

Variability in root production, phenology, and turnover rate among 12 temperate tree species

M. LUKE McCORMACK,^{1,2} THOMAS S. ADAMS,^{1,3} ERICA A. H. SMITHWICK,^{1,4} AND DAVID M. EISSENSTAT^{1,3,5}

¹Intercollege Graduate Degree Program in Ecology, Pennsylvania State University, University Park, Pennsylvania 16801 USA

²Key Laboratory of Ecosystem Network Observation and Modeling, Synthesis Research Center of Chinese Ecosystem Research Network, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, 22A Datun Road, Chaoyang District, Beijing 100101 China

³Department of Ecosystem Science and Management, Pennsylvania State University, University Park, Pennsylvania 16801 USA

⁴Department of Geography, Pennsylvania State University, University Park, Pennsylvania 16801 USA

Abstract. The timing of fine root production and turnover strongly influences both the seasonal potential for soil resource acquisition among competing root systems and the plant fluxes of root carbon into soil pools. However, basic patterns and variability in the rates and timing of fine root production and turnover are generally unknown among perennial plants species. We address this shortfall using a heuristic model relating root phenology to turnover together with three years of minirhizotron observations of root dynamics in 12 temperate tree species grown in a common garden. We specifically investigated how the amount and the timing of root production differ among species and how they impact estimates of fine root turnover. Across the 12 species, there was wide variation in the timing of root production with some species producing a single root flush in early summer and others producing roots either more uniformly over the growing season or in multiple pulses. Additionally, the pattern and timing of root production appeared to be consistent across years for some species but varied in others. Root turnover rate was related to total root production ($P < 0.001$) as species with greater root production typically had faster root turnover rates. We also found that, within species, annual root production varied up to a threefold increase between years, which led to large interannual differences in turnover rate. Results from the heuristic model indicated that shifting the pattern or timing of root production can impact estimates of root turnover rates for root populations with life spans less than one year while estimates of root turnover rate for longer lived roots were unaffected by changes in root phenology. Overall, we suggest that more detailed observations of root phenology and production will improve fidelity of root turnover estimates. Future efforts should link patterns of root phenology and production with whole-plant life history traits and variation in annual and seasonal climate.

Key words: carbon allocation; common garden; ecosystem modeling; fine root turnover; heuristic model; minirhizotron; nutrient uptake; phenology; plant competition; root biomass; root life span; standing crop.

INTRODUCTION

Identifying broad patterns of fine root phenology, production, and turnover is critical for understanding how plants respond to their local environment and how they compete with one another. Each year, new fine roots are produced and existing fine roots are shed with the timing and relative balance between the two processes determining the total amount of roots available for resource acquisition. Aboveground, leaf phenology is characterized by seasonal patterns of growth and senescence and recent studies have highlighted critical feedbacks between variation in leaf phenology and ecosystem productivity (Morin et al. 2009, Richardson et al. 2012). Similarly, root phenology

may be characterized by pronounced pulses of root production during favorable periods of plant growth. For many species, this corresponds to a primary flush of root production between late spring and summer (Burke and Raynal 1994, Tierney et al. 2003, Steinaker et al. 2010). However, this simple pattern may not be typical for the production of fine roots in all species and can be further complicated as patterns change between years and with varying climatic conditions.

Conceptually, root phenology can be characterized by several alternate patterns of root production (Fig. 1). Concentrated patterns in root production may occur where resources are available during a single seasonal pulse, whereas bimodal patterns could occur in response to multiple periods of favorable environmental conditions. Equally distributed production may occur in aseasonal areas like wet tropical sites (Barbhuiya et al. 2012) where resource availability can be relatively constant annually. Within these broad patterns it is also possible that subtle differences in timing of root

Manuscript received 5 December 2013; accepted 18 December 2013; final version received 17 January 2014.
Corresponding Editor: R. W. Ruess.

⁵ Corresponding author. E-mail: dme9@psu.edu

production occurring over just a few weeks could have large impacts on the ability of a root system to capitalize on variable, ephemeral supplies of nutrient and water resources. Overall, there has been little direct observation of root phenology in woody plants and basic understanding of how fine root phenology varies among species and across years is lacking.

In addition to the timing of fine root production, the total annual amount of fine root production and fine root turnover play important roles defining how plants interact with their environment. Root production and turnover together determine the total size of a root population, yet there is little appreciation for how production and turnover vary from year to year. This limits understanding of the patterns and rates of carbon (C) and nutrient cycling between plants and soils and hinders efforts to model terrestrial biogeochemistry (Jackson et al. 2000, Ostle et al. 2009). Despite this limitation, fine root production and turnover are estimated to account for between 10 and 60% of net primary productivity (NPP) in most terrestrial ecosystems and result in a large flux of C and nutrients into soil on relatively short time scales of months to years (Grier et al. 1981, Aerts et al. 1992, Jackson et al. 1997, Silver and Miya 2001, Ruess et al. 2003).

Fine root turnover rate may be defined simply as the number of times a root population is replaced over a given time (e.g., annually), but the measurement and calculation of fine root turnover is varied and complex. Calculations are often based on dividing annual root production or mortality by the average, maximum, or minimum root standing crop (Dahlgren and Kucera 1965, Hendrick and Pregitzer 1993, Pritchard et al. 2008). With the more recent approach of tracking the fate of individual roots with minirhizotron cameras, fine root turnover has also been calculated as the inverse of fine root life span (Majdi et al. 2005). Additionally, estimates based on C isotopes yield a measure of mean residence time that can be used to estimate turnover times for root C (Gaudinski et al. 2001, Matamala et al. 2003). Differences among these methods are not trivial and can result in calculated turnover rates that differ by an order of magnitude (Guo et al. 2008).

Limited understanding of root production and turnover rates have resulted in highly simplified descriptions of belowground processes in models and contributes to significant model uncertainty (Chapin et al. 2009, Ostle et al. 2009, Iversen 2010). Recent studies specifically cite uncertainty in estimates of root turnover rates and root processes as important factors driving whole-model uncertainty (Tatarinov and Cienciala 2006, Ciais et al. 2008, Medvigy et al. 2009). Despite this uncertainty, models require estimates of root turnover or root life span to parameterize the rate at which C leaves the root biomass pool. Additionally, for models that couple nutrient and/or water uptake to standing root biomass, root turnover rates, as well as root phenology, will also impact potential uptake of these

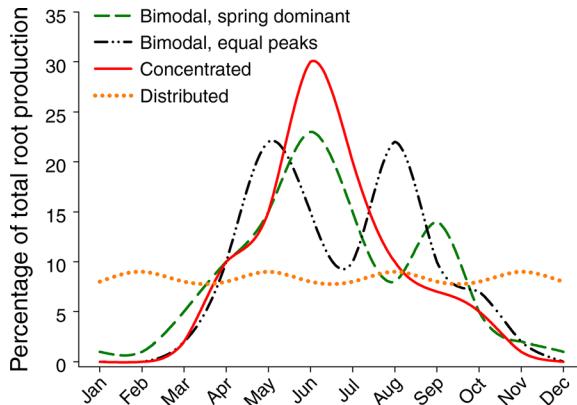


FIG. 1. A range of possible patterns of root phenology in temperate regions of the northern hemisphere.

resources as standing root biomass is mediated by root production and turnover.

