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Research Article

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Posted Date: September 26th, 2025

DOI: <https://doi.org/10.21203/rs.3.rs-7626492/v1>

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Shifts in plant nutrient acquisition strategies under nitrogen addition: a global meta-analysis

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Background and aims

Plants acquire nutrients by extending root length to explore soil resources and by metabolically exploiting the nutrients encountered. While global nitrogen (N) deposition has substantially enhanced aboveground productivity, it remains unclear how plants sustain this increase by coordinating changes in fine-root biomass and traits to restructure exploration–exploitation strategies.

Methods

We compiled fine-root trait data from 138 field experiments across 156 global sites and employed meta-analysis to quantify responses of fine-root biomass, morphological fine-root traits, nutrient uptake rate proxies, and mycorrhizal traits under N-only and N+P additions.

Results

N-only addition enhanced both exploration and exploitation capacities globally but reduced plant dependence on mycorrhizal fungi. In woody plants, fine-root biomass remained unchanged, but increased root tissue density (RTD, +11.9%) reduced root length density (RLD, −7.9%), while root nitrogen concentration (RN, +13.2%) and respiration rate (Rs, +21.5%) boosted exploitation capacity. Herbaceous plants adopted an acquisitive strategy, increasing fine-root biomass (+71.3%), specific root length (SRL, +67.8%), RN (+9.8%), and Rs (+24.6%), driving substantial RLD gains (+88.0%) and nutrient exploitation. N+P addition sustained mycorrhizal reliance and enhanced woody exploration (RLD +25.5%). Low baseline SRL predicted stronger biomass and RLD responses, identifying SRL as a key driver of belowground investment under N-only

addition.

Conclusions

Our results reveal contrasting strategies between woody and herbaceous plants and highlight SRL as a critical predictor of root biomass responses. These findings provide new insights into how plants adjust nutrient acquisition strategies under N addition and inform predictions of ecosystem carbon–nutrient dynamics under global change.

Keywords

nitrogen addition, fine roots, nutrient acquisition strategies, root traits, phosphorus addition.

Introduction

Fine roots are the primary organs for plant nutrient acquisition, playing a critical role in sustaining terrestrial ecosystem productivity (Jackson et al., 1997; Klimešová et al., 2023). Nutrient acquisition involves two key processes: exploration, where dense root systems forage for heterogeneously distributed soil resources, and exploitation, where roots metabolically absorb available nutrients (Hutchings et al., 1994; Hodge et al., 2004; Lambers et al., 2008; Parseval et al., 2016; Freschet et al., 2021). Exploration capacity is quantified by root length density (RLD), which determines the likelihood of encountering nutrient hotspots (Chen et al., 2016). RLD reflects the combined effects of belowground biomass investment and root morphology: greater fine-root biomass (RB) provides more material to deploy, while higher specific root length (SRL)—typically associated with smaller root diameter (RD) and/or low root tissue density (RTD) roots—yields more root length per unit biomass. Exploitation capacity, defined as nutrient uptake flux per unit ground area over time, depends on both fine-root biomass and uptake rate per unit biomass. Due to scarce direct measurements of uptake rates under N addition, we use root nitrogen concentration (RN) and root respiration rate (Rs) as proxies for uptake rate. RN reflects amino acid pools available for synthesizing high-affinity transport proteins, with higher values indicating greater metabolic activity and nutrient absorption potential (Schachtman et al., 1998; Bergmann et al., 2020; Liu et al., 2020; Freschet et al., 2021; Yi et al., 2023). Elevated Rs reflects increased ATP production, which supplies the energy required for sustained active ion transport (Reich et al., 2008; Griffiths et al., 2021; Jiang et al., 2023). Thus, exploitation capacity can be operationalized as the combination of fine-root biomass and uptake rate, proxied by RN and Rs, providing a mechanistic framework for nutrient acquisition in the absence of direct uptake measurements.

Global nitrogen (N) deposition has increased aboveground productivity (Matson et al., 2002; Galloway et al., 2008), requiring plants to meet higher nutrient demands by increasing fine-root biomass or adjusting traits. Greater biomass enhances nutrient acquisition by expanding root networks, while trait adjustments, such as higher SRL to increase RLD or elevated RN/Rs to improve uptake, can enhance acquisition without biomass increases (Li et al., 2015; Ma et al., 2021; Zhao et al., 2022). Mycorrhizal

74 symbioses further expand accessible soil volume, facilitating nutrient acquisition (Genre
75 et al., 2020). However, how plants coordinate fine-root traits, biomass, and mycorrhizal
76 associations under N addition remains unclear.

77 Chronic N addition often shift ecosystems from N to phosphorus (P) limitation
78 (Peñuelas et al., 2013). Combined N and P (N+P) addition may alter root–fungal
79 interactions differently from N-only addition. Some studies suggest N+P inputs increase
80 nutrient availability, reducing root biomass and mycorrhizal reliance (Phillips & Fahey,
81 2007; Chen et al., 2014), while others indicate stimulated root growth and sustained or
82 enhanced mycorrhizal dependence (Leppälammi-Kujansuu et al., 2013; Camenzind et al.,
83 2016; Wang et al., 2018). Understanding these dynamics is essential for ecosystem
84 management under rising N deposition.

