relate the minirhizotron observations only to the short-lived pool. Modelled fine-root dynamics, though, should represent the whole spectrum of fine-root dynamics observed with both techniques. Furthermore, the use of a single metric (median longevity) to represent minirhizotron observations throws away the majority of the information content of minirhizotron data. Finally, Strand *et al.* (2008) noted that *median* longevities yields turnover time estimates that are systematically too fast. This, in turn, possibly yields too slow turnover times of the long-lived root pool for the parameterization of the *Radix* model in Gaudinski *et al.* (2010).

We therefore want to make full use of the information content of minirhizotron data, and aim to quantify root turnover with minirhizotron and bomb-radiocarbon data as true joint constraints. To this end we developed a unified evaluation framework (Ahrens & Reichstein, 2014) that makes it possible to compare survival functions against both bomb-radiocarbon and minirhizotron data. We assess the performance of several survival functions that are commonly used to evaluate data from either technique: the *exponential*, *Weibull* and *log-normal* model (Gaudinski *et al.*, 2001; Pritchard & Strand, 2008; Strand *et al.*, 2008; Gaul *et al.*, 2009; Fröberg, 2012). Furthermore we test *two-pool* models, coupled either in parallel (equivalent to the live root-pool structure of *Radix*) or in series (as in Ahrens & Reichstein, 2014).

In Ahrens & Reichstein (2014) we already pointed to the possibility of accounting for biases of the minirhizotron and the bomb-radiocarbon technique. In this paper, we refine the unified evaluation framework by including prior knowledge on possible biases. First, one cannot rule out that carbon reserves are used for the growth of fine roots. This constitutes a bias for the bomb-radiocarbon technique because we cannot use the atmospheric ^{14}C record as a direct proxy for the ^{14}C content of newly grown roots, but must employ an (unknown) storage residence time. Thus, ^{14}C fine-root turnover times that do not include storage residence times yield estimates of root turnover that are too slow.

Second, it is hard to identify roots as dead or still alive in minirhizotron studies. Hence, the time-to-disappearance of a root segment is sometimes used instead of the time-to-death as a measure of fine-root longevity (Withington *et al.*, 2006; Gaul *et al.*, 2009). This overestimates root longevity by the time it takes for a root to be decomposed.

Our objectives in this study are: to quantify root turnover with bomb-radiocarbon and minirhizotron data as joint constraints using different survival functions; to assess the performance of these survival functions; and to address systematic biases of bomb-radiocarbon and minirhizotron data in the joint calibration framework.

Using Bayesian parameter estimation we calibrate the survival functions from our joint calibration framework with published ^{14}C contents in fine roots (Fröberg, 2012) and minirhizotron data (Hansson *et al.*, 2013) from the organic layer of Norway spruce forests in southern Sweden.

Materials and Methods

Fine-root ^{14}C data

Fröberg (2012) measured the radiocarbon content of fine roots from archived O-horizons of middle-aged to mature stands dominated by Norway spruce (*Picea abies* (L.) Karst.) in southern Sweden. Well preserved roots (diameter 0–0.5 mm) were selected to represent predominately live fine roots (Fröberg, 2012). We used the ^{14}C (% Modern) contents reported by Fröberg (2012) of fine roots from 1964, 1972, 1985 and 1998 and their analytical uncertainties as observational constraints for a comparison against the tested survival functions (Table 2).

Minirhizotron data

Hansson *et al.* (2013) studied fine-root turnover with minirhizotrons in eight different forest stands in southern Sweden. Here, we use fine-root minirhizotron data with the same diameter as for the ^{14}C data (0–0.5 mm) of the three mature Norway spruce stands in the Tönnersjöheden Experimental Forest. We use data from 14 tubes, five of which are solely located in the O-horizons, while nine others also include the upper 10 cm of the mineral soil. One of these nine tubes was from understorey spruce in a pine stand. Starting 1 yr after tube installation, roots were monitored throughout four growing seasons (2007–2010) and 14 photo sessions. Roots were monitored from growth to disappearance, so that root longevity is possibly overestimated by the timespan a dead root needs to be decomposed. Hansson *et al.* (2013) assume that this systematic bias is in the range of 1–4 months.

Analysis of minirhizotron data with survival functions

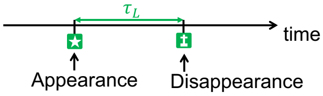
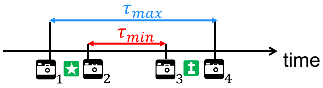
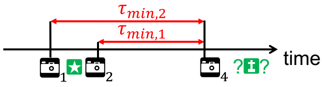
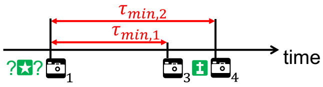
Ideally, minirhizotron tubes allow monitoring of fine-root segments from their formation to death. Unfortunately, it is difficult to actually classify fine roots as dead or alive, so fine-root segments are monitored from their first appearance until their disappearance (Table 1, Case C0). Four different cases can be distinguished (Table 1).

In the most common case, C1, the lifetime data are interval-censored, where both the appearance and the disappearance of a root segment occur in the time period between two photo sessions. Consequently, we can define a minimum (τ_{min}) and maximum lifetime (τ_{max}) for these root segments (Table 1, C1).

All other cases can be classified as right-censored because we know that the true lifetime, τ_L, of a root segment is longer than a certain minimum lifetime, τ_{min}. If a root segment did not disappear until the last photo session, we can define two possible minimum lifetimes, $\tau_{min,1}$ and $\tau_{min,2}$ (schematic drawing in Table 1, C2). Similarly, if a root segment has already been present before the first photo session, but died before the last photo session, we also can define two possible minimum lifetimes, $\tau_{min,1}$ and $\tau_{min,2}$ (schematic drawing in Table 1, C3). Finally, if a root segment has been present throughout the study period (from first to last photo session), we get an absolute minimum lifetime, τ_{min} (right-censoring, *sensu strictu*; Kleinbaum & Klein, 2005).

