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Measuring fine root turnover in forest ecosystems

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Abstract

Development of direct and indirect methods for measuring root turnover and the status of knowledge on fine root turnover in forest ecosystems are discussed. While soil and ingrowth cores give estimates of standing root biomass and relative growth, respectively, minirhizotrons provide estimates of median root longevity (turnover time) i.e., the time by which 50% of the roots are dead. Advanced minirhizotron and carbon tracer studies combined with demographic statistical methods and new models hold the promise of improving our fundamental understanding of the factors controlling root turnover. Using minirhizotron data, fine root turnover (y^{-1}) can be estimated in two ways: as the ratio of annual root length production to average live root length observed and as the inverse of median root longevity. Fine root production and mortality can be estimated by combining data from minirhizotrons and soil cores, provided that these data are based on roots of the same diameter class (e.g., <1 mm in diameter) and changes in the same time steps. Fluxes of carbon and nutrients via fine root mortality can then be estimated by multiplying the amount of carbon and nutrients in fine root biomass by fine root turnover. It is suggested that the minirhizotron method is suitable for estimating median fine root longevity. In comparison to the minirhizotron method, the radio carbon technique favor larger fine roots that are less dynamics. We need to reconcile and improve both methods to develop a more complete understanding of root turnover.

Introduction

Fine root production has been estimated to account for up to 33% of global annual Net Primary Production, NPP (Gill and Jackson, 2000). Thus, fine root turnover has important implications for individual plant growth, plant interactions, and below-ground carbon and nutrient cycling. Root turnover varies widely within and among species and across ecosystems, but our ability to predict root lifespan for particular species or systems is poor (Eissenstat and Yanai, 1997).

Understanding the factors controlling fine root production and mortality, which we collectively call turnover, is therefore important for understanding element fluxes in ecosystems. Several methods have been used to calculate

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rates of root production and mortality (Aerts et al., 1992; Hendrick and Pregitzer, 1992; Majdi and Andersson, 2005), and there is currently no standard approach for defining root turnover. The contribution of fine root turnover and associated mycorrhiza to total ecosystem carbon and nutrient budgets remains uncertain because, inter alia, it has always been difficult to directly quantify fine root turnover (Trumbore and Gaudinski, 2003).

In the last decade several methods for estimating fine root turnover in forest ecosystems have been developed, but turnover rates obtained seem to vary according to the method used (Gill and Jackson, 2000; Hertel and Leuschner, 2002; Tierney and Fahey, 2002).

The aim of the present review was to discuss the status of knowledge on fine root turnover and to suggest methods for measuring fine root turnover in forest ecosystems.

Development of methods

Sequential soil coring

Soil coring was the first method used to estimate fine root production and mortality (Fahey and Hughes, 1994; Nadelhoffer and Raich, 1992; Persson, 1979; Santantonio and Hermann, 1985; Vogt et al., 1986). This method is suitable for measuring standing biomass, but has several limitations when used for assessing root turnover and requires assumptions about root growth and mortality that can be difficult to ascertain. First, it must be assumed that each observed change in live root biomass during a sampling interval is solely due to either production or mortality and that the two processes did not occur simultaneously (Kurz and Kimmins, 1987; Singh et al., 1984; Vogt et al., 1998). The second assumption is that no additional peak or trough in either live or dead root biomass occurs between the sampling dates. Publicover and Vogt (1993) analyzed the sensitivity of fine root production estimates obtained by sequential coring to a variety of measurement errors and concluded that a principal problem was obtaining reliable information on fine root decomposition *in situ*. Depending on how production is calculated, there may be 2- to 3-fold differences in production estimates derived using the same sequential coring data (Gholz et al., 1986; McClaugherty et al., 1982). Sala et al. (1988) suggested that below-ground NPP based on sequential soil coring data is always overestimated because of sampling errors that accumulate as the frequency of sampling increases during a year.

A low-key debate has been ongoing for the last 15 years regarding alternative ways of estimating the turnover and the reliability of obtained data (see review by Vogt et al., 1998).

