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**Irreconcilable Differences: Fine-Root Life Spans and Soil Carbon Persistence**

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## Supporting Online Material

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Materials and Methods

Table S1  
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# Irreconcilable Differences: Fine-Root Life Spans and Soil Carbon Persistence

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The residence time of fine-root carbon in soil is one of the least understood aspects of the global carbon cycle, and fine-root dynamics are one of the least understood aspects of plant function. Most recent studies of these belowground dynamics have used one of two methodological strategies. In one approach, based on analysis of carbon isotopes, the persistence of carbon is inferred; in the other, based on direct observations of roots with cameras, the longevity of individual roots is measured. We show that the contribution of fine roots to the global carbon cycle has been overstated because observations of root lifetimes systematically overestimate the turnover of fine-root biomass. On the other hand, isotopic techniques systematically underestimate the turnover of individual roots. These differences, by virtue of the separate processes or pools measured, are irreconcilable.

**F**ine roots (those with diameters <2.0 mm) serve at least two roles of global importance: They act as conduits transporting carbon (C) into belowground C pools, and they acquire soil resources. Consequently, predictive models of plant function, forest nutrition, and global C cycling depend on accurate quantification of fine-root longevity and turnover rate.

Considerable effort has been expended to quantify the potential for fine roots to absorb C from the growing pool of atmospheric CO<sub>2</sub> and to sequester it in mineral soil. Globally, soil C pools are particularly important because they contain approximately 3.3 times more C than the atmospheric pool and 4.0 times more C than

the aboveground terrestrial biomass pool (1–4). Much of the C present in soil is probably derived from fine roots (5).

Understanding fine-root dynamics is also critical for understanding how plants acquire water and nutrients from soil. Because most uptake occurs in roots <1 mm in diameter, fine-root pool size may limit forest productivity by limiting plant absorptive capacity. Fine roots are also the primary site of infection by mycorrhizal fungi, which influence a wide range of ecosystem properties, including productivity, biodiversity, and soil structure.

There is currently an ongoing debate on the efficacy of methods that measure C residence time in fine roots using <sup>13</sup>C-depleted atmospheric enrichment (6) versus methods that observe roots directly by means of microvideo cameras (minirhizotrons) (6–8). This debate has been fueled by the observation that isotope-based estimates of C residence times in fine roots are much longer (>4 years) than estimates of root longevity determined by repeated observation with minirhizotrons (<1 year) (9, 10).

Several sources of discrepancy between these approaches have been identified: (i) differences in the pool of roots sampled with isotope versus minirhizotron methods (8, 11), (ii) the confounding effects of carbohydrate storage on depletion rates of C isotopes (12), (iii) the appropriateness of underlying survival functions assumed by isotope methods (10, 13), (iv) overestimation of turnover rate because of using median longevity as a surrogate for mean longevity in minirhizotron studies (11), and (v) slow return to equilibrium root dynamics after the installation of minirhizotron access tubes (14).

Although technical issues inherent to isotopic and minirhizotron methods have led to disparate conclusions about fine-root dynamics, arguments regarding the validity of these methods skirt the issue that multiple belowground processes require characterization and, although related, may best be measured with different approaches. In this study, we set out to reconcile measures of fine-root C pool dynamics derived with isotopic methods and fine-root dynamics obtained from minirhizotrons. First, we assess the relative magnitudes of several sources of measurement error associated with isotope and minirhizotron approaches; second, we attempt to quantify the differences between C residence and individual root-dynamic-focused studies. We used survival analysis to examine the root dynamics in the CO<sub>2</sub>-enriched plots at the Duke University free-air CO<sub>2</sub> enrichment (FACE) facility (15). The longevity of 2181 individual roots, with diameters <2 mm, was recorded over 8 years from repeated video images; 64% of these roots were followed until senescence and death. The remainder were alive at the end of the experiment and were treated as right-censored in survival analyses. We then compared our results to estimates of root turnover derived using isotopic techniques from the same forest plots, published by Matamala *et al.* (6).

