Sensitivity of four ecological models to adjustments in fine root turnover rate

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Abstract Large uncertainties surrounding root-specific parameters limit model descriptions of belowground processes and ultimately hinder understanding of belowground carbon (C) dynamics and terrestrial biogeochemistry. Despite this recognized shortcoming, it is unclear which processes warrant attention in model development, given the computational cost of additional model complexity. Here we tested the sensitivity of four models to adjustments in fine root turnover in forested systems: CENTURY, ED2, MC1, and LANDCARB. In general, faster root turnover rates resulted in lower total system carbon (C) and within model changes ranged from 1% to 38% following 100-year simulations. However, the underlying mechanisms driving these changes differed among models as some expressed lower net primary productivity (NPP) with faster turnover rates and others had similar NPP but large shifts in C allocation away from wood to fine roots. Based on these findings we expect that different model responses to changes in fine root turnover will be determined by 1) whether C is allocated to fine roots as fixed portion of NPP or to maintain a fixed biomass ratio between fine roots and leaves or stems and 2) whether soil nutrient and water uptake is a function of both resource availability and fine root biomass or based on resource availability alone. These results suggest that better constrained estimates of fine root turnover will represent a valuable improvement in many terrestrial models.

Key Points

- Changes in root turnover rate altered total system C by up to 40 percent
- Model sensitivity depends on approach to C allocation and soil resource acquisition

49 • Constrained estimates of turnover will improve model skill and aid
50 intercomparisons
51 **Keywords:** root production, carbon cycle, ecosystem, model sensitivity, carbon
52 allocation, belowground processes

1. Introduction

Terrestrial biosphere models simulate a range of natural phenomena in ecosystems across the globe including basic patterns of plant growth and senescence, carbon (C) fluxes and storage, as well as aspects of nutrient and hydrological cycles. Together, these models attempt to forecast the responses of terrestrial systems to changes in local environments and global climate and may inform better management and policy decisions (Stocker *et al.*, 2013). However, due in large part to a lack of empirical data, many belowground processes are poorly represented in ecological models (Ostle *et al.*, 2009; Iversen, 2010; Smithwick *et al.*, 2014), with complex belowground behaviors (e.g. autotrophic and heterotrophic respiration, C allocation, decomposition) represented by a small set of critical parameters. Of these, fine root turnover is one of the most common parameters included in terrestrial process models and is often used to tune belowground C fluxes. Empirically, fine root turnover is the process by which live roots die and transfer C into the soil where it may be respired to the atmosphere or accrue in soil C pools. In addition to its influence on C fluxes between soil pools and the atmosphere, fine root turnover rates also affect the total amount of root standing biomass, thus potentially influencing nutrient and water uptake by plants.

While the importance of root turnover in terrestrial systems is increasingly recognized (Ciais *et al.*, 2008; Malhi *et al.*, 2011), accurately and consistently quantifying root turnover empirically has proven difficult. Most estimates of root turnover have been derived through indirect means including sequential soil coring, in-growth core methods, and whole-system budget approaches (Dahlman & Kucera, 1965; Hendrick & Pregitzer, 1993). More recently, minirhizotrons have enabled direct observations of root dynamics

and root turnover (Majdi *et al.*, 2005; Pritchard, *et al.*, 2008; McCormack *et al.*, 2014) and isotopic tracers have enabled researchers to estimate the age of C in fine roots (Gaudinski *et al.*, 2001; Matamala *et al.*, 2003). However, data regarding turnover rates from minirhizotrons and isotopic techniques are still relatively sparse compared to coring approaches. Furthermore, while each method ostensibly measures the same process of root turnover there are indications of general bias among the different methods regarding both the method itself and the actual pool of fine roots being observed (Guo *et al.*, 2008; Strand *et al.*, 2008). The slowest fine root turnover rates are generally derived from isotopic methods and range from 0.1 to 0.4 yr⁻¹ (Gaudinski *et al.*, 2001; Matamala *et al.*, 2003), while coring approaches and minirhizotron observations tend to yield faster turnover estimates in the range of 0.3 to 1.5 yr⁻¹ and 0.6 to 3.0 yr⁻¹, respectively (Aerts *et al.*, 1992; Gill & Jackson, 2000; McCormack *et al.*, 2014). Some model applications have also used fine root turnover rates of 5.0 yr⁻¹ or greater under some conditions (Medvigy *et al.*, 2009; Parton *et al.*, 2010). Though some of the variation is due to differences across sites and species (Gill & Jackson, 2000; Yuan & Chen, 2010) it is also clear that a large portion of the variability is due to broader uncertainties regarding descriptions of fine roots and the methods used to estimate of root (Smithwick *et al.*, 2014).

Many models operating in perennial systems include an explicit fine root pool (separate from coarse roots), though it is not always clear what exactly constitutes a *fine root*. In most cases, this pool is intended to represent the most metabolically active roots that are responsible for water and nutrient uptake. Historically, this has been considered as all roots ≤ 2 mm in diameter, which is reflected in biomass estimates used to

parameterize most models (e.g. (Smithwick *et al.*, 2009), though the specific cutoff may vary (e.g. Dymond *et al.*, 2012). However, it is important to note that determining which roots represent active, absorptive roots is not trivial and assessing turnover rates for the most distal, absorptive fine roots separately from more proximal, transport fine roots represents a significant challenge. For example, minirhizotrons tend to be biased towards the most distal, absorptive pool of fine roots where isotopes likely capture the more transportive and persistent roots (Guo *et al.*, 2008; Strand *et al.*, 2008). This has resulted in a wide range in fine root turnover rates measured and reported both across and within ecosystems.