Ingrowth cores

Ingrowth cores have been used to estimate fine root production in various ecosystems. They can be used to get a quick and less laborious estimate of relative fine root production (Flower-Ellis and Persson, 1980; Vogt and Persson, 1991) when root growth is rapid. The method can be used to obtain relative growth estimates and to observe the effects of experimental manipulations on root production. The great advantages of the ingrowth core method are its simplicity and low cost. However, it has four major limitations: (i) it provides no information on the time scale of root-ingrowth or mortality; (ii) many of the in-growing roots are from damaged roots as all the roots in the plane of the core are cut; (iii) nutrient availability and soil structure are altered when soil is placed in the cores; and (iv) as with sequential cores, concurrent growth and mortality during the recolonization interval cannot be measured directly.

Recovering intact fine root systems from the soil using soil cores is far from trivial. In order to determine biomass, for example, fine roots have traditionally been sampled destructively and sorted into arbitrary size classes (e.g., 0−1 or 0−2 mm in diameter), dried and then weighed. Such an approach carries the underlying assumption that all roots of a given size class have the same life expectancy and physiological characteristics (Pregitzer, 2002). Furthermore, if species are being compared to one another, the arbitrary size class approach assumes that the roots of all species are constructed and function in the same way. Traditional harvest techniques also assume there is no bias in recovering roots of different sizes, e.g., that the probability of recovering roots that are 1.0 or 2.0 mm in diameter from a soil core is the same. Finally, although

soil cores can be used to estimate mycorrhizal biomass, the methodologies are problematic since it is difficult to recover mycorrhizal hyphae, which account for ca. 10% of total NPP (Leake et al., 2001).

Minirhizotrons

The minirhizotron technique is a non-destructive method that can be used to monitor the same root(s) over selected time intervals, which can vary from days to years. Transparent cylindrical tubes are installed horizontally and vertically in the soil (Majdi and Andersson, 2005) and root intersections along the tubes are viewed and recorded at appropriate times with a miniature video camera (Upchurch and Ritchie, 1983). Minirhizotrons are used to estimate fine root (<1 mm diameter) production, mortality and longevity. By comparing series of images it is possible to identify the same roots on successive dates (Hendrick and Pregitzer, 1992; Majdi, 1996). Quantitative data can be obtained on root length production, root length mortality, longevity, rooting density and root diameter (Andersson and Majdi, 2005; Hendrick and Pregitzer, 1996). Minirhizotrons can also provide qualitative information, on variables such as the frequency of short mycorrhizal roots, root color, branching characteristics and root decomposition.

The use of minirhizotrons in recent years has improved our knowledge of fine root dynamics because they allow the concurrent measurement of fine root production and mortality (Andersson and Majdi, 2005; Baddeley and Watson, 2005; Cheng et al., 1991; Green et al., 2005; Hendrick and Pregitzer, 1992; Johnson et al., 2001; Ruess et al., 2003; Tierney and Fahey, 2001). However, short-term minirhizotron studies (i.e., within-year) do not adequately track the longevity of longer-lived fine roots and the tubes themselves can influence root lifespan (Withington et al., 2003). In addition, the selected sampling intervals affect estimates of root longevity (Johnson et al., 2001).

After installing the tubes, root growth and death at the soil–minirhizotron tube interface may not be representative of these processes in bulk soil since a lag period of up to a year is required to stabilize the density of fine roots (Joslin and Wolfe, 1999). Another limitation of the minirhizotron technique is that if roots are only classified as dead when they disappear, their longevity will be overestimated.

Furthermore, although minirhizotron studies have been used to study the effects of changes in a wide range of environmental conditions, we still do not understand the mechanisms controlling fine root turnover (Pregitzer, 2002).

Statistical analysis of minirhizotron data

In recent years there has been increasing use of the Kaplan–Meier and Cox proportional hazards regression approaches to analyze root demographic data. The Kaplan–Meier approach (Altman, 1991; Kaplan and Meier, 1958) can be used to estimate survivorship functions for single and multiple cohorts of fine roots (Andersson and Majdi, 2005; Baddeley and Watson, 2005). Fine roots are followed until the end of the study period and classified as either dead (censored) or alive (uncensored). The rationale for using median longevity is that a large proportion of the roots are not followed until their death, as they are still alive at the end of the study period, which make it impossible to calculate the true mean turnover time. Survivorship analysis requires an adequate sample size of cohorts of individual roots because small cohorts, e.g., 10–15 roots, may not be representative of the entire population. This approach to understanding median longevity can be complicated by the long dormant season in temperate and boreal forests (Andersson and Majdi, 2005).