85 Plant responses to N addition likely depend on inherent root traits, analogous to the
86 leaf economics spectrum, where species with “fast” leaf traits (e.g., high leaf nitrogen and
87 specific leaf area) show stronger growth responses to nutrient addition than those with
88 “slow” traits (Leishman et al., 2010; Yang et al., 2025). Root traits follow a similar “fast–
89 slow” continuum: high RN and low RTD indicate rapid nutrient turnover, while low RN
90 and high RTD reflect conservative strategies (Bergmann et al., 2020). Whether “fast” root
91 traits species invest more in belowground biomass under N addition, compared to “slow”
92 species, is critical for understanding plant adaptation to global change.

93 To address these gaps, we conducted a global meta-analysis of 138 field experiments
94 across woody and herbaceous species, compiling ten fine-root and mycorrhizal traits: SRL,
95 RD, RTD, RN, Rs, RLD, RB, colonized root length, hyphal length, and mycorrhizal biomass.
96 We asked: (1) How does N addition reshape root exploration–exploitation strategies? (2)
97 To what extent does N+P co-addition alter mycorrhizal dependence? (3) Do species with
98 “fast” versus “slow” root traits differ in belowground biomass investment under N
99 addition?

101 **2. Materials and Methods**

102 **2.1 Data collection**

We systematically compiled experimental data through comprehensive searches in Web of Science and China National Knowledge Infrastructure (CNKI) databases, encompassing studies published through June 2024. The Boolean search strategy combined nitrogen perturbation terms (“nitrogen fertilization” OR “nitrogen addition” OR “nitrogen application” OR “nitrogen supply” OR “nitrogen input”) with belowground component descriptors (“root” OR “fine root” OR “absorptive root” OR “mycorrhizal fungi” OR “arbuscular mycorrhiza” OR “ectomycorrhiza”). The following criteria were utilized during data screening: (1) Field-scale manipulative experiments excluding greenhouse/pot studies; (2) Minimum experimental duration of 12 months; (3) Focus on N-only or N+P treatments in multi-factor designs; (4) Root diameter specifications (≤ 2 mm, ≤ 1 mm, ≤ 0.5 mm) or absorptive root orders (1, 1-2, 1-3); (5) Quantitative reporting of means with variability measures (SD/SE). For non-tabulated data, we employed Engauge Digitizer 11.1 for graphical data extraction.

The final dataset comprised 138 peer-reviewed studies across 156 globally distributed sites and included 101 plant species (Fig. S1), categorized into three functional groups (Table 1): (1) Fine root traits comprising RD, SRL, RTD, RN and Rs; (2) Root system operationalized through RB and RLD; (3) Mycorrhizal symbiosis metrics including colonized root length (derived from mycorrhizal colonization rate $\times$ RLD), mycorrhizal fungi biomass, and hyphal length, quantifying fungal-mediated nutrient acquisition pathways.

2.2 Meta-Analysis

In this study, a meta-analysis approach was employed to analyze the responses of plant belowground traits to N addition, utilizing the “metafor” package in R. The analysis involved the following steps:

First, the natural logarithm of the response ratio (LnRR), was used as the effect size to measure the influence of N addition on plant nutrient acquisition strategies. The formula is:

$$\text{LnRR} = \text{Ln}(\bar{X}_t) - \text{Ln}(\bar{X}_c) \quad (1)$$

where $\bar{X}_t$ and $\bar{X}_c$ represent the mean values for the treatment and control groups, respectively.

The variance (v) was calculated as:

$$v = \frac{S_t^2}{n_t X_t^2} + \frac{S_c^2}{n_c X_c^2} \quad (2)$$

where S_t and S_c are the standard deviations, and n_t and n_c are the sample sizes of the treatment and control groups, respectively.

The weight for each observation (w_{ij}) was calculated as the inverse of the variance:

$$w_{ij} = \frac{1}{v} \quad (3)$$

For locations with multiple observations, weights were adjusted by dividing by the total number of observations at each location:

$$w' = \frac{w}{n} \quad (4)$$

where n is the total number of observations at the location.

The weighted effect size ($\ln RR'$) was calculated as:

$$\ln RR' = w' \times \ln RR \quad (5)$$

The average effect size (RR_{++}) was computed as:

$$RR_{++} = \frac{\sum_i \frac{w_i}{n} \ln RR_i}{\sum_i \frac{w_i}{n}} \quad (6)$$

Here, w_i and $\ln RR_i$ are the weights and natural log response ratios for the i th observation.

A random-effects meta-analysis model was employed. When the 95% confidence interval of an effect size did not include zero, the effect of N addition on the trait was considered statistically significant. A positive effect size indicates a positive effect, and a negative effect size indicates a negative effect.

To interpret changes in belowground traits under N addition, we converted the average effect size into percentage change using the formula:

$$(e^{RR_{++}} - 1) \times 100\% \quad (7)$$

Liner mixed-effects models were employed to evaluate the effects of N addition amount and duration on belowground traits and can be expressed as:

$$\ln RR = \beta_0 + \beta_1 N + \beta_2 D + \beta_3 N \times D + \pi_{\text{site}} + \epsilon \quad (8)$$

where β represents the coefficients, π_{site} is the random effect for each site, and ϵ is the sampling error.

Mean imputation was used to calculate any missing standard deviations, sd_m :

$$sd_m = \frac{\sum(sd_t, sd_c)}{n} \quad (9)$$

where sd_t and sd_c are the standard deviations of the treatment and control groups, and n is the number of non-missing values. Missing standard deviations were replaced with sd_m .

