



Fine-root functional trait response to nitrogen deposition across forest ecosystems: A meta-analysis

Xiaoxiang Zhao^{a,b}, Qiuxiang Tian^{a,c}, Lin Huang^{a,b}, Qiaoling Lin^{a,b}, Junjun Wu^{a,c}, Feng Liu^{a,c,*}

^a Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, China

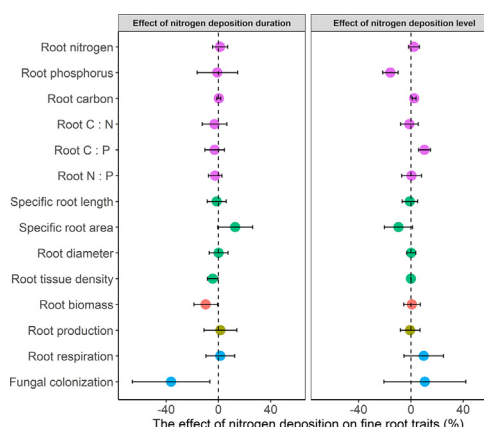
^b University of Chinese Academy of Sciences, Beijing 100049, China

^c Center of Plant Ecology, Core Botanical Gardens, Chinese Academy of Sciences, Wuhan, China

HIGHLIGHTS

- We conducted a meta-analysis to synthesize the effects of nitrogen (N) deposition on fine root traits of woody plants.
- N deposition mainly affected root nutrient content and stoichiometry.
- N deposition effects on fine-root biomass decreased with N deposition duration, especially under high deposition.
- The effect of N deposition on fine root diameter decreased with mean annual temperature and mean annual precipitation.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Zhaozhong Feng

Keywords:

Fine root traits
Root biomass
Root diameter
N deposition duration
N deposition level
Abiotic factors

ABSTRACT

Nitrogen (N) deposition has complex effects on vegetation dynamics and nutrient cycling in terrestrial ecosystems. However, how N deposition alters fine root traits remains unclear in forest ecosystems. Here, we carried out a synthesis based on 890 paired observations of 14 fine root traits from 79 articles to assess the effects of N deposition on fine root traits. The results showed that N deposition mainly affected root nutrient content and stoichiometry. Specifically, N deposition increased the root N content, root carbon: phosphorus (C:P) and root nitrogen: phosphorus (N:P) ratio, but decreased the root P content and root C:N ratio. Moreover, N deposition increased fine root respiration, but had no significant effect on other root morphological and physiological traits. N deposition effects on fine root biomass, root tissue density and fungal colonization decreased with N deposition duration. Compared to fine root P content, N deposition effects on fine root C content and C:P ratio increased with N deposition level. Moreover, the interaction between N deposition level and duration significantly affected fine root biomass. N deposition effects on fine-root biomass decreased with greater N deposition duration, especially in high N deposition experiments. Moreover, the effect of N deposition on root diameter decreased with mean annual temperature and mean annual precipitation. N form, forest type and soil depth significantly affect the effect of N deposition on fine root C:P. Therefore, the effects of N deposition on fine root traits were not only determined by N deposition level, duration and their interactions, but also regulated by abiotic factors. These findings highlight the diverse responses of fine root traits to N deposition have strong implications for forest ecosystems soil carbon stocks in a world of increasing N deposition associated with decreased root-derived carbon inputs and increases in fine-root respiration.

* Corresponding author at: CAS Key Laboratory of Aquatic Botany and Watershed Ecology, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, China.
E-mail address: liufeng@wbcas.cn (F. Liu).

1. Introduction

Anthropogenic activities have greatly changed nutrient cycling in terrestrial ecosystems, especially the nitrogen (N) cycle at the global scale (Vitousek et al., 1997). In the past decades, atmospheric N deposition in terrestrial ecosystem has sharply increased (Galloway et al., 2008; Reay et al., 2008), which caused a large amount of N entering in terrestrial ecosystems (Reay et al., 2008; Mo et al., 2008). N deposition not only affects species composition, plant growth and carbon allocations (Bobbink et al., 2010), but also ecosystem C and nutrient cycles (Chapin et al., 2009; Lu et al., 2014; Yuan and Chen, 2015; Lu et al., 2018; Tian et al., 2019). Forest ecosystem covers around 30 % of the global surface area and sequesters >70 % of total C of terrestrial ecosystems (Cai and Chang, 2020). Increasing N deposition will pose strong threats to forest biodiversity and its ecosystem function (Galloway et al., 2004; van Groenigen et al., 2017; Bobbink et al., 2010). However, previous studies associated in N deposition mostly focused on aboveground processes, how belowground processes of forest ecosystems response to N deposition remain relatively unknown.

Fine root (diameter ≤ 2 mm) is the key plant organ for water and nutrients acquiring (Cornelissen et al., 2003; Weemstra et al., 2016; Li et al., 2017). Fine root functional traits are attributes related to its morphology, chemistry and physiology, which are the results of long-term plant adaptation and response to the environment (Freschet et al., 2021). Moreover, fine root biomass turnover accounts for approximately 30 % of the net primary productivity at the global scale (Jackson et al., 1997) and is a dominant organic C input into soil (Adamczyk et al., 2019; Keller et al., 2021). Many studies have indicated that N deposition has significant effects on fine root functional traits and fine root biomass, which potentially affect carbon and nutrient cycles. Therefore, exploring the responses of fine root traits of forest ecosystems to N deposition is central to predicting the response of forest ecosystems to N deposition.

In past decades, field experiments of N addition have been widely used to study fine root traits response to N deposition, but no consistent conclusion has been reached for woody plants. Generally, fine root C:N ratio of woody plants decreased with N deposition due to the increased soil N availability and enhanced plant N absorption (Li et al., 2015; Ma et al., 2021). For the morphological traits, some studies have shown that N deposition decreased fine root diameter and increased specific root length (SRL) (Wang et al., 2013; Wang et al., 2019), which suggested that fine roots can regulate their morphological traits to adapt N deposition. However, other studies showed that N deposition had no significant effects on fine root morphological traits (Li et al., 2015; Ma et al., 2021). The responses of N deposition on fine root biomass and production are also inconsistent since negative (Nadelhoffer, 2000; Hendricks et al., 2006; Jourdan et al., 2008), positive (Kou et al., 2018) or no significant responses (Peng et al., 2017) have all been observed. These inconsistencies results might be attributed to different N deposition level and the duration of N deposition. However, how N deposition level, the duration of N deposition and their interactions affect fine root traits response to N deposition in forest ecosystems has been rarely evaluated at the global scale.

N deposition level and N deposition duration affect fine root traits. A lower level of N deposition has been shown to cause higher root tissue density (RTD) (Gong and Zhao, 2019), while higher N levels had the opposite effect (Wang et al., 2018). Meanwhile, fine root biomass commonly decreased after short-term N deposition (Mo et al., 2008), and increased after long-term N deposition (Ostertag, 2001). While, in a temperate forest, fine root biomass had no significant change after 15-year N deposition with a low N deposition level ($3 \text{ g N m}^{-2} \text{ yr}^{-1}$) (Burton et al., 2012). These results indicate that N deposition level and duration have interaction effects on fine root traits. Given the various combinations of natural N deposition levels and deposition durations across the globe (Ackerman et al., 2019), a better understanding of their joint effects on fine root traits would improve our ability to accurately predict carbon and nutrient cycles under future N deposition.

The effects of N deposition on fine root traits could vary with climate factors (e. g. mean annual temperature and mean annual precipitation).

Since different biomes have distinct climate conditions, the effects of N deposition on fine root traits can be different among biomes (Vogt et al., 1996). N deposition increased fine root biomass in boreal forest, but had no effect in other forest ecosystems (Li et al., 2015). Meanwhile, N deposition increased fine root diameter in boreal forests (Yan et al., 2017), but had no effect in subtropical bamboo forests (Chen et al., 2017). Assessing how climate factors regulate the effects of N deposition on fine root traits is critical to predict the impact of N deposition on root dynamics and soil C cycles in different biomes.

Two previous studies have been conducted to explore the effect of N deposition on fine root traits (Li et al., 2015; Ma et al., 2021), and these studies have improved our understanding of fine root trait expression under N deposition. But these studies didn't disentangle the effects of N deposition from different forest ecosystem types, N forms and soil depths, and didn't discuss the effects of N deposition level and N deposition duration on fine root traits. To comprehensively understand the relationships between fine root traits of woody plants and N deposition under natural conditions, we conduct a meta-analysis with newly reported studies and a larger number of fine root traits (14 traits).