Variability in reported fine root turnover rates and limited empirical understanding of the patterns and processes controlling root turnover have made it difficult to constrain estimates of fine root turnover in models. Where sufficient data are available and relevant to a given species or study system, ecoinformatic approaches which combine information from multiple data streams may be useful in constraining parameter estimates in the future (LeBauer *et al.*, 2013; Wang *et al.*, 2013). However, in many systems where little to no data are available it is likely that model estimates will remain uncertain for some time. As a result, models commonly use estimates of fine root turnover that span an order of magnitude. Table 1 reports turnover rates used in 18 different models parameterized for temperate forest ecosystems, estimates for which range from 0.15 yr⁻¹ to > 5.0 yr⁻¹. The large variation in turnover rates used raises questions about how these different turnover rates impact results across different models. If a model that uses a turnover rate of 0.3 yr⁻¹ instead used a turnover rate of 3.0 yr⁻¹, how would different pools of C within the modeled ecosystem change? Or, would they

change at all? It is unclear how sensitive different types of models are to variation in root turnover rates.

Though differences in fine root turnover rates in natural systems have direct implications for C, nutrient, and water cycling; the sensitivity of these cycles to root turnover in models will depend largely on model structure. Two specific areas likely to impact model sensitivity to root turnover include the simulated approach to allocate C among biomass pools and the treatment of soil resource acquisition. First, most models determine C allocation to fine roots one of two ways: either C is allocated as a fixed proportion of net primary productivity (NPP) or it is allocated as necessary to maintain a fixed biomass ratio between fine roots and leaves (Smithwick *et al.*, 2014), though in some models the ratio or proportion allocated may be adjusted based on nutrient or water availability. The resulting sensitivity and path by which altered fine root turnover impacts forest C pools including total fine root biomass, aboveground forest biomass, total soil organic C and ecosystem net primary productivity (NPP), is likely to differ between the two. Second, acquisition of soil resources may simply be a function of resource availability or may be a function of root capacity (usually standing fine root biomass) to obtain those resources. Models incorporating root capacity as a factor limiting resource uptake should express greater changes in forest productivity and C stores with changes in root turnover, which alters root biomass. However, the degree to which model outcomes depend on these choices remain unclear.

In this study we focus on two questions, 1) are models sensitive to changes in fine root turnover rates? And, 2) what differences in structure are likely to lead models to be more or less sensitive to changes in root turnover? Our overall goal is to identify models

that are likely to be sensitive or insensitive, but not to compare absolute sensitivity among models as this will likely vary depending on the context of specific site and climate parameterizations. Regarding our second question, we pay particular attention to model approaches to C allocation to fine roots and acquisition of soil resources. To address these questions we used four models: CENTURY v4.5, Ecosystem Demography model (ED2) v2.1, LANDCARB v3.3.5.2, and MAPSS-CENTURY 1 (MC1). These models vary both in their complexity and spatial extent (Figure 1) and can be parameterized for a wide range of ecosystems. To determine sensitivity, each model was parameterized for a temperate forest ecosystem and run using a suite of fine root turnover rates ranging from very slow (0.1 yr^{-1}) to very fast (5.0 yr^{-1}). Sensitivity of each model was assessed through changes in total system C as well as changes in fine root biomass, aboveground live forest biomass, soil organic matter, and NPP.

2. Methods and Materials

2.1. Approach

Model sensitivity to adjustments in fine root turnover rate was compared by running each model using five different fine root turnover rates: 0.1, 0.3, 1.0, 3.0, and 5.0 yr^{-1} . Each model run was conducted in an ecosystem dominated by temperate forest ecosystems (Table 2) and during each simulation all parameters other than the fine root turnover rate of trees were held constant within a given model using the default/local site parameter values. Each model was initialized and/or run to steady state conditions according to model-specific protocols (Appendix A) using a fine root turnover rate of 1.0 yr^{-1} . Following initialization, 100 yr simulations were conducted using the adjusted root

turnover rates. During the 100 yr simulations, each model was run in the absence of disturbance (*i.e.* fire or timber harvest) so as not to conflate long-term changes in ecosystem C due to variable fine root turnover with short-term differences in ecosystem recovery following disturbance.

Additional simulations were conducted using ED2 and MC1 as both models have been previously used to simulate ecosystems with and without feedbacks from N limitation. First, both models were run in modes where N limitation on forest productivity was absent, and then again with potential nitrogen (N) limitation enabled. This was done to determine the effects of resource (*i.e.* N) limitation on model sensitivity. Second, both models simulated forest growth within Harvard Forest (Petersham, MA; 42.53° N, -72.19° W) following model specific parameterization (Appendix A). We included additional simulations of forest growth in the Walker Branch Watershed (East Tennessee; 35.96° N, -84.33° W) using MC1. Running all four models with identical sites and parameter sets was not logistically feasible in this study and results should be interpreted carefully. Still, simulations with MC1 and ED2 at the same site, MC1 across two sites, and broader simulations across all four models enable baseline tests to determine the degree to which changes in model outcomes with adjusted fine root turnover rates result from differences between site-environment conditions rather than model structure or parameterization.

The sensitivity of each model to adjustments in fine root turnover rate was measured by changes in total system C. Total system C includes live biomass (leaves, fine roots, branches, stems, live coarse roots and live wood), dead plant litter (standing and fallen dead wood, leaf, branch and root litter, dead coarse roots), and SOC.

Differences between model simulations were calculated as the percent difference between the simulations using very fast (5.0 yr^{-1}) and very slow (0.1 yr^{-1}) fine root turnover rates. Additionally, changes in total system C over time are shown in Figure 2 by calculating the percent difference of each simulation from the average of the five turnover simulations for a given model and site.

3. Results

Among the four models, CENTURY and ED2 were the most sensitive to changes in fine root turnover rate while LANDCARB and MC1 were relatively insensitive (Figure 2). Both CENTURY and ED2 (with and without feedbacks from N limitation) accumulated over 30% more total system C when run with slower compared to faster fine root turnover rates. Increases in total system C were associated with increased NPP in CENTURY (and to a lesser extent in MC1) with slower root turnover rates. However, unlike CENTURY, the increase in total system C with ED2 was not the result of greater NPP (Table 3). Instead, slower root turnover resulted in increased C allocation to woody biomass. This occurs as the model maintains a fixed biomass ratio between fine roots and leaves. With slower fine root turnover rates less C is allocated to fine roots and more is available for wood production. Furthermore, because fine roots turnover on the order of months to years and woody biomass turns over on the order of centuries, C allocated to wood consistently adds to total system C while C allocated to fine roots is mostly lost from the system as respiration after a few years. Consistent with changes in total system C, aboveground tree biomass was also greater with slower root turnover reflecting greater investment in biomass pools other than roots (*i.e.* wood).