2.3 Data analysis

To evaluate the effects of N-only addition and combined N+P addition on plant nutrient acquisition strategies, we categorized the dataset into N-only and N+P co-addition treatments. Comparisons between N+P and N-only treatments isolated the regulatory role of P. Analyses of N addition focused solely on N-only experiments to assess direct impacts on fine-root and mycorrhizal traits.

To explore mechanisms underlying N-only addition effects on nutrient acquisition, we stratified the dataset by life growth form (woody vs. herbaceous). Within woody, we further distinguished plants responses by dominant mycorrhizal association, following Soudzilovskaia et al. (2020). Species were classified as arbuscular mycorrhizal (AM) or ectomycorrhizal (EM), with dual-mycorrhizal taxa (e.g., Salicaceae) assigned as EM to reflect their ecological dominance.

We evaluated the influence of outlier studies on effect sizes using Cook's distance, calculated with the metafor package in R. For each fitted meta-analytic model (`rma()`), Cook's distance was extracted using the `influence()` function, with values > 1 indicating potentially influential studies. Only one study (ID 25, reporting RB and RLD) exceeded this threshold; all others fell below it. Sensitivity analyses, excluding this study, showed qualitatively similar results, so it was retained in the overall meta-analysis. However, due to its disproportionate leverage in trait-response regressions, it was excluded from those analyses to ensure robust parameter estimation.

Publication bias was assessed using Egger's regression test, which detects funnel-plot asymmetry by regressing effect sizes against their standard errors (Table S1). A significant intercept deviation from zero indicated bias. Where asymmetry was detected, we applied the trim-and-fill procedure to adjust for missing studies, interpreting corrected estimates cautiously if they diverged substantially from original results (Table S2). Egger's regression was implemented using the `regtest()` function in the R package `metafor`.

To examine whether baseline trait variation modulated responses to N-only addition, we used control-treatment trait values as proxies for species' initial trait states. These were correlated with effect sizes for RB and RLD to identify trait-mediated mechanisms driving plant responses to N-only addition.

Results

3.1 Effects of nitrogen addition on nutrient acquisition strategies

N-only addition enhanced both root exploration and exploitation capacities globally. RB increased by 8.5%, SRL by 1.5%, and RLD by 84.6%, boosting soil exploration. Concurrently, RN rose by 13.2% and Rs by 21.5%, enhancing nutrient uptake rate. In contrast, N addition reduced reliance on mycorrhizal fungi, with declines in colonized root length (−18.7%), hyphal length (−7.5%), and mycorrhizal biomass (−32.7%).

Woody plants exhibited reduced exploration but increased exploitation under N-only addition (Fig. 1b). Fine-root biomass remained unchanged, but increased RTD (+11.9%) led to a reduced RLD (−7.9%). Enhanced exploitation was driven by higher RN (+13.2%) and Rs (+21.7%). When partitioned by mycorrhizal type, AM- and EM-associated woody plants showed divergent responses. AM woody species slightly increased SRL (+2.7%), resulting in higher RLD (+9.5%), whereas EM species increased RTD (+12.9%) and reduced RLD (−8.2%; Fig. S3).

Herbaceous plants, however, increased both exploration and exploitation capacities (Fig. 1c). RB rose substantially (+71.3%), RTD decreased (−33.3%), and SRL increased markedly (+67.8%), driving an 88.0% increase in RLD. Increases in RN (+9.8%) and Rs (+24.6%) further strengthened nutrient exploitation capacity. Notably, smaller sample

sizes for RTD and SRL warrants cautious interpretation.

3.2 Effects of combined nitrogen and phosphorus addition

N+P addition enhanced both root exploration and exploitation capacities (Fig. 2). RB increased by 19.4%, RTD decreased by 7.2%, SRL rose by 9.0%, and RLD expanded by 42.3%. RN increased by 13.9%, indicating improved uptake rate. Unlike N-only treatments, N+P addition sustained mycorrhizal reliance, with mycorrhizal biomass increasing by 41.9%. However, publication-bias diagnostics indicated instability: after trim-and-fill, the 95% CI became extremely wide (−34.5% to +264.0%), so this result should be treated cautiously and interpreted as directional only (Tables S1–S2).

In woody plants, N+P addition significantly boosted exploration without altering RB. Reduced RTD (−7.2%) and increased SRL (+9.0%) drove a 25.5% increase in RLD (Fig. S2).

3.3 Trait mediation of fine-root biomass and RLD responses

SRL emerged as a key predictor of plant responses to N-only addition (Fig. 3). Species with low baseline SRL showed stronger positive responses of RB ($r^2 = 0.13$, $p < 0.001$) and RLD ($r^2 = 0.19$, $p < 0.001$) to N-only addition, whereas species with high SRL exhibited much weaker responses. In contrast, RN was not significantly associated with RB responses ($p > 0.1$) but positively correlated with RLD responses ($r^2 = 0.27$, $p < 0.01$; Fig. S4).

3.4 Relationships between N addition intensity, duration, and belowground traits

N-only addition level and duration influenced root and mycorrhizal traits responses (Fig. 4; Table S1). RB responses showed a weak but significant positive correlation with N-only addition level ($r^2 = 0.02$, $p < 0.05$), whereas mycorrhizal biomass responses exhibited a stronger negative correlation ($r^2 = 0.29$, $p < 0.05$). The interaction between N-only addition level and duration negatively impacted RB and RLD, and duration negatively affected RTD responses (Table S3).