Proportional hazards regression is a statistical model that allows the effect of each covariate to be evaluated while accounting for effects of other covariates (Allison, 1995; Cox, 1972). Coefficients are then estimated for each covariate in the model, with negative and positive signs indicating that mortality decreases and increases, respectively, as the values of the covariates increase (Wells and Eissenstat, 2001). Using this model, individual roots are evaluated for their risk or 'hazard' of mortality, which can be considered as the instantaneous probability of mortality. Cox's proportional hazards regression analysis (Altman, 1991; Hosmer and Lemeshow, 1999) can also be used to analyze the risk of mortality in response to different covariates, e.g., treatments, root

diameter and soil depth (Baddeley and Watson, 2005; Green et al., 2005).

Standard demographic statistical techniques that are widely understood and applied in fields such as human medicine and wildlife biology hold significant promise for improving our understanding of how fine root systems function (Ruess et al., 2003).

Radiocarbon ^{14}C measurements

Radiocarbon measurements of SOM, CO_2 and roots provide useful data for determining soil carbon dynamics. Carbon reservoirs that exchange with the atmosphere reflect the rate of exchange through the amount of 'bomb' ^{14}C incorporated into particular pools of carbon. The ^{14}C content of a homogeneous C pool in any given year since 1963 can be predicted from the turnover time and the known record of atmospheric $^{14}CO_2$. Utilization of bomb-produced ^{14}C as a continuous isotopic label has advantages over other isotopic methods because it can be used in undisturbed ecosystems and can resolve dynamic changes that operate on annual to decadal time scales (Gaudinski et al., 2001). The interpretation of ^{14}C data generally, and bomb ^{14}C in particular, is far from trivial and the results are sensitive to the particular model used for interpretation (Franklin et al., 2003; Trumbore and Druffel, 1995). In order to adequately utilize this tool to understand root turnover, it is essential to define the root carbon pools of interest appropriately (Trumbore and Gaudinski, 2003). Simplistic or poorly founded assumptions regarding the definition of root carbon pools can confound our understanding of actual rates of carbon turnover calculated using tracer methods (Trumbore and Gaudinski, 2003). Using carbon isotopes, Gaudinski et al. (2001) estimated mean ages of fine root carbon between 3 and 18 years and Matamala et al. (2003) between 1.2 and 9 years. However, these results are sensitive to the distribution of the lifespans of the fine roots, and changing the model for this distribution has significant implications for estimates of fine root turnover (Gaudinski et al., 2001; Lou, 2003; Tierney and Fahey, 2002). The ^{14}C method requires a model to interpret root turnover from ^{14}C data and the time-dependent steady-state model, which assumes that age of the fine-root population is normally distributed, and therefore the probability of death does not vary with root age (Gaudinski et al., 2001). Refined methods that describe the distribution of root lifespan may be required in certain applications where a tail of very long-lived roots can have large impacts on the estimation of root turnover rates, e.g., estimates obtained using ^{14}C techniques (see Tierney and Fahey, 2002).

What is a fine root?

Fine root systems of perennial plants are complex networks, with millions of lateral branches associated with mychorrizal hyphae. Because of the complexity of the root system it is important to define fine roots not only by diameter size but also by their function and behavior.

Previously, many root ecologists have used the assumptions that all roots have the same function and behavior, regardless of their diameter or position in the branching root system. In many cases this approach may be overly simplistic. Eissenstat et al. (2000) found that root longevity was enhanced by mycorrhizal colonization and negatively correlated with nitrogen concentration, root maintenance respiration and specific root length. Pregitzer et al. (2002) showed that specific root length and nitrogen content depend fundamentally on the position of a root in the branching root system. Distal roots have the highest specific root length and nitrogen contents, and by inference, are the most metabolically active. Most fine roots are much smaller than commonly assumed (Pregitzer et al., 2002) and species differ in the way in which their fine roots are constructed (Baddeley and Watson, 2005). Another commonly used assumption is that all fine roots within an arbitrary size class or among species have similar rates of turnover, which is not the case since root diameter is correlated with root turnover (Baddeley and Watson, 2005; Eissenstat et al., 2000; King et al., 2002; Matamala et al., 2003; Wells and Eissenstat 2001). Thus, roots of the same diameter may differ in branching structure, function, and rates of turnover (Baddeley and Watson, 2005).

