META-ANALYSIS

Global patterns of root dynamics under nitrogen enrichment

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ABSTRACT

Aim Root production and turnover play a key role in regulating carbon (C) flow in terrestrial ecosystems. However, a general pattern reflecting the responses of roots to increasing nitrogen (N) input has yet to be described.

Location Global terrestrial ecosystems.

Methods We conducted a meta-analysis to assess the central tendencies of root production, turnover rate and standing crop with respect to the experimental addition of N. We evaluated the effect of the form of N, root diameter and climatic (mean annual temperature, MAT; mean annual precipitation, MAP), biotic (ecosystem type, plant type and forest stand age) and forcing factors (experimental duration, N addition rate and cumulative amount of N) on the variations in root response.

Results Globally, the addition of N significantly decreased root production and turnover rate but had only a minor impact on root standing crop. In different ecosystems, the three root variables exhibited heterogeneous responses to N enrichment. Additionally, root production and turnover rate responded distinctly to diverse forms of N. The responses of root production and turnover rate to the addition of N were generally positively correlated with MAT and MAP but negatively related to forest stand age and experimental duration. The response pattern of root standing crop was negatively affected by MAT, MAP and forest stand age. However, none of the three root parameters had any obvious correlations with N addition rate or cumulative amount of N.

Main conclusions Our results demonstrate that, on aggregate, the addition of N decreased root production and turnover rate at the global scale. These root response patterns and the regulatory factors can be incorporated into earth system models to improve the prediction of belowground C dynamics.

Keywords

Carbon (C) cycle, nitrogen (N) input, root production, root standing crop, root turnover, soil organic carbon.

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INTRODUCTION

Root production and turnover have dominant roles in terrestrial carbon (C) cycling (Matamala *et al.*, 2003). It is estimated that root production could contribute as much as 30–60% of global annual net primary production (NPP) (Jackson *et al.*, 1997; Hendricks *et al.*, 2006). Root production and turnover also have important effects on the rate of accrual of C in soil organic matter (Nie *et al.*, 2013), as well as water and nutrient cycling (Chen *et al.*, 2013b). Similar to other belowground processes, root dynamics may be altered by changes in the availability of soil nitrogen (N) (Nadelhoffer, 2000). Anthropogenic activities, such as the application of N fertilizer, fossil fuel combustion and legume cultivation, have roughly doubled the amount of N entering the biosphere over several decades (Galloway *et al.*, 2008), resulting in increased availability of soil N across various ecosystems (Lu *et al.*, 2011a). Therefore, examining how and to what extent additional N input affects root dynamics is

essential for a better understanding of the terrestrial C cycle under scenarios of increasing N deposition (Yuan & Chen, 2012).

Numerous individual studies have been conducted to examine how root dynamics, including production, turnover and standing crop, respond to the addition of external N. However, the results obtained from different experiments are highly variable. Among those studies, the addition of N may substantially stimulate (King *et al.*, 2002; Bai *et al.*, 2008), significantly inhibit (Kern *et al.*, 2004; Jourdan *et al.*, 2008) or have little influence on (Ostertag, 2001) root dynamics. A previous meta-analysis indicated that, in temperate forests, external N input had a minor impact on fine root production (Janssens *et al.*, 2010). However, the root standing C pool showed a significantly positive response to N input across all terrestrial ecosystems (Lu *et al.*, 2011b). While excluding croplands, Liu & Greaver (2010) observed minimal changes in root C input following the addition of N in natural ecosystems. Although these studies provided some evidence of the response patterns of root production and standing biomass to N enrichment, how root turnover responds to the experimental addition of N over a broad range remains unknown. Therefore, a comprehensive analysis is needed to understand the explicit patterns of the responses of root production, turnover and standing crop to experimental addition of N at the global scale.

Experimental conditions (e.g. the form of N and classification of root diameter) and a number of climatic (e.g. mean annual temperature, MAT; mean annual precipitation, MAP), biotic (e.g. ecosystem type, plant type and forest stand age) and forcing factors (e.g. experimental duration, N addition rate and cumulative amount of N) may influence the response of roots to the addition of N. Different forms of N fertilizer can exert different influences on root dynamics. For instance, Baldi *et al.* (2010) observed that the application of organic N significantly increased root production and lifespan in a nectarine (*Prunus persica* L.) orchard, while inorganic N had less effect on root dynamics. MAT and MAP are also of great significance in regulating the responses of roots to external N input because of the influence of climatic factors on plant above- and belowground C allocation (Mokany *et al.*, 2006). A recent study revealed that this allocation process was governed by allometric constraints on and trade-offs among the components of gross primary production, and the trade-offs were regulated by N availability, precipitation and temperature (Chen *et al.*, 2013a). Therefore, climatic factors may interact with N to regulate root production and further turnover or standing biomass. In addition, Aber *et al.* (1998) proposed that external N inputs initially stimulate root growth when ecosystems are N-limited, and have no influence on, or even a negative impact on, root production after N saturation. Consequently, the responses of root production and mortality to N addition may be time dependent and may also be influenced by the N application rate and the cumulative amount of N.

Nevertheless, how these factors regulate the responses of roots to N addition remains unclear.

Here, we conducted a meta-analysis to examine the effects of N addition on root production, turnover rate and standing crop across global terrestrial ecosystems using data from 83 peer-reviewed papers. We also assessed the effects of the form of N, root diameter and climatic, biotic and forcing factors on variations in response. The aims of the present analysis are: (1) to reveal general response patterns of root production, turnover rate and standing crop to experimental N addition at the global scale, and (2) to examine the influences of experimental conditions as well as climatic, biotic and forcing factors on the N-induced changes in root dynamics.