Together, variations in fine root phenology and fine root turnover will impact competitive interactions among species as well as carbon, nutrient, and water cycles at the ecosystem level. Importantly, these two processes are also likely to be linked both empirically and analytically. For example, a species with high root turnover may experience high root mortality in late fall and have relatively few roots surviving through the winter. The resulting low root standing biomass potentially puts that species at a competitive disadvantage as it has fewer roots with which it can acquire nutrients and water in spring. However, this may be compensated for by producing new roots in early spring. Production of new roots to obtain limiting soil resources before nearby competitor species may then be an advantage (Harris 1977, Eissenstat and Caldwell 1988), particularly if it avoids extra expenditures of building and maintaining more costly, longer-lived roots to survive through the dormant season. The disadvantage of maintaining older roots may be further compounded as uptake rates tend to decline with root age and the capacity for resource acquisition by these older roots has likely diminished by spring (Bouma et al. 2001). Analytically, calculations of root turnover often depend on estimates of root production and standing root biomass, both of which are sensitive to the timing of root production and the timing and frequency of field measurements used to determine root biomass. Despite the potential interplay between fine root phenology and fine root turnover rates there has been little effort to characterize the relationships between the two.

In this study, we use three years of minirhizotron observations of fine root dynamics across 12 temperate tree species grown in a common garden setting together with a heuristic model that relates root phenology to root turnover to address four objectives. Our primary objectives were to determine if broad patterns of fine root production phenology varied among temperate tree

TABLE 1. Different methods for calculating fine root turnover.

Method	Calculation
T_{Max}	(annual fine root production)/ (maximum fine root standing crop)
T_{Avg}	(annual fine root production)/ (average fine root standing crop)
T_{Min}	(annual fine root production)/ (minimum fine root standing crop)
T_{Inv}	inverse of fine root life span

Note: In steady state systems where production and mortality are roughly equal between years, annual root production can be replaced with annual root mortality to yield similar estimates of root turnover.

species or groups of temperate tree species (i.e., deciduous vs. evergreen, fast vs. slow growing, arbuscular vs. ectomycorrhizal association); determine if interspecies and interannual variation in the total amount of annual fine root production leads to predictable changes in fine root turnover rate; and determine whether estimates of fine root turnover rate are sensitive to variable patterns of fine root phenology. Additionally, we investigate how estimates of root turnover rates vary with different methods of calculating root turnover rate and their sensitivity to changes in root phenology. Estimates of fine root turnover rate were calculated using four common methods relating turnover to total root production and root standing crop or directly to root life span (Table 1) allowing for comparisons of sensitivities of each method to changes in annual fine root production and root phenology.

MATERIALS AND METHODS

To address our primary objectives we used common garden observations that allowed us to measure natural patterns and variability in fine root dynamics across 12 temperate tree species. We then used the heuristic model as a way to control the phenology of root production independently of total root production and root life span and to explore the relative influence of each factor on annual fine root turnover rate. Turnover estimates are reported as rates per year (yr^{-1}). To estimate absolute turnover ($[\text{g root}][\text{m}^{-2} \text{ ground area}]\text{yr}^{-1}$), rates reported in this study could be combined with measures of standing fine root biomass determined using soil cores (Hendrick and Pregitzer 1996).

Common garden observations

Minirhizotron cameras were used to observe fine root dynamics separately for 12 temperate tree species growing in a common garden in central Pennsylvania, USA (40°42' N; 77°57' W). The species used in this study represent important and common species found in temperate forests across much of the eastern United States: *Acer negundo*, *A. rubrum*, *A. saccharum*, *Carya glabra*, *Juglans nigra*, *Liriodendron tulipifera*, *Pinus strobus*, *Pinus virginiana*, *Populus tremuloides*, *Quercus alba*, *Q. rubra*, and *Sassafras albidum*. The site and

methods for observing fine root life span have been previously described (McCormack et al. 2012). Briefly, for each species, 16 minirhizotron tubes were installed to a vertical depth of 20 cm. Images were collected on both the upper and lower surfaces using a Bartz 1.125-inch (28.575-mm) digital camera with I-CAP v. 4.01 software (Bartz Technology, Carpinteria, California, USA). Minirhizotron tubes were installed in June 2005, and image collection for production and standing crop did not begin until spring 2008. Minirhizotron observations of fine roots were limited to first- and second-order roots. Fine root turnover rate was calculated as described in Table 1 using numbers of roots produced. In general, root number and root length are well correlated (Crocker et al. 2003). Root number rather than root length was used here as the total length of a given root may not be visible along the tube surface and because estimates of median root life span were also based on individual roots. Preliminary analyses of fine root production and turnover rates were also calculated using root length and results were similar to those reported here.

Average annual precipitation measured at the site was 894 mm (years 2005–2011) and during the study annual precipitation was 922, 780, and 974 mm in years 2008, 2009, and 2010, respectively (USDA Natural Resources Conservation Service, Site 2036 “Rock Springs”). Rainfall was distributed roughly evenly across each year (Appendix: Fig. A1). Mean July temperature ranged from 18.7° to 22.4°C and mean January temperature ranged from –3.6° to –0.8°C. Total root production, mortality, and standing crop were observed using minirhizotrons approximately every four weeks during the growing season (April–November). Roots were counted as newly produced when they first appeared along the observation tube and mortality was determined when the roots fractured, shriveled to approximately one-half their original diameter, or disappeared. Roots whose birth date and/or death date could not be assessed confidently due to tubes shifting in the soil were not used in the analysis. Lost observations due to tube movement occurred roughly equally across species and years and primarily occurred during the transition from winter to spring due to slight frost heaving. These accounted for <25% of the total roots observed.

Temporal patterns of fine root production were determined for each species and each calendar year (January–December) separately. Root production is expressed as the percentage of total annual root production produced per day. Daily production was calculated as the percentage of new roots that were observed during an image session divided by the number of days between that session and the previous session. Estimates of daily production were used rather than point measurements from each image session as the length of time between sessions varied. In the first year of observation (2008), roots observed during the first

image session were not counted as new production but were included to establish the initial standing crop. For the first image session in years 2009 and 2010 (23 April and 2 April, respectively) the daily production was calculated as $([\text{the number of new roots observed during the first session}]/[\text{the day of year for that session}]) - 75$, which corresponds to the middle of March. Root production was assumed to be zero for the months of December–March. This simplifying assumption was made as it was not possible to collect images over winter months during the study. However, images collected during the winter prior to the start of the current study confirmed that little to no production occurred during these months at our site. In total, two new roots were observed in a December 2007 image session and no new roots were observed in a February 2008 image session. The two roots observed in December represented less than 1% of root production observed in 2007. For each year, smooth spline curves were fit to the point estimates of daily root production from each minirhizotron image session using SAS JMP 9.0.2 (SAS Institute, Cary, North Carolina, USA). R^2 values for each fit ranged from 0.54 to 0.96 and averaged 0.81. The relatively conservative $\lambda = 10\,000$ (a measure of how precisely the curve followed the data) was used for the spline curves as smaller values for λ appeared to over-fit the data.