Approaches to derive fine-root turnover estimates include nonparametric and parametric approaches. Common to both approaches is the definition of so-called survival functions which – in the case of roots – describe the fraction of roots that survive until age τ. The nonparametric Kaplan–Meier survival function is basically a cumulative frequency function of the observed fine-root lifetimes. The Kaplan–Meier approach has been used in numerous studies to estimate median longevities of fine-root segments, although Pritchard & Strand (2008) rightly argue that

Table 1 Likelihood functions (L) for minirhizotron observations are depending on the timing of image collection

Schematics of hypothetical lifetimes of root segments in minirhizotrons τ_{max} := max. lifetime τ_{min} := min. lifetime 📷$_i$:= photo at time i	Lifetime (τ_L)	Likelihood (L)	Case	n
	τ_L	$f(\tau_L)$	C0	0
	$\tau_{min} < \tau_L < \tau_{max}$	$S(\tau_{min}) - S(\tau_{max})$	C1	1435
	$\tau_L > \tau_{min,1}$ or $\tau_L > \tau_{min,2}$	$½(S(\tau_{min,1}) + S(\tau_{min,2}))$	C2	1088
	$\tau_L > \tau_{min,1}$ or $\tau_L > \tau_{min,2}$	$½(S(\tau_{min,1}) + S(\tau_{min,2}))$	C3	54
	$\tau_L > \tau_{min}$	$S(\tau_{min})$	C4	42

The schematics show how well the fine-root lifetime (τ_L) can be constrained for typical cases. n is the number of respective cases for the Norway spruce minirhizotron data (0–0.5 mm) in Hansson *et al.* (2013).

median longevity underestimates mean longevity and thereby the fine-root turnover time.

Parametric survival functions should be preferred over non-parametric ones, because the mean longevity and, hence, the fine-root turnover time are well defined. Parametric survival functions, $S(\tau)$, are commonly derived from cumulative distribution functions $F(\tau)$:

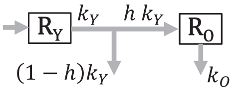
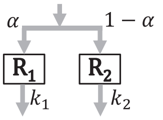
$$S(\tau) = 1 - F(\tau)$$

Throughout the study we used five different survival functions (Table 2). *Exponential* survival functions have been commonly used to determine fine-root turnover from the ^{14}C in fine roots (Gaudinski *et al.*, 2001; Gaul *et al.*, 2009; Fröberg, 2012), while *Weibull* and *log-normal* survival functions have been used to determine mean longevity from minirhizotron data (Strand *et al.*, 2008; Gaul *et al.*, 2009; Hansson *et al.*, 2013). Additionally, we tested two *two-pool* models – one in a serial setting as in Ahrens & Reichstein (2014), and one in a parallel setting which is equivalent to the pool structure of live fine roots of the *Radix* model (Riley *et al.*, 2009). The survival functions corresponding to the *serial-two-pool* and *parallel-two-pool* model are also given in Table 2.

The formulation of the likelihood for cases C1 and C4 (Table 1) can be directly taken from textbooks on survival analysis (Kleinbaum & Klein, 2005). For cases C2 and C3 we also applied the likelihood function for the right-censored case C4, but assumed that the overall likelihood is the mean of the individual likelihoods of both possible minimum lifetimes, $\tau_{min,1}$ and $\tau_{min,2}$ (Table 1). This definition accounts for the probability of a shorter minimum lifetime $\tau_{min,1}$ in comparison to the probability of longer minimum lifetime $\tau_{min,2}$. This formal definition of likelihood functions is able to deal with apparently shortened root lifetimes due to transparent root material (Tierney & Fahey, 2001) or due to the disappearance of root segments because of causes other than death (Hansson *et al.*, 2013). The likelihood functions only rely on the minimum observed time that root segments are actually present (Table 1). Table 1 also gives an overview about the frequency of cases C1 to C4 at the Tönnersjöheden Experimental Forest.

The parameters of the different survival functions can be summarized with metrics like mean residence time, τ_r, or mean age, τ_a (Ahrens & Reichstein, 2014). For the quantification of root turnover, mean residence time is the most important metric and is used interchangeably with notions like mean longevity, mean lifespan or mean lifetime (Strand *et al.*, 2008; Gaul *et al.*, 2009;

Table 2 Overview of tested survival functions; τ denotes the age of a root, $\#\theta$ is the number of parameters of a survival function

Survival function	Equation	Model structure	$\#\theta$
Exponential[a]	$S(\tau) = e^{-k\tau}$		1
Weibull[b]	$S(\tau) = e^{-(\frac{\tau}{\gamma})^{\beta}}$		2
Log-normal[c]	$S(\tau) = 0.5\left[\mathrm{erf}\left(\frac{\log_e(\tau) - \mu}{\sigma\sqrt{2}}\right)\right]$		2
Serial-two-pool[d]	$S(\tau) = \frac{e^{-(k_Y+k_O)\tau}[(k_Y(1-h) - k_O)e^{k_O\cdot\tau} + h\cdot k_Y e^{k_Y\cdot\tau}]}{k_Y - k_O}$		3
Parallel-two-pool[e]	$S(\tau) = \alpha e^{-k_1\tau} + (1-\alpha)e^{-k_2\tau}$		3

[a] The only parameter for the *exponential* survival function is the turnover rate k.

[b] The *Weibull* survival function can be described by the scale parameter γ and the shape parameter β.

[c] The *log-normal* model can be described by the location parameter μ and the shape parameter σ. erf(x) denotes the Gaussian error function.

[d] In the *serial-two-pool* model new roots belong at first to a fast-cycling root pool, R_Y. These roots are turning over with rate k_Y. A fraction h of the turnover from the fast-cycling pool R_Y is transferred to the slow-cycling pool R_O which is turning over with rate k_O.This survival function is based on the derivation by Manzoni et al. (2009).

[e] In the *parallel-two-pool* model roots either belong to the fast-cycling pool R_1 or the slow-cycling pool R_2. The pools are turning over with the respective rates k_1 and k_2. α describes the fraction of roots belonging to pool R_1. This survival function is based on the derivation by Manzoni et al. (2009).

Riley *et al.*, 2009; Kikuzawa & Lechowicz, 2011). In steady state, the mean residence time can be calculated as

$$\tau_r = \int_0^{\infty} S(\tau)\,\mathrm{d}\tau \qquad \text{Eqn 1}$$

(Manzoni *et al.*, 2012).

Throughout this study we assume that the root system is in steady state; therefore, the root turnover time, τ_0, is equal to the mean residence time, τ_r (Rodhe, 1992). The root turnover time, τ_0, is defined as the ratio of the root biomass over the root litter input. Consequently, one can calculate the root litter input to the soil organic carbon pool from root biomass measurements and estimates of τ_r.

