Low-level nitrogen and short-term addition increase soil carbon sequestration in Chinese forest ecosystems

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Abstract

Soil carbon (C) sequestration plays a vital role in mitigating global climate change. Human activities have vastly increased nitrogen (N) deposition rate in China, which in turn influences belowground C cycle processes. We performed a meta-analysis based on 61 published studies on N addition experiments, including 4072 observations across China, to quantify the responses of belowground soil C dynamics and sequestration to N enrichment in Chinese forest ecosystems. The results showed that, on average, N enrichment significantly enhanced C dynamics in boreal and temperate forests by an average of 24% and 10% while it reduced in subtropical and tropical forests by 11% and 19%. The response of C pools and C input to N addition were more pronounced in boreal forests with +17% and +10% while it was lower in subtropical forests with -0.4% and -19% respectively. The N enrichment enhanced soil C output by in boreal (6%) and temperate (7%) forests and a negative effect in subtropical (-30%) and tropical forests (-10%). This can be explained by the higher reduction levels in C respiration, despite the slightly lower litter and root-derived C inputs. Notably, N addition specifically increased belowground C sequestration, at low N addition rates (<30 kg N ha^{-1} yr^{-1}) and during a short-term period (<1 year). These C sequestration effects were reversed at higher N deposition levels and /or during a longer time period. This implies that soil C sequestration is currently most likely not enhanced in (large) parts of China, as forests are characterized by long-term elevated N deposition levels.

Keywords: Carbon sequestration; Nitrogen addition; belowground soil C processes; Forests; China.

1. Introduction

Growing fossil fuel consumption, human population, industrialization, animal husbandry expansion, and agricultural intensification have strongly enhanced China's emissions and deposition of reactive nitrogen (N) (Liu et al., 2019). China is one of the global hotspots areas for N deposition, which amounted on average 20.4 ± 2.6 kg N ha^{-1} yr^{-1} in 2011–2015 (Yu et al., 2019) compared to the United States and Europe, where the rate is relatively low, being about 6.7 kg N ha^{-1} yr^{-1} (Walker et al., 2019) and 9.2 kg N ha^{-1} yr^{-1} for the year 2015 (de Vries et al., 2017), respectively. N deposition level affects the forest carbon (C) cycle by stimulating biomass production (Fowler et al., 2013; LeBauer and Treseder, 2008), and this is also held in large parts of China, where forest ecosystems are N-limited and characterized by young forest age. However, long-term addition can also threaten forest health by altering the N cycle in forested ecosystems and inducing nitrogen saturation (Aber et al., 1998; Gundersen et al., 2006; (de Vries and Schulte-Uebbing, 2019). The C sink due to enhanced forest growth results from several processes, including N deposition, but also age-related growth (regrowth) after land-use change, forest management practices, and elevated CO_2 (Albani et al., 2006; Luyssaert et al., 2008; Reay et al., 2008; Schimel et al., 2000; Yu et al., 2014).

To better understand the effects of N addition on C sequestration, it is crucial to distinguish impacts on above—and belowground C dynamics in forest ecosystems (Chen et al., 2015; Deng et al., 2018; Liu and Greaver, 2010). Recently, several studies have been carried out to assess the impacts of N addition on aboveground C sequestration by a meta-analysis of N addition experiments (Chen et al., 2015; Schulte-Uebbing and de Vries, 2018). However, changes in mineral soil C pools, representing the largest pool of terrestrial organic C in the biosphere (Hyvönen et al., 2007), were not considered. It has been shown that the belowground C cycle does not always mirror that of the aboveground soil C and has lower turnover times than aboveground C (De Vries et al., 2007; Deng et al., 2018; Liu and Greaver, 2010). Belowground C response to N addition is determined by N-induced changes in biochemical composition, litter inputs, and soil respiration (Frey et al., 2014; Zak et al., 2017), and it can thus be different from aboveground C response, which is mainly determined by N-induced forest growth changes (Pregitzer et al., 2008). Where N deposition nearly always (apart from N saturated systems) enhanced forest growth and related C sequestration, soil C sequestration depends on the balance of the impacts on litter C inputs and soil respiration C outputs. Several studies have been conducted to assess N addition effects on belowground C dynamics in forests, but they give contradicting results. For example, Frey et al. (2014) and Zak et al. (2017) reported that N deposition could increase soil C sequestration due to increased litter inputs and/or reduced soil respiration. Several studies and meta-analysis confirmed this N induced stimulation of soil C sequestration, specifically by reduced soil respiration (De Vries et al., 2007; Janssens et al., 2010; Lu et al., 2021; Nave et al., 2009), but Liu and Greaver (2010) reported that soil respiration was not altered by N addition. Several other studies also outlined that N addition can deplete the soil C pool (Van Miegroet and Jandl, 2007) or does not affect soil C sequestration (Lu et al., 2011).