Heuristic model

The heuristic model was used to investigate analytically, in a controlled manner, how a suite of predetermined root phenology patterns and life span estimates influences estimates of root turnover. The model consisted of 20 life-span–production scenarios using five different root life spans and four patterns of root production phenology (Fig. 1 and Table A1). Three values of root life span (91, 182, and 365 days), were chosen to reflect the range of root life spans typically measured across different species using minirhizotrons (~90–600 days; Arnone et al. 2000, Pritchard et al. 2008, McCormack et al. 2012). These roots generally represent fine roots that are more active in nutrient and water uptake. In addition, two values (1215 and 3650 days) were chosen to represent life spans typically measured using isotopic techniques (Matamala et al. 2003, Gaudinski et al. 2010) and that might be assumed given the slowest turnover rates used in some models (i.e., 0.1–0.3 yr⁻¹). These longer life span estimates more likely capture higher order fine roots responsible for conducting resources toward coarse roots and to aboveground pools. Alternate life span scenarios allowed for the exploration of whether root phenology impacts turnover rates equally across shorter-lived and longer-lived roots.

The patterns of root production were chosen to reflect the range of patterns observed both in our data and in other studies of perennial species (Steinaker et al. 2010, Barbhuiya et al. 2012). For each life-span–production

scenario, 100 units of roots produced annually were allocated to monthly production according to one of the four patterns of root production (concentrated, distributed, bimodal with dominant spring production, and bimodal with equal production in spring and fall; Fig. 1). Roots produced in a given month counted toward the standing crop for that month and persisted into the following months depending on prescribed fine root life span (Table A1). For example, roots under the life span scenario of 91 days and produced in June would be counted towards the standing crop for June and persist through July and August but would be considered dead by September.

Analyses

Common garden observations were analyzed using a general linear model to determine the effect of species, total annual root production, duration of root production, year, and the interaction between species and total root production on estimates of root turnover rate (T_{Max} , T_{Avg} , and T_{Min} ; see Table 1). However, because root production is used in the calculation of root turnover, relationships between annual root production and annual root turnover should be treated with caution. This approach does provide information determining whether species with high production are likely to also have high rates of root mortality and replacement (turnover) or to maintain greater amounts of root biomass. Tukey's honest significant difference test was used to determine differences in turnover rates among species. Linear regression was used to test the relationship between estimates of annual fine root turnover rate and annual root production as well as the relationship of median root life span with T_{Max} , T_{Avg} , and T_{Min} . Patterns of production phenology were also assessed visually using the fitted curves of root production per day for each species and year. Analyses were done using SAS JMP 9.0.2.

The duration of root production in the common garden, which is a measure of the root production phenology, was calculated for each year and each species. Duration equaled the sum of days between the first and last observation date where the total root production exceeded the average root production across all image sessions during the year. This was intended to capture the breadth of the active root growing season where concentrated patterns of production will have shorter duration than bimodal patterns and evenly distributed patterns will have the longest duration.

Fine root turnover was calculated four ways for both the common garden observations and the heuristic model (Table 1). These four methods were chosen as they represent the most common approaches for calculating fine root turnover rate in terrestrial ecosystems. Estimates for T_{Max} , T_{Avg} , and T_{Min} were calculated annually in the common garden and for each life span–production scenario in the heuristic model. Estimates for T_{Inv} were calculated as the inverse of

median fine root life span. Median fine root life span was determined separately for each species using Kaplan-Meier survival estimates (Kaplan and Meier 1958) based on observations from 2007 to 2010 (reported in McCormack et al. 2012). As described above, life span was explicitly prescribed in the heuristic model (e.g., 91, 182, 365, 1215, and 3650 days) and does not vary with different production scenarios. Therefore, calculations of turnover from T_{Inv} are not related to phenology in either the common garden or the heuristic model.

RESULTS

Variation across species

Root production phenology varied among the 12 species and across the three years of observation in the common garden. Many species tended to follow a general concentrated pattern of root production with the peak production typically occurring between late May and early July (e.g., *P. tremuloides* and *Q. rubra*, Fig. 2). However, patterns of more evenly distributed root production as well as examples of bimodal production were also observed (e.g., *A. saccharum*, *C. glabra*, and *J. nigra*). There was also noticeable variation across years for some species. For example, *A. negundo* shifted the timing of peak root production by nearly 100 days between 2008 and 2010. By comparison, other species had nearly identical timing of peak root production across the three years (e.g., *L. tulipifera*). The greatest variability in patterns of root production within species appeared in *J. nigra* and *P. strobus*. However, both species produced relatively few roots compared to the other species in the study (Table 2), which may have led to poor characterization of their root phenology.

Large variation in fine root turnover rates among species was also observed at the common garden. *P. tremuloides* had the fastest turnover rates and *L. tulipifera*, *P. virginiana*, and *Q. alba* had the slowest turnover rates (Table 2, Appendix: Fig. A2). For many species, interannual variability in fine root turnover rate was as great as or greater than differences among species. For example, the coefficient of variation (CV) within species and across years for *A. negundo*, *J. nigra*, and *Q. alba* ranged from 24% to 82%. Other species like *P. strobus* and *P. tremuloides* had relatively consistent rates of fine root turnover and low CV across years (Table A2). Interannual variation in total root production was also high with CV above 50% for six of the 12 species.

Total production and phenology impact turnover rates

Observations from the common garden and the heuristic model indicated that both the amount and phenology of fine root production affected estimates of fine root turnover rate. Across species in the common garden, there was a two- to six-fold increase in variation in turnover rates depending on method of calculation. Greater total root production was associated with faster

root turnover rates ($P < 0.001$; Table 3) indicating that species with high root production were likely to have high rates of replacement (turnover) and do not simply maintain higher standing root biomass (Fig. 3, Table 2).

Production phenology strongly influenced turnover rates in the heuristic approach but effects were more difficult to discern in the common garden. In the heuristic model, turnover rates calculated with maximum (T_{Max}) and minimum (T_{Min}) standing crop were highly sensitive to production phenology (Table 4). Variation in turnover estimates with different production phenology was greatest for short-lived roots (91 days) with a nearly threefold increase in T_{Max} and even larger differences in T_{Min} as phenology was shifted from concentrated to distributed root production. When root life span was equal to 182 days, similar changes were observed with a 60% difference in estimates of T_{Max} between the concentrated and distributed production phenology. For roots with life spans ≥ 1 year, there were minimal effects of production phenology on estimates of root turnover rates. Here, differences ranged from 0 to 10% as the longer life spans led to more stable root standing crop across the year.

Phenology and duration of fine root production varied across the 12 species in the common garden (Fig. 2). Yet, the duration of root production did not appear to affect estimates of root turnover rate at the site-level ($P > 0.05$; Table 3), likely because, as indicated by the heuristic model, variation in duration should only impact estimates of turnover rate for species with relatively short root life spans ($\ll 1$ year). Therefore, only species like *P. tremuloides* and *A. negundo* with relatively short median root life spans would likely be sensitive to changes in root phenology. For *A. negundo*, the 50% increased root turnover rate observed in 2009 was coupled with increased duration of root production, which is consistent with the heuristic model (Fig. 2, Table 3). However, the increased duration coincided with an increase in total root production making it unclear if the change in turnover rate was driven primarily by the pattern of root production or by the amount of root production. In the case of *P. tremuloides*, the patterns and duration of root production observed were similar across the three years of observation in the common garden. Accordingly, there was little variation in estimates of turnover rate (Table 2).

