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Rhizosphere processes are quantitatively important components of terrestrial carbon and nutrient cycles

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Abstract

While there is an emerging view that roots and their associated microbes actively alter resource availability and soil organic matter (SOM) decomposition, the ecosystem consequences of such rhizosphere effects have rarely been quantified. Using a meta-analysis, we show that multiple indices of microbially mediated C and nitrogen (N) cycling, including SOM decomposition, are significantly enhanced in the rhizospheres of diverse vegetation types. Then, using a numerical model that combines rhizosphere effect sizes with fine root morphology and depth distributions, we show that root-accelerated mineralization and priming can account for up to one-third of the total C and N mineralized in temperate forest soils. Finally, using a stoichiometrically constrained microbial decomposition model, we show that these effects can be induced by relatively modest fluxes of root-derived C, on the order of 4% and 6% of gross and net primary production, respectively. Collectively, our results indicate that rhizosphere processes are a widespread, quantitatively important driver of SOM decomposition and nutrient release at the ecosystem scale, with potential consequences for global C stocks and vegetation feedbacks to climate.

Keywords: carbon cycle, global change, nitrogen cycle, priming effects, soil organic matter

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Introduction

More carbon (C) is stored in soil organic matter (SOM) than that found in plant biomass and as CO_2 in the Earth's atmosphere combined (Schimel, 1995). As a major reservoir of C and the primary source of nutrients that fuel primary production (Cleveland *et al.*, 2013), it is essential to understand the factors regulating SOM turnover to predict terrestrial feedbacks to future climate change. Historically, soil temperature and moisture have been viewed as the primary drivers of SOM decomposition. However, an emerging but largely untested view argues that plant C allocation to roots and rhizosphere microbes is a major driver of the decomposition process and that it is quantitatively important at ecosystem scales (Fontaine *et al.*, 2007; Bardgett *et al.*, 2008; Schmidt *et al.*, 2011). Plants rapidly transfer photosynthate into the soil around roots (i.e., the rhizosphere, Hogberg *et al.*, 2001; De Deyn *et al.*, 2011), which stimulates microbial activity and microbial demand for nutrients (Ekblad & Nordgren, 2002). This, in turn, stimulates microbial production of exoenzymes that decompose SOM and release nutrients (Schimel & Weintraub, 2003) through priming effects (Bengtson *et al.*, 2012). While components of this general principle have long been recognized (Bingeman *et al.*, 1953; Cheng *et al.*, 2003; Hinsinger *et al.*, 2009; Iversen, 2010; Jenkinson *et al.*, 1985; Jones *et al.*, 2004; Kuzyakov *et al.*, 2000; Löhnis, 1926), remarkably few studies have examined the magnitude of root-induced changes in nutrient cycling and decomposition across vegetation types or quantified the ecosystem-scale consequences of such rhizosphere effects.

Given that global change alters the flux of C belowground (Uselman *et al.*, 2000; Johansson *et al.*, 2009; Drake *et al.*, 2011; Phillips *et al.*, 2011; Yin *et al.*, 2013), it is essential to develop scaling techniques for empirical measurements of rhizosphere processes. One such approach is to estimate the percentage of soil that is in a 'rhizosphere' state as a function of the distribution and architecture of fine root systems and model the contribution of rhizosphere C and nutrient fluxes to total fluxes in the entire soil volume. By mapping rhizosphere volume to the distribution of fine roots, a parameter that is now being included in many land surface models (Iversen, 2010), it may ultimately be possible to study rhizosphere processes at the spatial scales relevant to climate change research. For the purposes of

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this study, we use the term 'exudation' to encompass rhizosphere C inputs to the soil derived from rhizodeposits (e.g., root cap sloughing) and exudation of soluble C- and N-containing compounds from the root surface.

While previous studies have estimated exudation rates (Smith, 1976; Phillips *et al.*, 2011; Brzostek *et al.*, 2013) and rhizosphere effects (Phillips & Fahey, 2006) in forests, few studies have linked these processes at the ecosystem scale or provided a framework for incorporating these dynamics into large-scale models. To the extent they have been incorporated into models (e.g., Wutzler & Reichstein, 2013; Cheng *et al.*, 2014; Foereid *et al.*, 2014; Perveen *et al.*, 2014), their representation is relatively crude and lacks representation of the actual processes taking place. For example, while the spatial extent of the rhizosphere is largely a function of a root system's depth distribution, architecture and exudation rate, these components are absent from the current generation of ecosystem and land surface models. Further, root and microbial processes are rarely coupled in most large-scale models. As such, microbial responses to localized and transient root-derived inputs of DOC and DON, and their role in promoting feedbacks to plant productivity under changing environmental conditions, cannot be predicted.

This study provides a novel, quantitative framework for investigating how changes in root and microbial processes (e.g., such as those triggered by rising atmospheric CO_2, N deposition, warming, etc.) may influence ecosystem C and N cycling and ultimately feedbacks to climate. Here, we use a meta-analytical approach to quantify rhizosphere effects – defined as the enhancement of a rhizosphere pool or process rate relative to that in the bulk soil – on microbial biomass and activity in soils from agricultural, herbaceous and woody growth forms. We then use the results of the meta-analysis in conjunction with published data on the distribution of root biomass and root architecture to model the contribution of the rhizosphere to total soil C and N mineralization to a depth of 1 m in temperate forest soil. Finally, we use a stoichiometrically constrained microbial decomposition model to estimate the quantity of exuded C that is required to achieve the modeled rhizosphere contributions. Our results show that (i) the magnitude and direction of rhizosphere processes are similar among plant growth forms, (ii) root-induced changes in SOM decomposition and nutrient flux can account for up to one-third of the total C and N mineralized in temperate forest soils, and (iii) the magnitude of such rhizosphere effects in forests can be induced by relatively small inputs of root-derived C.

Materials and methods

Meta-analysis

We used a number of search strings in Thompson ISI® Web of Science and Google Scholar to identify rhizosphere data in the literature for the meta-analysis. For each study, we tabulated information on mean microbial activity, its standard deviation and the sample size (see Tables S1–S6). When necessary, we used DataThief III to obtain mean and standard deviation (or standard error) estimates from plotted data. We also collected information about each experiment, including ecosystem and vegetation type (i.e., woody, nonwoody, agricultural), growing environment (e.g., greenhouse, field, elevated CO_2, N fertilization) and the location of the study.