Compared to the responses of CENTURY and ED2, MC1 was less sensitive to changes in fine root turnover rate with essentially no difference among simulations when MC1 was run without N limitation. However, when MC1 was run with potential feedbacks from N limitation the model sensitivity increased from less than 1% to roughly 6% difference in total system C at Walker Branch. By comparison, shifts at Harvard Forest were slight, increasing to a roughly 3% difference with N feedbacks. Interestingly, the greatest differences in total system C did not occur between the simulations using the slowest and fastest roots turnover rates as was observed in all other simulations. Instead, when feedbacks from N were incorporated the maximum values for total system C and most biomass components (except fine root biomass) occurred with intermediate turnover rates (e.g. 1.0 yr^{-1} ; Figure S1). The decrease in productivity (live aboveground biomass, SOC, NPP, Total system C) observed with the slowest turnover rate (0.1 yr^{-1}) compared to the more intermediate turnover rates likely occurs as the large buildup of fine root biomass saturates the max N uptake function such that further increases in biomass do not result in increased uptake of soil resources. At the same time, the increased root biomass does represent an increased respiratory cost, thereby reducing overall NPP. This is different from simulations without N limitation where N fixation rates are set to meet plant demand, effectively increasing the available N pool and avoiding uptake saturation. Accordingly, the total system C accumulated in simulations without N feedbacks was generally twice that as N limited simulations (Table S1).

Similar feedbacks between root biomass and N uptake might be expected in simulations with ED2 incorporating N limitation, yet these were not observed in this

study. In this case, the relatively modest effects of N limitation observed in the MC1 model were greatly exceeded by differences related to C allocation schemes in ED2. Specifically, the ED2 model maintains fixed leaf to root biomass ratios which results in smaller absolute differences in fine root biomass among simulations with faster and slower root turnover rates in ED2 compared with MC1 (Tables 3 and S1). By maintaining more reasonable amounts of root biomass under simulations with fast fine root turnover, the ED2 model effectively ensures adequate N uptake, even under N limited simulations. At the same time, surplus C that is not needed to maintain fine root biomass is then allocated to woody biomass which has a much greater effect on total system C than relatively small changes in N uptake.

LANDCARB was also relatively insensitive to adjustments in fine root turnover with less than 6% difference among model simulations. However, unlike the other models, slightly more C accumulated under the fastest root turnover rate (5.0 yr^{-1}) compared to the slowest (0.1 yr^{-1} ; Figure 2). Here, slower root turnover rates were associated with lower NPP and slower forest growth which eventually led to the slightly lower total system C. While the reduction in NPP with slower root turnover was approximately 15%, this was partially balanced by nearly 20% lower ecosystem respiration in the slow root turnover simulations leading to the muted differences in total system C. Another interesting difference in LANDCARB was that simulations using turnover rates of $\geq 1.0 \text{ yr}^{-1}$ returned nearly identical results indicating that above some threshold, changes in turnover rate have no impact on model results. For all other models, each increase in turnover rate resulted in incremental changes total system C.

Across all models, slower fine root turnover rates resulted in greater standing fine root biomass (Table 3). In models that maintain a fixed allocation of NPP to fine roots (see Table 4), the relative decrease in standing fine root biomass with fast root turnover rates results from rapid loss (mortality) of fine roots following root production. Fine root biomass accounted for less than 1% of total tree biomass in runs with fast root turnover rates but accounted for *ca.* 6%, 1.7%, and 17% of tree biomass with slow turnover rates in MC1, LANDCARB, and CENTURY, respectively. The loss of fine root biomass eventually led to reduced NPP and reduced total ecosystem C with fast root turnover rates in the CENTURY model as the less roots equated to lower capacity for uptake of soil resources. Incorporating feedbacks from N limitation in MC1 slightly increased the contribution of fine root biomass to total tree biomass from 5.6% to 6.7% at Harvard Forest and from 3.9% to 4.7% at Walker Branch. In the ED2 model, where fine root biomass is maintained as a fixed ratio with leaf biomass, the overall contribution of fine root biomass to total tree biomass was 28% and 21% with fast and slow root turnover, respectively. The greater proportion represented by fine roots with faster turnover was the product of there being less wood accumulated (and therefore less total tree biomass) in runs with faster turnover and not the result of increased buildup of fine roots.

Despite the variable contribution of fine root biomass to total tree biomass among the model simulations, the overall contribution of differences in fine root biomass to changes in total ecosystem C with altered root turnover rates was relatively small as changes generally manifested in other forest C components (*i.e.* wood or soil C). For example, in the CENTURY model, the roughly 200% increase in fine root biomass with slow root turnover rates only accounted for approximately 20% of the observed increase

in total system C after 100 years. At the same time, increases in aboveground biomass accounted for approximately 75% of the change in total system C. Furthermore, when simulations are extended beyond 100 years fine root biomass generally plays an even smaller role as soil organic C increases over time and accounts for a larger portion of observed differences in total system C (data not shown).

4. Discussion

4.1. Model responses to altered rates of fine root turnover

The ability to accurately describe and model terrestrial biogeochemistry is an important step towards understanding and anticipating land-based responses to environmental perturbations and shifting climate. Here, we addressed two main questions of whether different terrestrial models are sensitive to adjustments in fine root turnover rate (1), and how different model structures contributed to the sensitivity of each model (2). Importantly, the range of fine root turnover rates used in this study was based on the range of fine root turnover rates currently used in different models (Table 1).

In answer to our first question, we found that for some models, adjustments of fine root turnover rates clearly resulted in substantial changes in total system C. The extent of changes to total ecosystem C ranged from < 6% in LANDCARB and MC1 to greater than 30% in CENTURY and ED2. Given that the models were run across different sites it cannot be concluded that LANDCARB and MC1 would always be relatively insensitive while ED2 and CENTURY would always be highly sensitive to changes in fine root turnover rate. However, the general responsiveness of many of the simulations indicates that careful choice and testing of fine root turnover rates used to

parameterize many models is broadly important. Interestingly, model responses were not broadly related to their potential scale or complexity (i.e. Figure 1). Instead, the observed changes in total ecosystem C resulted from tradeoffs between different plant (e.g. allocation to roots vs. wood) and ecosystem (e.g. increased resource uptake and NPP vs. increased respiration) components and not simply from direct changes in fine root biomass (Figure 3). This further indicates the importance of model structure and our second question.