We hypothesized that (1) N deposition could significantly affect fine root nutrient content and stoichiometric ratios due to the enhanced plant N absorption; (2) fine root biomass decreased with N deposition duration, and the decreasing trend was much stronger at higher N deposition, which could be a result of enhanced soil environmental stress; and (3) the effects of N deposition on fine root traits decreased with MAT due to the relatively higher N limitation in temperate forest and higher P limitation in tropical forest.

2. Materials and methods

2.1. Data collection

We collected publications through the Web of science (www.isiknowledge.com) and China National Knowledge Infrastructure (CNKI; www.cnki.net) before March 2021. The search terms were as follows: ("nitrogen addition" OR "nitrogen deposition" OR "nitrogen fertilization" OR "nitrogen enrichment" OR "nitrogen application" OR "nitrogen elevated" OR "nitrogen supply" OR "nitrogen input") AND ("root" OR "fine root" OR "belowground") AND ("biomass" OR "nitrogen" OR "phosphorus" OR "carbon" OR "stoichiometric ratio" OR "diameter" OR "morphology" OR "production" OR "respiration" OR "area" OR "physiology" OR "fungal colonization"). Afterward, we screened the articles according to the following criteria: (1) only forest ecosystems (woody plants) were considered; (2) only fine roots (diameter ≤ 2 mm) were considered; (3) only field manipulative experiments were included, greenhouse and pot experiments were excluded; (4) if a study had multifactorial treatments (e.g., warming, precipitation change, multiple nutrient addition), only the control and N addition treatments were considered; (5) the articles should reported the mean value, standard deviation and number of replications for the control and treatments or these data can be retrieved directly from graphs using GetData Graph Digitizer (version 2.25).

In our dataset, we collected 14 fine root traits: root N content, root phosphorus (P) content, root C content, root C:N ratio, root C:P ratio, root N:P ratio, specific root length (SRL), root tissue density (RTD), specific root area (SRA), root diameter, root production, root biomass, root respiration and fungal colonization. Root biomass and root production were estimated either by a soil auger or by ingrowth core. The morphological trait of fine roots (such as diameter and area) was scanned by scanner and then calculated by WinRHIZO Pro (Regent Instruments, Quebec, Canada) or other software (e.g. ImageJ).

Data associated in N deposition level ($\text{N kg ha}^{-1} \text{ yr}^{-1}$), N deposition duration (year^{-1}), background N deposition and forest types were also collected. The forest was classified into four different forest types (tropical forest, subtropical forest, temperate forest and boreal forest) according to the information provided in each study. We also collected the geographic coordinates (latitude and longitude), mean annual temperature (MAT, °C)

and mean annual precipitation (MAP, mm yr⁻¹) for each study. Based on the geographic locations, any missing MAT or MAP data were extracted using the raster R package from WorldClim version 2 (Fick and Hijmans, 2017).

2.2. Data analysis

The overall effects of N deposition on fine root traits were evaluated using the log-transformed response ratio (lnRR) as the effect size. The equation is:

$$\ln RR = \ln (X_t/X_c) = \ln X_t - \ln X_c \quad (1)$$

(Hedges et al., 1999) where X_t and X_c are the mean values of a fine root traits in the N deposition treatment and control, respectively. The lnRR and its CIs (95 %) were transformed into percentages as effect size according to:

$$\text{Effect size (\%)} = (e^{\ln RR} - 1) \times 100 \% \quad (2)$$

To evaluate the effects of N deposition level, N deposition duration and forest type on the N response for each fine root trait we then constructed a complete linear mixed effect model. This model was in the following structure:

$$\ln RR = \beta_0 + \beta_1 L + \beta_2 D + \beta_3 Z + \beta_4 L \times D + \beta_5 L \times Z + \beta_6 D \times Z + \beta_7 L \times D \times Z + \pi_{\text{study}} + \varepsilon \quad (3)$$

where β_n (n from 0 to 7) are coefficients, L is the N deposition level, D is the N deposition duration, Z is the forest type, π_{study} is each individual “study” as a random factor, and ε is the sampling error. In this model, we scaled L and D (observed values minus the mean and divided by one SD) to better compare fine root trait responses to L and D (Chen and Chen, 2019; Chen et al., 2020; Wang et al., 2021). As a result, in the mixed effect model, β_0 was the overall lnRR for fine root trait responses to N deposition at the mean levels of L and D (Cohen et al., 2013; Wang et al., 2021), and β_1 and β_2 were the effect sizes of fine root trait responses to L and D , respectively. We used maximum likelihood (ML) in the *lme4* package to fit the linear mixed model. In this linear mixed model, the $W_{\text{response ratio}}$ was considered as the weight for each study in the function of “*lmer*” in *lme4* (Bates et al., 2017) because meta-analysis should consider the weight of replications in each study when calculate the effect size (Ma and Chen, 2016; Wang et al., 2021). More importantly, weighting based on sampling variances could assign extreme importance to only a few individual observations, and consequently average lnRR would be determined predominantly by a small number of studies (Wang et al., 2021). Thus, the weights were calculated based on previous studies (Chen and Chen, 2019; Chen et al., 2020; Wang et al., 2021):

$$W_{\text{response ratio}} = (N_c \times N_t) / (N_c + N_t) \quad (4)$$

where the $W_{\text{response ratio}}$ is the weight associated with each lnRR and N_c and N_t are the replication numbers for the control and the N deposition treatment, respectively.

After creating the complete mixed model, we selected the most parsimonious model using the function “*dredge*” in the *MuMin* package (Barton, 2018). The model selection criteria were as follows: (1) the model should retain the N deposition level (L) and N deposition duration (D) to test their effects on fine root traits; (2) the model with the lowest AIC value was chosen as the most parsimonious model; and (3) forest types were excluded in all models (Wang et al., 2021) as L and D were key aspects of the N deposition to be tested. Publication bias was examined by a funnel of test asymmetry on our mixed effect models (Pellegrini et al., 2018). There was no significant publication bias in any tests (Table S5), which suggested no publication biases that might have prejudiced our results toward significant effects (Peng and Chen, 2021).

To graphically illustrate whether the effect of N deposition duration on lnRR differs with N deposition level, we explored the linear relationships between N deposition duration and the effect size of fine root traits at

different N deposition levels. N deposition levels were divided into low (<100 kg N ha⁻¹ yr⁻¹), medium (≥ 100 and <200 kg N ha⁻¹ yr⁻¹), and high (≥ 200 kg N ha⁻¹ yr⁻¹) levels following Li et al. (2015). Moreover, we also explored the relationship between the N deposition level and the effect size of the N deposition level on fine root traits when they were significant.

To evaluate how climate and other variables influence the effects of N deposition on fine root traits, we used a linear mixed model in the *lme4* package. The MAT, MAP, forest type, N form and soil depths was fixed factor and each study was a random factor. Pearson correlation analyses were also conducted to quantify the relationships between lnRR and MAT or MAP. Moreover, mixed model was also used to evaluate the effect of background N deposition on the effect size of N deposition on fine-root traits. The background nitrogen deposition was treated as a fixed factor, and each study was a random factor in the linear mixed model. All statistical analyses were performed in R 3.6.1. (R Core Team., 2019).

3. Results

3.1. Summary of the dataset

In our collection of studies, N deposition experiments were conducted worldwide (Fig. 1). The dataset of fine root traits included 890 paired observations and 14 fine root traits in 79 published studies. The forest fell into four distinct forest types: tropical (12 studies), subtropical (25 studies), temperate (38 studies) and boreal (4 studies). For the 14 fine root traits, the number of observations followed the rank of fine root biomass ($n = 191$) > root diameter ($n = 124$) > specific root length (SRL) ($n = 111$) > root N content ($n = 110$) > root tissue density (RTD) ($n = 83$) > root C:N ratio ($n = 55$) > root respiration ($n = 34$) = root production ($n = 34$) > fungal colonization ($n = 31$) > root P content ($n = 27$) > root N:P ratio ($n = 25$) > root C content ($n = 24$) > root C:P ratio ($n = 22$) > specific root area (SRA) ($n = 19$).