Although the mean age of roots, τ_a, cannot be used to constrain any component of the belowground carbon cycle, we also report the mean age of the root population. Mean ages were calculated as described in Ahrens & Reichstein (2014).

Convolution of the atmospheric bomb-radiocarbon curve with survival functions

Due to aboveground testing of thermonuclear weapons during the 1950s and 1960s the tropospheric ^{14}C content nearly doubled. After the Partial Test Ban Treaty in 1963, the atmospheric ^{14}C content declined quasi-exponentially due to the uptake of ^{14}C in the vegetation and oceans, but also due to fossil fuel emissions which practically contain no ^{14}C. The atmospheric bomb-radiocarbon record has proven to be a powerful tracer to shed light on carbon dynamics on annual to decadal timescales (Trumbore & Gaudinski, 2003; Trumbore, 2009). In ecological studies where bomb-radiocarbon is used as a tracer, ^{14}C contents are commonly reported in *percent Modern*, pM, or ^{14}C (% Modern). A ^{14}C (% Modern) value over 100 is typically indicative of the presence of bomb-radiocarbon and processes on yearly to decadal timescales, while a ^{14}C (% Modern) value below 100 may indicate carbon cycling on centennial or millennial timescales.

We showed that the same survival functions (Table 2) can be used to analyse both fine-root ^{14}C using the atmospheric radiocarbon curve as a tracer, and minirhizotron lifetime data (Ahrens & Reichstein, 2014). We formulated a generic time-shift model for the ^{14}C (% Modern) content of fine-roots, $Root^{14}\mathrm{C}(t)$, based on a framework proposed by Manzoni *et al.* (2009):

$$Root^{14}\mathrm{C}(t) = \int_0^{\infty} \frac{1}{\tau_0}\cdot Atm^{14}\mathrm{C}(t-\tau)\cdot S(\tau)\cdot e^{-\lambda\cdot\tau}\mathrm{d}\tau \qquad \text{Eqn 2}$$

(τ_0, turnover time, $Atm^{14}\mathrm{C}(t)$ the atmospheric ^{14}C (% Modern) value in year t; $S(\tau)$, survival function describing the fraction of roots surviving at least to age τ (cf. Niinemets & Lukjanova (2003), Manzoni *et al.* (2009, 2012)); $e^{-\lambda\cdot\tau}$, radioactive decay of ^{14}C). When the root population is in steady state, the turnover time τ_0 is equal to the mean residence time τ_r.

Eqn 2 essentially describes $Root^{14}\mathrm{C}(t)$ in a certain year t as the sum of ^{14}C inputs via root production from previous years τ weighted by the fraction of fine roots $S(\tau)$ that live for at least τ years. The atmospheric ^{14}C (% Modern) values, $Atm^{14}\mathrm{C}$, can be used as a proxy for the ^{14}C content of new roots. Consequently, the term $1/\tau_0\cdot Atm^{14}\mathrm{C}(t-\tau)$ describes the ^{14}C input via root production under the assumption that root biomass is in steady state.

Accounting for methodological biases

If neither of the methods had a systematic bias, we could directly compare $Root^{14}\mathrm{C}(t)$ and the corresponding $S(\tau)$ with the measured fine-root ^{14}C and time-to-disappearance data, respectively.

If, however, we cannot rule out that the above-mentioned systematic biases of the two methods are relevant, we need to modify the described framework.

In Eqn 2 we have to replace the atmospheric $Atm^{14}C(t-\tau)$ curve with a curve that actually represents the ^{14}C input to the root system and accounts for the possibility that stored carbon has been used to build new roots. This could be achieved by calculating a ^{14}C curve under the assumption that carbon to grow new roots ($NewGrowth^{14}C(t)$) is on average x years old. This can, for example, be modelled by a survival function that follows an exponential function with a storage turnover time, T_S:

$$NewGrowth^{14}C(t) = \int_0^{\infty} \frac{1}{T_S} \cdot Atm^{14}C(t-\tau) \cdot e^{-\frac{\tau}{T_S}} \cdot e^{-\lambda \cdot \tau} d\tau \qquad \text{Eqn 3}$$

The ^{14}C in fine roots is then calculated as (compare to Eqn 2):

$$Root^{14}C(t) = \int_0^{\infty} \frac{1}{\tau_0} \cdot NewGrowth^{14}C(t-\tau) \cdot S(\tau) \cdot e^{-\lambda \cdot \tau} d\tau \qquad \text{Eqn 4}$$

Minirhizotron data are biased because they often represent time-to-disappearance instead of time-to-death. This means that one should additionally account for the time-to-decomposition:

$$\text{time-to-disappearance} = \text{time-to-death} + \text{time-to-decomposition}$$
$$\tau_{dis} = \tau + \tau_{dec} \qquad \text{Eqn 5}$$

This corresponds to a transfer from a live-root pool to a dead-root pool. In the survival function framework we have to convolute the survival function $S(\tau)$ that accounts for the death of roots with an exponential function with a dead root turnover time, T_D:

$$S_{\text{time-to-disappearance}}(\tau_{dis}) = \int_0^{\infty} S(\tau_{dis} - \tau_{dec}) \cdot \frac{1}{T_D} \cdot e^{\frac{-\tau_{dec}}{T_D}} d\tau_{\text{dec}} \qquad \text{Eqn 6}$$

This gives a survival curve $S_{\text{time-to-disappearance}}(\tau_{dis})$ which describes the fraction of roots that are present (live or dead) at least for a time τ_{dis}. The term $1/T_D \cdot e^{-\tau_{dec}/T_D}$ in Eqn 6 is the decomposition function for dead roots which weights the relative contribution of fine-roots $S(\tau)$ that have lived for a time $\tau = \tau_{dis} - \tau_{dec}$ to fine-roots that have not disappeared until time τ_{dis}. This curve should be directly compared with the minirhizotron data. In the calibration we use prior knowledge for the two parameters, T_S and T_D, describing the systematic biases of both techniques (see next section).