Comparison of methods estimating root turnover rate

Of the four methods used to calculate fine root turnover, T_{Max} consistently yielded the slowest turnover rates while T_{Min} yielded the fastest. Three-year species-averages for turnover rates from the common garden ranged from 0.7 yr^{-1} to 1.3 yr^{-1} , 0.9 yr^{-1} to 2.1 yr^{-1} , and 1.3 yr^{-1} to 7.6 yr^{-1} for T_{Max} , T_{Avg} , and T_{Min} respectively. Estimates from T_{Inv} ranged from 1.1 yr^{-1} to 3.8 yr^{-1} . Turnover estimates based on maximum (T_{Max}) and minimum (T_{Min}) standing crop were the

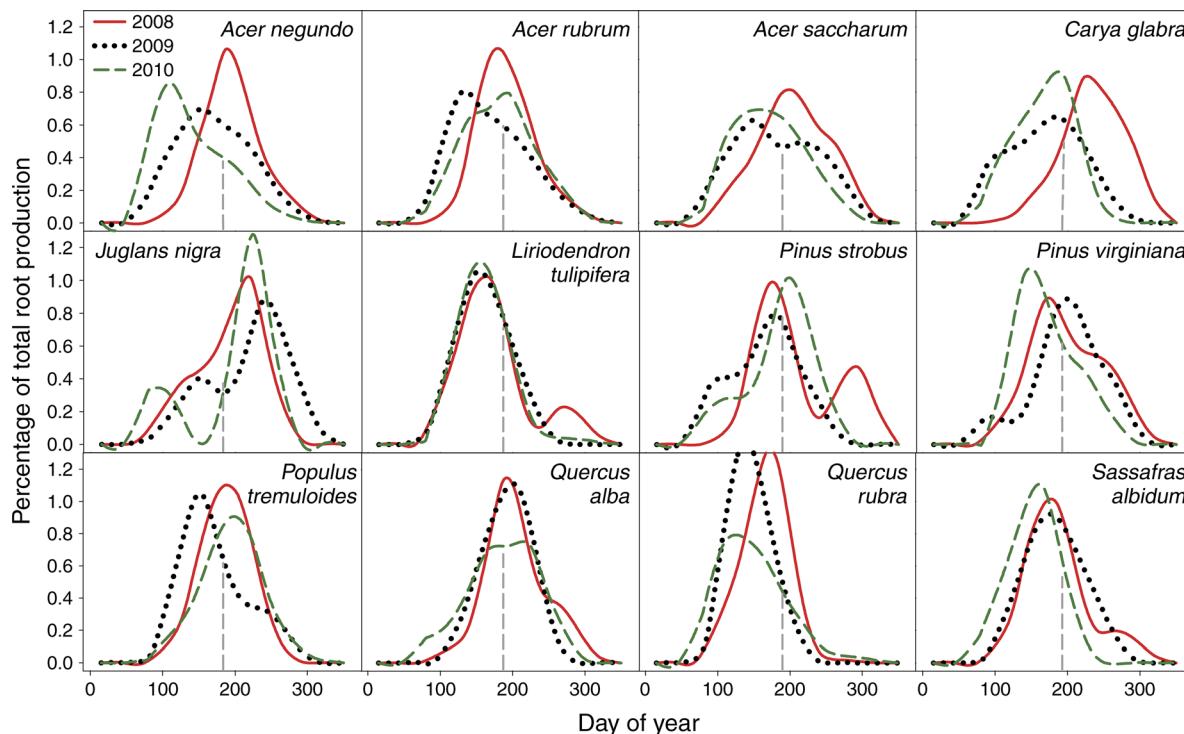


FIG. 2. Patterns of root production phenology observed during years 2008–2010 for 12 temperate tree species in central Pennsylvania, USA. Absolute differences in total annual production are given in Table 2. Vertical gray bars are included for reference on 1 July.

most sensitive to changing phenology. For example, T_{Max} experienced a threefold increase in turnover rate from the concentrated to the distributed pattern for the shortest-lived roots while estimates of T_{Min} decreased from 100 yr^{-1} to 4.0 yr^{-1} . When root life spans were ≥ 1 yr, neither T_{Max} nor T_{Min} were sensitive to production pattern. The heuristic model found no effect of phenology on T_{Avg} , though, when the calculation for average standing crop was limited to months during the active growing season, values for T_{Avg} followed a similar pattern of sensitivity to phenology as T_{Max} (data not shown). Restricting the calculation to the growing season mimics observation frequencies found in many minirhizotron studies, including our common garden study, where observations often do not occur over winter due to difficult weather conditions. Estimates of T_{Inv} did not vary because root life span was held constant in the heuristic model and was determined using multiple years of observations from the common garden.

Across the common garden observations and the heuristic model, both T_{Max} and T_{Avg} yielded reasonable and relatively consistent estimates of root turnover rate (Appendix: Fig. A2, Table 2). In contrast, estimates from T_{Min} were more variable and were frequently above 5.0 yr^{-1} . Estimates of root turnover rate as the inverse of life span should also be treated with caution. In this case, species with root life spans < 1 yr,

calculations of T_{Inv} implicitly assume that roots are produced throughout the year (i.e., no dormant season) unless the reported rate is explicitly confined to a measured growing season (e.g., Sun et al. 2012). However, fine root life span, from which T_{Inv} is derived, does correlate well with the multi-year averages of T_{Max} and T_{Avg} ($P < 0.001$, $R^2 = 0.76$ and 0.71 respectively; Fig. A3) making it a useful predictor of more traditional estimates of root turnover rate.

DISCUSSION

Fine root production and turnover control a large flux of C from plants and into soil and their dynamic patterns represent important ways in which plants respond to climatic variation and structure belowground interactions among species. From both empirical and modeling perspectives it is of considerable value that the patterns and rates of fine root phenology and turnover are quantified consistently and accurately. At the ecosystem level, differences in terminology and methodology have made comparisons of productivity across sites difficult (Chapin et al. 2006, Lovett et al. 2006). Similarly, current understanding of root dynamics is hindered by differences in study approach and methodology as well as limited understanding of variability inherent to natural systems. Previous studies have discussed extensively variation in estimated turnover rates based on methods of observation (Tierney and

TABLE 2. Root dynamics observed in 12 temperate tree species grown in a common garden in central Pennsylvania, USA.