Discussion

Our findings reveal that plants respond to N-only addition by increasing RB and adjusting functional traits, thereby enhancing both nutrient exploration and exploitation to meet elevated aboveground nutrient demands (Galloway et al., 2008). Globally, N-only addition increased RB by 8.5% and SRL by 1.5%, contributing to an 84.6% increase in RLD. Concurrently, RN and Rs, key indicators of uptake rate, rose by 13.2% and 21.5%, respectively.

Woody and herbaceous plants exhibited divergent strategies under N-only addition. Woody plants maintained stable RB but reduced exploration capacity through morphological traits adjustments while enhancing exploitation via increased RN and Rs. Specifically, increased RTD (+11.9%) led to a 7.9% reduction in RLD (Fig. 1b), indicating reduced exploration. This likely reflects greater soil N availability, decreasing the need for extensive root proliferation (Aber et al., 1989). When stratified by mycorrhizal type, AM woody species reduced RB (-5.4%) but increased SRL (+2.7%), resulting in a 9.5% RLD increase, whereas EM species reduced RB (-3.8%), increased RTD (+12.9%), and decreased RLD (-8.2%; Fig. S3). These patterns align with resource contexts: AM species, prevalent in P-limited environments (Steidinger et al., 2019), likely face exacerbated P limitation under N addition (Du et al., 2020), prompting root proliferation for P acquisition. Conversely, EM species in N-limited systems (Steidinger et al., 2019) experience alleviated N limitation (De Schrijver et al., 2008), reducing exploration needs. Woody plants enhanced nutrients uptake rate through increased RN (+13.2%) and Rs (+21.7%), suggesting that, rather than increasing biomass investment, they meet elevated nutrient demands through physiological rate gains.

Herbaceous plants adopted a more acquisitive strategy by increasing RB and adjusting morphological traits to enhance exploration capacity, while simultaneously elevating RN and Rs to strengthen exploitation capacity. Specifically, increasing RB by 71.3%, reducing RTD by 33.3%, and raising SRL by 67.8%, driving an 88.1% RLD increase (Fig. 1c). Concurrent increases in RN (+9.8%) and Rs (+24.6%) further enhanced exploitation capacity. This acquisitive strategy aligns with herbaceous plants' ecological traits, including strong nutrient limitation, high intraspecific competition, and rapid root

turnover (Illuminati et al., 2025). Abundant soil N likely prompts herbs to allocate heavily belowground, rapidly expanding root networks to preempt resources.

N-only addition reduced mycorrhizal reliance, with declines in mycorrhizal biomass (−32.7%), colonized root length (−18.7%), and hyphal length (−7.5%; Fig. 1a). These findings align with prior syntheses (Han et al., 2020; Ma et al., 2021), which suggest that mycorrhizal networks, while beneficial in nutrient-poor soils, incur high carbon costs that become disadvantageous under N enrichment (Han et al., 2021).

Surprisingly, combined N+P addition increased mycorrhizal biomass by 41.9% (Fig. 2), contrasting with greenhouse and pot studies where co-fertilization typically reduces fungal reliance (Ma et al., 2021). This discrepancy may stem from environmental heterogeneity: diverse soil microbial communities and strong P adsorption to soil particles in field settings sustain plant reliance on fungal networks for P mobilization (Leppälammi-Kujansuu et al., 2013; Camenzind et al., 2016; Wang et al., 2018). In contrast, low-diversity substrates in controlled experiments limit mycorrhizal fungal network development, favoring direct nutrient uptake by plants (Brundrett, 2009). Although N+P co-addition increased mycorrhizal biomass on average, trim-and-fill produced very wide CIs (−34.5% to +264%), indicating substantial uncertainty, we therefore treat this pattern as directional only and emphasize the need for paired within-study contrasts to isolate P-mediated regulation. Besides, while N-only treatments reduced woody plant exploration capacity, N+P addition enhanced it. Without altering RB, woody plants decreased RTD (−7.2%) and increased SRL (+9.0%), leading to a 25.5% increase in RLD (Fig. S2). This likely reflects P's low soil mobility compared to N, which diffuses readily via mass flow, prompting plants to expand root systems to access discrete P patches (Moreau et al., 2019; Jiang et al., 2019).

Contrary to our third hypothesis, SRL, not RN or RTD, was the strongest predictor of RB responses to N-only addition. Species with low baseline SRL exhibited stronger positive responses of RB and RLD to N-only addition (Fig. 3), enhancing exploration capacity, whereas high-SRL species showed much weaker or even negative responses. This may reflect differing mycorrhizal reliance: low-SRL species, often more dependent on

mycorrhizal fungal symbioses (Bergmann et al., 2020), compensate for reduced symbiotic function under N addition (Fig. 1a) by investing in roots. High-SRL species, with inherently dense root systems, scale back investment under N-only addition. Moreover, as RB is a major component of belowground carbon pools (Jackson et al., 1997), the linkage between SRL and biomass responses offers a mechanistic framework for understanding trait-driven modulation of ecosystem carbon cycling under global change (Díaz et al., 2007; McCormack et al., 2013). RN positively correlated with RLD responses (Fig. S4b), suggesting that species with higher baseline RN enhance root proliferation to maximize nutrient capture under N enrichment.