The data used for microbial activity was limited to studies using a manual separation of bulk from rhizosphere soil. The most common is the gentle shaking of the roots collected from soil cores, with the soil adhering after shaking considered the rhizosphere. For analysis of rhizosphere effects on microbial biomass and respiration, extracellular enzyme activity and N mineralization (gross and net), we tabulated data from studies using this definition of rhizosphere soil (Table S1). To this data set, we added four additional studies. One study used a 2-mm distance from the root as the cutoff between rhizosphere (<2 mm) and bulk soil (>2 mm). The remaining three studies employed a bag-separation method, where plants were grown in a nylon bag with a small volume of soil that allows the movement of water and nutrients to the root system. A large number of studies measured 'rhizosphere respiration' in the field (e.g., trenching experiments, ^{13}C and ^{14}C labeling), but these analyses confound the contributions of roots and microbes, particularly for CO_2 production, and were therefore excluded. The method used to generate rhizosphere and bulk soil in each study is listed in Table S1.

This study also collected information on the rate of SOM decomposition in the rhizosphere compared to bulk soil, using information from planted and unplanted mesocosms. Only studies using isotopes were considered in this analysis. The mesocosms were established such that CO_2 produced from the metabolism of labeled photosynthate had an isotopic composition unique from that of SOM. In these studies, the flux and isotopic composition of the respired CO_2 was collected over a period of weeks to months. A two-end member-mixing model was then used to calculate the fraction of total microbial respiration derived from SOM in the planted mesocosms. Multiplying this fraction by total CO_2 efflux provided a quantitative estimate of SOM decomposition due to the presence of a rhizosphere. When compared to the rate of CO_2 efflux in the unplanted controls, these studies estimate the combined effects of root activity (e.g., soil structure and moisture) and root-derived organic matter (e.g., exudates, mycorrhizal activity) on SOM loss.

Despite the variety of experimental designs and sampling schemes, most of the data on microbial biomass and activity were measured on a mass-specific basis (e.g., mg CO_2 g^{-1} h^{-1}). Data presented on a per unit area or pot basis were converted to a mass-specific basis prior to statistical analysis, using information on soil bulk density and sampling depth

provided in the paper. The data were then scaled to consistent units of mass (i.e., CO_2-C) and time (hour). The methods and assumptions required to scale the data are found in the Supplementary Information (Tables S2–S6). This approach enabled us to plot rhizosphere microbial activity as a function of bulk-soil microbial activity and also to calculate the stimulation of microbial activity in rhizosphere compared to bulk soil at the median bulk-soil value for each microbial process studied (c.f., Norby *et al*., 2005).

We used meta-analysis to assess differences in microbial activity between rhizosphere and bulk soil (Meta-Win V2.0, Rosenberg *et al*., 1999). Meta-analysis provides a quantitative statistical approach for synthesizing the results of multiple independent experiments. We calculated a single response ratio (RR), defined here as the mean of the process of interest in the rhizosphere sample divided by its corresponding mean in the bulk-soil sample, for experiments with repeated measurements of the same sample over time (i.e., the average across all time points). Data were also averaged when a particular study categorized data according to criteria that were not relevant to our study [e.g., different depths of soil, different watering treatments, or similar enzyme types (e.g., acid and alkaline phosphatase)]. If a study had samples from different plant species and different years or used different methods of analysis (e.g., substrate-induced respiration and chloroform fumigation extraction), these were considered independent observations and were not averaged.

For each pair of observations (rhizosphere, bulk soil), Meta-Win calculates the effect size of a given treatment by calculating the natural log of the response ratio [i.e., *ln(RR)*]. Each response ratio is weighted in the overall analysis of variance based on the sample size and standard deviation around each mean, which when necessary, we calculated from standard errors and sample size. Values of *ln(RR)* >0 indicate stimulatory effects and values <0, inhibitory effects. For each data set, average *ln(RR)* ± 95% confidence intervals not overlapping zero indicated a significant treatment response. Given the assumption of log-normal distribution in meta-analysis, in-text references to percent rhizosphere stimulation are presented at the original scale using the transformation mean [ln (*RR*)] = $e^{(\mu+\sigma\text{^}2/2)}$, the mean of the log-normal distribution (Clark, 2007).

Of the >1000 papers we reviewed, 52 were suitable for meta-analysis of microbial and exoenzyme activity and nine for SOM decomposition. The data for microbial and exoenzyme activity were analyzed by experimental setting (field vs. greenhouse) and vegetation type (woody vs. herbaceous vs. agricultural species). Similarly, given the abundance of enzyme data, it was possible to estimate an effect size for different enzyme functional groups. The five functional groups were as follows: labile-C-degrading enzymes (glucosidase, galactosidase, endocellulase, saccharase), recalcitrant-C-degrading enzymes (phenol oxidase, peroxidase), enzymes involved in the depolymerization and mineralization of N (N-acetylglucosaminidase, peptidase, protease, urease, asparaginase), P (acid & alkaline phosphatase, phosphodiesterase) and S (sulfatase, Table S4). The data on N mineralization were separated according to whether the observation was a gross or net flux (Table S5). Finally, due to relatively small sample size (nine studies and 30 observations), it was only possible to test for differences in SOM decomposition between planted and unplanted controls.

Scaling rhizosphere processes

Estimates of root length, depth distribution and architecture were used to upscale meta-analysis results to the ecosystem scale. We focused the upscaling on temperate forests because this ecosystem type had the most data available. Together, published data in Gale & Grigal (1987) and Jackson *et al*. (1997) were used to estimate the cumulative distribution of fine root length (FRL, km m^{-2}) to 1 m depth in temperate forest soils. This distribution was asymptotically nonlinear viz (Jackson *et al*., 1997):

$$r(d) = 1 - \beta^d \quad (1)$$

where *r(d)* is the cumulative fraction of roots above profile depth, *d* (in cm, including the organic horizon), and β is an estimated shape parameter equivalent to 0.95 in this study (Gale & Grigal, 1987). From the cumulative distribution, we calculated the proportion of FRL in 1 cm depth increments in the soil (Fig. S1a). This proportion multiplied by total FRL (km m^{-2}) distributed FRL in 1 cm depth increments to 1 m depth.

Previous research on fine root architecture in nine North American tree species found that the majority of FRL is found in the finest roots (Pregitzer *et al*., 2002). There is large variability among these tree species, so for this study, we conservatively assumed that 75% of total FRL is found in roots ≤0.5 mm. To estimate the proportion of roots in different diameter classes, we used a logistic (sigmoid) function. With an asymptote of 1 (i.e., all roots have a diameter ≤2 mm), the cumulative root diameter function was estimated as:

$$CRL = \frac{1}{1 + \alpha * e^{-\gamma * rootD}} \quad (2)$$

where *CRL* = cumulative root length and *rootD* is root diameter in mm (Fig. S1b). The values of α (=75, intercept) and γ (=11, exponential decay coefficient) fit the CRL distribution to the requirement that 75% of roots are ≤0.5 mm diameter. From the cumulative root-length distribution, we calculated the proportion of FRL in 0.02-mm-diameter increments for each cm of soil to 1 m depth.