Parameter estimation with minirhizotron and bomb-radiocarbon data

We optimized the parameters $\boldsymbol{\theta}$ of the different survival functions, $S(\tau)$, (Table 2) and the two additional bias parameters, T_S and T_D, by maximizing the logarithm of the posterior of the joint evaluation framework with the DiffeRential Evolution Adaptive Metropolis algorithm (Guillaume & Andrews, 2012). The posterior distribution of parameters expresses the uncertainty of the parameters after accounting for the prior knowledge we have about the parameters, and the likelihood of reproducing the minirhizotron and fine-root ^{14}C data with the model using these parameters. Because we aim to reconcile minirhizotron fine-root lifetimes and the ^{14}C content of fine roots, we define a joint likelihood function for both techniques. For mathematical convenience we use the logarithm of the joint likelihood, which is the sum of the log-likelihood of the minirhizotron data, $\ell_{Mini}(\boldsymbol{\theta})$, and the log-likelihood of the fine-root ^{14}C data, $\ell_{14C}(\boldsymbol{\theta})$.

The log-likelihood for the minirhizotron data can be formulated as:

$$\ell_{Mini}(\boldsymbol{\theta}) = \sum_{i=1}^{case} \boldsymbol{n}_i \cdot \log\left(L_i(\boldsymbol{\theta}|\boldsymbol{D}_{Mini,i})\right) \qquad \text{Eqn 7}$$

(L_i, likelihood function for one of the cases i (cases C1-C4, Table 1); $\boldsymbol{n}$, respective number of roots with the same time-to-disappearance $\boldsymbol{D}_{Mini,i}$)

The log-likelihood for the fine-root ^{14}C data can be formulated as:

$$\ell_{14C}(\boldsymbol{\theta}) = \sum_{t=1964}^{\text{meas.yrs.}} \left(-0.5\left(\frac{\boldsymbol{D}_{14C}(t) - M(t,\boldsymbol{\theta})}{\sigma(t)}\right)^2 - 0.5\log(2\pi) - \log(\sigma(t)) \right) \qquad \text{Eqn 8}$$

($\boldsymbol{D}_{14C}(t)$, fine-root ^{14}C data; $M(t,\boldsymbol{\theta})$, model results of a certain survival function for the proposed set of parameters; t, points in time when fine-root ^{14}C measurements are available; $\sigma(t)$, respective measurement uncertainty).

We only defined priors for the two bias parameters, T_D and T_S. Based on considerations by Hansson *et al.* (2013), we chose a log-normal prior for T_D with its mode at 2 months and its 90th percentile at 7 months (Fig. 1a). We chose the 0.4 yr of mean storage time found by Gaudinski *et al.* (2009) as the mode for a log-normal prior for T_S. The 90th percentile for this log-normal prior was set to 2 yr (Fig. 1b). Both log-normal priors were

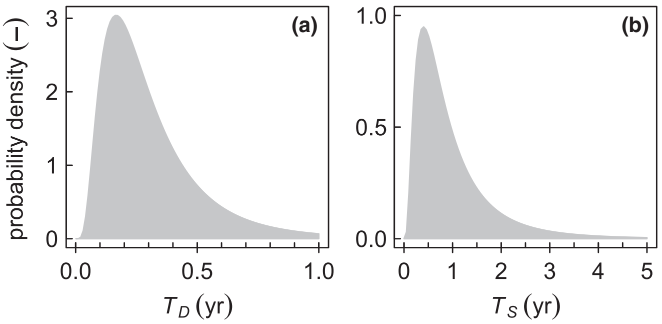


Fig. 1 Priors for the bias parameters T_D (a) and T_S (b). T_D describes the time it takes for a fine-root segment to disappear from a minirhizotron photo after its death. T_S accounts for the time carbon has potentially spent in storage pools after its photosynthetic fixation before it it used to grow new roots.

truncated – at 1 yr for T_D and at 5 yr for T_S – to avoid the possibility that the observations would solely be explained by the two bias parameters.

Results

Performance of different survival functions in explaining bomb-radiocarbon and minirhizotron observations of fine roots

The two *two-pool* models (Table 2) were best able to capture both the minirhizotron time-to-disappearance data and the bomb-radiocarbon in fine-roots (Table 3). Although the *two-pool* models have the largest number of parameters (three + two bias parameters), they have by far the best likelihoods of all survival functions relative to the number of parameters as indicated by the Bayesian information criterion (BIC; Kass & Raftery, 1995; Table 3). The BIC would favour survival functions with a lower complexity (fewer parameters) if they achieve a similar maximum likelihood. The *serial-two-pool* survival function and the *parallel-two-pool* survival function perform equally well in terms of the BIC (Table 3).

The differences in BIC (ΔBIC in Table 3) are considerable between the *two-pool* survival functions and the *log-normal*, *Weibull* and *exponential* survival functions. The *exponential* (*one-pool*) survival function performs particularly poorly and is neither able to capture the dynamics of long-lived roots in minirhizotrons (Table 3, blue dashed line vs orange step function) nor the time-series of fine-root ^{14}C (Table 3). Both the *Weibull* and *log-normal* survival functions perform much better than the *exponential* survival function. The *Weibull* survival function is better able to capture fine-root ^{14}C compared to the *log-normal* survival function, while the *log-normal* survival function is better at capturing the minirhizotron time-to-disappearance data (Table 3, blue dashed line vs orange step function). However, the *serial-two-pool* and the *parallel-two-pool* survival function outperform the *Weibull* and *log-normal* survival function both in explaining the minirhizotron data and the ^{14}C of fine-roots.

Minirhizotron bias – T_D The bad performance of the *exponential* survival function is also reflected in the posterior distribution of the bias parameter for minirhizotron observations, the dead root turnover time, T_D. The posterior distribution is the combination of the prior knowledge we had about this parameter and the information contained in the data to further constrain this parameter. The posterior distribution of T_D (Fig. 2, blue line) for the *exponential* survival function is hitting the edge of the truncated log-normal distribution that describes our prior knowledge about T_D (Fig. 2, grey area). This indicates that our optimization algorithm strives for longer dead root turnover times in order to be able to explain the quite long-lived roots observed with the minirhizotrons (Table 3, orange step function).

For the other survival functions we do not see any edge hitting for T_D, although the posterior mean of T_D is located in the 90th percentile of the prior distribution for the *two-pool* and *Weibull* survival functions (Fig. 2). The posterior uncertainty of T_D is best constrained compared to our prior knowledge for the *log-normal* survival function with a dead root turnover time of 0.23 ± 0.04 yr (posterior mean ± SD). For the *two-pool* survival functions we obtain the same posterior T_D of 0.60 ± 0.08 yr (mean ± SD).