3.2. Overall effects of nitrogen deposition on fine root traits

N deposition mainly affects fine root chemical traits and stoichiometric ratio. Fine root N content increased by 14.76 % (95 % CIs, 8.60 % to 20.92 %, $P < 0.001$, $n = 111$), while the root P content decreased by 20.76 % (95 % CIs, -39.31 % to -2.21 %, $P < 0.05$, $n = 27$) under N deposition. The fine root C:P ratio increased by 21.29 % (95 % CIs, 10.34 % to 32.23 %, $P < 0.05$, $n = 22$) under N deposition (Fig. 2). N deposition increased the fine root N:P ratio by 16.56 % (8.11 % to 25 %, $P < 0.001$, $n = 25$), but decreased the fine root C:N ratio by 9.51 % (95 % CIs, -18.90 % to -0.12 %, $P < 0.05$, $n = 55$, Table S4). N deposition increased fine root respiration by 12.05 % (2.52 % to 21.55 %, $P < 0.05$, $n = 34$, Fig. 2). However, N deposition had no significant effects on fine root C content, morphological traits (SRL, RTD, SRA and root diameter) and fungal colonization (Fig. 2).

3.3. N deposition level and duration regulating N deposition effects

N deposition duration decreased the effect size of fine root biomass by 9.70 % (95 % CIs, -18.70 % to -0.69 %, $P < 0.01$, Fig. 3), the effect size of fine root tissue density by 4.37 % (95 % CIs, -8.43 % to -0.32 %, $P < 0.01$, Fig. 3), and the effect size of fine root fungal colonization by 36.21 % (95 % CIs, -65.9 % to -6.53 %, $P < 0.05$, Fig. 3), respectively. However, N deposition duration had no significant effect on the effect size of other fine root traits (Fig. 3, Table S4). The effect sizes of root biomass, and fungal colonization were negatively correlated with N deposition duration ($R^2 = 0.04$, $P < 0.01$; $R^2 = 0.12$, $P < 0.05$, Fig. 4e, f). Meanwhile, the effect size of root tissue density with N deposition duration was barely significant ($R^2 = 0.04$, $P < 0.05$, Fig. 4d).

N deposition level decreased the effects size of root P content by 15.69 % (95 % CIs, -21.61 % to -9.77 %, $P < 0.001$, Fig. 3, Table S4). However, the N deposition level increased the effect size of root C content

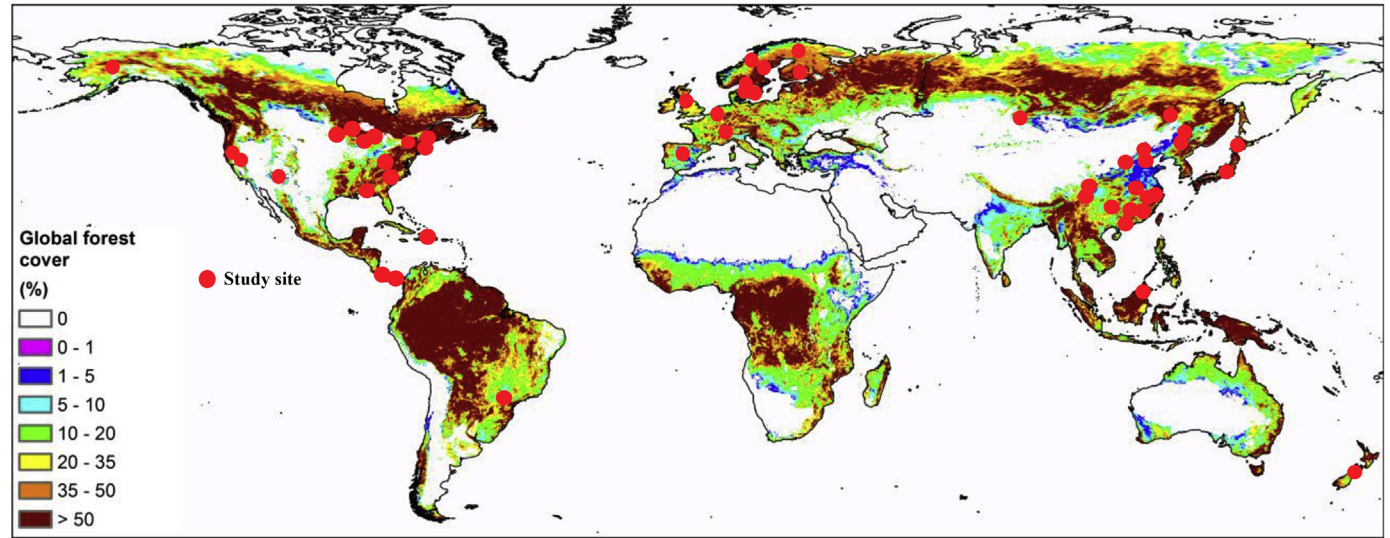


Fig. 1. Geographical distribution of the study sites across the 79 references (Schwede et al., 2018). The red dot represents the study site.

and root C:P ratio by 2.49 % and 10.40 % (95 % CIs, 1.05 % to 3.92 %, $P < 0.01$; 5.90 % to 14.90 %, $P < 0.001$; Fig. 3, Table S4), respectively. The effect sizes of root P content and N deposition level was negatively correlated with N deposition level ($R^2 = 0.59$, $P < 0.001$, Fig. 4a), while the

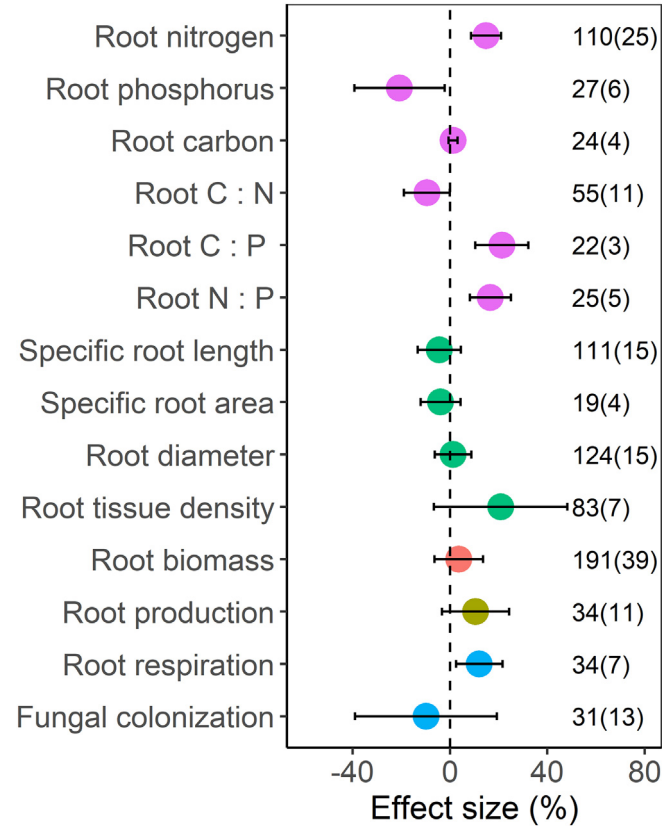


Fig. 2. The effect of nitrogen deposition on 14 fine root traits at mean nitrogen deposition level and nitrogen deposition duration (coefficient of β_0 was estimated at bootstrapped means $\pm$ 95 % CIs). Dashed lines represent the effect size (InRR) = 0; in the right of figure, numbers within and outside the brackets represent studies and observations, respectively. When 95 % CIs was cover zero, the effect of nitrogen deposition was not significant, in contrast it was significant $P < 0.05$. Traits of root chemistry, morphology, fine root biomass, dynamics and physiology are colored in purple, green, red, orange and blue, respectively.

effect sizes of root C content and root C:P ratio were positively related to N deposition level ($R^2 = 0.21$, $P < 0.05$; $R^2 = 0.66$, $P < 0.001$, Fig. 4b, c).

The interaction effect between N deposition level and duration on the effect size of fine root biomass was also significant ($P < 0.01$, Fig. 4f, Table S4). As the N deposition duration increased, the effect size of N deposition on fine root biomass shifted from positive to negative, and the shift was much faster under higher N deposition level (Fig. 4f).