The relationships between N-only addition level, duration, and belowground responses highlight complex ecosystem feedbacks. RB responses showed a weak positive correlation with N addition level, while mycorrhizal biomass responses declined strongly (Fig. 4). These align with N-induced suppression of soil microbial communities (Zhang et al., 2018). However, our observed RB responses contrasts with studies reporting no effect (Zhao et al., 2022; Gao et al., 2023), possibly due to compensatory root investment offsetting mycorrhizal fungal declines amid alleviated nutrient limitation and higher aboveground productivity (Deng et al., 2017). However, the low explanatory power of the biomass regression ($r^2 = 0.2$) suggests caution. These contrasting root and fungal responses underscore how N-only addition reshapes belowground biogeochemical processes. Future long-term, multifactorial experiments are needed to disentangle the interactive effects of N rate, duration, and co-limiting nutrients on belowground dynamics, improving predictions of ecosystem functioning under chronic N deposition.

Limitations

Despite compiling a larger dataset than previous syntheses, evidence for nutrients addition effects on fine-root traits remains constrained. Significant publication bias in studies reporting RD and SRL (Tables S1–S2) necessitates cautious interpretation of our findings. Additionally, no studies directly measured fine-root nutrient uptake rates under N addition, leading us to use RN and Rs as proxies for uptake rate. Although higher RN

supports synthesis of high-affinity transport proteins and elevated R_s indicates greater ATP availability for ion uptake, direct evidence linking these traits to increased nutrient fluxes is lacking. We hypothesize that elevated soil N enhances root N storage, boosting protein synthesis potential, and that higher R_s provides ATP for active uptake. Future research should quantify nutrient uptake rates across ecosystems to validate these proxies. Unexpected SRL increases in woody plants (Fig. 1b) also diverge from theoretical expectations, as increased RTD should reduce SRL when RD is constant ($SRL = 4 / (\pi \times RD^2 \times RTD)$). This discrepancy may reflect an overemphasis on datasets with large response magnitudes, potentially reducing representativeness. Finally, some herbaceous data reflect community-level shifts rather than intraspecific plasticity, as analyses included community contrasts alongside species-specific manipulations. Thus, trait changes in herbaceous plants may partly stem from altered community composition, a key caveat for interpreting their root strategies under N addition.

Conclusion

N-only addition enhances root-driven nutrient exploration and exploitation capacities while reducing mycorrhizal reliance, indicating a shift from symbiont-mediated to root-centric nutrient acquisition. Woody plants reduced RLD, reflecting diminished exploration, but compensated with increased RN and R_s to meet aboveground nutrient demands. Conversely, herbaceous plants exhibited robust increases in RB, RLD, RN and R_s enhancing both exploration and exploitation capacities. N+P addition sustained mycorrhizal reliance, with plants leveraging mycorrhizal fungal networks for P acquisition under nutrient-rich conditions. Notably, fine-root traits were strong predictors of belowground biomass responses: species with low SRL showed stronger RB and RLD responses to N-only addition, while those with high SRL responded weakly. These findings elucidate trait-mediated strategies for belowground allocation under nutrient addition, highlighting a fundamental shift in nutrient acquisition under global change.

Acknowledgements

This study was supported by the Natural Science Foundation of Xiamen, China (grant nos. 3502ZZ202471075), the Xiamen Institute of Technology High Level Talent Project (grant nos. YKJ24012R). We would like to acknowledge the use of ChatGPT for providing assistances with the polishing of the English language in this manuscript.

Competing interests

None declared.

Author contributions

L.K. and H.G. conceived the idea, H.G. performed the data analysis and wrote the manuscript. L.K., Y.Z., B.X.Z, Y.H. and L.W. substantially contributed to revisions.

Data availability

Supplementary data to this article can be found online.

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FIGURES

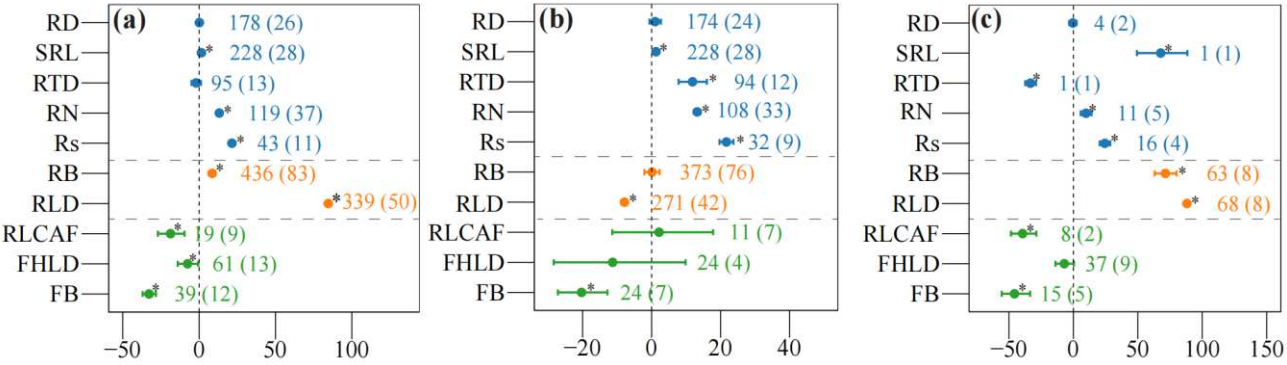


Figure 1 Effect sizes of fine root and mycorrhizal fungal traits in response to N-only addition.