Our results indicate that certain types or families of models may be more sensitive to changes in root turnover rates (question 2, Table 4). Irrespective of spatial scale, models which incorporate feedbacks between root processes and plant productivity will likely be more sensitive to adjustments in fine root turnover rates than those that treat fine roots as passive portals through which plant C enters the soil. While this statement may not be surprising it should be noted that determining whether these feedbacks exist and how they manifest within models is not always clear. In the models used here we found two pathways by which this occurred; through root mediated uptake of soil resources and through shifting patterns of C allocation among different plant components (leaves, wood, sapwood, coarse and fine roots). First, slower turnover rates in CENTURY and MC1 (with N limitation) resulted in decreased root mortality, increased total root biomass and subsequently, increased NPP. This occurs as uptake of nutrients is explicitly tied to fine root biomass such that as root biomass increases, the proportional uptake of available nutrients also increases (Metherell *et al.*, 2010) (Table 4), alleviating nutrient limitation to the plant. Though water did not appear to play an important role in the simulations reported here, in models and systems where water is an important constraint to NPP, we

further hypothesize that increases in fine root turnover would result in similar decreases in NPP as total uptake capacity for water declines with reduced root biomass.

The second mode of altered total system C occurs as models shift patterns of C allocation among plant components. In many of the models, a fixed proportion of NPP is allocated to fine root production and this proportion may be increased in response to limiting soil resources (e.g. CENTURY and MC1, Table 4). However, for models that maintain a fixed biomass ratio between roots and leaves, changes in root turnover rate can substantially alter the amount of NPP required to maintain steady root biomass levels at the expense of other plant components. This occurred with ED2 as the model compensates for increased root turnover rates by increasing total allocation to fine root production. This resulted in substantially less C allocated to woody biomass and eventually less total system C. Thus, the increased C allocation to roots comes at the expense of allocation to other plant components (Litton *et al.*, 2007). The concept and utility of fixed and dynamic root:shoot ratios has received substantial discussion in the literature (Wilson, 1988; Reich *et al.*, 2002). Additionally, recent studies have identified strong tradeoffs between NPP allocated to fine roots and wood in forest ecosystems (Dybzinski *et al.*, 2011; Malhi *et al.*, 2011). Using model simulations and empirical measurements, these studies showed that the proportion of NPP allocated to foliage remains relatively stable while allocation to wood and fine roots was more variable. Consequently, increased allocation of NPP to woody biomass generally resulted in decreased C allocation fine root production and vice versa.

While many models incorporate feedbacks between fine roots and plant C acquisition or allocation, some models do not. Depending on the goal of the model it

may not be necessary to explicitly incorporate root-mediated processes to capture desired ecosystem behaviors. In these simulations, LANDCARB as well as MC1 (without N feedbacks) were largely insensitive to adjustments in fine root turnover. In both cases the models aim to capture a large portion of the variation in photosynthesis and growth as functions of available light and available soil moisture and/or soil temperature (Bachelet, 2001; Harmon, 2011). For these and other models that do not incorporate feedbacks between root turnover or root biomass with soil resource acquisition or C allocation it is likely unnecessary to devote limited resources to constraining turnover estimates to capture long-term behaviors at ecosystem and larger scales. Though, it is also likely that this approach will limit the ability of a model to capture ecosystem or larger scale responses to changes or limitations in soil resource availability.

4.2. Ecosystem responses to altered fine root turnover

Shifts in species composition or environmental conditions may alter fine root turnover rates and drive varied and complex responses within an ecosystem. Limited descriptions and feedbacks between fine root dynamics and ecosystem processes in models are partly due to uncertainties associated with many empirical observations and a lack of sound mechanistic understanding. Still, there is sufficient appreciation of belowground processes to identify several key aspects of ecosystem biogeochemistry that would likely be affected by altered fine root turnover (Figure 3). The following is an attempt to identify several factors that may be broadly relevant and translatable to current and future model applications.

373 4.2.1. *Carbon cost at the root level.* Increasing root turnover rates may lead to
374 increased or decreased total C cost for root systems depending principally on whether
375 similar levels of absolute standing root biomass are maintained. For most models a
376 relatively simple distinction can be made. Does the model maintain a fixed biomass ratio
377 between roots and leaves? Or, is the standing biomass of roots flexible while the total
378 amount of C allocated to roots is maintained as a fixed proportion of NPP? In the first
379 case, if fine root turnover rates increase then the plants (or model) would necessarily
380 allocate increasing amounts of C to fine roots in an effort to maintain roughly fixed
381 biomass ratios between roots and leaves (*e.g.* ED2). In the second case, where the
382 proportion of C (NPP) allocated to root production is roughly constant, the increasing
383 turnover rates will at first reduce root standing root biomass and lead to reduced
384 respiratory cost of the whole root system. This is similar to the pathway captured by the
385 LANDCARB model that led to slightly higher NPP with faster root turnover. However,
386 in models where nutrient and/or water uptake are dependent on the amount of roots
387 present in the system (*e.g.* CENTURY, ED2) then reduced standing root biomass should
388 result in decreased capture of soil resources which, if those resources (nutrients and/or
389 water) limit plant growth, will then reduce NPP and total system C with time.