3.4. Abiotic factors regulating N deposition effects

The effect sizes of N deposition on fine root C:P ratio ($P < 0.001$, Table S3) and diameter ($P < 0.01$, Table S3) were affected by MAT. The

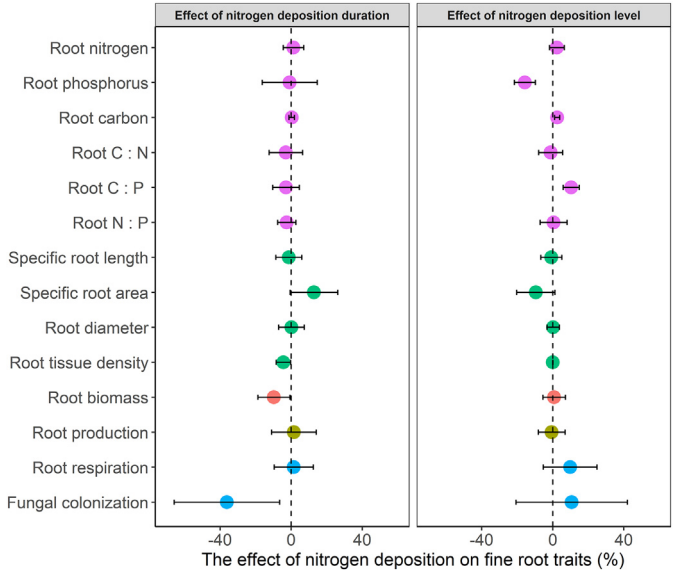


Fig. 3. The effect of nitrogen deposition duration and nitrogen deposition level on 14 fine root traits, respectively. Effect size from the coefficients of β_2 and β_1 (bootstrapped means $\pm$ 95 % CIs), which was estimated by linear mixed effect model based on Eq. (3). When 95 % CIs was cover zero, the effect of nitrogen deposition duration or nitrogen deposition level was not significant, in contrast it was significant $P < 0.05$. Traits of root chemistry, morphology, fine root biomass, dynamics and physiology are colored in purple, green, red, orange and blue, respectively.

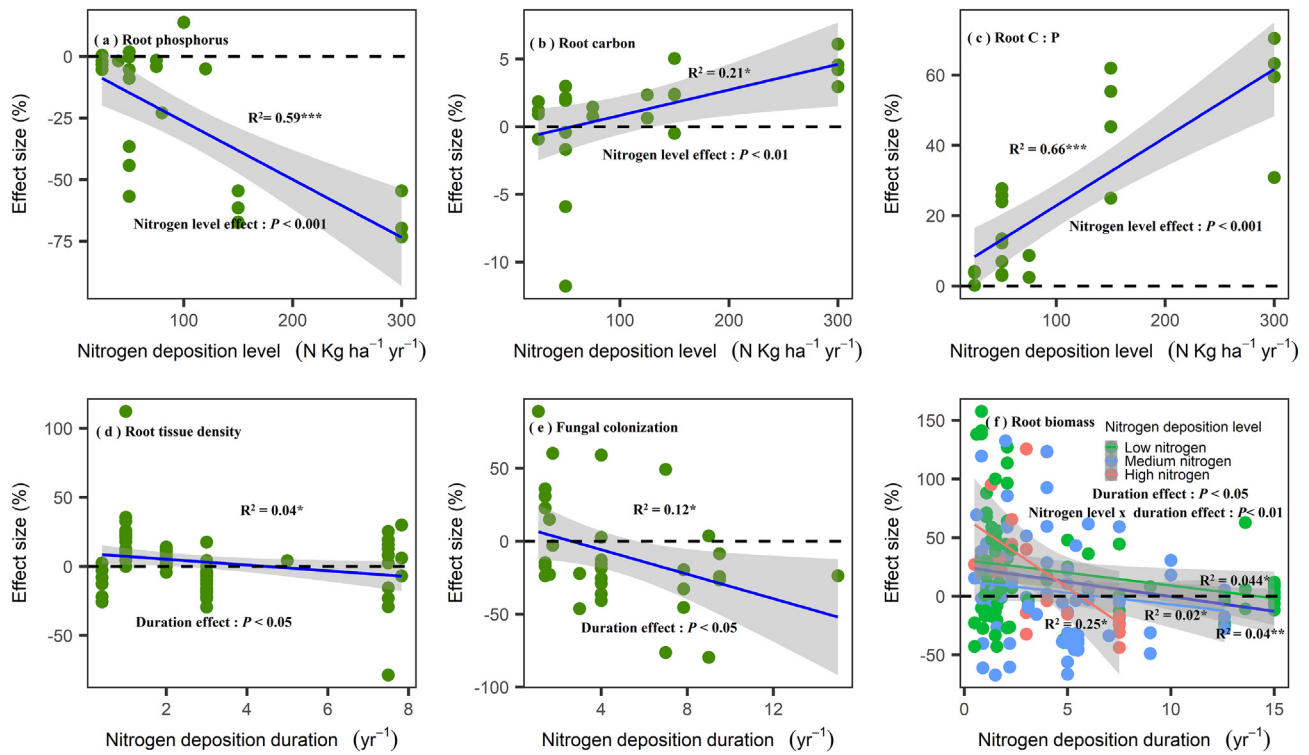


Fig. 4. The effect of nitrogen deposition level or nitrogen deposition duration on root phosphorus content, root carbon content, root C: P ratio, root tissue density, fungal colonization and root biomass. The dot with different color indicates different groups in nitrogen deposition level and blue solid line indicate three group as a group (f). In these figures, horizontal dashed lines represent no effect size and blue lines are fitted by Pearson linear regressions with 95 % confidence intervals (CIs) in grey shading. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

effect size of root diameter decreased with MAT ($R^2 = 0.25$, $P < 0.001$, Fig. 5a).

The effect size of N deposition on fine root diameter was affected by MAP ($P < 0.01$, Table S3). The effect size of root diameter decreased with MAP ($R^2 = 0.17$, $P < 0.001$, Fig. 5b). The effect size of the root C:P ratio and root diameter were affected by forest type ($P < 0.001$ and $P = 0.01$, Table S2, Fig. S3), while other fine root traits did not show significant responses to forest type (Table S2). Compared with temperate forests,

subtropical forests have higher effect size of fine root C:P, but lower effect size of fine root diameter (Fig. S2).

N form had significant effect on the effect size of root P content ($P < 0.001$) and root C:P ratio ($P < 0.001$), but it had no significant effects on effects size of other fine root traits (Table S1, Fig. S2). Moreover, the effect size of the root C:P ratio was affected by soil depths ($P < 0.001$, Table S6), while effects size of other fine root traits were similar among soil depths.

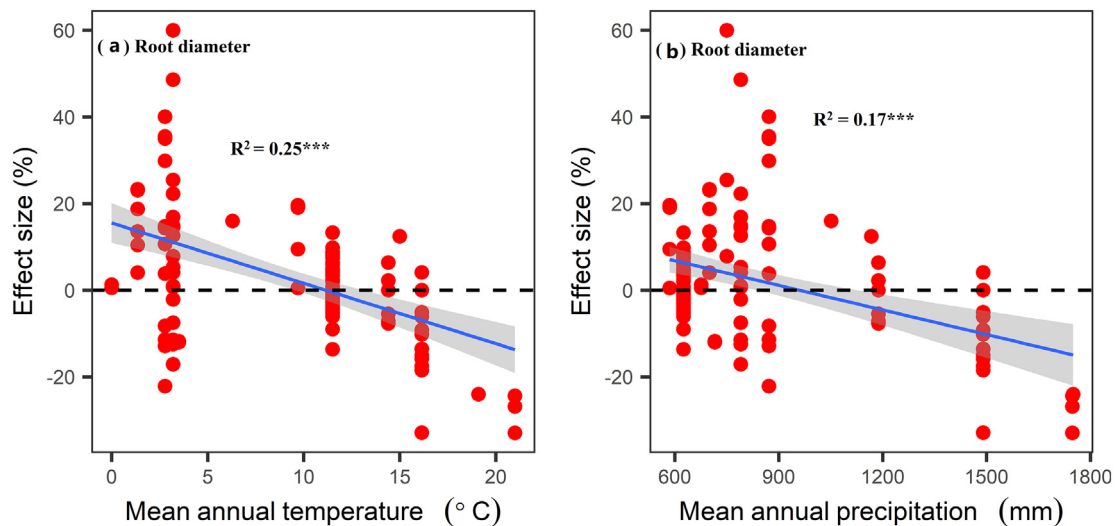


Fig. 5. The relationships between effect size of fine root traits and mean annual temperature (MAT) and mean annual precipitation (MAP) using Pearson linear regression. In these figures, horizontal dashed lines represent no effect size and blue lines are fitted by Pearson linear regressions with 95 % confidence intervals (CIs) in grey shading. *** $P < 0.001$.