Bomb-radiocarbon bias – T_S Similar to the findings for the minirhizotron bias parameter, T_D, we also observe edge-hitting of the storage turnover time, T_S, for the *exponential* survival function. For the *exponential* model the posterior distribution of T_S (Fig. 2, blue line), which accounts for the use of stored carbon to grow new roots, is concentrated at the upper edge of the truncated log-normal prior knowledge (Fig. 2, grey area). This again indicates that the *exponential* model is not remotely able to fit the minirhizotron and bomb-radiocarbon data jointly without attributing too much of the observed variation to the bias parameters.

The posterior distribution of the *log-normal* model again follows most closely our prior knowledge, while the posterior means of T_S of the *two-pool* models and the *Weibull* survival functions are located in the 10th percentile of the prior distribution (Fig. 2). The uncertainty of T_S is best constrained compared to our prior knowledge (Fig. 2) for the *two-pool* survival functions with a storage turnover time of 0.08 ± 0.04 yr (posterior mean ± SD).

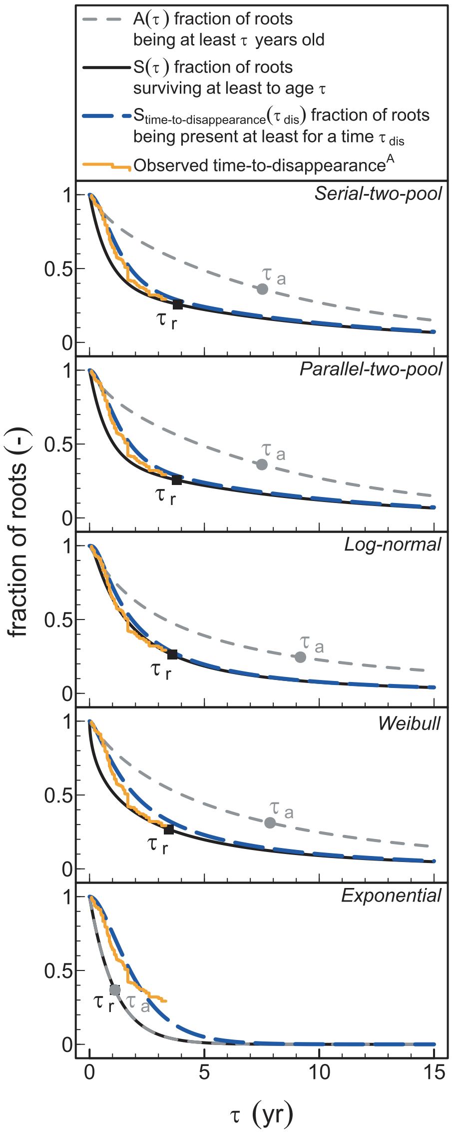
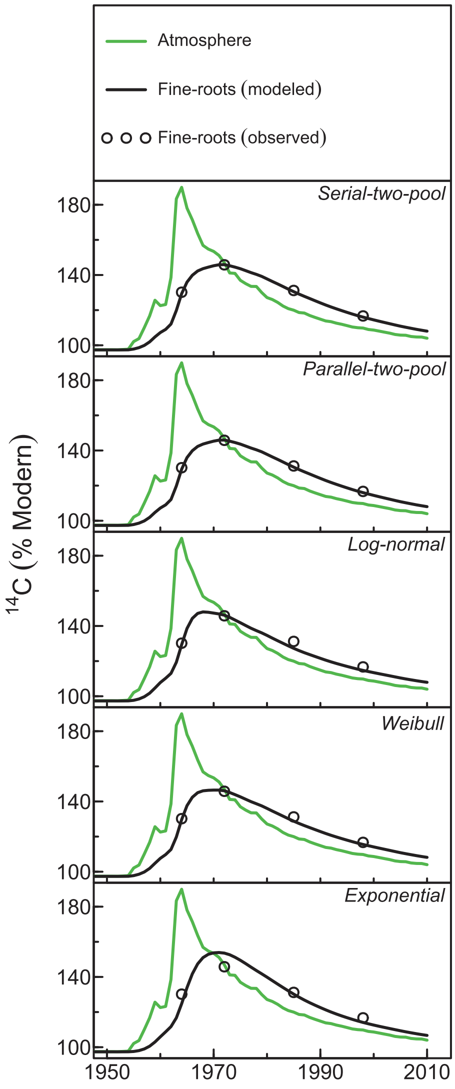
Mean residence times and mean ages

The mean residence time estimate, τ_r, for the *exponential* survival function is seriously biased because the model error is considerable. The model error of the *exponential* model can be illustrated by its inability to reproduce the short and long lifetimes observed in the minirhizotrons (Table 3, column 1) and by its inability to fit all ^{14}C measurements of fine roots reasonably well (Table 3, column 2). The τ_r estimates for the other survival functions can be reliably interpreted because the model error does not dominate in these cases. τ_r ranges from 3.53 ± 0.16 yr for the *Weibull* survival function to 3.80 ± 0.16 yr for the two *two-pool* survival functions (Table 3).

Apart from the mean residence times, the individual parameters that describe the shape of the survival curves can give interesting insights on the timescales that fine roots are turning over. For the one-parameter *exponential* survival function the inverse of the decomposition rate k already constitutes the mean residence time: $1/k = \tau_r = T$ (Fig. 2).

Also the parameters of the *two-pool* survival functions can be readily interpreted. In the *parallel-two-pool* model 60 ± 2% of fine roots belong to a fast-cycling pool with a turnover time T_1 of 0.75 ± 0.10 yr (mean ± SD), while the remainder belongs to a slow-cycling pool with a turnover time T_1 of 8.4 ± 0.2 yr (mean ± SD) (Fig. 2). The parameters of the *log-normal* and *Weibull* model elude such a straightforward interpretation, because the shape and scale parameters cannot directly be translated into how many roots are turning over on a certain timescale.