Previously published isotopic estimates of turnover for this forest (6) have been criticized on

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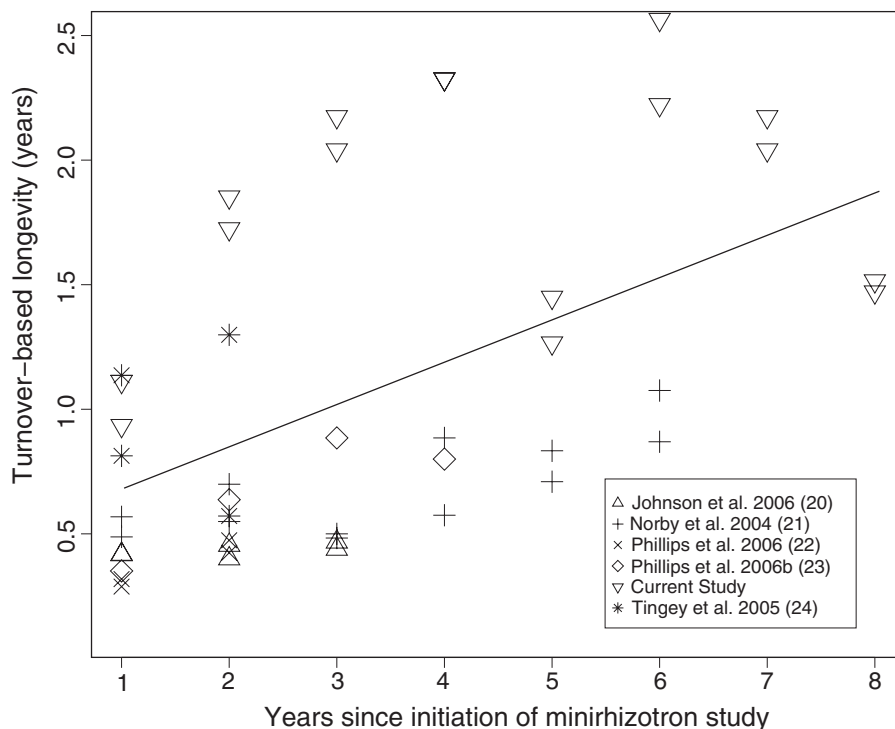
the basis of speculation that they were derived using an inappropriate survival model (7). It was suggested that a more appropriate model would lower longevity estimates (10). We used direct measurement of individual root life spans to identify the most appropriate model and then applied this model to previously published isotopic data for these plots (6). For root survival, comparison among several models indicated that a log-normal survival model fit best with a Bayesian information criterion (BIC) score of 3248.12 as compared to BIC scores for Weibull and exponential distributions of 3463.17 and 3463.18, respectively. Although the log-normal model fit root survival best, reanalyzing published isotopic data using this model instead of the exponential model used previously failed to increase the earlier estimate of turnover rate. The model invoked to estimate turnover of fine roots, in this case, did not explain the difference in turnover rates obtained with isotope and minirhizotron techniques.

Projections of the longevity of roots, or the  $C$  they contain, assume that belowground processes are in equilibrium. Insertion of minirhizotron tubes is a necessary disturbance. It has been unclear to date how rapidly disturbed soil will return to equilibrium conditions or if this even occurs during the course of a given minirhizotron study. We took both a meta-analysis and a single-study approach to estimate this rate. Data from seven minirhizotron studies that were at least 2 years in duration were used to estimate root turnover (per year) from yearly production and the average yearly standing crop, using a flux approach (15, 16). We then took the reciprocal of fine-root turnover to estimate mean longevity for each year of each study. Although heterogeneity among studies was observed for absolute longevity, longevity estimates increased significantly with increases in study duration (Fig. 1). For instance, fine-root longevity increased from an average of 0.7 year in minirhizotron studies conducted over 1 year as compared to 1.0 year for studies conducted over 3 years, an increase of over 40%. We also examined this process for individual root survival at the Duke FACE site by directly measuring root life spans and estimating the mean longevity of roots initiated in each of the years of the study. We observed that roots initiated in early years exhibited lower mean life span and a return to equilibrium by year three (Fig. 2). Based on this return to equilibrium, we separated the individual roots into those initiated during the first 3 years (pre-equilibrium) and those initiated in the last 5 years (post-equilibrium). The longevity of fine roots established during the pre-equilibrium period was 50% shorter as compared to the longevity of roots that developed during the post-equilibrium period (Fig. 1 and Table 1). This result indicates that short-duration experiments, characteristic of most minirhizotron studies, may have contributed to inflated estimates of fine-root turnover rates.