The volume of rhizosphere soil was estimated from the distribution and architecture of the roots. Exudation rates and sloughing of necromass associated with root growth are thought to vary as a function of root diameter with fine, actively growing first- and second-order roots exuding more than wider diameter, third-order and above roots (Rovira, 1969). We therefore modeled the distance exudates travel from the root surface using a first-order, exponential decay model as a function of root diameter. This approach merges the idea that finer roots are likely to exude more than coarser roots and that a larger pulse of exudates is likely to travel further from the root surface than a small pulse of exudates.

The distance exudates travel from the root surface was limited to 2 mm. This assumption is conservative relative to that reported in the literature (Table 1) where the median, mean and upper bound on exudate distance from the root surface are 2.3, 3.4 and 12 mm, respectively. Exudate diffusion distance from the root surface was modeled as a negative exponential function of root diameter viz.:

$$\textit{exudate diffusion distance}\ (\text{mm}) = 2 * \exp^{-k*rootD} \quad (3)$$

where k describes the rate at which exudate distance declines as a function of *rootD* (mm) and 2 is the y-intercept (i.e., maximum exudate diffusion distance). We conservatively assumed that an exudate produced by a 1-mm-diameter root extended no farther than 0.5 mm from the root surface ($k = -1.5$).

Mass-specific rates of rhizosphere processes reported in the meta-analysis were extrapolated to the ecosystem scale (i.e., g m^{-2} $time^{-1}$) in a two-step process: (i) estimating the volume of fine roots, rhizosphere and bulk soil and (ii) accounting for the decline in the quantity of SOM with depth. The volume of soil occupied by roots was based on the modeled FRL and diameter distribution to 1 m depth, assuming the roots were cylindrical. We similarly estimated root plus rhizosphere volume, from which we calculated rhizosphere volume by difference (Fig. S1c). All calculations assumed a constant soil bulk density throughout the profile (1 g cm^{-3}). Declines in microbial activity with depth in the soil profile mirror reductions in the quantity of SOM with increasing depth as reported in Jobbagy & Jackson (2000). Hence, rates of microbial respiration and net N mineralization in bulk and rhizosphere soil were greatest at the soil surface and declined exponentially with depth viz.:

$$\textit{SOM multiplier}\ [\textit{dimensionless}] = 1 * e^{-0.55*\textit{soil depth}} \quad (4)$$

There is substantial uncertainty associated with the distance exudates travel from the root surface and large variations in root architecture and depth distribution among species and ecosystems. To assay the sensitivity of the model to these uncertainties and variations, we doubled and halved the coefficients relative to our initial model parameters (Table 2). An annotated version of the scaling model code and empirical data on root distributions can be found in Appendices S1 and S2.

Modeling exudation flux

To estimate the rhizosphere C flux, we coupled the microbial decomposition model [MCNiP, Drake *et al.*, 2013a,b; Cheng *et al.*, 2014;] with the depth, length and architecture of roots estimated for temperate forests (Fig. S2). In brief, MCNiP adds an N cycling subroutine to the C-only microbial physiology model of Allison *et al.* (2010), using stoichiometric principles of Schimel & Weintraub (2003). In the model, litter inputs (leaf, root) are partitioned to SOC and DOC pools at each time step (h^{-1}). Root exudates are, however, input only into the DOC pool. Microbes take up DOC and DON according to Michaelis–Menten kinetics. The rates of C and N mineralization are dependent on system stoichiometry and temperature via Arrhenius kinetics (Davidson *et al.*, 2012).

Depth-dependent variation in microbial processes was added to MCNiP by creating 100 soil layers, each 1 cm deep (i.e., to a depth of 1 m). Mirroring the change in SOM content, inputs to SOC and DOC pools declined exponentially with depth (Jobbagy & Jackson, 2000). Within each soil layer, the soil volume was separated into bulk and rhizosphere soil based on the output generated by Eqns (1)–(3). The exudation rate into the rhizosphere soil volume was increased from a starting point of 10^{-4} mg C cm^{-3} root until the model reproduced the microbial respiration effect size for woody plants in the meta-analysis to a depth of 15 cm ($lnRR = 0.4077$). For the purpose of model calibration, temperature was held constant at 20 °C, the same temperature at which the majority of the meta-analysis studies were conducted.

Once parameterized (Table S7, see Appendix S1 for spin up parameters), the model was used to predict annual root exudation flux (g C m^{-2} yr^{-1}) for a hypothetical temperate forest ecosystem, assuming roots exude C 24 h d^{-1} during a 200-day growing season – an average growing season length for temperate forests (Churkina *et al.*, 2005; Wu *et al.*, 2014).

Table 1 Published estimates of the distance plant root exudates were found from the surface of roots

Reference	Exudate diffusion distance from the root surface
Dessureault-Rompre *et al.* (2007)	>5 mm
Jones (1998)	0.2–1 mm
zu Schweinsberg-Mickan *et al.* (2010)	2.6 mm
Sauer *et al.* (2006)	2–12 mm
De Neergaard and Magid (2001)	1–3 mm
Toussaint *et al.* (1995)	5–10 mm
Darrah (1991)	2 mm
Jones *et al.* (1996)	5 mm
Nuruzzaman *et al.* (2006)	3–4 mm
Dick and Kandeler (2005)	0–1.3 mm
Herman *et al.* (2006)	2 mm
Landi *et al.* (2006)	2 mm
Cheng (2009)	5 mm
Falchini *et al.* (2003)	2 mm

Table 2 Parameter values for sensitivity analysis of fine root length (FRL), cumulative root length (CRL) and exudate diffusion distance (EDD)

	Low	Int.	High
FRL (km m^{-2})	3.6	7.2	10.8
CRL (γ, unitless)	7.14	11	21.5
EDD (k, unitless)	2.9	1.45	0.73

We assumed that root exudation rates decrease with depth in the soil. The model was then used to explore temporal variations in the magnitude of rhizosphere effects on microbial activity as predicted by MCNiP. To add seasonality to the simulation, we scaled the calibrated model output by assuming a Q_{10} of 2 for microbial respiration and a Gaussian distribution for soil temperature that has a minimum of 0 °C on growing season days 1 and 200, and a maximum of 20 °C on day 100. Once again, we evaluated the sensitivity of the MCNiP model estimates of root C exudation and rhizosphere microbial activity to exudate diffusion distance, root architecture and fine root length.

Results

Meta-analysis

Microbial biomass was significantly greater in rhizosphere than bulk soil (Fig. 1a). This stimulation was significantly higher in herbaceous and agricultural compared to woody-dominated ecosystems (Fig. 1b). There were sufficient data to test for differences between chloroform fumigation extraction (CFE) and substrate-induced respiration (SIR). SIR estimates of biomass (*lnRR* = 0.54; CI = 0.52–0.56) were significantly higher than those of CFE (*lnRR* = 0.43; CI = 0.41–0.44). Across all studies, microbial biomass was 62% higher in rhizosphere compared to bulk soil (Fig. 2a).