MATERIALS AND METHODS

Data compilation

An exhaustive literature survey of peer-reviewed publications was undertaken using the ISI-Web of Science (Thomson Reuters, New York, NY, USA), Google Scholar (Google Inc., Mountain View, CA, USA) and the China Knowledge Resource Integrated database (TsinghuaTongfang Knowledge Network Technology Co, Ltd, Beijing, China) to identify articles published before 2015. By searching these databases, we compiled a database of 83 published papers, including 119 observations of root production, 64 observations of root turnover rate and 134 observations of root standing crop in response to the experimental addition of N. (A list of the literature sources is given in Appendix 1 and the relevant information is shown in Table S1 in the Supporting Information.) To avoid bias in reference selection, the following six criteria were applied.

1. Field experiments were selected in which at least one of the target variables (root production, turnover rate or standing crop) was measured and N was directly applied.

2. For studies that examined the interactions of N addition with other global change factors (e.g. elevated CO_2, climate warming, changing precipitation, etc.), only data from the control and N addition plots were included.

3. Studies conducted at distinct sites and with different rates of N addition were treated as independent (Liu & Greaver, 2010); discrete studies performed in the same general area or research site were also assumed to be independent (LeBauer & Treseder, 2008).

4. If multiple measurements across several years were reported for a study, data from the most recent year were used, and if multiple sampling was conducted within one year, the average was calculated to provide a single estimate. Furthermore, some studies reported root variables at different soil depths. In such cases, we calculated the mean values as one data point.

5. Root turnover rate was either directly extracted from the selected papers or calculated by the inverse value of the root life span (Yuan & Chen, 2010) and the ratio of root

production to root standing crop when both parameters were recorded in the same papers (Gill & Jackson, 2000).

6. It is widely recognized that methodological approaches have an effect on root research (Eissenstat & Yanai, 2002). Where the studies used more than one method to estimate root production and turnover rate, data obtained from each method were treated as independent estimates (Gill & Jackson, 2000). Root diameter also influences root dynamics (McCormack & Guo, 2014), and so root variables reported for different diameters were also assumed to be independent (Gill & Jackson, 2000).

The raw data were extracted from the text, tables and figures of the published papers. When the data were presented graphically, the numerical data were obtained using Origin-Pro 8.0 (OriginLab, Northampton, MA, USA). Some background information was also collected, including the MAT, MAP, forest stand age, experimental duration and N addition rate. Among the collected studies, MAT ranged from −11.5 to 27.6 °C, and MAP extended from 98 to 4300 mm. The forest stand age and experimental duration ranged from 1 to 400 years and from 1 to 34 years, respectively. The N addition rate varied from 1 to 60 g m^{-2} year^{-1}. For studies that did not report geographical and climatic characteristics, information was obtained from alternative sources, including other publications from the same location and the global database at http://www.worldclim.org/ using longitude and latitude coordinates.

Meta-analyses

To evaluate the responses of root production, turnover rate and standing crop to N addition, the response ratio (RR) from each individual study was calculated as an index of the direction and magnitude of the effect of N. The RR, the ratio of the mean value of the chosen variable in the N addition group (X_t) to that in the control group (X_c), was calculated as a natural log response ratio: $RR = \ln(X_t/X_c) = \ln X_t - \ln X_c$ (Hedges *et al.*, 1999). Typically, individual observations are weighted by the inverse of the variance, assuming that individuals with a lower variance should be weighted more highly. Not all of the collected studies in our database reported the sampling variance (e.g. the standard deviation), but all reported the sample size. Thus, we weighted the RR by sample size, i.e. weight$_n = n_c n_t/(n_c + n_t)$, where n_c and n_t are the sample sizes for the control and treatment groups, respectively (Adams *et al.*, 1997). Under these conditions, higher weighting is given to well-replicated studies with larger sample sizes (Adams *et al.*, 1997). To avoid assigning relatively high weights to those studies that had multiple records from various sampling methods, root diameters or both, the weight$_n$ values from such studies were downweighted by multiplying by the inverse of the corresponding number of methods, diameters or their products (Chen *et al.*, 2013a).

Resampling techniques were used to calculate the mean effect size and 95% confidence interval (CI). Resampling

methods such as bootstrapping can generate their own distributions and are thus free from the distribution assumptions of parametric tests (e.g. a normal distribution) (Adams *et al.*, 1997). In many cases, this method may be more powerful when the obtained data violate the assumptions of parametric approaches (Adams *et al.*, 1997). The program METAWIN 2.1 (Sinauer Associates Inc., Sunderland, MA, USA) was used to calculate the mean RRs and the 95% bootstrap CI. If the 95% bootstrap CI values did not overlap with zero, a significant N-induced response was considered. Otherwise, N was considered to have no significant effect on those variables.

To test whether the various factors affect the magnitude of the response to N addition, we categorized all observations of root production, turnover rate and standing crop into five ecosystems, four plant types, six forms of N and five diameter classes. The five ecosystems included tropical forests, temperate forests, boreal forests, grasslands and tundra (Fig. S1). Forests were classified based on latitude, with tropical forests situated between 23.5° S and 23.5° N and boreal forests between 46° N and 66° N, with temperate forests including all those between the tropical and boreal forests (Yuan & Chen, 2012). Notably, in this analysis, all grassland root turnover data are from Inner Mongolia (Bai *et al.*, 2008; Li *et al.*, 2011) and all tundra root turnover data are from Toolik Lake, Alaska (Sullivan *et al.*, 2007; Nowinski *et al.*, 2008). Therefore, this limited data set may not be an accurate representation of all grassland and tundra ecosystems. The four plant types included broadleaf forests, conifer forests, mixed forests and grasses. The six forms of N included NH_4NO_3, NH_4^+–N, NO_3^-–N, urea, NH_4NO_3 + urea and other types of N fertilizer. Other types of N fertilizer usually included commercial fertilizer, slow-release fertilizer, balanced nutrient solutions, etc. Root diameter classes were categorized as 0.0–1.0 mm, 0.0–2.0 mm, 1.0–2.0 mm, 2.0–10.0 mm and >10.0 mm.