These contradictions may partly be due to the amount of N that is applied in the experiments. According to De Vries et al. (2014), N addition enhances growth and thus likely C input by litterfall, but it may also stimulate soil respiration at lower levels (near 20-30 kg N $ha^{-1}yr^{-1}$) while reducing at higher addition rates. This distinction in addition rates is crucial since the lower rates more realistically mimic N deposition on forests in most parts of the world. Along the same lines, Janssens et al. (2010) also mentioned that reduced soil respiration mainly occurs at high N addition. Many studies indeed only report enhanced SOC contents in response to high N addition rates (>50 kg N ha^{-1} yr^{-1}) (Lu et al., 2021; Maaroufi et al., 2015; Tian et al., 2019). Conversely, other studies reported that SOC content is more responsive at a low N addition level (≤ 50 kg N ha^{-1} yr^{-1}) (Deng et al., 2018). There is thus a need to investigate further the relation between N deposition level and the increase or decrease in soil C sequestration. Apart from the varying responses of soil C sequestration to N deposition at different levels, no studies to date have provided a holistic picture of belowground soil C sequestration response to N addition in Chinese forests (boreal, temperate, subtropical, and tropical). This is a knowledge gap considering that China has a significant spatial variation in climatic conditions and diverse ecosystems. Furthermore, China represents a region where atmospheric N deposition is projected to increase because of the intensification of agricultural and industrial activities (Chen et al., 2015; Deng et al., 2018; Liu et al., 2013). Finally, China contains a large area of tropical forest ecosystems, which are often N-rich (Lu et al., 2021) and where N induced aboveground C sequestration is thus found to be low (De Vries et al., 2007; Deng et al., 2018; Liu and Greaver, 2010).

To address this critical gap in our knowledge, we performed a meta-analysis, synthesizing the effects of N addition on belowground C cycling (input, output, and pool) in Chinese forest ecosystems. The main aim was to assess the impact of N deposition level on the changes in C inputs, C output, and C pools. We hypothesized that belowground C sequestration is mainly affected by low N addition rates, reflecting current N deposition levels, considering that under these circumstances, both growth might be enhanced and respiration reduced, with impacts being less pronounced in long-term N addition experiments.

2. Materials and Methods

2.1. Data collection

We searched the peer-reviewed journal articles that studied N addition effects on belowground C dynamics (Table S1) in Web of Science and Google Scholar (1900–2020), using the following keywords: "forest" and "carbon" and "nitrogen addition or nitrogen enrichment or nitrogen deposition or nitrogen fertilization or boreal forests, subtropical, temperate, and tropical." This search returned 2086 papers, the titles of which were scanned to eliminate irrelevant papers.

The following criteria were used to select appropriate studies and avoid bias in publication: (1) the experiments must be conducted in the field in China, and only field studies performed in forest ecosystems were used; (2) the experiments were performed on forest areas older than 10 years at the start of the experiment; (3) the experiments included a control treatment, and if many levels of N addition were applied in the same experiment, then the measurements for different N application rates were considered as independent observations and (4) the levels and types of N addition and experiment duration were reported or extracted through the figures or tables (Fig. S1). The following framework was used in this study to select, classify the studies, describe, and analyze the data by using the method described by Arksey and O'Malley (2005). This led to a compilation of 4072 field observations from 61 studies (publications) across China. Four types of forests were included in this analysis: boreal (n=125), temperate (n=961), subtropical (n=870) and tropical forests (n=130) (Fig. 1). The means, standard deviations (SD) or standard errors (SE), and sample sizes were reported, calculated, or extracted using OriginPro version 2021 software (Origin Lab Corporation, Northampton, MA, USA) or Graph Grabber version 2.0.2, Quintessa Ltd if the data were graphically presented.

The compiled database of belowground contained 8 variables including, C input fluxes, i.e., litter inputs and fine root inputs, C output fluxes, i.e., soil respiration (Rs) and heterotrophic respiration (Rh), and soil C contents/pools, i.e., microbial biomass (MBC), total C (TC), soil organic carbon (SOC) and dissolved organic C (DOC). All the variables were compared among different forest types (i.e., boreal, temperate, subtropical, and tropical forests), N addition forms (NH_4NO_3 and Urea), N addition rates (<30, 30–70, and >70 kg N ha^{-1} yr^{-1}), N deposition rate (i.e., <10, 10–20 and >20 kg N ha^{-1} yr^{-1}) and N fertilization duration (<1, 1–3 and >3 years). Microbial respiration and root respiration variables were excluded from the analysis due to insufficient or lack of data.