Many studies suggest that none of these commonly accepted assumptions about the fine roots of trees are necessarily correct, nor are common sampling protocols necessarily unbiased (King et al., 2002; Pregitzer et al., 2002; Ruess et al., 2003; Tierney and Fahey, 2002; Wells and Eissenstat, 2001).

In conclusion, a fine root is not always a fine root as roots of the same diameter may differ in branching structure, function, and rates of turnover (Baddeley and Watson, 2005).

Fine root turnover

There are many factors that may affect the lifespan of a root. For instance, Eissenstat and Yanai (1997) hypothesized that herbivore pressure, competition for carbon among various plant parts and seasonality may all affect root lifespan. As noted above, fine roots can differ substantially in form and function (Pregitzer et al., 2002) and this can translate into very different patterns of carbon turnover (Matamala et al., 2003). Baddeley and Watson (2005) clearly show that the life expectancy of individual roots in the branching root system varies widely, with smaller roots having significantly shorter lifespans, on average. Current understanding suggests that the average life expectancies of roots of different sizes located on different portions of the same branching root system can be represented by a continuum of probabilities (see for example, Baddeley and Watson, 2005; King et al., 2002; Majdi et al., 2001; Wells and Eissenstat, 2001). The seasonal timing of production may influence root longevity, since roots produced before trees bloom in the spring have shorter lifespans than those produced later, probably because they have lower carbohydrate reserves (Anderson et al., 2003). Furthermore, there is no concrete evidence to support the common assumption that root turnover is the same among species, and growing evidence that root turnover of the same sized roots varies significantly among species (Matamala et al., 2003).

Here we define fine root turnover time (median root longevity) obtained from minirhizotrons, as the time during which 50% of the fine roots die (Andersson and Majdi, 2005; Baddeley and Watson, 2005; Green et al., 2005). Majdi and Andersson (2005) used the minirhizotron technique to estimate fine root turnover (y^{-1}) in two ways: as the ratio of annual root length production to average live root length observed and as the inverse of median root longevity. Thus, the fluxes of carbon and nutrients via fine root mortality can be estimated by multiplying the amount of carbon and nutrients in fine root biomass by the fine root turnover.

From minirhizotron data, root biomass production can be estimated through time in two ways. One is to combine standing fine root (<1 mm) biomass data from soil cores with median fine root longevity data obtained from minirhizotrons (Hendrick and Pregitzer, 1993; Majdi and Andersson, 2005). This approach requires the root pools measured by the two techniques to be adequately matched, i.e., the diameter class(es) of the roots examined (e.g., roots <1 mm in diameter) and the times spans used in the soil core and minirhizotron analyses should be the same. The other approach is based on volumetric calculations (see review by Johnson et al., 2001), whereby minirhizotron data are converted to root lengths per unit soil volume. Fine root biomass ($g\ m^{-2}$) at any time is then estimated by multiplying root length density ($m\ m^{-3}$) by specific root length ($m\ g^{-1}$) values obtained from soil cores. Again, estimates of specific root length must match the specific root length observed in the minirhizotrons.

Modeling fine root turnover

The use of models could improve the interpretation of fine root turnover data and elucidate the mechanisms behind fine root production and mortality. However, there seems to have been little development in this area since several attempts in the early 1970s (Ares and Singh, 1974; Bartos and Jameson, 1974; Hackett and Rose, 1972). Many current modeling efforts are directed, instead, towards root:shoot allocation (e.g., Ågren and Wikström, 1993) or root architecture (e.g., Lynch et al., 1997). However, Marshall and Waring (1985) predicted fine root turnover by monitoring root starch and soil temperature.