The sampling method has a significant affect on inferences made about root dynamics (Hendricks *et al.*, 2006). In our collected N addition experiments, minirhizotron, soil core and ingrowth core were the major sampling methods used for assessing the effects of N on root dynamics. Meanwhile, there are also three studies that used the C budgeting method to assess N-induced changes in root production. We divided the observations into those using 'high-quality' (i.e. minirhizotron) and 'low-quality' (i.e., non-minirhizotron) techniques for sampling root production and turnover rate in the analyses (Chen *et al.*, 2013a). Moreover, the method used to calculate root turnover rate may influence the results. In the collected studies, root turnover rate was calculated either by the inverse of the root lifespan or by the ratio of root production to standing crop. Hence, turnover rate was also divided into two groups based on the calculation method. The mean RR for each ecosystem, plant type, N form and root diameter was calculated across all methods, as well as minirhizotron and non-minirhizotron methods. To examine whether the RR differed among diverse ecosystems, plant types, N forms and root diameters, the total heterogeneity
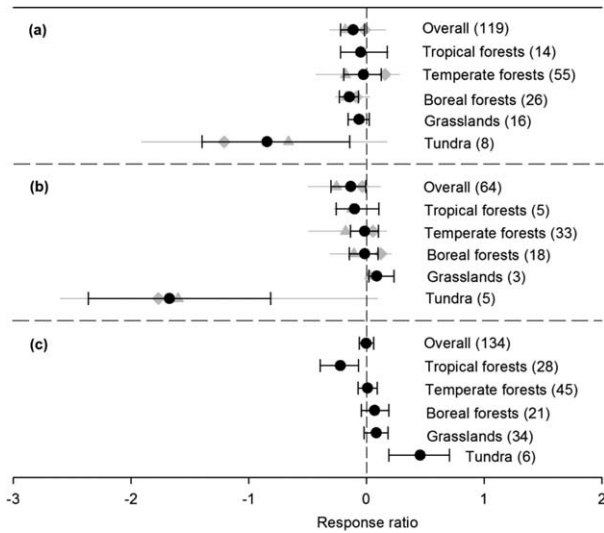
Figure 1 Effect of N addition on root production (a), turnover rate (b) and standing crop (c) for all ecosystems, tropical forests, temperate forests, boreal forests, grasslands and tundra. The black circles with error bars indicate the mean response ratios (RRs) with 95% bootstrap CIs across all sampling methods. The grey diamonds and triangles indicate the mean RRs from minirhizotron and non-minirhizotron methods, respectively. The vertical line is drawn at RR = 0. The sample size for each variable is shown in parentheses.

among groups (Q_t) was partitioned into within-group heterogeneity (Q_w) and between-group heterogeneity (Q_b). A significant Q_b suggests that the RRs differ among these experimental conditions (Hedges *et al.*, 1999). If none of the categorical groups displayed a significant Q_b, there was no statistical justification for further subdivision of the data. When there were fewer than two observations in a subgroup, that subgroup was excluded owing to a lack of statistical power.

Weighted least squares (WLS) regression analysis was performed to examine the relationships between the RRs of root production, turnover rate and standing crop, as well as climatic and forcing factors. The WLS regression analysis assumed that observations with larger weights provide more reliable information about the regression function than those with smaller weights. The weight$_n$ was used as the WLS weight in the analysis. Because the RR of the root turnover rate did not satisfy the assumption of normality, it was power-transformed before the analysis. All WLS regressions were conducted using SPSS 16.0 (IBM SPSS, Chicago, IL, USA).

RESULTS

Responses of root production, turnover rate and standing crop to N addition

Averaged across all studies, external N addition significantly decreased root production and turnover rate, but had no overall effect on root standing crop (Fig. 1). Roots in different ecosystems exhibited various responses to N addition (Table 1). Root production was inhibited by N addition in boreal forests

Table 1 Effect of N addition on between-group heterogeneity (Q_b) of root production, turnover rate and standing crop.

Categories*	Root production		Root turnover rate		Root standing crop	
	Q_b	*P*-value	Q_b	*P*-value	Q_b	*P*-value
Ecosystem type	3.66	<0.01	11.5	<0.01	0.38	<0.01
Plant type	0.05	0.98	0.14	0.75	0.35	0.14
N form	3.19	0.01	6.09	0.01	0.40	0.23
Root diameter	3.06	0.11	2.16	0.29	0.41	0.24

*Ecosystem type includes tropical forests, temperate forests, boreal forests, grasslands and tundra. Plant type includes broadleaf forests, conifer forests, mixed forests and grasses. N form includes NH_4NO_3, NH_4^+–N, NO_3^-–N, urea, NH_4NO_3 + urea and other types of N fertilizer. Root diameter is classified as 0.0–1.0 mm, 0.0–2.0 mm, 1.0–2.0 mm, 2.0–10.0 mm and >10.0 mm.

and tundra but was not significantly altered in tropical forests, temperate forests and grasslands (Fig. 1a). Root turnover rate displayed a positive response to N addition in grasslands, a negative response in tundra and a neutral response in tropical, temperate and boreal forests (Fig. 1b). N addition increased root standing crop in tundra, decreased it in tropical forests and had no significant impact on it in temperate forests, boreal forests and grasslands (Fig. 1c).