Parameter	<i>A.</i> <i>negundo</i>	<i>A.</i> <i>rubrum</i>	<i>A.</i> <i>saccharum</i>	<i>C.</i> <i>glabra</i>	<i>J.</i> <i>nigra</i>	<i>L.</i> <i>tulipifera</i>	<i>P.</i> <i>strobus</i>	<i>P.</i> <i>virginiana</i>	<i>P.</i> <i>tremuloides</i>	<i>Q.</i> <i>alba</i>	<i>Q.</i> <i>rubra</i>	<i>S.</i> <i>albidum</i>
2008												
Total production (no. roots)	47	224	57	103	14	29	9	89	162	102	48	26
Max stand crop (no. roots)	56	215	63	90	17	53	10	97	118	117	42	26
Avg stand crop (no. roots)	46	152	48	43	14	44	8	75	74	91	25	21
Min stand crop (no. roots)	34	40	29	14	10	34	5	40	16	58	4	7
Total duration (d)	107	74	104	96	56	153	150	94	74	104	38	85
T_{Max} (yr ⁻¹)	0.84	1.04	0.90	1.14	0.82	0.55	0.90	0.92	1.37	0.87	1.14	1.00
T_{Avg} (yr ⁻¹)	1.02	1.47	1.19	2.39	1.03	0.66	1.14	1.19	2.20	1.13	1.94	1.26
T_{Min} (yr ⁻¹)	1.38	5.60	1.97	7.36	1.40	0.85	1.80	2.23	10.1	1.76	12.0	3.71
2009												
Total production (no. roots)	120	118	64	88	25	50	17	56	142	49	16	80
Max stand crop (no. roots)	100	142	71	90	20	54	21	68	95	112	20	72
Avg stand crop (no. roots)	73	129	60	77	12	42	16	55	61	93	17	47
Min stand crop (no. roots)	31	90	49	53	4	23	10	41	16	74	9	7
Total duration (d)	176	109	176	148	136	109	151	108	53	84	53	112
T_{Max} (yr ⁻¹)	1.20	0.83	0.90	0.98	1.25	0.93	0.81	0.82	1.49	0.44	0.80	1.11
T_{Avg} (yr ⁻¹)	1.65	0.92	1.06	1.14	2.13	1.18	1.05	1.01	2.32	0.53	0.93	1.69
T_{Min} (yr ⁻¹)	3.87	1.31	1.31	1.66	6.25	2.17	1.70	1.37	8.88	0.66	1.78	11.4
2010												
Total production (no. roots)	60	77	48	74	8	34	16	21	55	73	24	49
Max stand crop (no. roots)	76	101	72	84	10	45	18	39	49	78	23	66
Avg stand crop (no. roots)	62	84	65	57	7	36	14	32	29	69	18	51
Min stand crop (no. roots)	33	58	57	26	4	26	10	24	15	52	9	33
Total duration (d)	134	83	116	116	164	83	58	113	86	86	106	88
T_{Max} (yr ⁻¹)	0.79	0.76	0.67	0.88	0.80	0.76	0.89	0.54	1.12	0.94	1.04	0.74
T_{Avg} (yr ⁻¹)	0.97	0.92	0.74	1.29	1.14	0.96	1.15	0.65	1.89	1.07	1.36	0.97
T_{Min} (yr ⁻¹)	1.82	1.33	0.84	2.85	2.00	1.31	1.60	0.88	3.67	1.40	2.67	1.48
3 Year Average												
T_{Max} (yr ⁻¹)	0.94	0.88	0.82	1.00	0.96	0.75	0.87	0.76	1.33	0.75	0.99	0.95
T_{Avg} (yr ⁻¹)	1.21	1.10	1.00	1.61	1.43	0.93	1.11	0.95	2.14	0.91	1.41	1.31
T_{Min} (yr ⁻¹)	2.36	2.75	1.27	3.96	3.22	1.44	1.70	1.49	7.56	1.27	5.48	5.54
T_{Inv} (yr ⁻¹)	1.92	1.41	1.13	1.48	1.76	1.13	1.23	1.29	3.84	1.09	1.55	1.15

Notes: Observations were made across three years (2008, 2009, and 2010) and included total root production, maximum (max), average (avg), and minimum (min) root standing (stand) crop, total duration of root production, and root turnover calculated as shown in Table 1. Genera are *Acer*, *Carya*, *Juglans*, *Liriodendron*, *Pinus*, *Populus*, *Quercus*, and *Sassafras*.

Fahey 2002, Guo et al. 2008, Strand et al. 2008, Milchunas 2009) and differences in pools of roots being observed or measured (Guo et al. 2008, Gaudinski et al. 2010). However, there has been little discussion that addresses directly how estimates of root turnover rates vary within and across species based on differences in total annual root production or in the pattern and timing of root production. We address this gap using a

TABLE 3. Summary of analysis of variance for effects of species, total annual root production, duration of root production, and year on T_{Max} , T_{Avg} , and T_{Min} as well as the interaction of species and total root production.

Source	df	T_{Max}		T_{Avg}		T_{Min}	
		χ^2	$P > \chi^2$	χ^2	$P > \chi^2$	χ^2	$P > \chi^2$
Species	11	47.0	<0.001	57.3	<0.001	61.8	<0.001
Total production	1	17.8	<0.001	27.3	<0.001	18.3	<0.001
Duration	1	0.1	0.79	0.05	0.83	0.1	0.82
Year	2	1.1	0.58	2.8	0.25	2.7	0.25
Species \times production	11	30.2	0.002	40.5	<0.001	45.4	<0.001

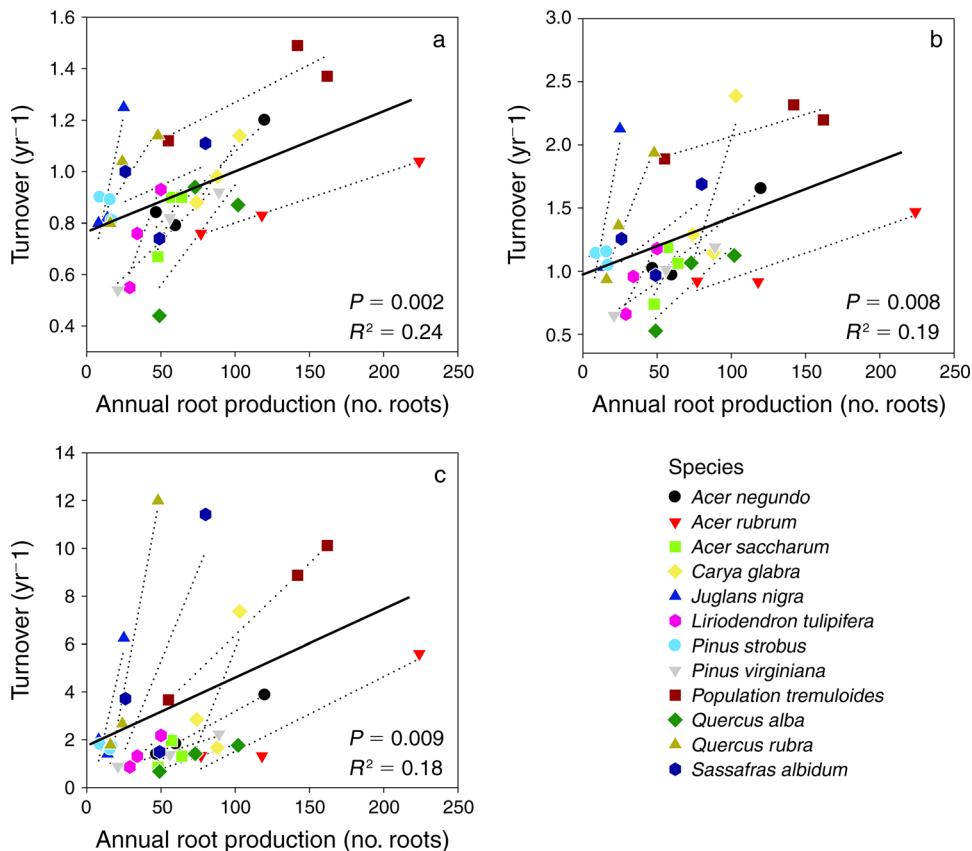


FIG. 3. Patterns of increasing turnover rates with greater total annual root production observed across 12 species grown in a common garden. Each panel represents turnover rate calculated using a different method (see Table 1 for definitions): (a) T_{Max} , (b) T_{Avg} , and (c) T_{Min} . Within each panel, the solid line represents a linear regression through all 12 species and all three years ($n = 36$), while the dotted lines represent regression lines through each species separately. Reported P values and R^2 are shown for regression lines across all species (solid line).

unique data set of three years of fine root observations across 12 species grown in a common garden together with a simple model of root phenology and turnover that was used to explore relationships between root production phenology and root life span in the absence of natural variation.