390 4.2.2. *Resource cost at the plant level.* At the whole-plant level changes in rates
391 of fine root turnover may have both positive and negative impacts for overall resource
392 acquisition. Decreased standing root biomass with increased fine root turnover should
393 lead to lower total uptake capacity for soil resources. However, root-specific resource
394 uptake rates may decrease with slower root turnover as depletion zones for relatively
395 immobile soil nutrients (*e.g.* phosphorus) form around older roots and uptake rates for

other more mobile nutrients (e.g. N) also tend to decline with root age (Bouma *et al.*, 2001; Volder *et al.*, 2005). Thus, maintaining younger root populations through increased turnover rates may represent an advantage for capturing soil resources under some circumstances, particularly if total root biomass remains relatively constant. Unfortunately, there is currently insufficient mechanistic understanding to adequately parameterize relationships between shifting root turnover rates, declining nutrient uptake rates with root age, and the total uptake capacity of a root population and these nonlinear processes likely vary with species and soil conditions. It should also be noted that some of the decline in uptake for both mobile and immobile resources by older roots may be compensated for through mutualisms with mycorrhizal fungi, though the point at which declining uptake directly by roots is offset by increasing uptake by fungi offset is unclear. Furthermore, these potential interactions are complicated, have relatively little empirical data available to constrain parameters, and are not explicitly included in most models (but see (Orwin *et al.*, 2011; Deckmyn *et al.*, 2014).

In addition to impacting the potential for resource uptake, increasing root turnover rates may also represent a significant loss of nutrients through the repeated construction and subsequent death and decomposition of fine roots. This flux of nutrients through the turnover of root biomass into soil is substantial (Silver & Miya, 2001). If plants are not capable of recapturing the majority of the nutrients lost through root turnover, faster turnover rates will then represent a large expenditure of valuable resources.

4.2.3. *Impacts on microbial communities, soil organic matter, and soil nitrogen.*

Faster turnover rates of fine roots may result in greater C and N inputs into soils which has important implications for decomposition and mineralization processes mediated by

microbial communities. Several studies have reported that increasing C flux belowground in response to elevated atmospheric CO₂ results in increased microbial activity, faster decomposition of fresh organic matter, and increased breakdown of more recalcitrant pools of soil organic C (Langley *et al.*, 2009; Drake *et al.*, 2011). These results are consistent with more basic expectations that increasing simple carbohydrates to microbial communities increases, or primes the degradation of soil C and increases mineralization of nutrients previously immobilized in recalcitrant soil organic C (Kuzyakov *et al.*, 2000). Should these responses to increased C input be broadly applicable across ecosystems it would suggest that increasing root turnover rates may prime microbial communities and the breakdown of soil organic matter. Additionally, increases or decreases in N availability resulting from altered fine root turnover may feedback on the amount of root biomass maintained in an ecosystem to capture limiting soil resources. However, predicting these responses will be partially contingent on whether or not the quality of root and mycorrhizal litter changes which may also mediate rates of decomposition, nutrient mobilization, and subsequently, fine root biomass (Silver & Miya, 2001; Chen *et al.*, 2002; Koide & Malcolm, 2009; Goebel *et al.*, 2011; Fernandez & Koide, 2012).

Widely integrating one or a few of the above processes into models remains a daunting task. Further research teasing apart specific effects of shifting turnover rates on ecosystem biogeochemistry is needed. Identifying which processes are most important to models will be vital so that field efforts can be focused to collect those data which are most needed to improve model design and parameterization.

4.3. Variation in turnover rates used by different models

Evidence presented here suggests that adjusting fine root turnover rates in models can have significant impacts on total system C and C partitioning across plant and ecosystem components (leaves, roots, wood, soil organic C). Therefore, accurately parameterizing fine root turnover should be a priority whenever possible. Yet, as shown in Table 1, current estimates used in models can vary by an order of magnitude. Why then do we see variation in the root turnover parameter across models even though they all describe ostensibly similar ecosystems (i.e. temperate forests)? This is due in part to the variation in methodologies used to determine root turnover and the specific root populations they are likely to capture (Guo *et al.*, 2008; Strand *et al.*, 2008; Gaudinski *et al.*, 2010). Additionally, some of the variation may be due to actual differences between species and sites or due to differences between years of observation (Gill & Jackson, 2000; Iversen *et al.*, 2008; McCormack *et al.*, 2014), though the magnitude of variation across species and sites tends to be smaller than that observed among different methods. A third factor contributing to the different rates across models may also be the result of different approaches to derive and describe fine root turnover used by different models. Recent studies using the FORCENT model (Parton *et al.*, 2010) and ED2 (Medvigy *et al.*, 2009; Kim *et al.*, 2012) cite turnover rates between 3.5 and 9.6 yr⁻¹ which are much higher than are typically measured for even the shortest-lived fine root populations in temperate trees, but are logically derived based on logic implicit to each model.

First, the FORCENT model uses a two-pool model of fine roots, termed *juvenile* and *mature*, with separate maximum turnover rates of 9.6 and 2.2 yr⁻¹, respectively. Importantly, the actual turnover rates used in the model vary based on soil temperature

and water stress and would rarely be expressed at the maximum rate for the entirety of any given year. There is strong empirical evidence to support this two pool approach that divides fine roots into a fast turnover, ephemeral fine root pool and a slow turnover, persistent fine root pool (Gaudinski *et al.*, 2010; Lynch *et al.*, 2013). Still, care must be taken to accurately quantify and parameterize turnover rates for each pool which may be best achieved through a combination of root observation methods including minirhizotrons for smaller and more distal absorptive roots and isotopic approaches for higher order, transport fine roots. Given proper parameterization, the approach modeling fine roots as two separate pools will likely enable models to better capture and describe more variability associated with fine root turnover and function in perennial plant systems (McCormack *et al.*, *In prep*).

Based on logic separate from the two-pool approach used in FORCENT, recent applications of ED2 settled on turnover rates much higher than the default value of 0.33 yr⁻¹ first used in the model. Through model optimizations, Medvigy *et al.* (2009) established a fine root turnover rate of 5.1 yr⁻¹ for mixed temperate forests and Kim *et al.* (2012) a rate of 6.6 yr⁻¹ for an Amazonian rainforest. If empirical observations of fine root turnover are generally below 2.0 yr⁻¹ and often below 1.0⁻¹, why are these values so high? First, the ED2 model incorporates C loss through root exudates as part of root turnover. Most exudates have relatively short turnover times of hours to weeks, but are rarely included as a separate model pool. Capturing root plus exudate behaviors with a faster turnover rate may achieve model phenomenological objectives but allow little flexibility to describe mechanistic relationships among complex exudates and root

processes. Furthermore, the term ‘exudates’ may refer to many different processes and should be unpacked before interpreting.