Different forms of N had a significant influence on root production and turnover rate (Table 1). The supply of NH_4NO_3 and NH_4^+–N fertilizers significantly inhibited root production, while other types of N fertilizer had only a minor influence on root production (Fig. 2a). Root turnover rate was repressed by NH_4NO_3 but stimulated by urea, while

Table 2 Effect of N addition on between-group heterogeneity (Q_b) of root production and turnover rate for minirhizotron and non-minirhizotron methods.

Categories*	Minirhizotron				Non-minirhizotron			
	Root production		Root turnover rate		Root production		Root turnover rate	
	Q_b	*P*-value	Q_b	*P*-value	Q_b	*P*-value	Q_b	*P*-value
Ecosystem type	3.52	<0.01	6.40	<0.01	1.16	0.33	4.99	0.02
Plant type	0.00	0.88	0.00	0.88	0.18	0.87	0.63	0.23
N form	3.21	<0.01	4.49	0.02	0.98	0.42	2.02	0.28
Root diameter	1.70	0.19	1.02	0.57	1.38	0.20	2.05	0.09

*Ecosystem type includes tropical forests, temperate forests, boreal forests, grasslands and tundra. Plant type includes broadleaf forests, conifer forests, mixed forests and grasses. N form includes NH_4NO_3, NH_4^+–N, urea, NH_4NO_3 + urea and other types of N fertilizer. Root diameter is classified as 0.0–1.0 mm, 0.0–2.0 mm, 1.0–2.0 mm, 2.0–10.0 mm and >10.0 mm.
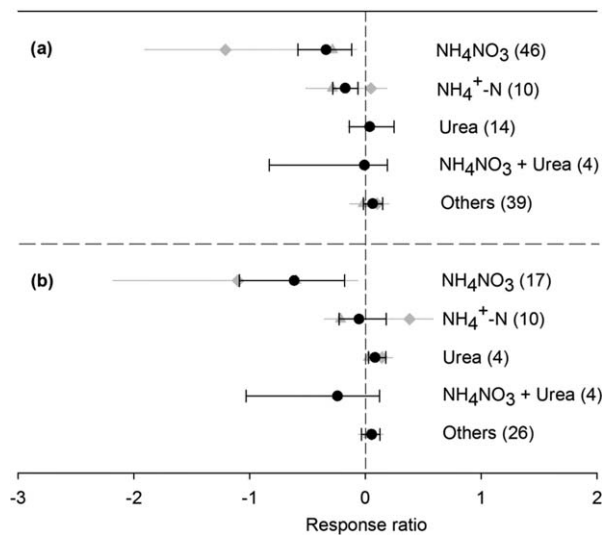
Figure 2 Effect of N addition on root production (a) and turnover rate (b) for various N forms, including NH_4NO_3, NH_4^+-N, urea, NH_4NO_3 + urea and other types of N fertilizer. The black circles with error bars indicate the mean response ratios (RRs) with 95% bootstrap CIs across all sampling methods. The grey diamonds and triangles indicate the mean RRs from minirhizotron and non-minirhizotron methods, respectively. The vertical line is drawn at RR = 0. The sample size for each variable is shown in parentheses.

the effects of the other forms of N were not pronounced (Fig. 2b). Since no study examined root production and only one reported root turnover rate responses to NO_3^-–N addition (see Table S1), the effect of NO_3^-–N, on both variables was excluded in the analysis. Other factors, such as plant type and root diameter, did not significantly influence root dynamics (Table 1). The method of root sampling (i.e. minirhizotron or non-minirhizotron) generally did not alter the direction of root production and turnover rate in response to N addition among the various ecosystem types and N forms, except for root production in temperate forests and turnover rate in temperate and boreal forests, as well as the influence of NH_4^+–N fertilizers on both root production and turnover rate (Table 2; Figs 1 & 2). Moreover, the method for calculating root turnover rate did not significantly affect the RR of root turnover rate in our analysis ($P = 0.10$).

Factors regulating the responses of root production, turnover rate and standing crop to N addition

Climatic, biotic and forcing factors influenced the direction and magnitude of root responses to N addition. The N-induced changes in root production significantly increased with MAT ($r^2 = 0.18$, $P < 0.01$; Fig. 3a) and MAP ($r^2 = 0.13$, $P < 0.01$; Fig. 3b) but decreased with forest stand age ($r^2 = 0.12$, $P < 0.01$; Fig. 3c) and experimental duration ($r^2 = 0.13$, $P < 0.01$; Fig. 3d). However, the RR of root production did not show any significant correlations with the rate of N addition or the cumulative amount of N (Fig. 3e,

f). Similar to root production, the RR of root turnover rate exhibited significantly and marginally positive correlations with MAT ($r^2 = 0.19$, $P < 0.01$; Fig. 4a) and MAP ($r^2 = 0.06$, $P = 0.06$; Fig. 4b) and negative correlations with forest stand age ($r^2 = 0.09$, $P = 0.03$; Fig. 4c) and experimental duration ($r^2 = 0.19$, $P < 0.01$; Fig. 4d). There were no obvious correlations of the RR of root turnover rate with the N addition rate or the cumulative amount of N (Fig. 4e, f). The standing crop RR significantly declined with MAT ($r^2 = 0.12$, $P < 0.01$; Fig. 5a), MAP ($r^2 = 0.08$, $P < 0.01$; Fig. 5b) and forest stand age ($r^2 = 0.11$, $P < 0.01$; Fig. 5c) but did not trend with experimental duration, N addition rate or the cumulative amount of N (Fig. 5d–f).