Microbial respiration rates were significantly enhanced in rhizosphere compared to bulk soil (Fig. 1a), and this effect was far larger in agricultural species compared to woody plants (Fig. 1b). There were insufficient data to test for nonwoody species effects on rhizosphere respiration. Across all studies, respiration in rhizosphere soil was 80% higher than bulk soil (Fig. 2b).

Exoenzyme activity was significantly higher in rhizosphere compared to bulk soil (Fig. 1a). Exoenzyme activity in the rhizosphere of woody and nonwoody plants was significantly higher than that in agricultural plants (Fig. 1b). The activity of labile-C-degrading enzymes in the rhizosphere was 55% greater than the bulk soil (Fig. 1c). The activity of N-degrading enzymes increased 35% in rhizosphere relative to bulk soil. This stimulation excludes the activity of urease reported by Zhang *et al*. (2012). Their data, plotted in gray, report a significant repression of urease activity in excess of any other study of exoenzyme or microbial activity. The activity of P- and recalcitrant-C-degrading enzymes was 45% and 44% greater in rhizosphere compared to bulk soil, respectively. Across all studies and enzyme classes, exoenzyme activity was 28% greater in rhizosphere compared to bulk soil (Fig. 2c).

The rate of inorganic N production was significantly greater in rhizosphere than bulk soil, and this effect held whether production was measured as net mineralization, gross NH_4 mineralization or net nitrification (Fig. 1a). The stimulation of N production in the

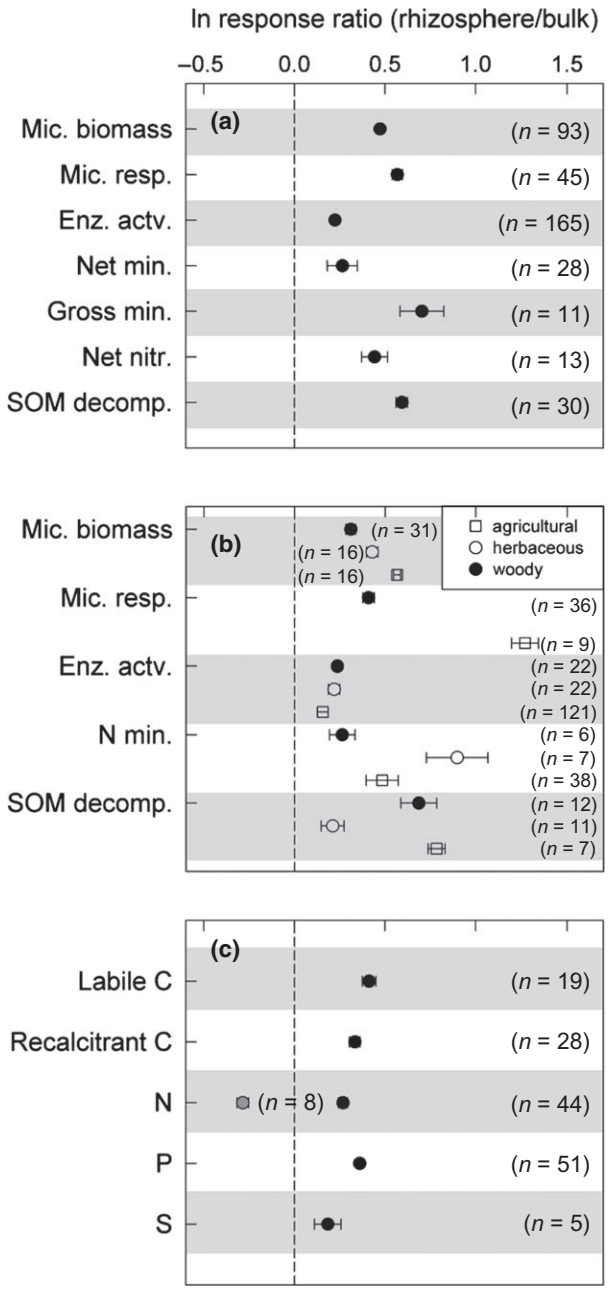

Fig. 1 Meta-analysis results [mean *ln*(RR) ± 95% confidence intervals]. (a) Microbial, exoenzyme and SOM decomposition effects in rhizosphere compared to bulk soil across all observations, (b) effects sorted by growth form and (c) separation of enzymes by functional class. The black symbol for N-degrading enzymes is the mean *ln*(RR) for all enzymes excluding urease values reported by Zhang *et al*. (2012, see text for details), which is plotted in gray. The list of enzymes in each class can be found in the *Methods* section.