Grayston *et al.* (1996) identified five distinct classes of compounds exuded directly by roots which have short lifespans (hours to days), but also usually represent a fairly small amount (*ca.* 1 to 5%) of total plant C allocation. However, other authors also classify sugars given to mycorrhizal fungi in exchange for soil nutrients or water as root exudates. Here, turnover rates may range from days to months for fungal hyphae (Godbold *et al.*, 2006) or months to years for mycorrhizal tips and rhizomorphs (Pritchard, *et al.*, 2008; McCormack *et al.*, 2010). The amount of C allocated to mycorrhizal fungi is also substantially greater than that allocated to other exudates and may be as high as that allocated directly to roots (Wallander *et al.*, 2004). However, given the variability in the amount of C resources that are estimated to be allocated to mycorrhizal fungi and the range in turnover times from days to years among the components of the root to mycorrhizal fungal system it is unclear what exactly would be a reasonable, single estimate for turnover rate. Separating mycorrhizal fungi from roots altogether, work by Orwin *et al.* (2011) used a turnover rate of 3.2 yr⁻¹ for mycorrhizal fungi, which is still substantially lower than the turnover rates used for roots + exudates in the ED2 model. It is possible that the consistent optimization results within the ED2 model are capturing aspects of C flow through the entire root and fungal complex that has not yet been considered or well quantified. However, even if this is the case, the turnover rates used are only being applied to root biomass and not explicitly to root *plus* mycorrhizal biomass, which may misrepresent total C allocation and flux through the belowground plant and mycorrhizal pools.

Given the wide range of uncertainty associated with fine root turnover rates it may seem a daunting task to adequately narrow the field of potential estimates to parameterize models. Recent work coupling ED2 with a novel workflow tool (PEcAN) to inform model parameterization demonstrated that uncertainty in model results could be greatly reduced by constraining the range of potential estimates of fine root turnover rate used in the model (LeBauer *et al.*, 2013; Wang *et al.*, 2013). This and other similar approaches may prove invaluable to reduce uncertainty regarding estimates of many difficult to measure parameters, though they are still dependent on availability of robust and relevant data. In the case of fine root turnover, to ensure that appropriate constraints for turnover rates are set for models there are likely several important questions that require further investigation. How should fine root turnover be modeled, as one root pool or two (Smithwick *et al.*, 2014)? How do turnover rates vary across species and landscapes (McCormack *et al.*, 2013; McCormack *et al.*, 2014)? How should C allocation associated with fine roots (e.g. root exudation and allocation to mycorrhizal fungi) be treated in models (see discussion above; (Orwin *et al.*, 2011; Deckmyn *et al.*, 2014)?

4.4. Conclusion

Future improvements in modeling terrestrial processes and their responses to environmental change will be partly contingent on developing better understanding of root dynamics and how they interact and mediate resource acquisition and productivity at the whole-plant and ecosystem level. When attempting to determine *a priori* if an untested model will be sensitive to changes in fine root turnover rate, asking two initial questions may help predict how the model is likely to respond. First, is standing root

biomass determined to be a fixed biomass ratio with leaves or is root biomass the product of a fixed allotment of NPP (root production) and subsequent turnover (root mortality)?

Second, is the acquisition of soil resources dependent on the amount of standing root biomass? For models that base soil resource acquisition on soil availability and not root biomass and that do not maintain a fixed biomass ratio between roots and leaves, changes in root turnover rates are unlikely to be of significant consequence to overall model predictions. However, for applications that base soil resource uptake on direct root uptake or that maintain fixed ratios between root and leaf biomass (Figure 3), fine root turnover rates should be selected carefully and model sensitivities to different turnover rates should be explicitly tested. Improvements here should enable models to better capture and predict responses of terrestrial ecosystems to complex and interactive changes in climate, atmospheric CO₂, and soil resource availability. Continued work identifying the patterns and processes influencing root lifespan and turnover will lead to more confident assignment of root turnover rates in models. Future field- and model-based research should further focus on building better empirical understanding of how changes in root turnover impact ecosystem C and nutrient dynamics.

Author Contributions

MLM and ES designed the experiments. MLM, EC, and BR performed model simulations with assistance from ES and FS. MLM prepared the manuscript with contributions from EC, DE, BR, and FS.

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Appendix

Appendix A. Description of Models

CENTURY v4.5 is an ecosystem-process model that describes C, nitrogen (N), phosphorus, sulfur, and hydrological dynamics in terrestrial ecosystems (Parton *et al.*, 1987; Parton *et al.*, 1993). The structure of each system is user-defined (*i.e.* forest, savanna, agricultural field) as are most system parameters (*i.e.* climate, soil, productivity). While the model can be parameterized for many different locations it is neither spatially explicit nor spatially interactive. For our analysis we parameterized the CENTURY model for a site within Yellowstone National Park (YNP; 44.60° N, -110.50° W) that was dominated by lodgepole pine (*Pinus contorta*) following Smithwick *et al.* (2009). The model was initialized with site-specific values for soil and vegetation parameters for mature forests. Using these initial parameters, the model was run for 2000 years with stand-replacing fires prescribed every 200 years until long-term soil C pools

became stable. Once stable, the 100 year simulation with adjusted root turnover rates was conducted without subsequent disturbance. Climate was provided as monthly means for precipitation and temperature based on modeled historical averages from Western Regional Climate Center (<http://www.wrcc.dri.edu/>; site 485345).