2.2. Analysis and statistics

A general linear model was used to analyze the relationships between the variables across all samples. We also used Pearson correlations to explore the relationships between the variables and MAP, MAT, N addition. Differences were evaluated at P <0.05. All analyses were analyzed using SPSS version 26.0 (SPSS Inc., Chicago, IL, USA). While the meta-analysis method, described by Hedges et al. (1999), was conducted to assess belowground C responses to N addition using the METAWIN (Sinauer Associates, Inc. Sunderland, MA, USA). The effects of N additions were estimated based on the natural log-transformed response ratio (RR):

$$\ln RR = \ln\left(\frac{\overline{X}_t}{\overline{X}_c}\right) \quad (3)$$

Where (Xt) and (Xc) are the mean values of a variable in the treatment and control group, respectively. The variance (n) of RR was estimated as:

$$v = \frac{S_t^2}{n_t \overline{X}_t^2} + \frac{S_c^2}{n_c \overline{X}_c^2} \quad (4)$$

Where n_t and n_c are the sample sizes for the treatment and control groups, respectively, and S_t and S_c are the standard deviations for the treatment and control groups, respectively. For literature sources where the standard error (SE) rather than standard deviation (SD) was reported, we recalculated the SD by:

$$SD = SE \times \sqrt{N} \quad (5)$$

Where *N* is the number of replications.

For a better explanation, the mean of the response ratio was transformed back to the percentage change according to:

$$(\ln RR - 1) \times 100\% \quad (6)$$

Confidence intervals (CIs) on the weighted effect size were generated using bootstrapping (9,999 iterations). The N addition effect on a response variable was considered significant between two treatments if the 95% CI did not overlap with 1.0.

3. Results

The estimation of the changes in the C budget of belowground terrestrial ecosystems under N addition across forests ecosystems in China was summarized in Fig. 2. Our meta-analysis showed that N enrichment enhanced soil C pools, as indicated by the increased total C (TC) by 15%; and soil organic carbon (SOC) by 6% and inhibited C fluxes (C input and C output)(Fig. 2). Indeed, N addition decreased soil C input by aboveground litter and fine roots by 4% and 6%, respectively (Fig. 2). Similarly, N addition inhibited C output by soil respiration (Rs) and heterotrophic respiration (Rh), which declined on average by 5% and 12%, respectively (Fig. 2).

3.1. Boreal forests

Specifically, N addition significantly increased C dynamics in boreal forests by an average of 24% (Fig. 3a; $P>0.05$). The enrichment was positive for C pools, C inputs, and C outputs with an average increase of 17% and 10% and 6%, respectively (Fig. 3a; $P>0.05$). The positive effects were much more pronounced for DOC (+34%) and MBC (+31%)(Fig. 3a; $P>0.05$). Furthermore, impacts of N addition on C inputs reversed from negative in litter inputs (Fig. 3b, $P<0.05$). When data were subdivided into N fertilization rates, we found a positive and significant correlation between N addition and the response ratios of C concentration, but it was more pronounced at low N fertilization rate (<30 kg N ha^{-1} yr^{-1}, +33%; $P>0.05$)(Fig. 3a). In addition, our meta-analysis showed a tendency for an increase at a high ambient N deposition (>20 kg N ha^{-1} yr^{-1}, +27%; $P>0.05$) and intermediate-term (1-3 years, +35%; $P>0.05$)(Fig. 3a). Our meta-analysis showed that N enrichment had a negative impact on C:N ratio and pH in boreal forests (Fig. S2).