Observations of root dynamics in the common garden revealed that the timing of root production varied widely across species observed in this study (Fig. 2). The observation of both unimodal and multimodal patterns of root production is consistent with those observed in seedlings of different species by Lyr and Hoffman (1967) and by Steinaker et al. (2010). While it is currently unclear what specific processes cause this variation it is possible that it represents different strategies to utilize temporally variable resource supplies and to respond to seasonal or annual changes in local climate. Early root production may enable greater capture of nutrients mineralized over winter and mobilized with warmer temperatures and soil thawing (Brooks et al. 2011). Similarly, studies have highlighted the potential for greater early season root production to enable more effective capture of soil resources by occupying and

utilizing resource patches of soil before competitor species (Harris 1977, Eissenstat and Caldwell 1988).

While there are apparent benefits to producing roots early in spring, many species at our site consistently produced the majority of their roots later in the season around or after 1 July. Though the factors leading to later root production are unclear, it is possible that species with more conservative whole-plant growth also favor more conservative late-season root growth. This appears to be true for species like *C. glabra* and *Q. alba*, which experienced peak root production later in the season and had slower growth rates over their first 10 years after planting than species like *A. negundo*, *A. rubrum*, *L. tulipifera*, and *Q. rubra*, which tended to grow faster and produce the majority of their roots earlier in the season (Fig. 2; McCormack et al. 2012). However, there are clear examples where this pattern does not apply as *J. nigra* had moderately fast stem growth and produced the majority of its roots in late summer while *S. albidum* was one of the slowest growing species yet consistently produced most of its roots in spring.

TABLE 4. Results from heuristic model showing the effects of fine root phenology and fine root life span on fine root turnover.

Fine root life span (d)	Fine root turnover (yr^{-1})			
	T_{Inv}	T_{Avg}	T_{Max}	T_{Min}
Concentrated				
91	4.0	4.0	1.5	100
182	2.0	2.0	1.1	12.5
365	1.0	1.0	1.0	1.0
1215	0.3	0.3	0.27	0.33
3650	0.1	0.1	0.1	0.1
Distributed				
91	4.0	4.0	4.0	4.0
182	2.0	2.0	2.0	2.0
365	1.0	1.0	1.0	1.0
1215	0.3	0.3	0.3	0.3
3650	0.1	0.1	0.1	0.1
Bimodal, spring				
91	4.0	4.0	1.9	33.3
182	2.0	2.0	1.2	20.0
365	1.0	1.0	1.0	1.0
1215	0.3	0.3	0.28	0.33
3650	0.1	0.1	0.1	0.1
Bimodal, equal				
91	4.0	4.0	2.13	100
182	2.0	2.0	1.12	9.1
365	1.0	1.0	1.0	1.0
1215	0.3	0.3	0.27	0.29
3650	0.1	0.1	0.1	0.1

Notes: For all scenarios, total root production equaled 100 units. A representation for each production pattern (concentrated, distributed, bimodal with dominant spring production, and bimodal with equal production in spring and fall) is shown in Fig. 1.

It is also possible that associations with different mycorrhizal fungi could play a role in defining root phenology (Brundrett and Kendrick 1988) as it is possible that signaling from these fungi stimulates root growth (Oláh et al. 2005). In this study, most tree species that primarily associated with ectomycorrhizal fungi tended to have later peaks in root production (*C. glabra*, *P. strobus*, *P. virginiana*, and *Q. alba*) than tree species associated with arbuscular mycorrhizal fungi. However, this was not true for *Q. rubra*, which associates with ectomycorrhizal fungi and had earlier production, and for *J. nigra*, which associates with arbuscular mycorrhizal fungi but had later production. Given the limited number of species observed and the amount of interspecies and interannual variability, it is unclear if consistent patterns do or even should exist regarding mycorrhizal status and root phenology.

Finally, dates of peak root production may also be related to patterns of leaf emergence in spring. This is likely to be particularly relevant for species characterized by a unimodal pulse of root production. While aboveground phenology was not directly monitored in this study some broad patterns may still be assessed. Based on observations of leaf phenology made in years following this study there were no clear relationships between root and leaf phenology across all 12 species

(data not shown). However, within the *Acer* and *Quercus* genera there was an interesting pattern where peak root production among species was ordered the same as leaf emergence (M. L. McCormack, *personal observation*). For example, spring leaf emergence in the common garden occurs first in *A. negundo*, second in *A. rubrum*, and last in *A. saccharum*, which mirrors the pattern of peak root production among the three species (Fig. 2). The two *Pinus* species appeared to follow this pattern as well, though there was greater overlap between leaf and root production between the two species. Interestingly, evergreen conifers tended to produce a larger proportion of their roots later in spring and summer than did most (but not all) deciduous species, which is not consistent with an already established leaf canopy in early spring. However, evergreen species also produced new leaves several weeks later than deciduous species (M. L. McCormack, *personal observation*). Data reported elsewhere seem to partially support this trend (Lyr and Hoffmann 1967) but are less clear in other studies (Steinaker et al. 2010). It will be important for future studies to separate the role of peak root production from the timing when new root production is first initiated in spring and their relative importance to whole-plant resource acquisition and carbon allocation. This will require observations across multiple years and with greater temporal resolution (and more species) to determine the consistency of the trends suggested here as well as allow for greater appreciation of the observed exceptions.

While plants may express broad patterns of root phenology based on basic different life history strategies, it is likely that abiotic factors including temperature and precipitation also impact seasonal and annual dynamics of root growth and are particularly important for explaining interannual variations within species. During the course of this study, we did not observe strong year-to-year variation in climate making it difficult to determine which factors contributed most to interannual variation and peaks of late-season productivity observed in some species and years. Furthermore, the frequency of minirhizotron observations (approximately monthly) was not sufficient to confidently draw connections to distinct climatic events within seasons. As such, this remains a wide-open area for future research to better understand climatic drivers of fine root phenology and subsequent impacts on belowground resource capture and plant competition.

In addition to, and perhaps as a consequence of, the variation in root production phenology, we observed a wide range of total annual root production and turnover rates across the 12 species and three years (Appendix: Fig. A2, Table 2). At ecosystem-scales, models can readily incorporate differences in fine root turnover rate observed across species. However, the observation that total production and turnover rates often vary from year-to-year within a single species is particularly important as few models allow for interannual variation

in rates of fine root turnover. (For examples of models that allow for interannual variation, see Aber et al. 1997 and Parton et al. 2010.) While there are relatively few datasets that report trends in fine root turnover rates across three or more years, studies emerging from long-term, free-air-CO₂-enrichment studies generally support our findings here (Iversen et al. 2008, Pritchard et al. 2008, Ferguson and Nowak 2011). These results are further corroborated by a multi-year synthesis in a grassland ecosystem by Gill and Jackson (2000) along with other studies that have reported considerable variability in root production and turnover among years (Steele et al. 1997, Fitter et al. 1998). Based on these findings it is likely that turnover estimates based on a single or even a few years of observation may not capture the long-term patterns and average rates of fine root turnover for a given species or ecosystem.