4. Discussion

4.1. Effects of N deposition on fine root traits

Our research showed N deposition could significantly increase the fine root N content and N:P ratio, and decrease P content, which were consistent with previous studies (Li et al., 2015; Ma et al., 2021). Natural forests are generally in N limitation (Elser et al., 2007). N deposition increases soil N availability (Galloway et al., 2004), promoting N absorption by woody plants (Vanguelova and Pitman, 2019), which in turn increased root N (Hyvonen et al., 2008). P is an important nutrient for plant growth (Zambrosi et al., 2015). Previous studies have showed that N deposition had minimal effect on the fine root P content (Li et al., 2015; Ma et al., 2021), which was contrary with our result. N deposition can increase soil exchangeable Al^{3+} (Chen et al., 2017), which may inhibit P uptake at the root epidermis (Gassmann and Schroeder, 1994). Given the widespread P limitation in tropical/subtropical ecosystems (Hou et al., 2020), a forest ecosystem under N deposition is likely to experience aggravated P limitation, causing lower root P content (Zhou et al., 2018a). Generally, the C content of fine roots was consistent under N deposition (Liu et al., 2021). In this way, the increased N content and declined P content induced the lower C:N ratio and higher C:P ratio under N deposition (Chen et al., 2017).

Our research showed N deposition had no significant effects on fine root biomass and fine root production, which was contrary with some recent studies finding that fine root biomass and production were significantly changed under N deposition in forest ecosystems (Nadelhoffer, 2000; Kou et al., 2015; Ma et al., 2021; Li et al., 2015). The positive effect of N deposition on fine root production was generally explained that N deposition cause more total C amount allocated for fine root growth, but the negative effect of N deposition on fine root biomass was attributed to N-induced increase in fine root turnover was greater than the N-induced increase in fine root production (Ma et al., 2021). The lack of significant response of fine root biomass and production to N deposition is attributed to two possible reasons. First, we collected studies from 0 to 15 years with various N deposition levels (Fig. 4f), the effect of N deposition on root biomass might trade-off between short-term and long-term experiments since fine root biomass was negatively affected by N deposition duration, shifting from positive to negative responses as deposition duration increased (Figs. 3, 4f). Second, plants allocate photosynthetic C to fine root for nutrient acquisition. When plant was not in N limitation with high soil N availability, the marginal benefit of additional N uptake by their fine roots may be lower than the cost of the carbohydrates used to maintain the root system (Smithwick et al., 2013). Thus, long-term N deposition might potentially suppress fine root production and biomass due to the improved nutrient conditions (Eissenstat and Yanai, 1997).

N deposition did not significantly affect fine morphological traits in this study, which was consistent with previous studies (Eissenstat, 1992; Li et al., 2015; Ma et al., 2021). The key roles of fine roots are to acquire soil nutrients. The morphological traits have been used to indicate the root strategies for nutrient acquisition. Thus, the morphological traits of fine roots are supposed to change due to enhanced soil N availability after N deposition. The lack of significant response of morphological traits to N deposition is attributed to three possible reasons. First, the effect of N deposition might trade-off between short-term and long-term experiments. Second, long-term N deposition commonly induced soil acidity (Bradford et al., 2001; Vogt et al., 2006), which may limit the access of woody plants to nutrients and weaken the effect of N availability on fine root morphological traits. Third, some other physiological activities might be modified to regulate the nutrient acquiring. For example, recent studies showed that woody plants acquire nutrients by increasing the root acid phosphatase rather than changing fine root morphological traits under N deposition (Ma et al., 2021).

Our results demonstrated that simulated N deposition increased fine root respiration. This may be attributed to the fact that N deposition significantly increases the fine root N content, and fine root respiration was positively controlled by fine root N content (Han and Zhu, 2021).

4.2. N deposition effects were regulated by N deposition level and duration

The effects of N deposition on fine root biomass, RTD and fungal colonization changed with the N deposition duration. Short-term (2–3 years) N deposition increased fine root biomass because short-term N deposition stimulated the acquisition of N by plants and promoted root production, thus increasing root biomass (Li et al., 2021a, 2021b, 2021c). However, long-term N deposition could decrease soil pH (Bradford et al., 2001; Vogt et al., 2006) and cause the leaching of Ca^{2+} and Mg^{2+} cations from soil (Horswill et al., 2008), which suppress fine root production. Moreover, N deposition could cause other nutrients (e.g., P) deficiency and limitation, which in turn hinder fine root production (Hietz et al., 2011). Thus, the effect size of fine root biomass decreased with N deposition duration in our study. Plant can regulate the morphological and physiological traits of fine roots to adapt the nutrient and environmental conditions. Plant can also allocate photosynthetic C to mycorrhizae for nutrient acquisition. In short-term N deposition, RTD and fungal colonization increased to acquire more nutrients for plant production. In long-term N deposition, RTD and the mycelia growth were potentially suppressed due to the improved soil N availability (Nilsson and Wallander, 2003; Sims et al., 2007; Vitousek et al., 2010).

The effects of N deposition on the root P content and root C:P ratio varied with the N deposition level, and higher N deposition level caused stronger decrease in root P content and stronger increase in root C:P ratio. These results are consistent with the results in a bamboo forest (Chen et al., 2017), and probably due to the stronger soil acidization and increased exchangeable Al^{3+} which prohibit P uptake at higher N deposition levels, soil P becomes a more limiting nutrient in forest ecosystems as the soil N content is approaches saturation (Vitousek et al., 2010).

The interaction effects between N deposition level and duration on the effect sizes of fine root traits have rarely been explored in field manipulation experiments and global synthesis (Li et al., 2015; Ma et al., 2021). Our results indicated that the effect size of fine root biomass was affected by their interaction. Above analysis showed that the effect size of N deposition on fine root biomass decreased with deposition duration, and we further observed stronger decreasing trend at higher N deposition level ($\geq 200 \text{ kg N ha}^{-1} \text{ yr}^{-1}$, Table S4, Fig. 4f) which could be a combined result of stronger P or other nutrient limitation and stronger soil environmental stress at higher N deposition levels (Vitousek et al., 2010; Hietz et al., 2011). Therefore, long-term and high-level N deposition is detrimental to plant root health and ecosystem functioning. Meanwhile, long-term and low-level N deposition have much smaller effects on root traits. A 15-year N deposition experiment further certified the minimal effect of N deposition on fine root biomass at low N deposition level (Burton et al., 2012). These findings have important implications for forest management and mitigation in the context of future N deposition.

4.3. N deposition effects were regulated by abiotic factors

The morphological traits of fine roots can be easily affected by environmental factors (Zhang et al., 2020). In this study, the response of fine root diameter to N deposition decreased with MAT and MAP, shifting from a positive/neutral effect to negative effect as MAT and MAP increased, while the effect size of the fine root C:P ratio increased with MAT. These results were consistent with a field experiment showing that the interaction of warming and N decreased fine root diameter (Xiong et al., 2020). Under cold and dry conditions, N deposition increased fine root diameter mainly due to the increased stele (Wang et al., 2018). However, under warmer and humid conditions, N deposition decreased root diameter (Wang et al., 2019). In general, forest ecosystems shifted from N limitation to P limitation with decreasing latitude (Reich and Oleksyn, 2004; Yuan et al., 2011; Augusto et al., 2017; Hou et al., 2020). Therefore, thinner roots with shorter lifespans may be produced to enlarge the absorptive area per unit mass to increase nutrient acquisition efficiency under low-P conditions (Wells and Eissenstat, 2001; McCormack et al., 2012). Additionally, plant growth is generally limited by nutrients, especially P in warmer

environments (Du et al., 2020; Hou et al., 2020). Therefore, P limitation caused a decrease in the fine root P content which caused the effect size of the fine root C:P ratio increase with temperature.