Another important distinction between the isotopic and minirhizotron approaches involves units of measurement. Whereas isotopic methods are based on mean residence time of fine-

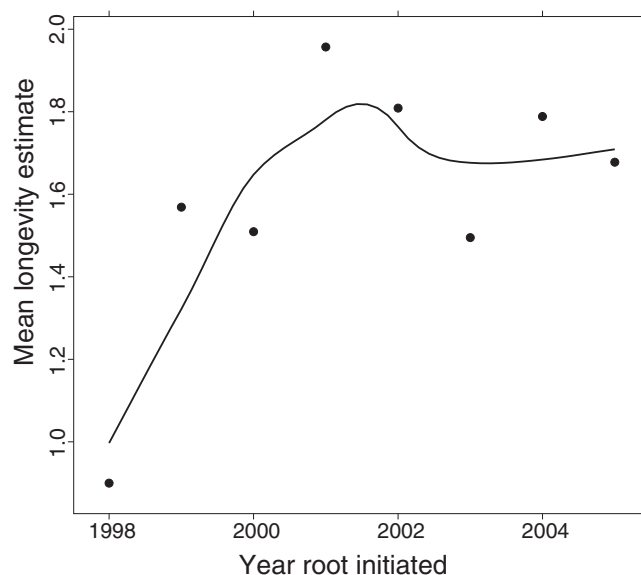
root  $C$  in units of biomass, most minirhizotron experiments report turnover of individual roots themselves. Because smaller-diameter, more numerous roots turn over more quickly than larger-diameter, less numerous roots, treating all roots equally could contribute to inflated  $C$  turnover rate estimates when using minirhizotrons. Moreover, studies conducted with minirhizotrons often use median root longevity values as a surrogate for

mean longevity. This assumption also contributes to underestimations of root longevity, because root survival functions are positively skewed (Table 1) (6, 7). To alleviate these sources of error, we applied parametric survival regression, based on units of root volume as a surrogate for root biomass, to estimate mean longevity for roots initiated in the last 5 years of the study. These survival curves were compared to those of individual roots and the



**Fig. 1.** Estimates of fine-root longevity from root turnover measurements as a function of the number of years since the initiation of the minirhizotron study. Turnover values were derived from annual production divided by average annual standing crop (14). Analysis of covariance supports the hypothesis that longevity estimates increase over time ( $P < 0.001$ ) and that there is little support for the hypothesis that this slope differs among studies ( $P = 0.97$ ). This analysis explains 81% of the variation in longevity estimates. The solid line represents a best linear fit to these data overall ( $y = 0.51 + 0.17x$ ). Numbers in parentheses are reference numbers.

**Fig. 2.** Estimates of the mean longevity of individual fine roots appearing at different times during the Duke FACE study. Mean estimates are derived from parametric regression of fine-root survival times, which also indicated significant variation among survival curves stratified by year of initiation ( $P < 0.0001$ , log-normal distribution of survival times). The solid line represents a loess fit to mean longevity for visualization.



residence time of C in the same plots (Fig. 3). We found that estimates based on the longevity of individual roots lead to a 50% exaggeration of fine-root biomass turnover rate.

It has been suggested that the finest roots are not adequately sampled by destructive soil coring because of the difficulty of extracting them from the cores (17). Missing the smallest ( $\leq 0.3$  mm) and most ephemeral roots could bias isotopic measures of longevity upward (11). We tested the potential for this sampling bias to contribute to the underestimation of fine-root turnover using the isotopic approach. Our results suggested that poor sampling of these shorter-lived smaller roots may significantly affect isotope-based C longevity estimates, because such sampling in our data increased the longevity of biomass in the soil (fig. S2) (15).

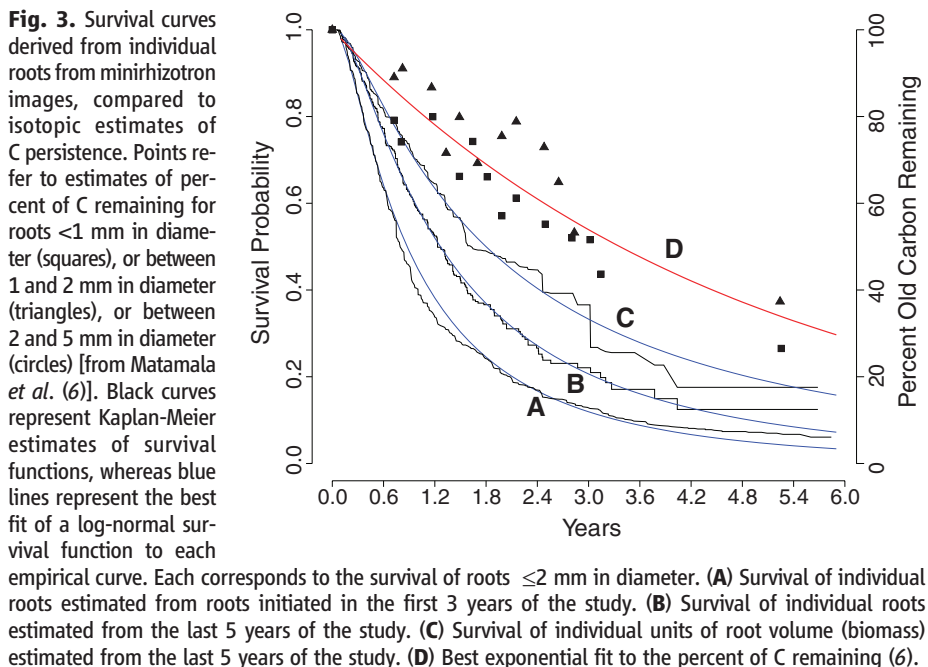
In this study, we have eliminated several biases proposed to explain the divergence in fine-root longevity common to isotope- versus minirhizotron-based methods. Because we controlled for time, place, and several technical assumptions of both isotope and minirhizotron analyses, the remaining differences result from several factors that we cannot control. The isotopic technique fails to account for heterogeneity in fine-root life span: The longevity of fine roots increases considerably with increasing soil depth and diameter and with branching