Separate analysis of root production by different methods indicated that minirhizotron and non-minirhizotron techniques had a minor influence on these relationships, except that no significant correlation was found between the RR of root production from the minirhizotron method with experimental duration (Fig. 3d). As for the RR of root turnover rate, only MAT has a positive affect on it in both methods (Fig. 4a); a negative impact was only observed with experimental duration for the RR derived from the non-minirhizotron method (Fig. 4d).

DISCUSSION

Reduced root production and turnover rate under N addition

Based on the data collected from global N addition experiments, our analysis demonstrated that additional N input significantly decreased root production (Fig. 1a). Generally, experimental addition of N causes a sudden large increase in the availability of soil N (Burton *et al.*, 2000; Lu *et al.*, 2011a). Therefore, it would be expected that, in N-limited ecosystems, the addition of N reduces C partitioning to roots. This response is in accordance with the theories of 'law of the minimum' (von Liebig, 1841) and 'optimal C allocation' (Chapin *et al.*, 1987), which suggest that C allocation is a function of limitations: if a plant is limited by N, it should invest proportionally more C to roots to acquire more N. If N is not limiting, then the plant should not necessarily increase the proportion of C to roots. However, it is unknown whether the ecosystems in our analysis are N-limited or not. To test this, we searched the studies that reported aboveground NPP (ANPP) in our database and found that the addition of N significantly increased ANPP by 36.8%, supporting the assumption that the majority of terrestrial ecosystems are N limited (LeBauer & Treseder, 2008; Lee *et al.*, 2010). Therefore, it is reasonable to state that addition of N decreased the proportion of C allocated to roots, as observed in our analysis.

Root turnover rate was also reduced by the addition of N (Fig. 1b). This may be best explained by a cost–benefit relationship, which suggests that roots may be maintained as long as the benefit of acquiring nutrients exceeds the C cost of keeping them alive (Burton *et al.*, 2000; Eissenstat & Yanai, 2002). Increasing the availability of soil N generally leads to a higher rate of uptake of N by roots and also greater
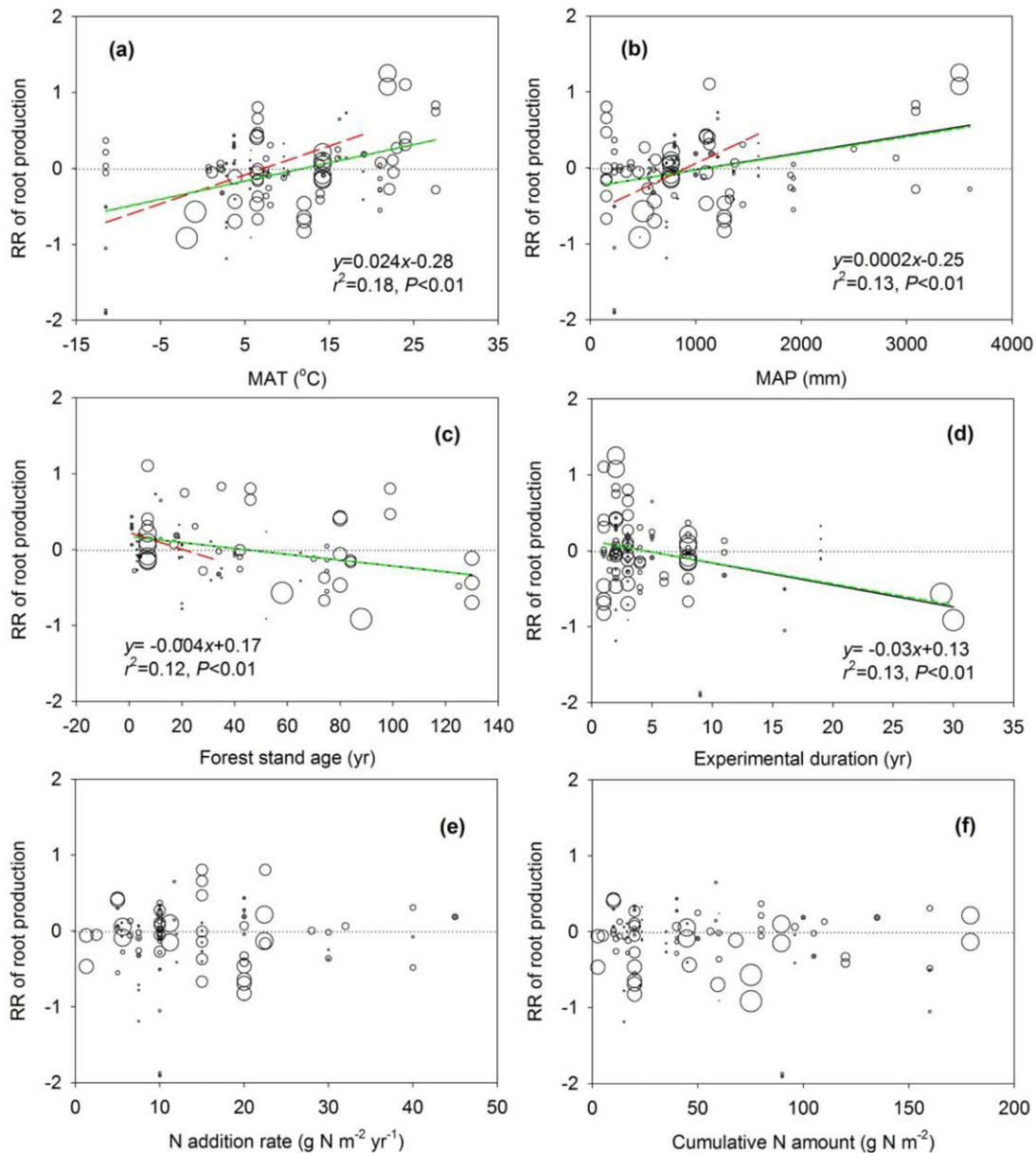
Figure 3 Bubble plots showing the relationships of the response ratio (RR) of root production with MAT (a), MAP (b), forest stand age (c), experimental duration (d), N addition rate (e), and cumulative N amount (f) across all N addition experiments. Grey bubbles indicate data from the minirhizotron method, open bubbles indicate data from non-minirhizotron methods, and the size of the bubble is the relative weight of the effect size (RR) in the weighted least squares (WLS) regression. Larger bubbles indicate study outcomes that contributed a greater overall weight in WLS regressions. Solid lines, long and short dashed lines are regression curves for the data from all methods, minirhizotron and non-minirhizotron methods, respectively. The horizontal dotted lines indicate RR = 0. MAT, mean annual temperature; MAP, mean annual precipitation.