Results from the heuristic model showed that turnover estimates for species with root life spans less than a year may be sensitive to differences in root phenology. Importantly, the model holds total root production and subsequent root mortality equal across the different patterns of root production, which, in a natural ecosystem, would mean that total C flux is the same despite variation in the calculated turnover rate. For example, estimates of T_{Max} increased substantially when production shifted from concentrated to distributed root production even though the absolute amount of annual root production and mortality were the same. For models that use a root turnover parameter to dictate C allocation to roots or root longevity, a nearly threefold increase in root turnover would alter C allocation to roots and could lead to a 10–40% difference in total system C (combined biomass, litter, and soil C; M. L. McCormack, E. Crisfield, B. M. Raczka, F. Schnakenburger, D. M. Eissenstat, and E. A. Smithwick, *unpublished manuscript*). Therefore it will be particularly important to ensure that dissimilar estimates of root turnover rate reported from the same or different sites actually represent a change in the rate of carbon-flow through root turnover and not simply a difference in the perceived rate due to differences in root phenology or the method used to calculate root turnover.

The heuristic model also indicated that, unlike with short-lived roots, there was little to no effect of phenology on estimates of turnover when root life spans were a year or longer. Recent work has highlighted that within a defined population of fine roots (e.g., ≤ 2 mm) there are two root pools that are best characterized with different life spans and turnover rates (Strand et al. 2008, Gaudinski et al. 2010, Xia et al. 2010). Lower-order, absorptive, fine roots have shorter life spans while higher-order, structural, fine roots have longer life spans, or residence times, in the range of several years to a decade. Our results illustrate the potential for the absorptive pool to be more dynamic and susceptible to variation in patterns of root production on seasonal to

annual timescales. Recent modeling efforts including the Radix (Riley et al. 2009, Gaudinski et al. 2010) and ForCent (Parton et al. 2010) models already describe production and turnover of fine roots as two separate pools. Here, an important next step may be to incorporate the timing of root production for the short-lived fine roots, improving estimates of turnover as well as capturing temporal variation in absorptive capacity for water and nutrients by the fine root pool.

CONCLUSIONS

In an effort to improve understanding of fine root dynamics, we investigated how total annual root production and root phenology vary among species and across years and determined how variation in fine root dynamics impacts estimates of fine root turnover. We observed a wide range in fine root phenology across the 12 species indicating that simple characterizations of fine root phenology dominated by a single pulse of root production may not be adequate for all species. Furthermore, for many species the pattern, timing, and total amount of root production varied substantially between years. Identification of these interannual patterns in root production is important and future efforts should focus on connecting these patterns with broader climatic variation. Our results also suggest that variation in both the total amount and the timing of root production impact estimates of fine root turnover rates. Impacts of production phenology were most pronounced for relatively short-lived roots while longer-lived roots were largely unaffected. This difference further emphasizes the need to measure and model fine roots as two separate pools based on root function rather than a single pool based on an arbitrary size classification. The occurrence and explanation of interannual variation in root turnover rates has not been well documented previously and limits the utility of turnover rates in terrestrial ecosystem and larger-scale models. Overall, we expect that future work identifying mechanistic drivers of fine root phenology and production will substantially improve understanding of root turnover rates and root life span as well as our ability to quantify and predict the fluxes of C, nutrients, and water at the whole-plant and ecosystem levels.

ACKNOWLEDGMENTS

We are grateful to the LEAPS Lab at Penn State, L. Archer, K. Davis, and R. Koide for helpful discussions in preparation of the manuscript and to D. Gear for inspiration. We are also grateful to very helpful comments from three anonymous reviewers. This work was supported by the National Science Foundation (Grants IOS0824704 and ARC1107381) to D. M. Eissenstat and the Department of Energy GREF to M. L. McCormack.

LITERATURE CITED

Aber, J., S. V. Ollinger, and C. T. Driscoll. 1997. Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecological Modelling* 101: 61–78.