Effect size of fine root traits were regulated by forest types, N forms and soil depths. Soil in subtropical forests tend to be more weathered and greater P deficiency compared to soil in temperate forests (Hou et al., 2018), which exacerbating P limitation in subtropical forests. Moreover, N deposition exacerbated P limitation in subtropical forests, which caused thinner roots with high efficiency in acquiring soil P (Wells and Eissenstat, 2001; McCormack et al., 2012). Thus, the effect size of fine root C: P in subtropical forests higher than temperate forests, but the effect size of fine root diameter lower than temperate forests. We also found a more pronounced response of fine root C:P ratio and P to N deposition in the form of nitrate N alone. This might be because plants preferentially take up nitrate N (Fenn et al., 2013). We also analyzed the effect of soil depths on effect size of N deposition for each fine root traits, most of the traits showed no significant difference among soil depths except fine root C:P ratio. However, the study sites and observations for depth analysis were small for each single trait. These results might cause misleading, and the effect of soil depths on N deposition effect need more field data in future study.

4.4. Limitations and prospect

There are certainly limitations associated with this study. First, the collected studies were mostly distributed in temperate and subtropical climate zones. Therefore, the findings of this study need further examination for tropical and boreal forests. We need to pay more attention to how fine root traits respond to N deposition in forests of South America and Africa (especially tropical forests) in the future. Moreover, the collected studies were mainly from China and the data for root P, root C:P, and root N:P are entirely from China, which may only reflect the effect of N deposition on fine-root traits in China. Therefore, the effects of N deposition on these three fine-root traits need to be examined with additional studies (outside China) in the future. Second, N deposition does not occur alone under global change and usually occurs with changes in other factors, such as warming, drying, and elevated CO₂. The effects of many other factors on fine root traits have been explored by meta-analyses at the global scale (Nie et al., 2013; Zhou et al., 2018b; Wang et al., 2020), but the interactive effects of N deposition and these factors are still unclear. Therefore, multi-factor interactive experiments should be conducted in forest ecosystems to clearly explore the response of fine root traits to global change. Third, the data for root P, root C:P, and root N:P are entirely from China, which only reflects the effect of N deposition on fine-root traits in China. Therefore, the effects of N deposition on these three fine-root traits need to be examined with additional studies (outside China) in the future. Finally, linear mixed model results showed that background N deposition could significantly influence the effect of N deposition on some fine root traits for forests (Table S7). Thus, the background N deposition level should be considered in future associated researches.

5. Conclusion

This meta-analysis explored the effect of N deposition on fine root traits across forest ecosystems. In general, N deposition mainly affected root nutrient contents and stoichiometry. N deposition increased the root N content, root C:P ratio, root N:P ratio and root respiration, but decreased the root P content. The effects of N deposition on fine root biomass, RTD and fungal colonization also changed with the N deposition duration. Short-term N deposition increased fine root biomass, RTD and fungal colonization, while long-term N deposition decreased these parameters. The effects of N deposition on the root P content varied with the N deposition level, and higher N deposition level caused stronger decrease in root P content. We observed a shift of the effects on root biomass from positive in the short-term to negative in the long-term in N addition experiments, and the shift was much faster under high-level N deposition. Moreover, the effect of

root diameter response to N deposition decreased with MAT and MAP, but the effect of root C:P ratio increased with MAT. These results indicate that the effects of N deposition on fine root traits were modulated not only by N deposition level, duration and their interaction, but also by abiotic factors. Overall, these results improved our understanding of root dynamics under N deposition and could improve the model of nutrient cycles under global change in forest ecosystems.

Credit authorship contribution statement

Xiaoxiang Zhao: Writing, Methodology, Data collection, Visualization.
Qiuxiang Tian: Writing, Visualization.
Lin Huang: Writing, Review & editing.
Qiaoling Lin: Writing, Review & editing, Data collection.
Junjun Wu: Methodology, Data collection.
Feng Liu: Writing, Review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

This study was supported by the National Natural Science Foundation of China (Grant numbers 32171599, 31870465). We are grateful to all scientists for their valuable studies used in the present synthesis. We thank Wang Jinsong from Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences for their helpful guidance in model construction and select in R. We also thank Kyle Tomlinson from Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences for his helpful teaching and guidance in linear mixed model.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.157111>.

References

- Ackerman, D., Millet, D.B., Chen, X., 2019. Global estimates of inorganic nitrogen deposition across four decades. *Glob. Biogeochem. Cycles* 33, 100–107.
- Adamczyk, B., Sietio, O.M., Strakova, P., Prommer, J., Wild, B., Hagner, M., Pihlatie, M., Fritze, H., Richter, A., Heinonsalo, J., 2019. Plant roots increase both decomposition and stable organic matter formation in boreal forest soil. *Nat. Commun.* 10, 1–9.
- Augusto, L., Achat, D.L., Jonard, M., Vidal, D., Ringeval, B., 2017. Soil parent material—a major driver of plant nutrient limitations in terrestrial ecosystems. *Glob. Chang. Biol.* 23, 3808–3824.
- Barton, K., 2018. MuMin: multi-model inference. R package version 1.42.1. <https://CRAN.R-project.org/package=MuMin>.
- Bates, D., Bolker, B., Walker, S., Christensen, R.H.B., Singmann, H., Dai, B., Grothendieck, G., 2017. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1–10. <https://cran.r-project.org/web/packages/lme4/index.html>.
- Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., 2010. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol. Appl.* 20, 30–59.
- Bradford, M.A., Ineson, P., Wookey, P.A., Lappin-Scott, H.M., 2001. The effects of acid nitrogen and acid sulphur deposition on CH₄ oxidation in a forest soil: a laboratory study. *Soil Biol. Biochem.* 33, 1695–1702.
- Burton, A.J., Jarvey, J.C., Jarvi, M.P., Zak, D.R., Pregitzer, K.S., 2012. Chronic N deposition alters root respiration-tissue N relationship in northern hardwood forests. *Glob. Chang. Biol.* 18, 258–266.
- Cai, Y., Chang, S.X., 2020. Disturbance effects on soil carbon and greenhouse gas emissions in forest ecosystems. *Forests* 11 (3), 297.
- Chapin III, F.S., McFarland, J., McGuire, A.D., Euskirchen, E.S., Ruess, R.W., Kielland, K., 2009. The changing global carbon cycle: linking plant-soil carbon dynamics to global consequences. *J. Ecol.* 97 (5), 840–850.
- Chen, X.L., Chen, H.Y.H., 2019. Plant diversity loss reduces soil respiration across terrestrial ecosystems. *Glob. Chang. Biol.* 25, 1482–1492.
- Chen, G.T., Tu, L.H., Peng, Y., Hu, H.L., Hu, T.X., Xu, Z.F., Liu, L., Tang, Y., 2017. Effect of nitrogen additions on root morphology and chemistry in a subtropical bamboo forest. *Plant Soil* 412, 441–451.