3.2. Temperate forests

Results from our meta-analysis showed that N addition positively affected C dynamics in temperate forests (+6%, Fig. 3b; $P>0.05$). N addition had a significant overall impact on C pools by an average of 10%, while C inputs decreased by -11% with N enrichment ($P>0.05$, for all). Also, N addition positively affected C outputs (+7%), but only Rs was significant (+11%, Fig. 3b; $P>0.05$). Our meta-analyses showed that C dynamics reversed from a positive effect at low N fertilization rates by an average of 8% (<30 kg N ha^{-1} yr^{-1}; $P<0.05$) to an adverse effect at above 30 kg N ha^{-1} yr^{-1} (Fig. 3b). N forms affect the response of C concentrations, with urea leading to a significant average increase of 11% (Fig. 3b, P<0.05), while NH_4NO_3 application decreased by only 3% (Fig. 3b, P<0.05). However, N addition only had a significant positive effect on C dynamics at intermediate N ambient N deposition (10–20 kg N ha^{-1} yr^{-1}, +9%; P<0.05) while it had a negative effect below 10 kg N ha^{-1} yr^{-1} (Fig. 3b). Similarly, it changed with N fertilization duration, significantly enhancing C dynamics in temperate forests below 1-year duration by an average of 9% (Fig. 3b; P>0.05). Overall, N addition decreased both C:N ratio and pH but no significant correlation with C:N ratio (Fig. S2).

3.3. Subtropical forests

N addition significantly reduced C dynamics in subtropical forests by an average of 19% (Fig. 3c, P<0.05). The enrichment insignificantly decreased C pools (-0.35%) but significantly reduced C inputs (-19%) and C outputs (-30%) in the subtropical forest (Fig. 3c, P>0.05 for all). Similarly, N fertilization rates negatively impact C dynamics following N fertilization rates by 10% (<30 kg N ha^{-1} yr^{-1}), 2% (30-70 kg N ha^{-1} yr^{-1}), and 19% (>70 kg N ha^{-1} yr^{-1}), but it had was significant only at low and high rates (Fig. 3c, P<0.05 for all). As with temperate forests, our meta-analysis showed that C dynamics is more sensitive to urea (-8%) compared to NH_4NO_3 (-12%)(Fig. 3c, P<0.05 for all). Besides, ambient N deposition rate had a significant effect on the response of C dynamics low (<20 kg N ha^{-1} yr^{-1}) and high (>20 kg N ha^{-1} yr^{-1}) fertilization rate leading to an average decrease between 22% and 7%, respectively (Fig. 3c). However, it was significant only at a high and low rate (Fig. 3c, P<0.05). Belowground C dynamics were found to decrease with time, but their decreasing extents were significantly larger under short-term N application (<1 year)(Fig. 3c, P<0.05) than that above 1-year (Fig. 3c, P<0.05). We found a significant and negative correlation between the response ratios of C:N ratio and pH to N enrichment (Fig. S2; P>0.05).

3.4. Tropical forests

In general, the results of our meta-analysis showed that N addition had a significant effect on C dynamics in tropical forests, with an average decrease of 19% (Fig. 3a, P<0.05). The enrichment was positive for C pools (+4%) but had a significant and negative effect on C inputs (-19%) and C outputs (-10%)(Fig. 3d, *P*<0.05). In addition, C dynamics decreased with the increase of N fertilization rate, but its response to N addition was positive only below 30 kg N ha^{-1} yr^{-1} (+9%) while it has a significant negative impact above 30 kg N ha^{-1} yr^{-1} by an average of 25% and 43% for intermediate (30-70 kg N ha^{-1} yr^{-1}) and high N fertilizer rate respectively (>70 kg N ha^{-1} yr^{-1})(Fig. 3d *P*<0.05 for all). Similar to N fertilization rate, N enrichment positively impacted C dynamics at low ambient N deposition by an average of 10% (<30 kg N ha^{-1} yr^{-1}). Fertilization duration influenced the responses of C dynamics to N addition. For example, short-term (<1 year) N fertilization duration had a positive and significant effect on C dynamics (+11%)(Fig. 3d *P*<0.05) while it was negative above 1 year (Fig. 3d). The negative effects were much more pronounced at long-term (3 years) N application (<10 kg N $ha^{-1}yr^{-1}$, *P*<0.05). Unlike to subtropical forests, impacts of N addition on C:N ratio and pH were negative but only significant for pH in tropical forests (Fig. 3b, *P*<0.05).

4. Discussion

4.1. C pools response to N enrichment

Results from our meta-analysis showed that N addition increased TC and SOC concentrations (pools) in boreal, temperate, and subtropical forests (Fig. 3a, b, and c). This increase in soil C pools under N enrichment is consistent. Previous studies reported that N addition had a significant positive effect on SOC concentration (Cusack et al., 2011; Fu et al., 2015; Gu et al., 2015; Lu et al., 2021) and with previous meta-analysis studies results (Deng et al., 2018; Hyvönen et al., 2008; Janssens et al., 2010; Nave et al., 2009). Considering that we found an overall decrease in both C inputs by litterfall and fine root production and in C outputs by heterotrophic (soil) respiration, the latter effect apparently dominates the net soil C budget.