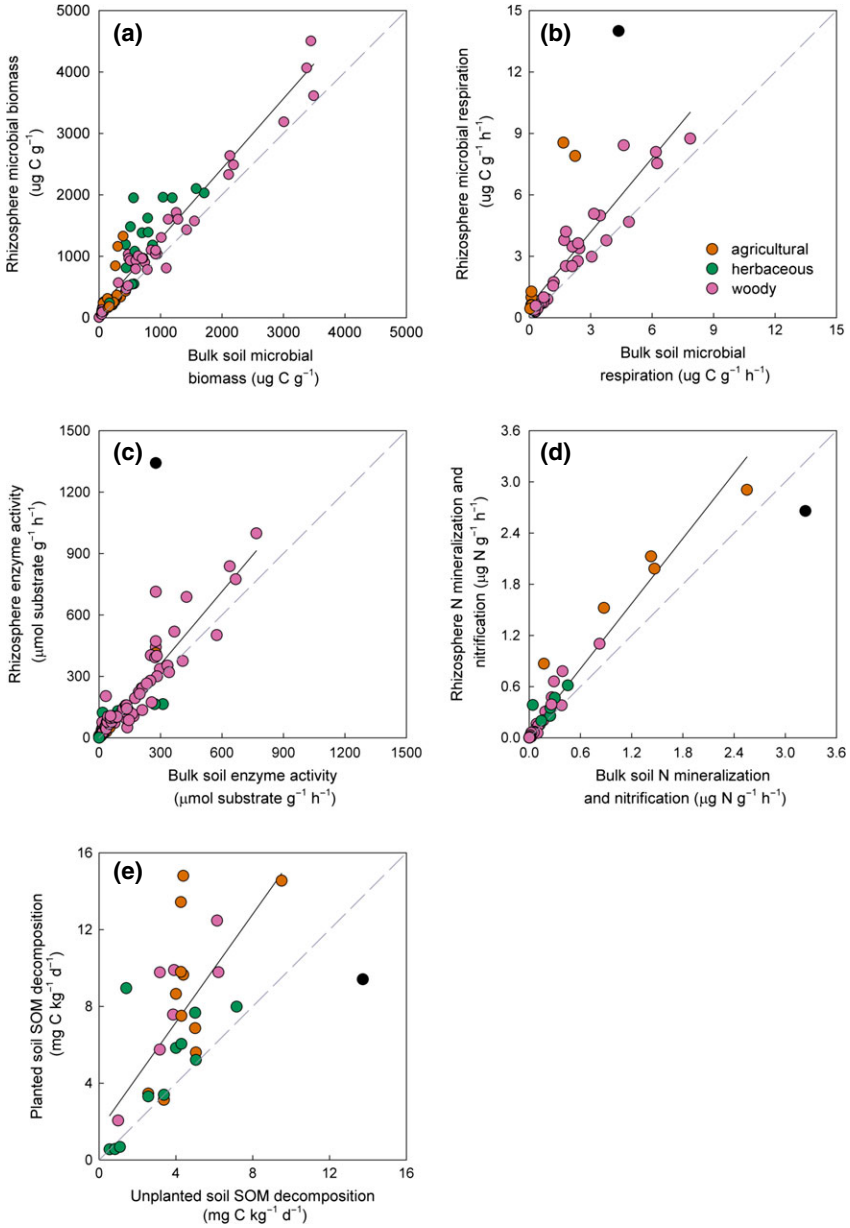

Fig. 2 Regression plots of microbial and exoenzyme activity, and SOM decomposition in rhizosphere (RS) vs. bulk soil (BS). (a) Microbial biomass [N = 93, RS = 142+1.14*BS, $P < 0.0001$, $R^2 = 0.91$], (b) microbial respiration [N = 43, RS = 0.57+1.20*BS, $P < 0.0001$, $R^2 = 0.73$], (c) exoenzyme activity [N = 164, RS = 3.07+1.18*BS, $P < 0.0001$, $R^2 = 0.89$], (d) net N mineralization and nitrification [N = 54, RS = 0.05+1.27*BS, $P < 0.0001$, $R^2 = 0.94$] and (e) SOM decomposition [N = 29, RS = 1.5+1.41*BS, $P < 0.0001$, $R^2 = 0.47$]. Black-fill points denote outliers that significantly influenced the regression line and were removed from the analysis. Solid lines = regression. Dashed lines = 1 : 1 line.

rhizosphere was highest in nonwoody plants, lower in agricultural plants and lowest in woody plants (Fig. 1b). Across all studies, the net rate of inorganic N production in the rhizosphere was 69% greater than in the bulk soil (Fig. 2d).

The rate of SOM decomposition was significantly stimulated in rhizosphere compared to bulk soil (Fig. 1a). The stimulation was largest in woody and agricultural ecosystems and smallest in herbaceous ecosystems (Fig. 1b). Across studies, SOM decomposition in the rhizosphere was 82% greater than the bulk soil though the coefficient of determination for this relationship was substantially lower than that of the other microbial processes analyzed (Fig. 2e).

Scaling rhizosphere processes

As parameterized, the distance exudates travel from the root surface declined exponentially with root diameter (Fig. 3a). Coupled with the decline in fine root length, there was a steep decline in rhizosphere soil volume with depth (Fig. 3b). Integrating to 10 cm depth, rhizosphere volume and soil mass comprise 8–26% of the total soil volume (Table 3). Integrating to 30 cm and 100 cm depths, these percentages decline to 5–17% and 2–6%, respectively. Although heterotrophic respiration and N mineralization rates in the bulk soil exceed rhizosphere respiration rates at all depths, rhizosphere microbial activity contributed significantly to respiration and N mineralization in surface soil (Fig. 3e,f). Integrating data to 10 cm depth, rhizosphere respiration and N mineralization accounted for 10–33% of total fluxes, with higher percentages at the very surface (Table 3).

Modeling exudation flux

The MCNiP model estimated that 0.47 μg C cm^{-3} of rhizosphere soil is necessary to simulate the stimulation of microbial respiration in the rhizosphere of temperate forest soils observed in the empirical data. The majority of exudation occurs in the upper 30 cm of the soil (Fig. 4a). When scaled to the ecosystem level at median parameterizations for diffusion distance, CRL and root length, 45 g C m^{-2} yr^{-1} are exuded from roots (Table 3). Microbial respiration in MCNiP was most sensitive to variations in rhizosphere diffusion distance and fine root length. It was least sensitive to variations in root architecture. At median parameterizations, MCNiP predicts total heterotrophic respiration rates of 365, 707 and 892 gC m^{-2} yr^{-1} at soil depths of 10, 30 and 100 cm, respectively (Table 3). MCNiP predicts that rhizosphere microbes account for 23%, 18% and 15% of these fluxes, respectively (Table 3).

Discussion

Accelerated organic matter decomposition owing to priming of microbial activity is widespread, occurring on land (Dijkstra & Cheng, 2007; Kuzyakov, 2010; Cheng *et al*., 2014), in freshwater (Guenet *et al*., 2010) and in the sea (Bianchi, 2011). In terrestrial ecosystems, the rhizosphere has long been regarded as a biogeochemical hot spot because plant-derived C inputs stimulate microbial activity. Indeed, microbial priming of SOM decomposition is arguably the most important of all rhizosphere effects, one that is likely to increase in importance with global change (Hungate *et al*., 1997; Carney *et al*., 2007; Talhelm *et al*., 2009; Cheng *et al*., 2012; Hartley *et al*., 2012; Van Groenigen *et al*., 2014).

While numerous studies have reported elevated rates of C and nutrient cycling in the rhizosphere for individual plant species, the ecosystem consequences of such effects have not been quantified. Consequently, few, if any, biogeochemical models meaningfully couple root and microbial processes in a manner that gives confidence in the inference drawn from their simulations. Using data compilation and a new modeling approach, we show that different plant growth forms converge in the magnitude and direction of rhizosphere effects (Figs 1 and 2) and that rhizosphere microbial activity significantly influences element cycling at the ecosystem scale (Fig. 3). We also show that relatively small

Table 3 Rhizosphere scaling and MCNiP simulation estimates of belowground pools and fluxes. Exudation rate (gC m^{-2} yr^{-1}) and rhizosphere respiration as a percentage of total respiration are integrated to 10 cm, 30 cm and 1 m depths assuming decreasing rates of root exudation with depth in the soil. See text for additional model details