Error bars indicate 95% confidence intervals (CIs), with effects considered significant when CIs do not overlap with 0, * indicates CIs do not overlap 0. Numbers outside brackets indicate sampling sites; numbers inside brackets denote total observations for each trait. (a) all plant species, (b) woody species, (c) herbaceous species. RD: root diameter; SRL: specific root length; RTD: root tissue density; RN: root nitrogen concentration; Rs: root respiration rate; RB: root biomass; RLD: root length density; RLCAF: root length colonized by arbuscular mycorrhizal fungi; FHLD: mycorrhizal fungal hyphal length density; FB: mycorrhizal fungal biomass.

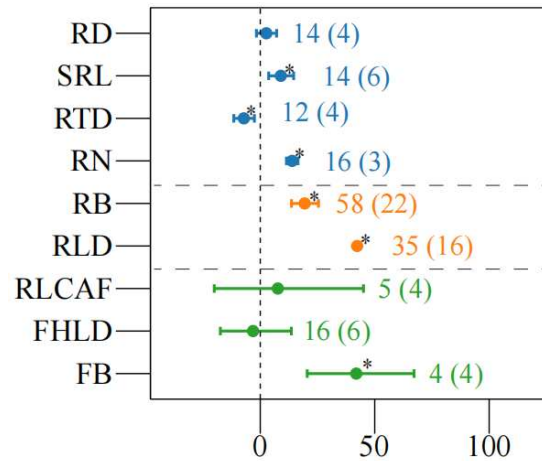


Figure 2 Effect sizes of fine root and mycorrhizal fungal traits in response to combined nitrogen and phosphorus additions.

Error bars indicate 95% confidence intervals (CIs), with effects considered significant when CIs do not overlap with 0, * indicates CIs do not overlap 0. Numbers outside brackets indicate sampling sites; numbers inside brackets denote total observations for each trait. RD: root diameter; SRL: specific root length; RTD: root tissue density; RN: root nitrogen concentration; RB: root biomass; RLD: root length density; RLCAF: root length colonized by arbuscular mycorrhizal fungi; FHLD: mycorrhizal fungal hyphal length density; FB: mycorrhizal fungal biomass.

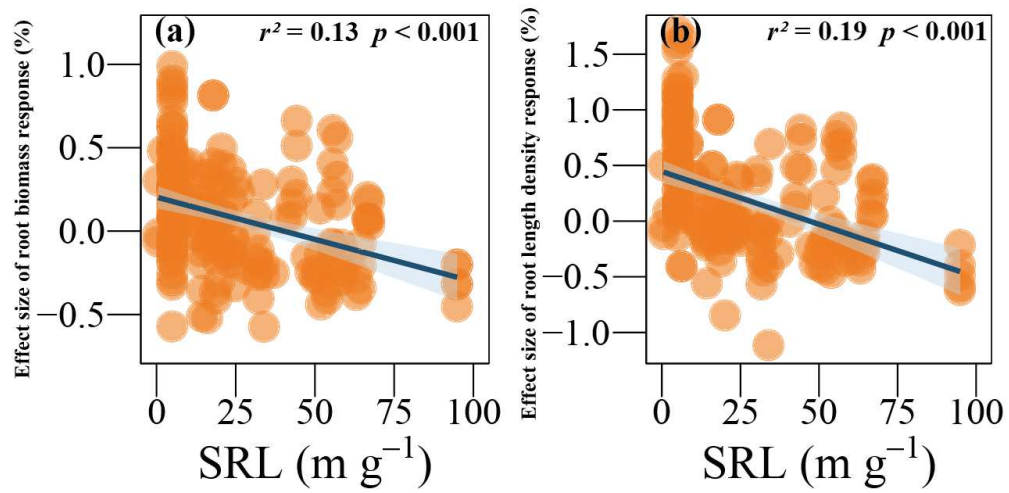


Figure 3 Scatterplot of effect sizes under N-only addition as a function of specific root length (SRL) for fine-root biomass (a) and root length density (b). Trendline for regression relationship are displayed with 95% confidence interval shaded regions.

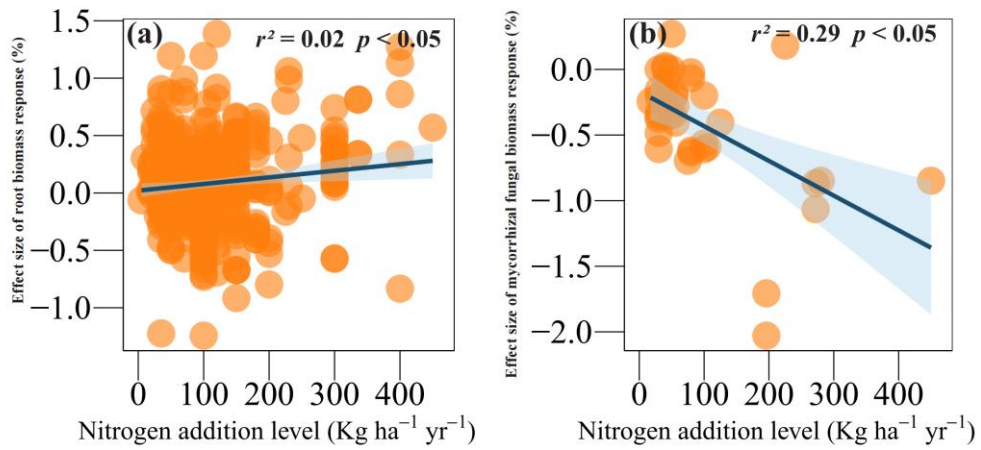


Figure 4 Scatterplot of effect sizes as a function of N-only addition level for fine root biomass (a) and mycorrhizal fungal biomass (b). Trendline for regression relationship are displayed with 95% confidence interval shaded regions.