metabolic activity (Minchin *et al.*, 1994; Bai *et al.*, 2008). Therefore, root activity remains high until the available N in the soil is depleted; hence, roots located in nutrient-rich soil have longer life spans and lower turnover rates (Burton *et al.*, 2000). However, an increased root N content may lead to more frequent grazing and infection by soil herbivores and pathogens, thus increasing the possibility of root mortality (Chen & Brassard, 2013; McCormack & Guo, 2014). Mycorrhizae can reduce the susceptibility of fine roots to soil

pathogens and herbivores, and increase root life span (Langley *et al.*, 2006). Although the addition of N generally reduces root mycorrhizal infection on a broad scale (Treseder, 2004), the influence of mycorrhizae on root lifespan is related to the diverse fungal species or types inducing different effects in plant roots (McCormack & Guo, 2014). Regardless of this, in our analysis a cost–benefit relationship may override other factors in explaining the response of root turnover to N addition, but further studies are needed to elucidate the
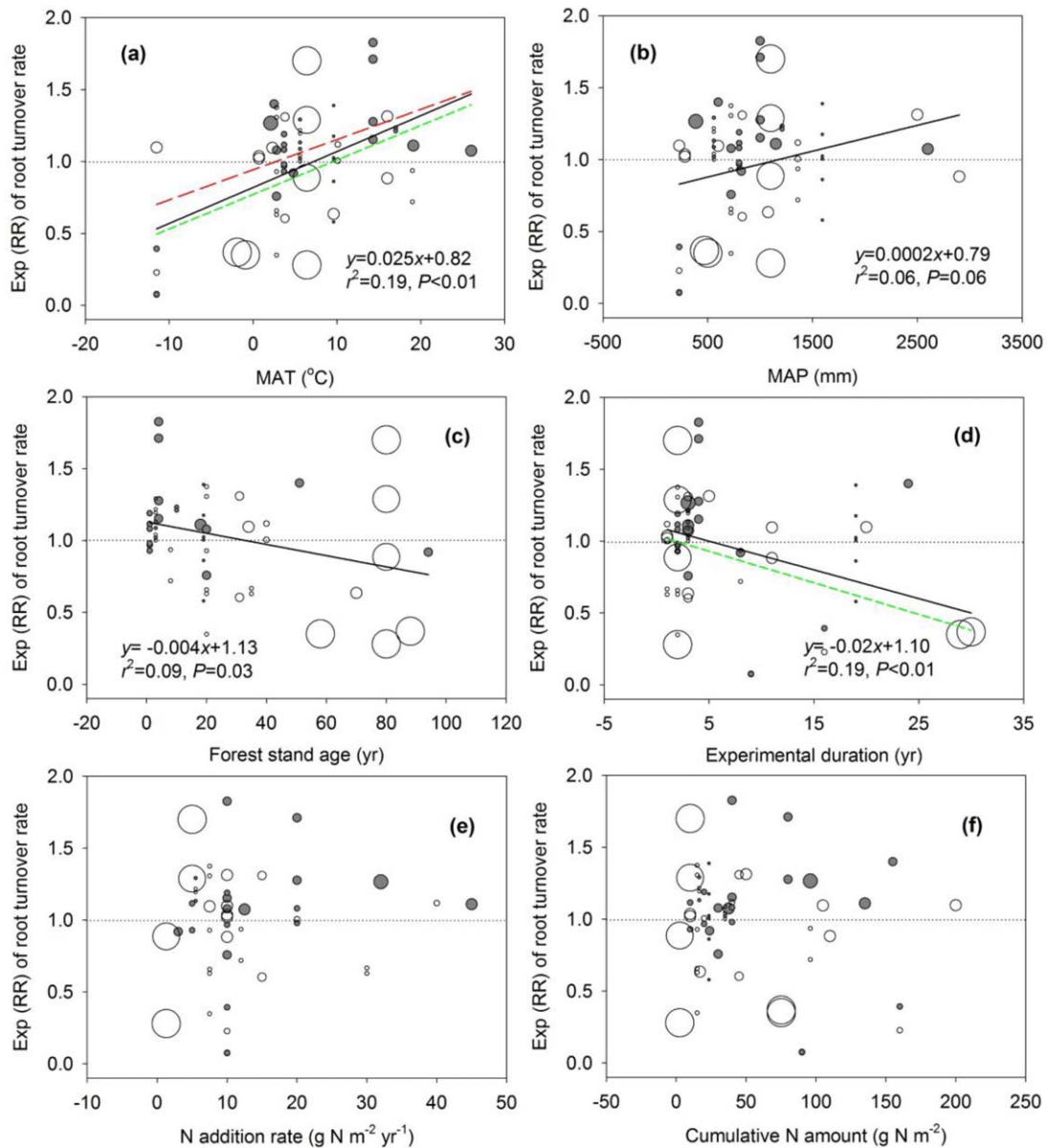
Figure 4 Bubble plots showing the relationships of the response ratio (RR) of root turnover rate with MAT (a), MAP (b), forest stand age (c), experimental duration (d), N addition rate (e), and cumulative N amount (f) across all N addition experiments. Grey bubbles indicate data from the minirhizotron method, open bubbles indicate data from non-minirhizotron methods, and the size of the bubble is the relative weight of the effect size (RR) in the weighted least squares (WLS) regression. Larger bubbles indicate study outcomes that contributed a greater overall weight in WLS regressions. Solid lines, long and short dashed lines are regression curves for the data from all methods, minirhizotron and non-minirhizotron methods, respectively. Note that the RRs were power-transformed before analysis. The horizontal dotted lines indicate RR = 1. MAT, mean annual temperature; MAP, mean annual precipitation.