Table 3 Modelled and observed time-to-disappearance of Norway spruce fine roots in minirhizotrons; modelled and observed ^{14}C in Norway spruce fine roots; performance of different survival functions as indicated by the difference of Bayesian information criterions (ΔBIC) between the respective survival function and the survival functions with the best performance (*serial-two-pool* and *parallel-two-pool*). τ_r is the mean residence time (mean ± SD), τ_a is the mean age of the root population

Minirhizotrons	Radiocarbon	ΔBIC	τ_r (yr); mean (SD)
		0	3.80 (0.16)
		0	3.81 (0.16)
		75	3.65 (0.12)
		103	3.53 (0.16)
		615	1.12 (0.04)

Minirhizotron data from Hansson *et al.* (2013) and radiocarbon data from Fröberg (2012).

[A]The observed time-to-disappearance data (orange step function) provides just an approximate visual depiction of the frequency of different times-to-disappearance, but does not account for the different cases of censoring (C2–C4 in Table 1). Here, we assumed that the time-to-disappearance is ½($\tau_{max} + \tau_{min}$) for case C1, ½($\tau_{min,1} + \tau_{min,2}$) for cases C2 and C3, and τ_{min} for case C4 in Table 1.

The turnover times of the *serial-two-pool* survival function are in accord with the turnover times of the *parallel-two-pool* model – the turnover time of the fast-cycling root pool, T_Y, is also 0.75 ± 0.10 yr (mean ± SD), and the turnover time of the slow-cycling pool is also 8.4 ± 0.2 yr (mean ± SD). 36 ± 2 % (mean ± SD) of the roots that turn over in the fast-cycling pool, R_Y, (Table 2) are entering the slow-cycling pool, R_O, via the transfer coefficient h (Table 2, Fig. 2).

This shows that the *serial-two-pool* model and the *parallel-two-pool* model are generally able to reproduce the same shape of survival curve with the same turnover times of the respective fast- and slow-cycling pools (T_{Fast}, T_{Slow}). The relationship between the parameters h and α is given by $h = (1-\alpha)\ (T_{Fast} - T_{Slow})/T_{Slow}$ (derived from equations for $S(\tau)$ in Table 2).

Although the mean age, τ_a, of a root population is not a really useful quantity for constraining belowground carbon cycling, the distance of τ_a to the mean residence time, τ_r, at least gives a quick

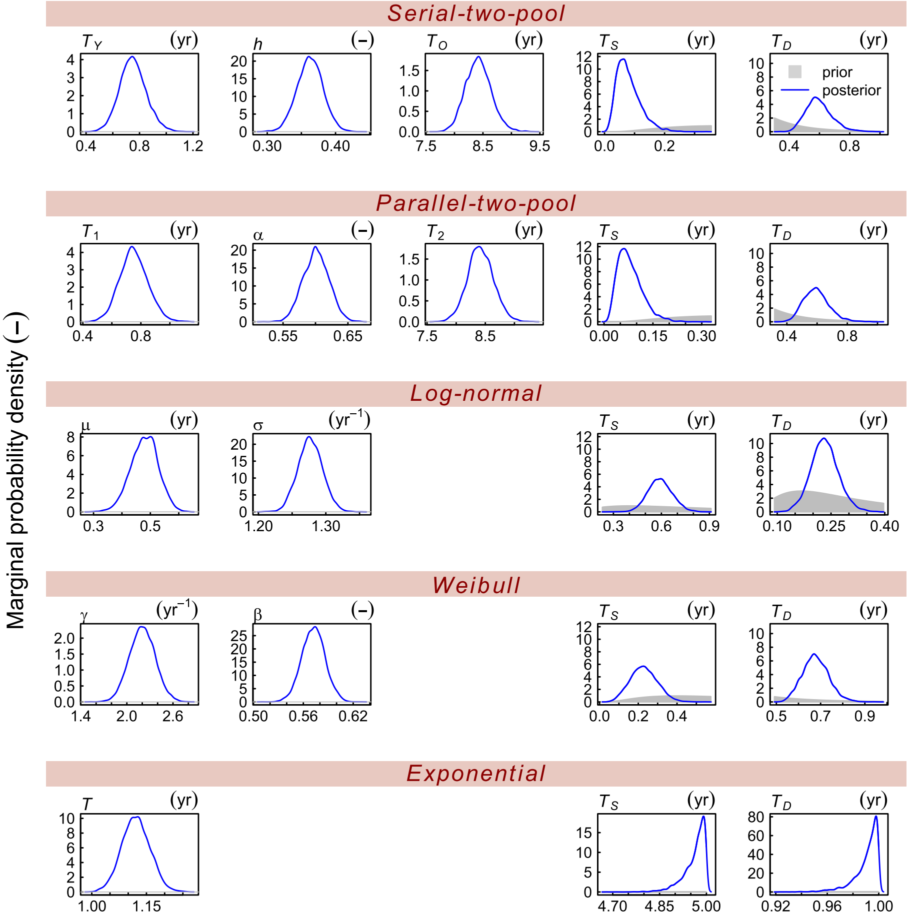


Fig. 2 Comparison of parameter probability distributions for different survival functions. The maximum density of the marginal posterior distribution (blue line) is an indicator for how well a parameter is constrained by the data. For the storage turnover time, T_S, and the dead root turnover time, T_D, the marginal posterior distribution (blue line) shows how much information is contained in the data compared to prior knowledge about these two parameters (grey area). *Serial-two-pool*: T_Y, turnover time of the young root pool R_Y; h, transfer coefficient from young to old root pool; T_O, turnover time of the old root pool R_O. *Parallel-two-pool*: T_1, turnover time of root pool R_1; T_2, turnover time of root pool R_2; α, fraction roots belonging to R_1. μ, location parameter and σ, shape parameter of the *log-normal* survival function. γ, scale parameter and β, shape parameter of the *Weibull* survival function. T, turnover time of the *exponential* model.

indication of how the survival probability of a root changes with increasing age τ (Table 3). For the *exponential* survival function the mean age is equal to the mean residence time (Table 3). This means that the probability for a root to die does not change with increasing root age τ. For all the other survival functions the mean age τ_a is longer than the mean residence time τ_r (Table 3). This indicates that most fine roots will die relatively soon after they grew, while a minority of roots survives for a relatively long time. The *log-normal* survival function shows the longest mean age of 9.3 ± 0.4 yr of fine roots (mean ± SD), while the *two-pool* models show the shortest mean age of 7.5 ± 0.2 yr (mean ± SD). The *Weibull* model has a mean age of 7.9 ± 0.3 yr (mean ± SD). Apart from the *exponential* model, the distance between τ_a and τ_r is shortest for the *two-pool* survival functions, indicating that the probability of a root dying does not decrease as strongly with increasing age as it does for the *Weibull* and *log-normal* survival functions.