order, and may be influenced by herbivory (18, 19). Interpretations of isotopic results could also be confounded if some proportion of new fine roots is constructed using C recycled from senescing tissues or storage pools (12). For example, some time may pass from the time when C is acquired through photosynthesis and the time when new roots are constructed from that C in spring. Furthermore, recycling of old C to support growth of newer roots could also cause individual C atoms to persist in the fine-root pool much longer than the individual roots themselves. Finally, the difficulty of obtaining the smallest roots from soil cores in isotopic analyses will bias isotope-based estimates of longevity upward.

Characterizing the persistence of C and the longevity of roots is not redundant; each is essential for understanding ecosystem function. Quantifying belowground C pools is also critical for parameterizing global C cycle models. Our results indicate that applying the median longevity of individual roots in short-term minirhizotron studies underestimated residence time of fine-root biomass by over 300% as compared to mean longevity of fine-root volume (biomass) derived from a long-term experiment. This suggests that previous estimates that fine-root turnover represents 33% of annual global net primary production (9) are probably unrealistically high. However, under-

standing soil C pools is of limited use in understanding ecosystem function in other ways. C pools may provide a gross reflection of root biomass, but because these pools are somewhat insensitive to the dynamics of the smallest roots, they provide little information on water and nutrient uptake potential, the demography of plant modules, or relative investments in absorption versus transport.

Unfortunately, the behavior of the soil C pool and the dynamics of the fine-root pool have often been conflated in the literature (table S1) (15). Misapplying the results of an isotope-based estimate of C persistence will underestimate root turnover rate by 60% and, more importantly, underestimate the rate at which the finest roots—the location of interaction between plants and soil—are produced. Conversely, misapplication of minirhizotron results, particularly those derived from short-term experiments, will dramatically overestimate the rate at which fine-root turnover transfers C into the soil. These methods are both fundamentally irreconcilable yet complementary.



**Fig. 3.** Survival curves derived from individual roots from minirhizotron images, compared to isotopic estimates of C persistence. Points refer to estimates of percent of C remaining for roots  $<1$  mm in diameter (squares), or between 1 and 2 mm in diameter (triangles), or between 2 and 5 mm in diameter (circles) [from Matamala *et al.* (6)]. Black curves represent Kaplan-Meier estimates of survival functions, whereas blue lines represent the best fit of a log-normal survival function to each empirical curve. Each corresponds to the survival of roots  $\leq 2$  mm in diameter. (A) Survival of individual roots estimated from roots initiated in the first 3 years of the study. (B) Survival of individual roots estimated from the last 5 years of the study. (C) Survival of individual units of root volume (biomass) estimated from the last 5 years of the study. (D) Best exponential fit to the percent of C remaining (6).

**Table 1.** Estimates of mean life span for individual roots and root biomass from parametric survival regression of root life spans compared to C residence time from a  $^{13}\text{C}$  study. CI, confidence interval.

Survival type	Time period	Mean life span in years (95% CI)	Median life span in years (95% CI)
Individual roots	Pre-equilibrium	1.51 (1.45, 1.59)	0.79 (0.75, 0.86)
Individual roots	Post-equilibrium	2.21 (2.08, 2.36)	1.23 (1.12, 1.41)
Biomass (volume)	Pre-equilibrium	2.61 (2.42, 2.81)	0.93 (0.92, 1.04)
Biomass (volume)	Post-equilibrium	3.24 (3.01, 3.49)	1.64 (1.55, 2.04)
Isotope-based	-	5.3 (4.8, 5.8)	-

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**Supporting Online Material**

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