in-depth mechanisms that control root turnover under altered soil N availability.

Responses of root dynamics to the addition of N among diverse ecosystems and N forms

Diverse root responses to additional N were observed across biomes (Fig. 1). However, root production, turnover rate and standing crop did not change synchronously following the addition of N at the ecosystem scale. For example, boreal forests exhibited a negative response of root production to the addition of N, but there were no changes in either root turnover or standing crop in response to N enrichment. Meanwhile in tropical forests, N addition did not significantly affect root production or turnover but considerably inhibited standing crop (Fig. 1a, b). This is probably because (1) forests generally allocate more C to aboveground biomass than to roots (lower root to shoot ratio, R/S) (Mokany *et al.*,
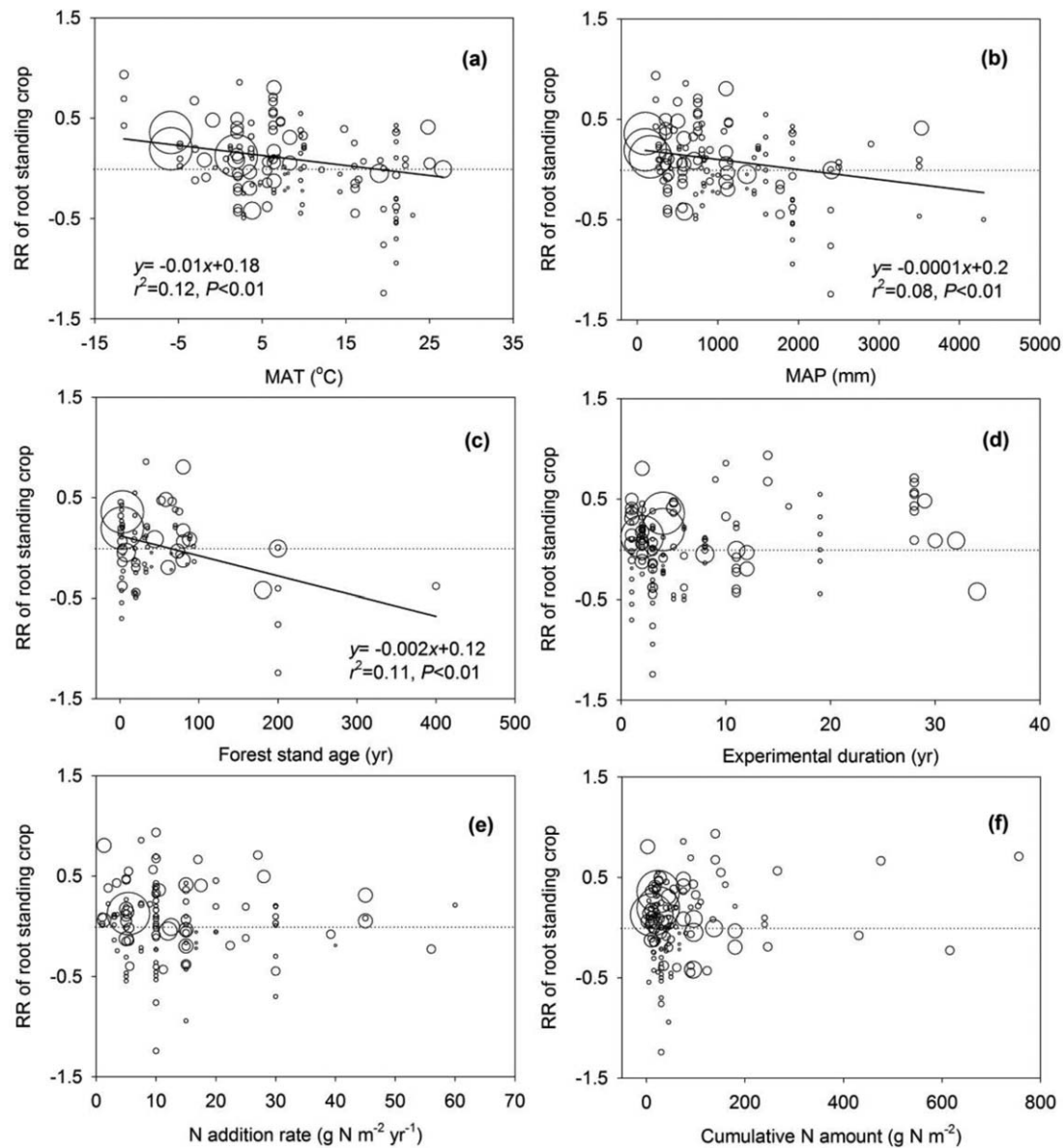
Figure 5 Bubble plots showing the relationships of the response ratio (RR) of root standing crop with MAT (a), MAP (b), forest stand age (c), experimental duration (d), N addition rate (e), and cumulative N amount (f) across all N addition experiments. The size of the bubble is the relative weight of the effect size (RR) in the weighted least squares (WLS) regression. Larger bubbles indicate study outcomes that contributed a greater overall weight in WLS regressions. The horizontal dotted lines indicate RR = 0. MAT, mean annual temperature; MAP, mean annual precipitation.