- Chen, X.L., Chen, H.Y.H., Chen, C., Ma, Z.L., Searle, E.B., Yu, Z.P., Huang, Z.Q., 2020. Effects of plant diversity on soil carbon in diverse ecosystems: a global meta-analysis. *Biol. Rev.* 95, 167–183.
- Cohen, J., Cohen, P., West, S.G., Alken, L.S., 2013. *Applied Multiple Regression/Correlation Analysis for the Behavioral Sciences*. Psychology Press, London, UK.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51, 335–380.
- Du, E., Terrer, C., Pellegrini, A.F., Ahlström, A., van Lissa, C.J., Zhao, X., Xia, N., Wu, X., Jackson, R.B., 2020. Global patterns of terrestrial nitrogen and phosphorus limitation. *Nat. Geosci.* 13, 221–226.
- Eissenstat, D.M., 1992. Costs and benefits of constructing roots of small diameter. *J. Plant Nutr.* 15, 763–782.
- Eissenstat, D.M., Yanai, R.D., 1997. The ecology of root lifespan. *Adv. Ecol. Res.* 27, 1–60.
- Elser, J.J., Bracken, M.E., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., Smith, J.E., 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* 10 (12), 1135–1142.
- Fenn, M.E., Ross, C.S., Schilling, S.L., Baccus, W.D., Larrabee, M.A., Lofgren, R.A., 2013. Atmospheric deposition of nitrogen and sulfur and preferential canopy consumption of nitrate in forests of the Pacific Northwest, USA. *For. Ecol. Manag.* 302, 240–253.
- Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* 37 (12), 4302–4315.
- Freschet, G.T., Roumet, C., Comas, L.H., Weemstra, M., Bengough, A.G., Rewald, B., Bardgett, R.D., De Deyn, G.B., Johnson, D., Klimesova, J., Lukac, M., McCormack, M.L., Meier, I.C., Pages, L., Poorter, H., Prieto, I., Wurzbarger, N., Zadworny, M., Bagniewska-Zadworna, A., Blancaflor, E.B., Brunner, I., Gessler, A., Hobbie, S.E., Iversen, C.M., Mommer, L., Picon-Cochard, C., Postma, J.A., Rose, L., Ryser, P., Scherer-Lorenzen, M., Soudzilovskaia, N.A., Sun, T., Valverde-Barrantes, O.J., Weigelt, A., York, L.M., Stokes, A., 2021. Root traits as drivers of plant and ecosystem functioning: current understanding, pitfalls and future research needs. *New Phytol.* 232, 1123–1158.
- Galloway, J.N., Dentener, F.J., Capone, D.G., Boyer, E.W., Howarth, R.W., Seitzinger, S.P., Asner, G.P., Cleveland, C.C., Green, P.A., Holland, E.A., Karl, D.M., Michaels, A.F., Porter, J.H., Townsend, A.R., Vorosmarty, C.J., 2004. Nitrogen cycles: past, present, and future. *Biogeochemistry* 70, 153–226.
- Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Martinelli, L.A., Seitzinger, S.P., Sutton, M.A., 2008. Transformation of the nitrogen cycle: recent trends, questions, and potential solutions. *Science* 320 (5878), 889–892.
- Gassmann, W., Schroeder, J.I., 1994. Inward-rectifying K⁺ channels in root hairs of wheat (a mechanism for aluminum-sensitive low-affinity K⁺ uptake and membrane potential control). *Plant Physiol.* 105, 1399–1408.
- Gong, L., Zhao, J., 2019. The response of fine root morphological and physiological traits to added nitrogen in Schrenk's spruce (*Picea schrenkiana*) of the Tianshan mountains, China. *PeerJ* 2019 (7), e8194.
- Han, M., Zhu, B., 2021. Linking root respiration to chemistry and morphology across species. *Glob. Chang. Biol.* 27, 190–201.
- Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80, 1150–1156.
- Hendricks, J.J., Hendrick, R.L., Wilson, C.A., Mitchell, R.J., Pecot, S.D., Guo, D.L., 2006. Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. *J. Ecol.* 94, 40–57.
- Hietz, P., Turner, B.L., Wanek, W., Richter, A., Nock, C.A., Wright, S.J., 2011. Long-term change in the nitrogen cycle of tropical forests. *Science* 334, 664–666.
- Horswill, P., O'Sullivan, O., Phoenix, G.K., Lee, J.A., Leake, J.R., 2008. Base cation depletion, eutrophication and acidification of species-rich grasslands in response to long-term simulated nitrogen deposition. *Environ. Pollut.* 155, 336–349.
- Hou, E., Chen, C., Luo, Y., Zhou, G., Kuang, Y., Zhang, Y., Heenan, M., Lu, X., Wen, D., 2018. Effects of climate on soil phosphorus cycle and availability in natural terrestrial ecosystems. *Glob. Chang. Biol.* 24 (8), 3344–3356.
- Hou, E., Luo, Y., Kuang, Y., Chen, C., Lu, X., Jiang, L., Luo, X., Wen, D., 2020. Global meta-analysis shows pervasive phosphorus limitation of aboveground plant production in natural terrestrial ecosystems. *Nat. Commun.* 11, 1–9.
- Hyvonen, R., Persson, T., Andersson, S., Olsson, B., Agren, G.I., Linder, S., 2008. Impact of long-term nitrogen addition on carbon stocks in trees and soils in northern Europe. *Biogeochemistry* 89, 121–137.
- Jackson, R.B., Mooney, H.A., Schulze, E.D., 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proc. Natl. Acad. Sci.* 94, 7362–7366.
- Jourdan, C., Silva, E.V., Goncalves, J.L.M., Ranger, J., Moreira, R.M., Laclau, J.P., 2008. Fine root production and turnover in Brazilian eucalyptus plantations under contrasting nitrogen fertilization regimes. *For. Ecol. Manag.* 256, 396–404.
- Keller, A.B., Brzostek, E.R., Craig, M.E., Fisher, J.B., Phillips, R.P., 2021. Root-derived inputs are major contributors to soil carbon in temperate forests, but vary by mycorrhizal type. *Ecol. Lett.* 24, 626–635.
- Kou, L., Guo, D.L., Yang, H., Gao, W.L., Li, S.G., 2015. Growth, morphological traits and mycorrhizal colonization of fine roots respond differently to nitrogen addition in a slash pine plantation in subtropical China. *Plant Soil* 391, 207–218.
- Kou, L., Jiang, L., Fu, X.L., Dai, X.Q., Wang, H.M., Li, S.G., 2018. Nitrogen deposition increases root production and turnover but slows root decomposition in *Pinus elliottii* plantations. *New Phytol.* 218, 1450–1461.
- Li, W.B., Jin, C.J., Guan, D.X., Wang, Q.K., Wang, A.Z., Yuan, F.H., Wu, J.B., 2015. The effects of simulated nitrogen deposition on plant root traits: a meta-analysis. *Soil Boil. Biochem.* 82, 112–118.
- Li, H.B., Liu, B.T., McCormack, M.L., Ma, Z.Q., Guo, D.L., 2017. Diverse belowground resource strategies underlie plant species coexistence and spatial distribution in three grasslands along a precipitation gradient. *New Phytol.* 216, 1140–1150.
- Li, W., Shi, Y., Zhu, D., Wang, W., Liu, H., Li, J., Shi, W., Ma, N., Fu, S., 2021. Fine root biomass and morphology in a temperate forest are influenced more by the nitrogen treatment approach than the rate. *Ecol. Indic.* 130, 108031.
- Li, X., Zhang, C., Zhang, B., Wu, D., Zhu, D., Zhang, W., Ye, Q., Yan, J., Fu, J., Fang, C., Ha, D., Fu, S., 2021. Nitrogen deposition and increased precipitation interact to affect fine root production and biomass in a temperate forest: implications for carbon cycling. *Sci. Total Environ.* 765, 144497.
- Li, X., Zhang, C., Zhang, B., Wu, D., Zhu, D., Zhang, W., Ye, Q., Yan, J., Fu, J., Fang, C., Ha, D., Fu, S., 2021. Canopy and understory nitrogen addition have different effects on fine root dynamics in a temperate forest: implications for soil carbon storage. *New Phytol.* 231, 1377–1386.
- Liu, G., Xing, Y.J., Wang, Q.G., Wang, L., Feng, Y., Yin, Z.W., Wang, X.C., Liu, T., 2021. Long-term nitrogen addition regulates root nutrient capture and leaf nutrient resorption in *Larix gmelinii* in a boreal forest. *Eur. J. For. Res.* 140, 763–776.
- Lu, X., Mao, Q., Gilliam, F.S., Luo, Y., Mo, J., 2014. Nitrogen deposition contributes to soil acidification in tropical ecosystems. *Glob. Chang. Biol.* 20, 3790–3801.
- Lu, X., Vitousek, P.M., Mao, Q., Gilliam, F.S., Luo, Y., Zhou, G., Zou, X., Bai, E., Scanlon, T.M., Hou, E., Mo, J., 2018. Plant acclimation to long-term high nitrogen deposition in an N-rich tropical forest. *Proc. Natl. Acad. Sci.* 115 (20), 5187–5192.
- Ma, Z.L., Chen, H.Y.H., 2016. Effects of species diversity on fine root productivity in diverse ecosystems: a global meta-analysis. *Glob. Ecol. Biogeogr.* 25, 1387–1396.
- Ma, X., Zhu, B., Nie, Y., Liu, Y., Kuzyakov, Y., 2021. Root and mycorrhizal strategies for nutrient acquisition in forests under nitrogen deposition: a meta-analysis. *Soil Boil. Biochem.* 163, 108418.
- McCormack, M.L., Adams, T.S., Smithwick, E.A., Eissenstat, D.M., 2012. Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytol.* 195, 823–831.
- Mo, J., Zhang, W.E.I., Zhu, W., Gundersen, P.E.R., Fang, Y., Li, D., Wang, H.U.I., 2008. Nitrogen addition reduces soil respiration in a mature tropical forest in southern China. *Glob. Chang. Biol.* 14 (2), 403–412.
- Nadelhoffer, K.J., 2000. The potential effects of nitrogen deposition on fine-root production in forest ecosystems. *New Phytol.* 147, 131–139.
- Nie, M., Lu, M., Bell, J., Raut, S., Pendall, E., 2013. Altered root traits due to elevated CO₂: a meta-analysis. *Glob. Ecol. Biogeogr.* 22, 1095–1105.
- Nilsson, L.O., Wallander, H., 2003. Production of external mycelium by ectomycorrhizal fungi in a Norway spruce forest was reduced in response to nitrogen fertilization. *New Phytol.* 158 (2), 409–416.
- Ostertag, R., 2001. Effects of nitrogen and phosphorus availability on fine-root dynamics in hawaiian montane forests. *Ecology* 82, 485–499.
- Pellegrini, A.F., Ahlström, A., Hobbie, S.E., Reich, P.B., Nieradzik, L.P., Staver, A.C., Scharenbroch, B.C., Jumpponen, A., Anderegg, W.R.A., Randerson, J.T., Jackson, R.B., 2018. Fire frequency drives decadal changes in soil carbon and nitrogen and ecosystem productivity. *Nature* 553, 194–198.
- Peng, S., Chen, H.Y., 2021. Global responses of fine root biomass and traits to plant species mixtures in terrestrial ecosystems. *Glob. Ecol. Biogeogr.* 30, 289–304.
- Peng, Y.F., Guo, D.L., Yang, Y.H., 2017. Global patterns of root dynamics under nitrogen enrichment. *Glob. Ecol. Biogeogr.* 26, 102–114.
- R Core Team., 2019. R: A Language and Environment for Statistical Computing Version.3.6.1. R Foundation for Statistical Computing, Vienna, Austria.
- Reay, D.S., Dentener, F., Smith, P., Grace, J., Feely, R.A., 2008. Global nitrogen deposition and carbon sinks. *Nat. Geosci.* 1 (7), 430–437.
- Reich, P.B., Oleksyn, J., 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc. Natl. Acad. Sci.* 101, 11001–11006.
- Schwede, D.B., Simpson, D., Tan, J., Fu, J.S., Dentener, F., Du, E., deVries, W., 2018. Spatial variation of modelled total, dry and wet nitrogen deposition to forests at global scale. *Environ. Pollut.* 243, 1287–1301.
- Sims, S.E., Hendricks, J.J., Mitchell, R.J., Kuehn, K.A., Pecot, S.D., 2007. Nitrogen decreases and precipitation increases ectomycorrhizal extramatrical mycelia production in a longleaf pine forest. *Mycorrhiza* 17 (4), 299–309.
- Smithwick, E.A., Eissenstat, D.M., Lovett, G.M., Bowden, R.D., Rustad, L.E., Driscoll, C.T., 2013. Root stress and nitrogen deposition: consequences and research priorities. *New Phytol.* 197 (3), 712–719.
- Tian, J., Dungait, J.A., Lu, X., Yang, Y., Hartley, I.P., Zhang, W., Mo, J., Yu, G., Zhou, J., Kuzyakov, Y., 2019. Long-term nitrogen addition modifies microbial composition and functions for slow carbon cycling and increased sequestration in tropical forest soil. *Glob. Chang. Biol.* 25 (10), 3267–3281.
- van Groenigen, J.W., van Kessel, C., Hungate, B.A., Oenema, O., Powlson, D.S., van Groenigen, K.J., 2017. Sequestering soil organic carbon: a nitrogen dilemma. *Environ. Sci. Technol.* 51, 4738–4739.
- Vangelova, E.I., Pitman, R.M., 2019. Nutrient and carbon cycling along nitrogen deposition gradients in broadleaf and conifer forest stands in the east of England. *For. Ecol. Manag.* 447, 180–194.
- Vitousek, P.M., Aber, J.D., Howarth, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H., Tilman, D.G., 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecol. Appl.* 7, 737–750.
- Vitousek, P.M., Porder, S., Houlton, B.Z., Chadwick, O.A., 2010. Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. *Ecol. Appl.* 20, 5–15.
- Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., Ohara, J., Asbjornsen, H., 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. *Plant Soil* 187, 159–219.
- Vogt, R.D., Seip, H.M., Larssen, T., Zhao, D., Xiang, R., Xiao, J., Luo, J., Zhao, Y., 2006. Potential acidifying capacity of deposition: experiences from regions with high NH₄⁺ and dry deposition in China. *Sci. Total Environ.* 367, 394–404.
- Wang, G.L., Fahey, T.J., Xue, S., Liu, F., 2013. Root morphology and architecture respond to N addition in *Pinus tabulaeformis*, West China. *Oecologia* 171, 583–590.