Table 1 Abbreviations, full names, trait types, and units of belowground plant traits

Abbreviation	Full name	Traits type	Unit
RD	root diameter	Root trait	mm
SRL	specific root length	Root trait	m g^{-1}
RTD	root tissue density	Root trait	g cm^{-3}
RN	root nitrogen concentration	Root trait	%
Rs	root respiration rate	Root trait	$\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$
RB	root biomass	Root system	g m^{-2}
RLD	root length density	Root system	m m^{-2}
RLCAF	root length colonized by arbuscular mycorrhizal fungi	Mycorrhiza trait	m m^{-2}
FHLD	mycorrhizal fungal hyphal length density	Mycorrhiza trait	cm g^{-1}
FB	mycorrhizal fungal biomass	Mycorrhiza trait	nmol mg^{-1}



Figure S1 Global distribution of 156 sites across 138 studies

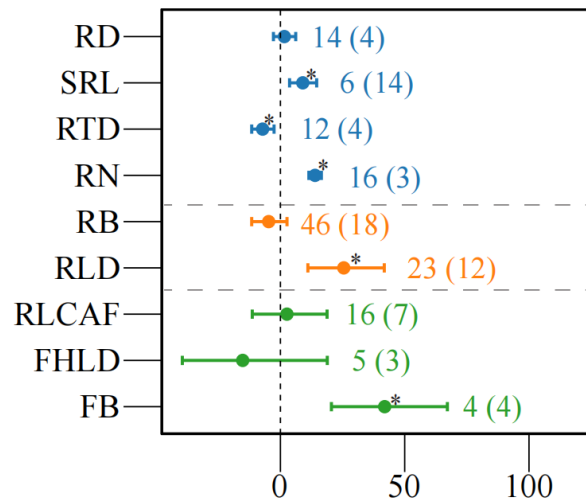


Figure S2 Effect sizes of nitrogen and phosphorus addition on fine root and mycorrhizal fungal traits for woody plants. Error bars indicate 95% confidence intervals (CIs), and effects are considered significant when CIs do not overlap with 0, * indicates CIs do not overlap 0. Numbers outside brackets indicate sampling sites; numbers inside brackets denote total observations for each trait. RD: Root Diameter; SRL: specific root length; RTD: root tissue density; RN: root nitrogen concentration; RB: root biomass; RLD: root length density; RLCAF: root length colonized by arbuscular mycorrhizal fungi; FHLD: mycorrhizal fungal hyphal length density; FB: mycorrhizal fungal biomass.

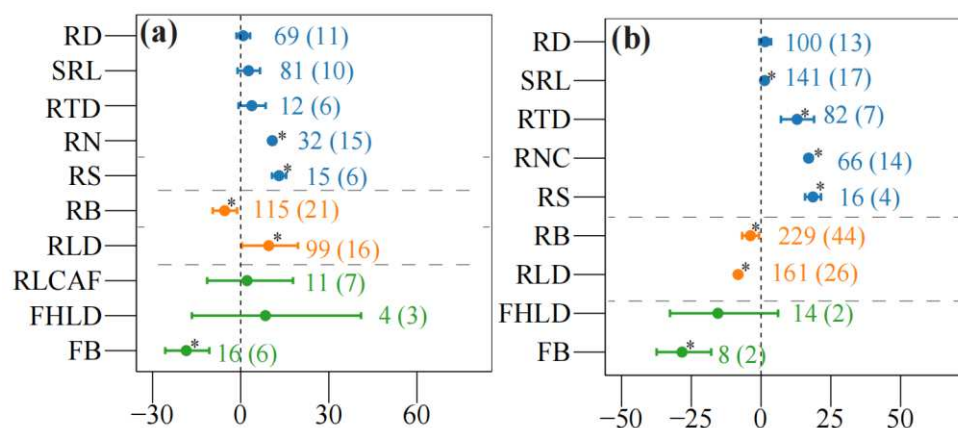


Figure S3 Effect sizes of N-only addition on fine root and mycorrhizal fungal traits in AM (a) and EM (b) woody plants. Error bars indicate 95% confidence intervals (CIs), with effects considered significant when CIs do not overlap with 0, * indicates CIs do not overlap 0. Numbers outside brackets indicate sampling sites; numbers inside brackets denote total observations for each trait. RD: Root Diameter; SRL: specific root length; RTD: root tissue density; RN: root nitrogen concentration; Rs: root respiration rate; RB: root biomass; RLD: root length density; RLCAF: root length colonized by arbuscular mycorrhizal fungi; FHLD: mycorrhizal fungal hyphal length density; FB: mycorrhizal fungal biomass.