	Depth (cm)	Median all parameters	Low EDD	Intermediate EDD	High EDD	Low CRL	High CRL	Low FRL	High FRL
Rhizosphere scaling (Rhizosphere as percentage of total in the soil)									
Soil mass	30	–	5%	11%	17%	–	–	–	–
	100	–	2%	4%	6%	–	–	–	–
Microbial	30	–	8%	17%	26%	–	–	–	–
Respiration	100	–	6%	14%	21%	–	–	–	–
N	30	–	7%	16%	25%	–	–	–	–
Mineralization	100	–	6%	13%	21%	–	–	–	–
MCNiP simulation									
Exudation	10	29	13	–	45	21	41	14	43
Rate	30	43	20	–	68	31	61	22	65
(gC m^{-2} yr^{-1})	100	45	21	–	71	33	64	23	68
Microbial	10	23%	11%	–	35%	17%	32%	12%	33%
Respiration	30	18%	8%	–	27%	13%	25%	9%	26%
(% total)	100	15%	7%	–	23%	11%	21%	8%	22%

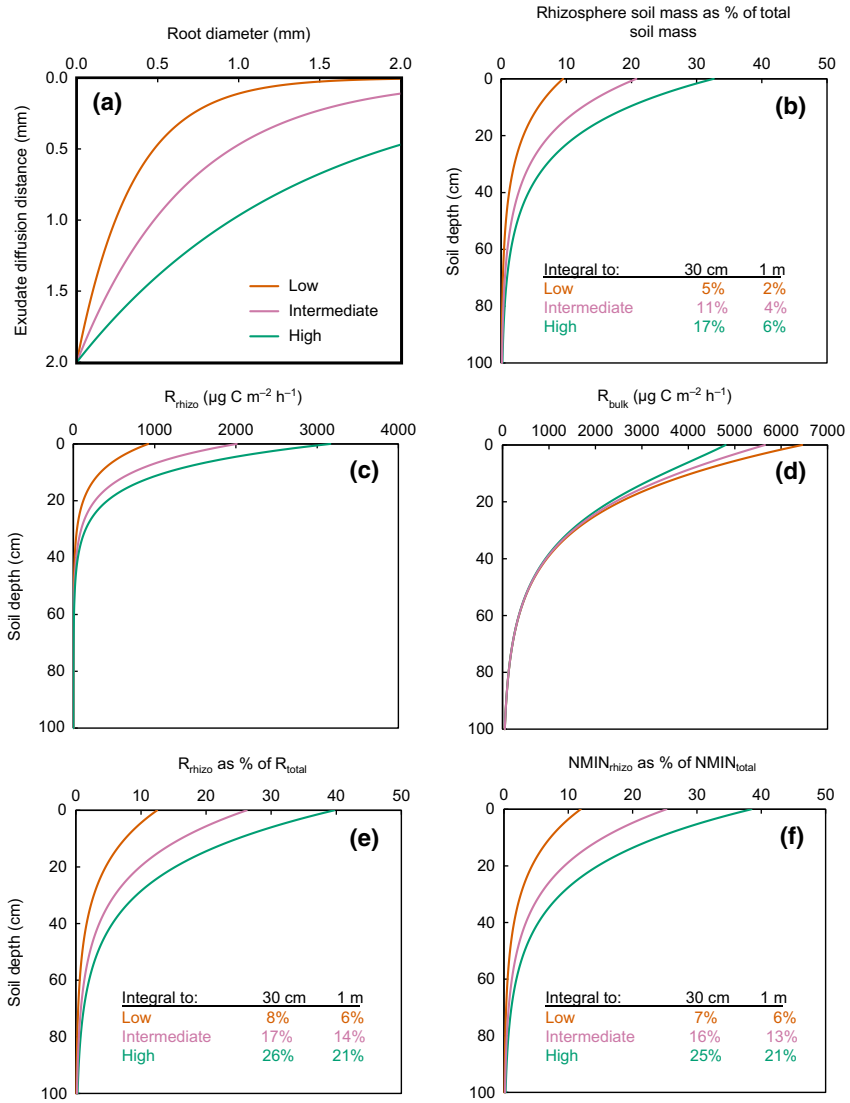

Fig. 3 Model results for rhizosphere processes. (a) Exudate diffusion distance as a function of root diameter. (b) Rhizosphere soil mass as a percentage of total soil mass. (c) Rhizosphere and (d) bulk-soil heterotrophic respiration rate as a function of soil depth to 1 m. Percentage of (e) total respiration and (f) net N mineralization in the rhizosphere as a function of soil depth. The three lines in each plot propagate the effect of different rhizosphere diffusion distances from the root surface. The inset tables in (b), (e) and (f) are integrated estimates of total rhizosphere soil mass, respiration and N mineralization to 30-cm and 100-cm depth, respectively.

inputs of root-derived C induce disproportionately large effects on soil biogeochemistry.

In addition to accelerated soil-C turnover, priming is likely responsible for the observed enhancement of rhizosphere N mineralization (Figs 1 and 2). Nitrogen in SOM must be depolymerized from larger molecules and in many instances mineralized before it can be become available to plants (Nasholm *et al.*, 1998; Schimel & Bennett, 2004; Finzi & Berthrong, 2005; Gallet-Budynek *et al.*, 2009). While the absence of a tracer (e.g., ^{15}N) prevents us from drawing a definitive conclusion regarding the source of N, the majority of soil N is bound to C and thus, it is nearly certain that the stimulation of N fluxes in the rhizosphere is driven in large part by the decomposition of SOM and not simply the recycling of N contained within the root exudates (Grayston *et al.*, 1997). Moreover, numerous other studies have reported positive correlations between gross N mineralization and SOM decomposition (Dijkstra & Cheng, 2007; Bengtson *et al.*, 2012; Zhu *et al.*, 2014), providing strong evidence that both microbial demand for N and exudate-induced shifts in microbial communities accelerate nutrient release from SOM (Chen *et al.*, 2014). We cannot, however, exclude the possibility of some N derived from enhanced rhizosphere N_2 fixation, a process favored under C-rich, anaerobic