A possible reason for the apparent neglect of turnover models are that fine root turnover has

been viewed as an intractable area with noisy data. As data quality improves, modeling development begins to seem meaningful. However, this raises questions about which aspects of the fine root system should be included in models. The variability in turnover time between different roots (see above) is a major issue and it is not clear at this time how pools of carbon should be defined. Other questions that should be addressed include the following. Is a mathematically sophisticated analysis with a continuous distribution of turnover times more meaningful than a simplistic approach with two different turnover times (see for example, Trumbore and Gaudinski, 2003)? In addition to root length (which is observable in minirhizotrons), how should other aspects of carbon and nutrient fluxes from the root system such as mycorrhiza and exudation be included? Can we even start modeling fine root turnover before we better understand factors that influence fine root mortality? Is mortality an endogenous or exogenous process (caused, for instance, by resource exhaustion in the vicinity of the root)?

The answer to most of these questions depends, of course, on the purpose of the model and its scale of application. For example, if the finest roots have a very short lifespan and are decomposed (almost) entirely within the time step of the model, then from a modeling perspective fine root turnover might as well be included with plant respiration. With a coarse temporal and spatial scale it might also be possible to look for shortcuts. Sapwood area and leaf area are strongly correlated in trees (e.g., Waring, 1983) and sizes of plant organs and growth of plant organs have strong allometric relationships over several orders of magnitude in size (Niklas and Enquist, 2002), although these relationships have not been tested in fine roots. It might be possible to deal with fine roots allometrically, but such an approach would require a more fundamental understanding of how long fine roots live and the factors that control their production and mortality.

Concluding remarks and remaining questions

It is suggested that the minirhizotron method is suitable for estimating median fine root longevity. Thus, we propose that if the annual average fine root biomass is near steady state, fine root production (g m^{-2} y^{-1}) can be estimated by multiplying standing fine root biomass (m^{-2}) data from soil cores (g) with median fine root turnover (y^{-1}) data obtained from minirhizotrons. This approach requires the root pools measured by the two techniques to be adequately matched, i.e., the diameter class(es) of the roots examined (e.g., roots <1 mm in diameter) and the time spans used in the soil core and minirhizotron analyses should be the same. The other method is based on volumetric calculations where minirhizotron data are converted to root lengths per unit soil volume. Fine root biomass (g m^{-2}) at any time is then estimated by multiplying root length density (m m^{-3}) by the specific root length (m g^{-1}) obtained from soil cores. It seems intuitively likely that the turnover times of roots in the same branching root system may vary substantially, and this has been demonstrated by both Baddeley and Watson (2005) and Tierney and Fahey (2002). Minirhizotrons are ideally suited for analyzing the turnover of small diameter roots with rapid dynamics, although roots with a slow turnover can sometimes be analyzed using minirhizotrons if the period of observation is long enough (Burton et al., 2004). Generally, however, radio carbon tracer methods are more suitable for larger fine roots with slower turnovers. We need to reconcile results from minirhizotron and ^{14}C methods and this should improve our fundamental understanding of how root systems function.

It was also suggested that we need to improve our understanding of the relationships between above- and below-ground biological processes, e.g., roots likely have 'flushes' of growth when the aboveground canopy has especially strong needs for additional water or nutrients, such as during the initiation of canopy expansion and the accompanying increase in transpiration in the spring. Other questions that need to be resolved include the following. What other biological or environmental 'triggers' control root turnover? How root production is affected by aboveground plant C and nutrient status? How do differences in the seasonal timing of root growth affect the longevity of fine roots? (cf. Anderson et al., 2003).

Plant root systems can respond to external signals from the soil to produce a localized flush

of fine roots (Hodge, 2004). Green et al. (2005) demonstrated, once again, how limiting soil resources (nutrients vs. water) can elicit different rates of fine root turnover. Obviously, plants can sense external signals from the soil and this can result in an increase in fine root production and mortality (Forde, 2002).

One fundamental question remains: what mechanisms control fine root turnover? The answer to this question is still elusive, but it seems likely that new methods such as functional genomics (e.g., Himanen et al., 2004) will be married to traditional field experiments in ways that will unravel the genes and signal transduction pathways involved in the initiation of lateral fine root production in response to different soil resources. One thing is obvious; we still have much to learn about fine root turnover.

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