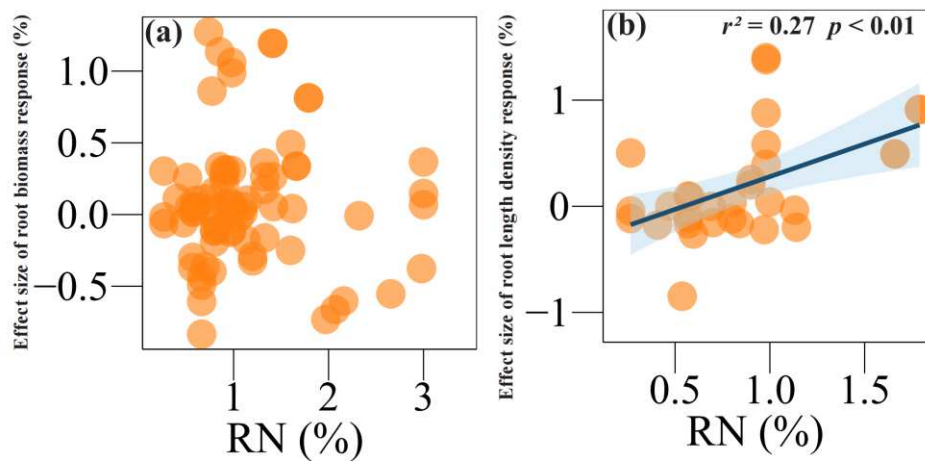


Figure S4 Scatterplot of effect sizes under N-only addition as a function of root nitrogen concentration (RN) for fine-root biomass (a) and root length density (b). Trendline for regression relationship are displayed with 95% confidence interval shaded regions.

Table S1 Bias analysis: $p < 0.05$ indicates the presence of publication bias (RD: root diameter; SRL: specific root length; RTD: root tissue density; RN: root nitrogen concentration; Rs: root respiration rate; RB: root biomass; RLD: root length density; RLCAF: root length colonized by arbuscular mycorrhizal fungi; FHLD: mycorrhizal fungal hyphal length density; FB: mycorrhizal fungal biomass.)

	N	N Woody	N herbaceous	N AM Woody	N EM Woody	N+P	N+P Woody
RD	$p < .01$	$p < .01$	$p = .09$	$p < .01$	$p = .77$	$p = .10$	$p = .90$
SRL	$p < .01$	$p < .01$		$p < .01$	$p = .17$	$p = .63$	$p = .59$
RTD	$p = .21$	$p = .31$		$p = .75$	$p = .32$	$p = .66$	$p = .66$
RN	$p = .20$	$p < .01$	$p = .62$	$p = .22$	$p < .05$	$p < .05$	$p < .05$
Rs	$p = .23$	$p = .11$	$p = .87$	$p = .24$	$p = .47$		
RB	$p = .47$	$p = .10$	$p = .83$	$p = .06$	$p = .08$	$p = .56$	$p = .81$
RLD	$p = .06$	$p = .08$	$p = .83$	$p = .08$	$p = .06$	$p = .32$	$p = .55$
RLCAF	$p = .07$	$p = .09$	$p = .23$	$p = .15$		$p = .32$	$p = .32$
FHLD	$p = .11$	$p = .47$	$p = .16$	$p = .95$	$p = .14$	$p = .24$	$p = .35$
FB	$p < .05$	$p = .10$	$p = .15$	$p = .61$	$p = .06$	$p < .05$	$p < .05$

Table S2 Trim-and-Fill correction for significant publication bias: * indicates a significant difference between the corrected results and the original results (RD: root diameter; SRL: specific root length; RN: root nitrogen concentration; FB: Fungal biomass).

	N	N Woody	N AM Woody	N EM Woody	N+P	N+P Woody
RD	-5.2* (-7.8, -2.6)	-5.1* (-7.8, -2.5)	-16.4* (-19.6, -13.1)			
SRL	-3.1* (-6.6, 0.4)	-3.2* (-6.6, 0.3)	2.0* (-4.9, 9.5)			
RN		12.2 (8.3, 16.2)		22.9 (18.0, 28.1)	13.8 (9.8, 17.9)	13.8 (9.8, 17.9)
FB	-34.3 (-42.9, -24.4)				54.4* (-34.5, 264)	54.4* (-34.5, 264)

Table S3. Significance analysis of N-only addition level, duration, and their interaction on fine root and mycorrhizal traits based on a mixed-effects model. Bold values indicate significant effects at $p < 0.05$. The table presents the effect sizes along with corresponding p -values for each trait.

	N	D	N*D
Root diameter	0.001 ($p = 0.43$)	0.063 ($p = 0.40$)	-0.000 ($p = 0.18$)
Specific root length	-0.002 ($p = 0.25$)	0.033 ($p = 0.56$)	0.001 ($p = 0.07$)
Root tissue density	-0.002 ($p = 0.55$)	-0.904 ($p < 0.001$)	0.000 ($p = 0.50$)
Root nitrogen concentration	0.001 ($p = 0.95$)	0.016 ($p = 0.62$)	0.000 ($p = 0.07$)
Root biomass	0.002 ($p < 0.05$)	0.015 ($p = 0.08$)	-0.001 ($p < 0.01$)
Root length density	0.003 ($p = 0.07$)	0.049 ($p = 0.43$)	-0.001 ($p < 0.05$)
Root length colonized by AM fungi	-0.008 ($p = 0.32$)	0.132 ($p = 0.57$)	-0.001 ($p = 0.75$)
Fungal hyphal length density	0.012 ($p = 0.55$)	0.261 ($p = 0.38$)	-0.003 ($p = 0.36$)
Fungal biomass	-0.012 ($p < 0.01$)	0.007 ($p = 0.90$)	0.000 ($p = 0.68$)

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- A total of 138 studies were included in this meta-analysis for data extraction
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