Discussion

Mechanistic interpretation of the *two-pool* models

We showed that we are able to obtain the same shape of the survival curve for the *serial-two-pool* model and the *parallel-two-pool* model using the same turnover times for the respective fast- and slow-cycling pools. Although the *two-pool* survival functions are obviously equivalent, these two models are open to different potential mechanistic interpretations.

***Serial-two-pool* model** After growth, all roots at first belong to a relatively fast-cycling pool where the majority of roots die after a relatively short period, while the remainder of fine roots are becoming suberized and are thereby able to increase their survival probability. Evidence from Pregitzer *et al.* (2002) for *Picea glauca* (we studied *Picea abies*) also suggests that in the < 0.5 mm size class at least the first three orders of roots are present. Branching of roots can generally be associated with enhanced transport, but also with the development of protective features such as suberin deposits or lignified cells (Eissenstat & Yanai, 1997; Hishi, 2007). Hence, branching is a process that should be taken into consideration when interpreting the transfer from the fast-cycling pool R_Y to the slow-cycling pool R_O.

***Parallel-two-pool* model** In this survival function structural differences between fine roots existing already at their establishment would predetermine their longevity. Similar to the *serial-two-pool* model, branching could play a major role in explaining the coexistence of a fast- and slow-cycling pool. However, the interpretation for the *parallel-two-pool* model has to be different because the two pools should describe roots whose function and structure would be predetermined at root establishment. The structural differences could stem from the interaction between root growth and ectomycorrhizal fungi which leads to a typical lateral root branching pattern with short lateral ectomycorrhizal roots and long supportive roots. This type of branching is commonly called heterorhizy (Brundrett *et al.*, 1996). Taylor *et al.* (2000) found that in a spruce forest in SW Sweden more than 99% of root tips are colonized by ectomycorrhiza. While the ectomycorrhizal infection of the slow-growing short lateral roots may prevent the deposition of suberin in cortical cells (Hishi, 2007), the longer roots may undergo more rapid secondary growth (Brundrett *et al.*, 1996), which is accompanied by suberization. Hence, the interactions of ectomycorrhizal fungi and plants could be interpreted as a predetermination of new roots to develop into short ectomycorrhizal roots (short-lived, T_1) or long suberized roots (long-lived, T_2).

Overall, the attribution of processes to either the *serial-two-pool* or the *parallel-two-pool* model is a rather philosophical exercise, which essentially reduces to a dichotomous decision between root development that could also depend on changing conditions in the micro-environment of the root (*serial-two-pool*), and the predetermination of root function at establishment regardless of changing micro-environmental conditions (*parallel-two-pool*). Nevertheless, given that both *two-pool* models are able to produce the same shape of the survival curve, our results do not support favouring just one of the two possible approaches.

Constraints on systematic biases

Overall, the estimates of the bias parameters for the bomb-radiocarbon and the minirhizotron technique did not converge across the different survival functions. As already mentioned, the *exponential* survival function could not reconcile both techniques, but both bias parameters, the dead root turnover time T_D and the storage turnover time T_S, were hitting the edge of the truncated log-normal prior distributions. Hence, the bias parameters would explain the major part of the apparent irreconcilability of both datasets for the *exponential* model.

The posterior distribution of the bias parameters, T_D and T_S, (Fig. 2, blue line) closely follows the prior knowledge (Fig. 2, grey area) for the *log-normal* survival function, which may indicate that its particular shape is actually helpful for explaining fine-root dynamics. For the *log-normal* survival function the risk of a root dying increases at first for rather short root ages τ, but declines after a certain age τ. For the other survival functions the risk of a root dying is either independent of its age (*exponential* model) or monotonically decreases with longer ages τ. The bias parameters, T_D and T_S, only influence the model output of the corresponding datastreams, as indicated by the weak correlations (r^2 between 0.008 and 0.09) between the posteriors of T_D and T_S (see Supporting Information Fig. S1 for correlation matrices of the parameters).

Although we have identified the storage turnover time and the dead-root turnover time as the most important biases of the ^{14}C and the minirhizotron technique, one cannot rule out that additional biases also influence the posterior estimates of our parameters. Adams & Eissenstat (2014) found evidence not only that stored carbon might be used for the growth of new roots, but also that recent photosynthate is incorporated into structural root tissue after root formation. This process would lead to a shorter storage turnover time T_S in our modelling framework. For the *Weibull* and both *two-pool* models, the fact that the posterior estimate of T_S is located in the 10th percentile of the prior knowledge (Fig. 2), could also be explained by a tradeoff between the use of stored carbon to grow new roots and the continuous incorporation of recent photosynthate into roots (Adams & Eissenstat, 2014).

Similarly, Fröberg (2012) selected the archived roots to represent predominately live roots, but he could not rule out the possibility that recently dead roots might have been included. This possible bias would lead to a longer estimate of T_S; this, however, does not seem to be relevant here, given that the posterior estimate of T_S is not located at the upper end of the prior knowledge (Fig. 2). This possible bias is also different from the dead-root turnover time that we proposed to account for the time-to-decomposition in minirhizotrons, because we would still sample a mixture of live and dead roots for the ^{14}C analysis, while in minirhizotrons root segments are most likely dead when they disappear.

Trade-off to single calibrations with minirhizotron or bomb-radiocarbon data

Trumbore & Gaudinski (2003) stated that both techniques – minirhizotrons and bomb-radiocarbon – would ‘gather information about different ends of the root lifetime continuum’. The validity of this statement relies on sampling and evaluation details of the two different techniques. The statement that minirhizotrons sample only at the younger end of the lifetime continuum is largely dependent on the length of the study period. Obviously, one strives to capture also the tails of the fine-root lifetimes monitored with minirhizotrons (Table 3), which is decisive for the extrapolation of root lifetimes outside the observed (also censored) lifetimes. The commonly reported *median* longevity estimates from *Kaplan–Meier point estimates* from minirhizotrons depend even more strongly on the length of the study period than in *parametric estimates* of *mean* longevity. Nevertheless, in parametric approaches, which are used to determine *mean* longevities/*mean* residence times (Table 2), the length of the study period also determines how much information is contained in the minirhizotron data, not only for the fast-cycling but also for the slow-cycling pool.