- Aerts, R., C. Bakker, and H. Decaluwe. 1992. Root turnover as determinant of the cycling of C, N, and P in a dry heathland ecosystem. *Biogeochemistry* 15:175–190.
- Arnone, J. A., J. G. Zaller, E. M. Spehn, P. A. Niklaus, C. E. Wells, and C. Körner. 2000. Dynamics of root systems in native grasslands: effects of elevated atmospheric CO₂. *New Phytologist* 147:73–86.
- Barbhuiya, A. R., A. Arunachalam, H. N. Pandey, M. L. Khan, and K. Arunachalam. 2012. Fine root dynamics in undisturbed and disturbed stands of a tropical wet evergreen forest in northeast India. *Tropical Ecology* 53:69–79.
- Bouma, T. J., R. D. Yanai, A. D. Elkin, U. Hartmond, D. E. Flores-Alva, and D. M. Eissenstat. 2001. Estimating age-dependent costs and benefits of roots with contrasting life span: comparing apples and oranges. *New Phytologist* 150: 685–695.
- Brooks, P. D., P. Grogan, P. H. Templer, P. Groffman, M. G. Öquist, and J. Schimel. 2011. Carbon and nitrogen cycling in snow-covered environments. *Geography Compass* 5:682–699.
- Brundrett, M. C., and B. Kendrick. 1988. The mycorrhizal status, root anatomy, and phenology of plants in a sugar maple forest. *Canadian Journal of Botany* 66:1153–1173.
- Burke, M. K., and D. J. Raynal. 1994. Fine-root growth phenology, production, and turnover in a northern hardwood forest ecosystem. *Plant and Soil* 162:135–146.
- Chapin, F. S., III, J. McFarland, A. David McGuire, E. S. Euskirchen, R. W. Ruess, and K. Kielland. 2009. The changing global carbon cycle: linking plant–soil carbon dynamics to global consequences. *Journal of Ecology* 97: 840–850.
- Chapin, F. S., III, et al. 2006. Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems* 9:1041–1050.
- Ciais, P. et al. 2008. Carbon accumulation in European forests. *Nature Geoscience* 1:425–429.
- Crocker, T. L., R. L. Hendrick, R. W. Ruess, K. S. Pregitzer, A. J. Burton, M. F. Allen, J. Shan, and L. A. Morris. 2003. Substituting root numbers for length: improving the use of minirhizotrons to study fine root dynamics. *Applied Soil Ecology* 23:127–135.
- Dahlman, R. C., and C. L. Kucera. 1965. Root productivity and turnover in native prairie. *Ecology* 46:84–89.
- Eissenstat, D. M., and M. M. Caldwell. 1988. Seasonal timing of root growth in favorable microsites. *Ecology* 69:870–873.
- Ferguson, S. D., and R. S. Nowak. 2011. Transitory effects of elevated atmospheric CO₂ on fine root dynamics in an arid ecosystem do not increase long-term soil carbon input from fine root litter. *New Phytologist* 190:953–967.
- Fitter, A. H., J. D. Graves, G. K. Self, T. K. Brown, D. S. Bogie, and K. Taylor. 1998. Root production, turnover and respiration under two grassland types along an altitudinal gradient: influence of temperature and solar radiation. *Oecologia* 114:20–30.
- Gaudinski, J., S. E. Trumbore, E. A. Davidson, A. C. Cook, D. Markewitz, and D. D. Richter. 2001. The age of fine-root carbon in three forests of the eastern United States measured by radiocarbon. *Oecologia* 129:420–429.
- Gaudinski, J. B., M. S. Torn, W. J. Riley, T. E. Dawson, J. D. Joslin, and H. Majdi. 2010. Measuring and modeling the spectrum of fine-root turnover times in three forests using isotopes, minirhizotrons, and the Radix model. *Global Biogeochemical Cycles* 24. <http://dx.doi.org/10.1029/2009GB003649>
- Gill, R. A., and R. B. Jackson. 2000. Global patterns of root turnover for terrestrial ecosystems. *New Phytologist* 147:13–31.
- Grier, C. C., K. A. Vogt, M. R. Keyes, and R. L. Edmonds. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington cascades. *Canadian Journal of Forest Research* 11:155–167.
- Guo, D., H. Li, R. J. Mitchell, W. Han, J. J. Hendricks, T. J. Fahey, and R. L. Hendrick. 2008. Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. *New Phytologist* 177:443–456.
- Harris, G. A. 1977. Root phenology as a factor of competition among grass seedlings. *Journal of Range Management* 30: 172–177.
- Hendrick, R. L., and K. S. Pregitzer. 1993. The dynamics of fine-root length, biomass, and nitrogen-content in two northern hardwood ecosystems. *Canadian Journal of Forest Research* 23:2507–2520.
- Hendrick, R. L., and K. S. Pregitzer. 1996. Applications of minirhizotrons to understand root function in forests and other natural ecosystems. *Plant and Soil* 185:293–304.
- Iversen, C. M. 2010. Digging deeper: fine-root responses to rising atmospheric CO concentration in forested ecosystems. *New Phytologist* 186:346–357.
- Iversen, C. M., J. Ledford, and R. J. Norby. 2008. CO₂ enrichment increases carbon and nitrogen input from fine roots in a deciduous forest. *New Phytologist* 179:837–847.
- Jackson, R. B., H. A. Mooney, and E. D. Schulze. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences USA* 94:7362–7366.
- Jackson, R. B., et al. 2000. Belowground consequences of vegetation change and their treatment in models. *Ecological Applications* 10:470–483.
- Kaplan, E. L., and P. Meier. 1958. Nonparametric-estimation from incomplete observations. *Journal of the American Statistical Association* 53:457–481.
- Lovett, G., J. Cole, and M. Pace. 2006. Is net ecosystem production equal to ecosystem carbon accumulation? *Ecosystems* 9:152–155.
- Lyr, H., and G. Hoffmann. 1967. Growth rates and growth periodicity of tree roots. *International Review of Forestry Research* 2:181–236.
- Majdi, H., K. Pregitzer, A. S. Moren, J. E. Nylund, and G. I. Agren. 2005. Measuring fine root turnover in forest ecosystems. *Plant and Soil* 276:1–8.
- Matamala, R., M. A. Gonzalez-Meler, J. D. Jastrow, R. J. Norby, and W. H. Schlesinger. 2003. Impacts of fine root turnover on forest NPP and soil C sequestration potential. *Science* 302:1385–1387.
- McCormack, M. L., T. S. Adams, E. A. Smithwick, and D. M. Eissenstat. 2012. Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytologist* 195: 823–831.
- Medvigy, D., S. C. Wofsy, J. W. Munger, D. Y. Hollinger, and P. R. Moorcroft. 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: ecosystem demography model version 2. *Journal of Geophysical Research Biogeosciences* 114. <http://dx.doi.org/10.1029/2008JG000812>
- Milchunas, D. G. 2009. Estimating root production: comparison of 11 methods in shortgrass steppe and review of biases. *Ecosystems* 12:1381–1402.
- Morin, X., M. J. Lechowicz, C. Augspurger, J. O'Keefe, D. Viner, and I. Chuine. 2009. Leaf phenology in 22 North American tree species during the 21st century. *Global Change Biology* 15:961–975.
- Oláh, B., C. Brière, G. Bécard, J. Dénarié, and C. Gough. 2005. Nod factors and a diffusible factor from arbuscular mycorrhizal fungi stimulate lateral root formation in *Mycobacterium truncatula* via the DMI1/DMI2 signaling pathway. *Plant Journal* 44:195–207.
- Ostle, N. J., et al. 2009. Integrating plant–soil interactions into global carbon cycle models. *Journal of Ecology* 97:851–863.

- Parton, W. J., P. J. Hanson, C. Swanston, M. Torn, S. E. Trumbore, W. Riley, and R. Kelly. 2010. ForCent model development and testing using the enriched background isotope study experiment. *Journal of Geophysical Research Biogeosciences* 115. <http://dx.doi.org/10.1029/2009JG001193>
- Pritchard, S. G., A. E. Strand, M. L. McCormack, M. A. Davis, A. C. Finzi, R. B. Jackson, R. Matamala, H. H. Rogers, and R. A. M. Oren. 2008. Fine root dynamics in a loblolly pine forest are influenced by free-air-CO₂-enrichment: a six-year-minirhizotron study. *Global Change Biology* 14:588–602.
- Richardson, A. D. et al. 2012. Terrestrial biosphere models need better representation of vegetation phenology: results from the North American carbon program site synthesis. *Global Change Biology* 18:566–584.
- Riley, W. J., J. B. Gaudinski, M. S. Torn, J. D. Joslin, and P. J. Hanson. 2009. Fine-root mortality rates in a temperate forest: estimates using radiocarbon data and numerical modeling. *New Phytologist* 184:387–398.
- Ruess, R. W., R. L. Hendrick, A. J. Burton, K. S. Pregitzer, B. Sveinbjornsson, M. E. Allen, and G. E. Maurer. 2003. Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. *Ecological Monographs* 73:643–662.
- Silver, W. L., and R. K. Miya. 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* 129:407–419.
- Steele, S. J., S. T. Gower, J. G. Vogel, and J. M. Norman. 1997. Root mass, net primary production and turnover in aspen, jack pine, and black spruce forests in Saskatchewan and Manitoba, Canada. *Tree Physiology* 17:577–587.
- Steinaker, D. F., S. D. Wilson, and D. A. Peltzer. 2010. Asynchronicity in root and shoot phenology in grasses and woody plants. *Global Change Biology* 16:2241–2251.
- Strand, A. E., S. G. Pritchard, M. L. McCormack, M. A. Davis, and R. Oren. 2008. Irreconcilable differences: fine-root life spans and soil carbon persistence. *Science* 319:456–458.
- Sun, J., J. Gu, and Z. Wang. 2012. Discrepancy in fine root turnover estimates between diameter-based and branch-order-based approaches: a case study in two temperate tree species. *Journal of Forestry Research* 23:575–581.
- Tatarinov, F. A., and E. Cienciala. 2006. Application of Biome-BGC model to managed forests: sensitivity analysis. *Forest Ecology and Management* 237:267–279.
- Tierney, G. L., and T. J. Fahey. 2002. Fine root turnover in a northern hardwood forest: a direct comparison of the radiocarbon and minirhizotron methods. *Canadian Journal of Forest Research* 32:1692–1697.
- Tierney, G. L., T. J. Fahey, P. M. Groffman, J. P. Hardy, R. D. Fitzhugh, C. T. Driscoll, and J. B. Yavitt. 2003. Environmental control of fine root dynamics in a northern hardwood forest. *Global Change Biology* 9:670–679.
- Xia, M., D. Guo, and K. S. Pregitzer. 2010. Ephemeral root modules in *Fraxinus mandshurica*. *New Phytologist* 188: 1065–1074.

SUPPLEMENTAL MATERIAL

Appendix

Background data and additional results for the heuristic model and observations of root dynamics in the Rock Springs Common Garden ([Ecological Archives E095-197-A1](#)).