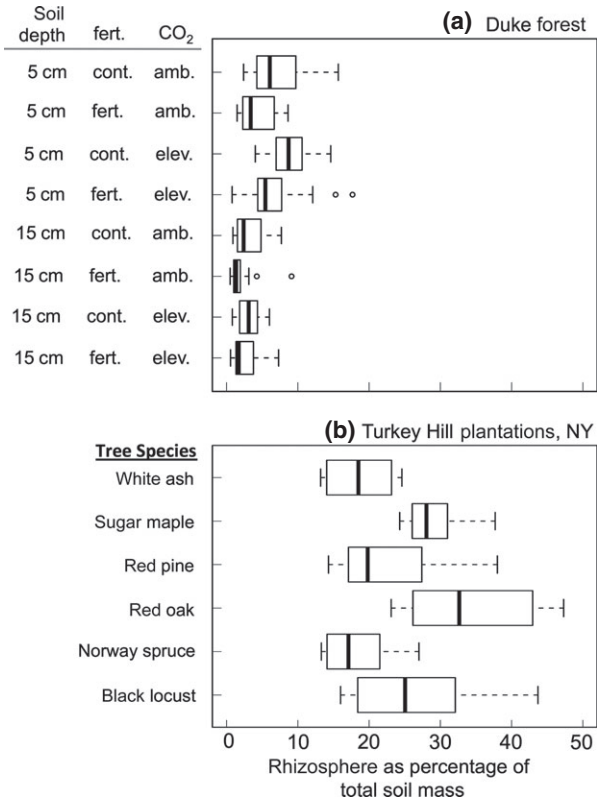

Fig. 4 Estimates of the percent rhizosphere soil mass as a function of total soil mass for the (a) Duke free-air CO_2 enrichment (FACE) study and (b) the Turkey Hill Plantation study (Phillips & Fahey, 2006). The Duke FACE data are separated by depth (0–5 cm, 5–15 cm mineral soil), CO_2 treatment (ambient, ambient + 200 ppm) and N fertilizer status (ambient, +110 kgN ha^{-1} yr^{-1}). The data from the Turkey Hill Plantation study were obtained from samples in the top 5 cm of mineral soil.

conditions that are presumably transiently present following exudation.

Rhizosphere scaling

The importance of scaling rhizosphere research is underscored by recent empirical and modeling studies showing their importance to the coupled cycles of soil C and N (Cheng, 2009; Bengtson *et al.*, 2012; Zhu *et al.*, 2014) and that the depolymerization of nutrients from SOM is essential to supporting long-term plant productivity in response to rising atmospheric CO_2 (Drake *et al.*, 2011; Zak *et al.*, 2011; Cheng *et al.*, 2012, 2014) and climate warming (Zhu & Cheng, 2011; Hartley *et al.*, 2012). To address the issue of rhizosphere scaling and develop a quantitative framework suitable for incorporation into the soil biogeochemistry components of models, we collected published information on fine root length (<2 mm), depth distribution, architecture and exudation. We coupled this information with the results of the meta-analysis and simple assumptions regarding soil properties with depth to generate a first-pass quantitative estimate of the ecosystem-scale consequences of rhizosphere microbial activity. The modeled estimate of rhizosphere soil volume (5–25% of the total soil volume) falls within the range of values reported in the literature (Fig. 5). Our model was not, however, calibrated or influenced by these data. Similarly, our estimate of exudate diffusion distance from the root is conservative relative to published estimates where exudate recovery distance frequently exceeds 2 mm from the root surface (Table 1).

At all depths, the rhizosphere contribution to C and N cycling exceeded its contribution to soil volume, and although bulk-soil microbial respiration and N mineralization rates exceed rhizosphere respiration rates at all depths in the soil, rhizosphere microbial activity made large contributions to C and N cycling in surface soil (Fig. 3cd). This is important because most of the microbial-respired CO_2 evading from the soil surface is generated near the surface rather than at depth where CO_2 readily accumulates at high concentrations (Gaudinski *et al.*, 2000). Thus, while the percentage contribution of the rhizosphere to total fluxes declined substantially with increasing depth in the soil (Fig. 3), this decline does not obviate the conclusion that rhizosphere processes are potentially a quantitatively important component of the heterotrophic C flux from soils.

Modeling exudation flux

Using the distribution of rhizosphere volume from the scaling exercise, MCNiP was used to estimate the mass-specific rates of root exudation needed to recreate the effect size for rhizosphere respiration in the meta-analysis (Table 3). Total exudation flux was 45 gC m^{-2} yr^{-1} at median parameter values. Given estimates of gross primary production (GPP) for temperate forests of ~1300 gC m^{-2} yr^{-1} (Turner *et al.*, 2003; Xiao *et al.*, 2004) and net primary production (NPP) of ~780 g C m^{-2} yr^{-1} (Huston & Wolverton, 2009), median estimates of exudation rate are ~4% and ~6% of GPP and NPP, respectively.

In addition to the estimate of C exudation, MCNiP simulations offer additional insights into the priming effect and the coupled cycles of C and N. In particular, there is clear evidence for priming induced losses of SOC (Fig. 6a) that are consistent with studies of elevated CO_2 where higher primary production results in greater C inputs to the soil but often no change or a decline in the quantity of SOC (Hungate *et al.*, 1997; Carney *et al.*, 2007; Lichter *et al.*, 2008; Talhelm *et al.*, 2009; Cheng *et al.*, 2012; Van Groenigen *et al.*, 2014).

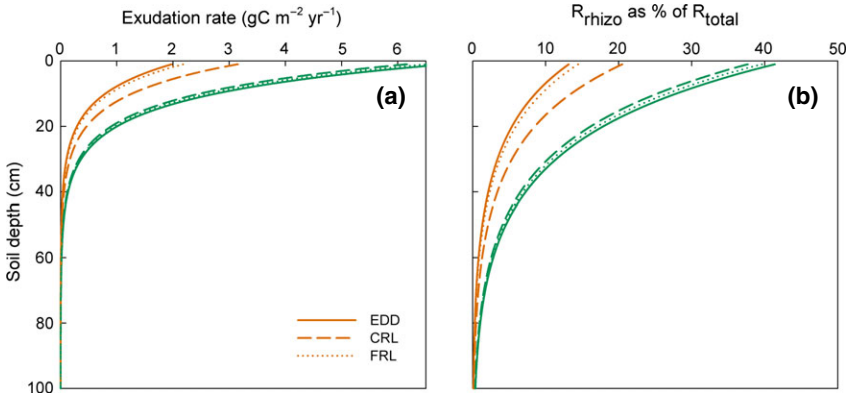

Fig. 5 (a) Exudation rate (gC m^{-3} soil growing season^{-1}) for each soil depth down to 1 m assuming a declining rate of exudation with depth. Paired colors represent estimation of exudation rate in low (red) and high (blue) parameterizations of exudation diffusion distance (solid), cumulative root length (dashed) and fine root length (dotted). (b) Rhizosphere respiration as a % of total respiration assuming a declining rate of exudation with depth. Paired colors represent estimation of percent rhizosphere respiration in low (red) and high (blue) parameterizations of exudation diffusion distance (solid), cumulative root length (dashed) and fine root length (dotted). Inset is the integral of exudation rate and percent rhizosphere respiration to 10-cm, 30-cm and 1-m soil depth.