Up to now, the evaluation of minirhizotron data has been inadequate for the nature of the data for two reasons. First, fitting parametric survival functions to Kaplan–Meier point estimates (Strand *et al.*, 2008; Gaul *et al.*, 2009; Hansson *et al.*, 2013) throws away a lot of information; in a least-squares fitting approach, longer survival times receive less weight because of the smaller numbers (fraction of roots surviving). Second, the information about censoring in the Kaplan–Meier survival curve is lost to a large degree when a parametric survival curve is fitted to the point estimates. In particular, the Kaplan–Meier approach is unable to account for the complex cases of censoring occurring in minirhizotron studies (Table 1, cases C2 and C3). In this study we employed a formal likelihood approach also for the minirhizotron data, which ensures a proper accounting for the different cases of censoring and a proper weighting also for long-living roots.

The information content of fine-root ^{14}C alone does not constrain the total fine-root turnover (fast- and slow-cycling roots) because survival functions with more than one parameter generally have enough flexibility to fit the same ^{14}C content in fine roots almost equally well with quite different mean residence times τ_r. However, the ^{14}C content of fine roots determines the mean age of fine-root τ_a to a large extent (Table 3; Ahrens & Reichstein, 2014), which is dominated by the slow-cycling pool. Overall, we conclude that minirhizotron data are the ideal complement to the ^{14}C measurements in fine roots, especially for studies without archived fine-root ^{14}C samples or a shorter minirhizotron sampling period: With minirhizotron data we are able to constrain the survival curve for short longevities τ, while the ^{14}C of fine roots alone would allow too much flexibility for short τ. Survival functions fitted to fine-root ^{14}C data alone had quite different mean residence times τ_r (1.9–7.1 yr; Ahrens & Reichstein, 2014), while the mean ages τ_a were quite similar (7.1–8.7 yr; Ahrens & Reichstein, 2014).

The mean residence times found in this study with the joint calibration to ^{14}C in fine roots and minirhizotron data (Table 3) showed that the joint calibration not only leads to a convergence of mean ages, but also to a convergence of mean residence times estimates (3.53–3.81 yr) between the different survival functions. Here, the exception is the *exponential* survival function which is generally unable to explain both datasets with its constant survival probability.

Implications, future research directions

Generally, one should probably take a step back and ask oneself ‘Why are we interested in estimating fine-root turnover times?’ The most general answer is ‘We want to quantify the input of root litter to the soil organic carbon pool’.

This also means that the mean residence time *per se* is not of primary interest, but the root litter input which is defined as root biomass/τ_r under the assumption that root biomass is in equilibrium. We argue for an overall more integrative approach for determining the root litter input to soils. Richardson *et al.* (2010) showed in a model-data fusion exercise with joint constraints (NEE, soil respiration, aboveground litterfall) that they were not able to constrain the turnover rate of fine roots. This indicates that the integration of minirhizotron data or fine-root ^{14}C into calibration exercises with whole ecosystem models might be beneficial to constrain the central parameter that determines the carbon input into the soil organic carbon pool.

Contrary to statistical survival functions (e.g. *log-normal* and *Weibull*), modelling the root turnover with *two-pool* models has the advantage of fitting seamlessly into ecosystem models. The survival functions for *two-pool* models essentially correspond to a system of ordinary differential equations. One would model the decrease of the fraction of roots still being alive without further new root growth. This curve can be used for comparison with the raw minirhizotron time-to-disappearance data. This would make it possible to use minirhizotron data along with the ^{14}C content of fine roots for calibrating parameters of ecosystem models in multiple constraint approaches. In addition, accounting for systematic biases of the minirhizotron and the bomb-radiocarbon technique, is more easily achieved in a traditional pool setting, while the convolution of two functions is quite uncommon for ecosystem models.

Overall, our results show that fine roots of trees are indeed cycling on quite different timescales. A *one-pool*, *exponential* model assumes a constant mortality risk for fine roots regardless of their age; it is impossible to reconcile minirhizotron and bomb-radiocarbon data using this assumption. Other survival functions, however, that exhibit a decreasing mortality risk with increasing age are able to reconcile the apparently contradictory datastreams. *Two-pool* survival functions, nonetheless, perform better than survival functions derived from statistical cumulative distribution functions, such as the *Weibull* and *log-normal* survival function. Moreover, the *two-pool* models can be better integrated into ecosystem models and are more open to a mechanistic interpretation. Therefore, the *two-pool* survival functions are best suited to represent fine-root turnover in models and to reconcile bomb-radiocarbon and minirhizotron data. The combination of both datasets is essential to reasonably constrain the proportion of short- to long-lived fine roots.

Our and other studies (Tierney & Fahey, 2002; Matamala *et al.*, 2003; Trumbore *et al.*, 2006; Gaudinski *et al.*, 2010) have shown that fine roots in rather well-drained forest ecosystems do not belong to just one homogenous pool. Whether fine roots in nonforested ecosystems also show this decreasing mortality risk with increasing age is questionable. Solly *et al.* (2013) found that fine-root ^{14}C in grasslands was generally much closer to the atmospheric ^{14}C curve than fine-root ^{14}C in forests, so the issue of reconciling minirhizotron observations with ^{14}C observations is probably less pressing for fine roots in grasslands. Nevertheless, Solly *et al.* (2013) found that the presence of perennial species in grasslands yields longer apparent ^{14}C fine-root turnover times. Also fine roots of grasslands could be modelled with our proposed framework, although the storage turnover time bias will be of minor importance for this ecosystem type. The use of the radiocarbon technique could be useful to study fine roots in grasslands with considerable amounts of perennial species, although using the minirhizotron technique might suffice. In poorly drained or even wetland soils the decomposition of dead roots might be impeded considerably (Iversen *et al.*, 2012). Therefore, it would be important to account for this substantial bias that would affect observations of fine-root turnover with minirhizotrons and bomb-radiocarbon.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Correlations between the posterior parameters of (a) the *serial-two-pool*, (b) the *log-normal*, (c) the *parallel-two-pool*, and (d) the *Weibull* survival function.