- Wang, W., Wang, Y., Hoch, G., Wang, Z., Gu, J., 2018. Linkage of root morphology to anatomy with increasing nitrogen availability in six temperate tree species. *Plant Soil* 425, 189–200.
- Wang, W.J., Mo, Q.F., Han, X.G., Hui, D.F., Shen, W.J., 2019. Fine root dynamics responses to nitrogen addition depend on root order, soil layer, and experimental duration in a subtropical forest. *Biol. Fertil. Soils* 55, 723–736.
- Wang, P., Huang, K.L., Hu, S.J., 2020. Distinct fine-root responses to precipitation changes in herbaceous and woody plants: a meta-analysis. *New Phytol.* 225, 1491–1499.
- Wang, J.S., Defrenne, C., McCormack, M.L., Yang, L., Tian, D.S., Luo, Y.Q., Hou, E.Q., Yan, T., Li, Z.L., Bu, W.S., Chen, Y., Niu, S.L., 2021. Fine-root functional trait responses to experimental warming: a global meta-analysis. *New Phytol.* 230, 1856–1867.
- Weemstra, M., Mommer, L., Visser, E.J., van Ruijven, J., Kuyper, T.W., Mohren, G.M., Sterck, F.J., 2016. Towards a multidimensional root trait framework: a tree root review. *New Phytol.* 211, 1159–1169.
- Wells, C.E., Eissenstat, D.M., 2001. Marked differences in survivorship among apple roots of different diameters. *Ecology* 82, 882–892.
- Xiong, D., Huang, J., Yang, Z., Cai, Y., Lin, T.C., Liu, X., Xu, C., Chen, S., Chen, G., Xie, J., Li, Y., Yang, Y., 2020. The effects of warming and nitrogen addition on fine root exudation rates in a young Chinese-fir stand. *For. Ecol. Manag.* 458, 117793.
- Yan, G., Chen, F., Zhang, X., Wang, J., Han, S., Xing, Y., Wang, Q., 2017. Spatial and temporal effects of nitrogen addition on root morphology and growth in a boreal forest. *Geoderma* 303, 178–187.
- Yuan, Z.Y., Chen, H.Y.H., 2015. Decoupling of nitrogen and phosphorus in terrestrial plants associated with global changes. *Nat. Clim. Chang.* 5, 465–469.
- Yuan, Z.Y., Chen, H.Y.H., Reich, P.B., 2011. Global-scale latitudinal patterns of plant fine-root nitrogen and phosphorus. *Nat. Commun.* 2, 334.
- Zambrosi, F.C.B., Ribeiro, R.V., Marchiori, P.E.R., Cantarella, H., Landell, M.G.A., 2015. Sugarcane performance under phosphorus deficiency: physiological responses and genotypic variation. *Plant Soil* 386, 273–283.
- Zhang, X., Xing, Y., Wang, Q., Yan, G., Wang, M., Liu, G., Wang, H., Huang, B., Zhang, J., 2020. Effects of long-term nitrogen addition and decreased precipitation on the fine root morphology and anatomy of the main tree species in a temperate forest. *For. Ecol. Manag.* 455, 117664.
- Zhou, G.Y., Zhou, X.H., Nie, Y.Y., Bai, S.H., Zhou, L.Y., Shao, J.J., Cheng, W.S., Wang, J.W., Hu, F.Q., Fu, Y.L., 2018. Drought-induced changes in root biomass largely result from altered root morphological traits: evidence from a synthesis of global field trials. *Plant Cell Environ.* 41, 2589–2599.
- Zhou, K., Lu, X., Mori, T., Mao, Q., Wang, C., Zheng, M., Mo, H., Hou, E., Mo, J., 2018. Effects of long-term nitrogen deposition on phosphorus leaching dynamics in a mature tropical forest. *Biogeochemistry* 138, 215–224.