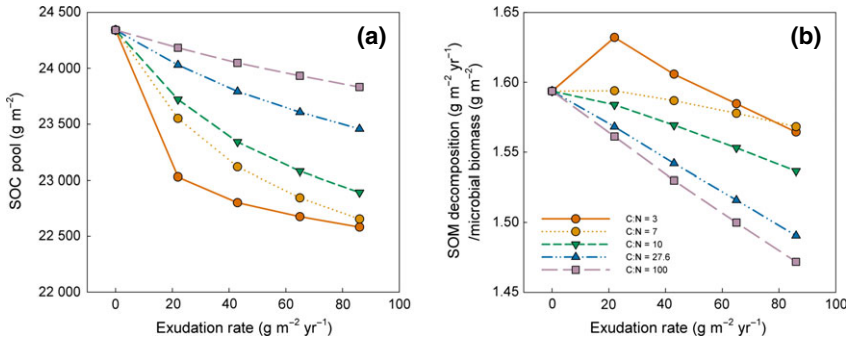

Fig. 6 (a) The size of the soil organic carbon pool down to 30 cm with different rates of exudation and C : N ratios ranging from 3–100. SOC pools decline with lower C : N ratio and higher rates of exudation. (b) The efficiency of SOM decomposition calculated as the quantity of SOM decomposed (mg cm^{-3} h^{-1}) divided by microbial biomass C (mg C cm^{-3}). If root exudate input C : N = 26.7, then efficiency declines with additional exudates. If root exudate input is more N rich (C : N < 7), microbial efficiency of SOM decomposition increases within a narrow range of inputs.

Beyond this qualitative agreement the model uncertainty in the exudation flux is associated with wide variation in the loss of SOC (Fig. 6a) that is related to the efficiency of SOM decomposition (Fig. 6b). The largest losses of SOC occur when the C:N ratio of exudates is <7 because of an increase in the efficiency of SOM decomposition, whereas SOC losses are dampened when exudate fluxes have C:N > 7 (Fig. 6a,b). Variation in the efficiency of SOM decomposition reflects the N constraint on exoenzyme synthesis in MCNiP. When exudates contain N, the N constraint on exoenzyme synthesis is alleviated, allowing for a large priming effect including an increase in the depolymerization of N from soil organic matter (Drake *et al.*, 2013b). The additional N is then taken up and allocated to growth and additional exoenzyme synthesis (Drake *et al.*, 2013a). When relatively little N is added in exudates, the priming effect still occurs but at lower levels and as a result of a larger microbial biomass rather than greater rates of SOM decomposition per unit microbial biomass.

Areas for future research

This study employed a three-pronged approach to quantify rhizosphere processes at the ecosystem scale (i.e., meta-analysis, rhizosphere scaling, simulation modeling). Collectively, these studies suggest that a relatively small proportion of C fixed is allocated to root exudation but that this flux has the potential for disproportionately large biogeochemical consequences. Admittedly, the magnitude of the effects reported here

are uncertain while the results reported here may be viewed with skepticism, it is precisely this skepticism that we hope will encourage new studies and model refinements by other investigators.

There are several areas where future research would greatly aid model development:

1. The meta-analysis results clearly indicate the rhizosphere is a biogeochemical hotspot. The data do not, however, provide any insight into the distribution of hot moments in the rhizosphere. How does microbial activity vary as a function of the quantity and timing of root inputs (*c.f.*, Herman *et al.*, 2006)?
2. How far do root exudates travel from the root surface and what determines this distance? The large range of values reported in the literature suggests that exudation diffusion distances are highly variable presumably owing to root and soil factors or the types of compounds that are exuded. The use of model systems and analysis tools (e.g., ^{11}C or ^{14}C labeling) could greatly aid in this respect.
3. What is the relationship between root order and exudation? Defining roots by size is convenient, but it does not always relate to function because species vary widely in their architecture, suberization and maturation (*c.f.*, Guo *et al.*, 2008; Valenzuela-Estrada *et al.*, 2008).
4. How does the timing of root production and turnover influence rhizosphere processes? Does exudation at particular times of the year result in greater effects on SOM decomposition and N mineralization? Models such as RADIX provide a framework for modeling root turnover (Gaudinski *et al.*, 2010), a recent analysis of root phenology can help understand the timing of root growth (Abramoff & Finzi, 2014), and simulation models where exudates are added in a temperature-dependent context (e.g., seasonal time scale) may begin providing insight (Davidson *et al.*, 2014). But, there is still a need for temporally resolved data and new methods to assay belowground production and turnover (*c.f.*, Strand *et al.*, 2008; Taylor *et al.*, 2013).
5. Given the prevalence of phosphorus (P) limitation to growth (Cleveland *et al.*, 2013), more work is needed to assess the consequences of enhanced exudation on P cycling. Exudates are likely to affect P cycling differently than N, as low molecular mass exudates can directly enhance P availability via chelation and pH-dependent changes in solubility (Lambers *et al.*, 2008). Further, phosphatase enzymes cleave ester-bonded P in SOM, and thus, elevated rhizosphere phosphatase activity will not affect SOM decomposition to the same degree as N-releasing exoenzyme activity (Dijkstra *et al.*, 2013). Given that phosphatase enzymes require N, however, it may be that more rapid N cycling in the rhizosphere also influences rhizosphere P cycling.

Conclusions

The ubiquity and magnitude of the effects in the meta-analysis demonstrate that rhizosphere processes are an important component of terrestrial element cycles and that resource investments by plants belowground exceed their cost, particularly in terms of nutrient uptake. Indeed, in the long-term, this must be true. The quantity of nutrients stored in plant biomass, especially in perennial ecosystems such as forests, exceeds that in microbial biomass often by orders of magnitude. The large majority of the nutrients plants acquire from the soil pass through the rhizosphere and may in fact be generated within the rhizosphere, a process that simultaneously affects C cycling. To the extent that root surfaces stimulate microbial activities while continuously exploring the soil, the total amount of N released from SOM is likely to have a large cumulative effect on element cycling over the lifetime of an individual root and across stand development. Given that root exudation and the activity of mycorrhizal fungi are increased by rising atmospheric CO_2 (Treseder, 2004; Alberton *et al.*, 2005) and rhizosphere inputs affect the apparent temperature sensitivity of SOM decomposition (Boone *et al.*, 1998; Zhu & Cheng, 2011), rhizosphere processes are likely to be an important control over element cycling and the response of ecosystems to global change.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Supplementary MCNiP Model figures.
Figure S2. A diagrammatic representation of the pools, fluxes and variables in the MCNiP model.
Table S1. Meta data for the studies that were suitable for meta-analysis
Table S2. Values for microbial biomass in rhizosphere and bulk soils.
Table S3. Values for microbial respiration in rhizosphere and bulk soils.
Table S4. Values for exoenzyme activity in rhizosphere and bulk soils.
Table S5. Values for gross and net N mineralization in rhizosphere and bulk soils.
Table S6. Values for SOM decomposition rates in planted and unplanted soils.
Table S7. Parameter values for MCNiP.
Appendix S1. Model description and equations
Appendix S2. Matlab Code for MCNiP simulation