ED2 is a hybrid model that predicts the vegetation structure and biogeochemical fluxes (e.g. C, water, N, sensible/latent heat) within a given landscape (Moorcroft *et al.*, 2001; Medvigy *et al.*, 2009). ED2 is spatially explicit and interactive and can operate at a range of scales and resolutions from ecosystems to regions. ED2 incorporates aspects of the CENTURY model to describe soil biogeochemistry and decomposition but uses its own approach (i.e. size and aged structured vegetation groupings) to determine ecosystem structure. The model is dynamic in that it allows for emergent behavior and changes in physical vegetation structure through time. Additionally, the model can be run in two separate modes; *with* feedbacks due to limited N availability and *without* feedbacks due to limited N availability. Here, the model was run both ways as both are common uses of the model. In this analysis we used ED2 v2.1 parameterized for Harvard Forest (Petersham, MA; 42.53° N, -72.19° W). The model was run for 100 yrs with the initial 12 yrs set to observed meteorology data from 1992 to 2003. For subsequent years, meteorology was randomly cycled through observed data from 1992 to 2003.

Atmospheric carbon dioxide (CO₂) was held constant leading to relatively stable climate conditions. Due to computational limitations, ED2 was run using only 4 sets of root turnover rate; 0.1 yr⁻¹ (very slow), 0.3 yr⁻¹ (slow), 1.0 yr⁻¹ (intermediate), and using the model default values which correspond to *very fast* turnover, ranging from 3.8 to 5.7 yr⁻¹

among the dominant tree types which included early, mid, and late successional deciduous species as well as late successional conifers.

LANDCARB describes terrestrial pools and fluxes of C across forested landscapes (Cohen *et al.*, 1996). Factors such as forest fire and timber harvest are key components of LANDCARB and are explicitly represented within the model. LANDCARB is spatially explicit and interactive with different processes such as disturbance and seed spread acting at different scales in a hierarchical manner. LANDCARB mimics stand level behaviors of a previous model, STANDCARB 2.0 (Harmon *et al.*, 2009) but simplifies many processes to capture behavior at a landscape scale with limited computational effort (Smithwick *et al.*, 2006). Here we used LANDCARB version 3.3.5.2 parameterized for the HJ Andrews Experimental Forest (44.21° N, -122.26° W). The model was run for a 2 x 2 grid set (each cell is 1 ha) and was scheduled so that no disturbances, including fire and timber harvest, took place within the simulated forests.

MC1 is a spatially explicit, though not spatially interactive, dynamic vegetation model (Bachelet *et al.*, 2000; Daly *et al.*, 2000). The model is composed of three separate modules including MAPPS (Neilson, 1995) which predicts vegetation type across landscapes based primarily on climate characteristics, a modified version of the CENTURY model that describes the biogeochemistry within each model cell; and a novel fire module that simulates fire disturbance and severity across the landscape (Lenihan *et al.*, 1998). The model is primarily concerned with distributions of vegetation and associated C fluxes and the simulations used in this study were performed at a 4 km x 4 km resolution. Similar to ED2, MC1 can be run with and without feedbacks due to

624 limited N availability. Here again, two sets of runs were conducted, with and without N
625 feedbacks. The model was initially run across the eastern United States following
626 Crisfield (2012). Taking advantage of this large spatial extent, data were extracted for
627 two separate points within the model domain to better discern whether results were model
628 specific or site specific. The first site corresponds to the same location used with ED2 in
629 Harvard Forest (42.53° N, -72.19° W) which was characterized as a temperate cool
630 mixed forest, defined in MC1 as “VTYPE 10”. The second site corresponds
631 approximately with the Walker Branch watershed (35.96° N, -84.33° W) in eastern
632 Tennessee and is characterized as a predominantly temperate deciduous broadleaf forest
633 (VTYPE 9). These two forests represent end-members of the broadly defined temperate
634 forests in the eastern and Northeast United States. To initialize the model, MC1 was first
635 set to run for 3000 years repeating an annual climate cycle based on average climate from
636 years 1895 to 2006. This was done to determine the spatial distribution of each
637 vegetation type. This was followed by a 1000 year spinup using detrended multi-year
638 climate taken from 1895 to 2006 scaled to the period of 1895 to 1909 (Bachelet *et al.*,
639 2008; Crisfield, 2012). The final model simulations were based on the historical climate
640 record in sequence from 1895 to 1995.

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Figure 1. Scale and complexity of four ecological process models (adapted from Ostle et al. 2009). Complexity refers approximately to the number parameters required relative to the spatial scale being described and is not necessarily a measure to the complexity of each model’s algorithms or approach.

Figure 2. Percent difference in total system carbon between model simulations using different fine root turnover rates; very slow (0.1 yr^{-1}), slow (0.3 yr^{-1}), intermediate (1.0 yr^{-1}), fast (2.0 yr^{-1}), and very fast (5.0 yr^{-1}). Site locations for each model are given in Table 1. Note that the y-axis scale is changed for Site 2 insets for the MC1 model.

Figure 3. Ecosystem pools and processes directly impacted by changes in fine root turnover rate. Carbon pools are indicated in boxes and plant processes are shown in circles. Changes in fine root turnover rate can impact C allocation to various plant components commonly resulting in tradeoffs between roots and woody biomass. Changes in fine root biomass also impact standing root biomass, uptake of soil resources and subsequently constrain net primary production (NPP) as well as alter rates of root litter inputs to soil organic matter (SOM).

Table 1. Review of 17 terrestrial models and their parameterization of fine root turnover in temperate forests. PFT = Plant Functional Type.