2006; Peng & Yang, 2016) and, thus, fine root dynamics in forests may be less responsive to N enrichment and difficult to detect, particularly compared with tundra (Fig. 1); (2) in our database, the same set of observations were not used for each analysis, i.e. some studies only reported root production, while others reported root turnover rate or standing crop (Appendix S1). This mismatched reporting of results from individual studies may erroneously indicate asynchronous responses of roots to N addition in the same ecosystems, especially in studies with small sample sizes (Janssens et al., 2010; Zhou et al., 2014).

Different forms of N influenced RRs of root production and turnover in response to N addition. Only the application of inorganic N tended to decrease root production and turnover rate (Fig. 2). One possible reason for this pattern is that increases in nitrate ions would reduce lateral root growth because NO_3^-–N may play a role in generating the inhibitory signal (Zhang et al., 1999; Ho et al., 2009). However, very few studies compared the effects of organic and inorganic N on root dynamics (Baldi et al., 2010), and the underlying mechanisms of how various forms of N regulate root growth are still unclear. Therefore, more studies are needed to better

understand the mechanisms underlying the distinct responses of root production, turnover and standing crop to different forms of N.

Effects of environmental factors on the magnitude of N-induced root dynamics

Climatic factors (i.e. MAT and MAP) regulated the responses of roots to the addition of N at the global scale. The response of root production to N addition was positively correlated with MAT and MAP (Fig. 3a, b). A possible reason is that the response of ANPP to N addition increases with increasing MAT and MAP (LeBauer & Treseder, 2008; Lee *et al.*, 2010). Following N addition, to acquire sufficient amounts of the other mineral nutrients needed for aboveground growth plants presumably also need to allocate more newly assimilated C to roots (Zhou *et al.*, 2014), thus leading to positive correlations of the N-induced changes of root production with MAT and MAP. The RR of root turnover rate showed a pattern similar to that of the RR of root production with climatic factors (Fig. 4a, b). Potential explanations may include the following. First, in terms of nutrient absorption, plant growth and N uptake increase with the addition of N (LeBauer & Treseder, 2008; Lee *et al.*, 2010; Lu *et al.*, 2011a). When temperature and water become limited, roots need to live as long as possible to acquire more N according to a cost–benefit relationship, thus reducing the turnover rate (Burton *et al.*, 2000; Eissenstat & Yanai, 2002). Second, from the perspective of respiration, root maintenance costs are comparably higher in warm and humid sites than in cold and dry regions (Hendrick & Pregitzer, 1993). Increasing the availability of N increases the tissue N concentration and generally results in higher root respiration (Reich *et al.*, 2008; Burton *et al.*, 2012). Therefore, sites with high MAT and MAP may have greater root turnover and decomposition rates under conditions of N enrichment owing to the high resource cost of maintenance respiration.

Forest stand age and experimental duration are also important factors that affect root dynamics in response to N addition. Mature forests are generally considered to have relatively complete root systems that would be more likely to exhibit neutral or negative responses to N, while young and rapidly expanding stands would be more likely to show a strong positive response to the addition of N (Chen & Brassard, 2013). Our results generally support this assumption, showing a negative correlation of RRs for root production, turnover rate and standing crop with forest stand age (Figs 3c, 4c & 5c). A similar response pattern of belowground C cycling was also reported by Janssens *et al.* 2010. The N-induced changes in root production and turnover rate were also negatively correlated with experimental duration (Figs 3c & 4c). This pattern can be potentially explained by changes in soil conditions (e.g. decreased soil pH and exchangeable base cations, and increased exchangeable aluminium) under long-term N input, which would result in unfavourable conditions for root growth (Bobbink *et al.*, 2010; Phoenix *et al.*, 2012).

Implications for understanding belowground C dynamics under N enrichment of ecosystems

The current analysis attempts to comprehensively evaluate the responses of root production, turnover rate and standing crop to changes in soil N availability from global N experiments. Our findings have three important implications for understanding belowground C dynamics under N enrichment of ecosystems. First, the decreased turnover rate of root production in response to N addition implies a limited contribution of C inputs from the roots to produce additional soil C sequestration under increasing N deposition. Second, the distinct root responses among various ecosystems and forms of N should be considered in future modelling and experimental studies to gain a better understanding of root dynamics under conditions of N enrichment. Third, the relationships between the N-induced changes in root dynamics and climatic and biotic factors (MAT, MAP, forest stand age and experimental duration) can be incorporated into earth system models to improve the prediction of belowground C dynamics. Overall, the responses of root dynamics to N addition and their correlations with climatic, biotic and forcing factors, as revealed in this study, provide valuable insights into the patterns and control of belowground C allocation and transformation, which should not be overlooked when predicting the responses of ecosystems to global change (Yuan & Chen, 2012; McCormack *et al.*, 2013).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Supporting information.
Table S1. Experimental conditions, climatic and biotic variables in papers from which the data were extracted for this meta-analysis.
Figure S1. Global distribution of N addition experiments included in this meta-analysis.
Figure S2. Bubble plots showing the relationships of the response ratios of root production, turnover rate and standing crop with latitude across all N addition experiments.

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APPENDIX 1: DATA SOURCES

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