Model	Fine root Turnover	Example	Reference
Biome-BGC	Initially set equal to leaf turnover, now can be user defined.	0.8 yr ⁻¹ spruce 1.0 yr ⁻¹ broadleaved	Tatarinov and Cienciala (2006)
CENTURY	User defined, single value for site at any given time, can be different between grasses and trees	0.9 yr ⁻¹ lodgepole pine	Parton <i>et al.</i> (1987); Smithwick <i>et al.</i> (2009)
CLM-CN	Defined as one of two possible rates depending on PFT	0.5 yr ⁻¹ or 1.0 yr ⁻¹	Levis <i>et al.</i> (2004)
ED2	User defined, can have different values for different species or PFTs	0.33 yr ⁻¹ , optimized range up to 6.6 yr ⁻¹ †	Medvigy <i>et al.</i> (2009); Kim <i>et al.</i> (2012)
Fire-BGC	Set equal to leaf turnover	1.0 yr ⁻¹ for leaves and fine roots	Keane <i>et al.</i> (2011)
FORCENT	User defined. Contains two separate pools of fine roots of faster and slower turnover times	Maximum rate of 2.2 to 9.6 yr ⁻¹	Parton <i>et al.</i> (2010)
IBIS	Fixed across all PFTs	1.0 yr ⁻¹	Kucharik <i>et al.</i> (2006)
JULES	Defined as one of two possible rates depending on PFT	0.15 yr ⁻¹ or 0.25 yr ⁻¹	Clark <i>et al.</i> (2011)
LANDCARB	Maximum turnover rate is user defined by species. Absolute rate varies with light absorbed by canopy.	0.5 yr ⁻¹	Harmon <i>et al.</i> (2009); Sierra <i>et al.</i> (2009)
LANDIS-II	Can be defined by species. May also temporarily increase to reflect losses in aboveground biomass.	0.6 or 1.0 yr ⁻¹	Dymond <i>et al.</i> (2012)
LM3V	Defined for different PFTs	1.0 yr ⁻¹ for temperate deciduous and 0.6 yr ⁻¹ for cold evergreen trees	Shevliakova <i>et al.</i> (2009)
LPJ	Defined as one of two possible rates depending on PFT	0.5 yr ⁻¹ or 1.0 yr ⁻¹	Sitch <i>et al.</i> (2003)
MC1	User defined, can have different values for different PFTs	1.1 yr ⁻¹ for deciduous broadleaf 1.3 yr ⁻¹ for evergreen needleleaf	Bachelet <i>et al.</i> (2000); Daly <i>et al.</i> (2000); Rogers <i>et al.</i> (2011)
Orchidee	User defined, can have different values for different PFTs	0.86 yr ⁻¹	Ciais <i>et al.</i> (2008)
PnET-CN	Varies as a function of annual nitrogen mineralization	Typical range of 0.48 yr ⁻¹ to 0.82 yr ⁻¹	Aber <i>et al.</i> (1997); Ollinger <i>et al.</i> (2002)
PPA	User defined	0.3 yr ⁻¹ , 0.7 yr ⁻¹	(Fisher <i>et al.</i> , 2010); Dybzinski <i>et al.</i> (2011)
SiBCASA	Fixed across all PFTs	1.0 yr ⁻¹	Schaefer <i>et al.</i> (2008)
TRIFFID	Set equal to minimum leaf turnover rate	0.25 yr ⁻¹	Cox (2001)

†Fine root turnover rate in ED2 incorporates production of short-lived root exudates.

Table 2. Four ecosystem models and sites used in analysis of model sensitivities to adjustments in fine root turnover rate. Further model details are given in Appendix A.

Model	Site	Location	Forest Ecosystem
CENTURY v4.5	Yellowstone National Park	44.60° N, -110.50° W	Evergreen temperate
ED2 v2.1	Harvard Forest	42.53° N, -72.19° W	Cool mixed temperate
LANDCAR B v3.3.5.2	HJ Andrews Experimental Forest	44.21° N, -122.26° W	Evergreen temperate
MC1	Site 1-Harvard Forest	42.53° N, -72.19° W	Cool mixed temperate
	Site 2-Walker Branch	35.96° N, -84.33° W	Warm mixed temperate

Table 3. Percent difference in live aboveground biomass, fine root biomass, and total soil organic carbon (SOC) as well as trends in total system C after 100 year simulations using very slow and very fast fine root turnover rates. Positive values indicate greater C under simulations with slower turnover rates. In MC1 simulations incorporating feedbacks from N limitation the maximum values in most C pools (except fine root biomass) were achieved with the intermediate fine root turnover rates instead of the very slow turnover rate. For these simulations the percent difference between intermediate and very fast fine root turnover rates are given in parentheses. Approximate site locations for each model are as follows: CENTURY (Yellowstone National Park, WY), ED2 (Harvard Forest, MA), LANDCARB (HJ Andrews Experimental Forest, OR), MC1 (Harvard Forest, MA; Walker Branch watershed, TN).

Model	Live aboveground biomass*	Fine root biomass	Total SOC	NPP†	Total system C
CENTURY	125	198	-1.5‡	102	38
ED2-unlimited N	70.8	49.1	-10.0	-7.7	33.4
ED2-limited N	70.6	49.4	-2.6	-7.0	32.8
LANDCARB	<1	76.7	-45.2	-15.6	-5.9
MC1-unlimited N					
Harvard Forest	<1	100	<1	<1	1.5
Walker Branch	<1	197	<1	<1	<1
MC1-limited N					
Harvard Forest	<1 (5.7)	197	<1. (3.6)	<1 (5.6)	2.5 (3.0)
Walker Branch	6.8 (9.8)	195	5.1 (8.3)	11.0 (15.0)	5.9 (6.2)

*For CENTURY and MC1 this corresponds to leaves, branches and wood (bole). For ED2 this corresponds to leaves and live sapwood. For LANDCARB this includes all live tree biomass aboveground plus roots.

†Percent difference was calculated using the average NPP from the final 10 years of the 100 year simulations.

‡Following extended model runs beyond 100 years, the -1.5% difference increases to +20% as greater soil organic C is built up with faster growth (more tree C) with the slowest turnover rate that is incorporated into soil organic C over time (data not shown).

Table 4. Structure of key root-related processes in four ecological models and their sensitivity to changes adjustments in fine root turnover rate. Model sensitivity was classified as either sensitive (S), moderately sensitive (M), or insensitive (I) based on the difference in total ecosystem C expressed between simulations (Table 3).

Model	C allocation to fine roots	Water uptake <i>Dependent or Independent</i> of fine roots	Nitrogen uptake <i>Dependent or Independent</i> of fine roots	Model Sensitivity
CENTURY	Fixed portion of NPP, adjusts in response to N limitation	Independent	Dependent	S
ED2-Limited N	Maintains fixed ratio between fine root and leaf biomass	Dependent	Dependent	S
Unlimited N			Independent	S
LANDCARB	Fixed portion of NPP	Independent	Independent	I
MC1-Limited N	Fixed portion of NPP, adjusts in response to N limitation	Independent	Dependent	M
Unlimited N	Fixed portion of NPP		Independent	I