Added N is usually first taken up by field- and ground-layer vegetation and microorganisms. This assertion is supported by the negative correlation between the response ratios of above litter production and SOC. A previous synthesis of field observations in tropical forests reported, for example, that belowground C storage enhancement under N addition increase could be driven by the changes in the mineral-associated C pool and alteration of microbial community composition (Cusack et al., 2011). Our regression analyses also showed that SOC, TC, and MBC correlated positively with fine roots (Table S2), indicating that root production is crucial for soil C accumulation.

Overall, we found that N addition inhibited microbial activity in Chinese forest ecosystems as indicated by a slight reduction in MBC content across forest types (Fig. 2 and 3), probably due to a reduction of litter production in the soil surface. MBC concentration patterns are usually linked to labile C from fresh litter input (Liu and Greaver, 2010; Sylvia et al., 2005). Although our results are consistent with previous meta-analysis studies (Lu et al., 2011), our value is lower (1%) compared to those found by Liu and Greaver (2010) and Treseder (2008), who reported a reduction of 20% and 15%, respectively. Moreover, the results indicated no significant correlation between the response ratios of MBC concentration and aboveground litter production (Table S2). This result is probably due to the toxicity effects caused by N enrichment-induced soil acidification (Liu and Greaver, 2010). Tian et al. (2018), in a meta-analysis assessing the effects of N addition on MBC in China's forest ecosystems, also reported that N additions significantly decreased MBC.

In the current study, SOC was negatively correlated with the response ratios of TC and litter input under N enrichment, probably due to the reduced microbial activity of decomposers (Table S2). According to Liu and Greaver (2010), litter might remain on the surface soil layer instead of mixing with SOC. According to Lorenz and Lal (2009), litter fragmentation, microbial metabolism, and root exudates are the major pathways for C accumulation. Our results indicated that the DOC concentration decreased by 3% under N enrichment (Fig. 4c), suggesting that N addition might inhibit C leaching loss in forest soil ecosystems. This evidence is contradictory with other meta-analysis studies reporting that N enrichment increased DOC concentration by 18% (Liu and Greaver, 2009) and 7.4% (Deng et al., 2018). These contradictory results could be due to the difference between vegetation types and diverse climatic zones resulting from the different scales in the various studies.

We observed that soil C sequestration enrichment following N addition was greater in boreal and temperate forests. In line with our finding, Pan et al. (2011) reported that temperate and boreal forests are the predominant global C sinks. Belowground C sequestration was higher in boreal and temperate forests (Fig. 3a, and b) than subtropical and tropical forests (Fig. 3c and d), which the N availability threshold level could explain in forest systems. Forests located in mid-to-high latitudes in the Northern Hemisphere (i.e., boreal and temperate) are more sensitive to N addition because they are mostly N-limited, enhancing net primary production (NPP) and aboveground litter production, while subtropical and tropical forests are more often N-rich (Lu et al., 2021; Matson et al., 1999). This difference between forest C sequestration levels can also be explained through the N saturation hypotheses. According to Aber et al. (1998), it occurs once an ecosystem reaches N saturation which leads to reduce soil functions (e.g., N retention and nutrient cycling) and plant performance (fine roots).

4.2. C flux response to N enrichment

There is currently some disagreement in the literature regarding the potential effects of N enrichment on belowground soil C dynamics in forests. Overall, N addition has been shown to decrease C inputs and C outputs except in boreal forests (Fig. 3). Specifically, N addition on average inhibited aboveground litter productivity by -6% -11% and -13% while it reduced fine root productivity by -13%, -25% in boreal, and temperate (Fig. 3a, and b). The slightly lower response of aboveground litter productivity than fine root productivity is most likely because of the negative effect of N addition on root: shoot ratio (Liu and Greaver, 2010). Similar observations have been observed in previous meta-analysis and field experimental studies (Chen et al., 2015; Knorr et al., 2005; Liu and Greaver, 2010). Responses of C input under N enrichment of individual forest ecosystem types varied across forest types. The negative response of litter and fine root production to N enrichment was more pronounced in subtropical and tropical forests, being more N-rich forest ecosystem types, due to the large natural N fixation (Menge et al., 2019; Yu and Zhuang, 2020). This trend could be attributed to the N-saturation, implying that the N supply exceeds the requirement of plants and microorganisms because further N addition to an N-saturated system will reduce plant performance, especially of fine roots (Aber et al., 1998). Interestingly, similar trends have also been observed for N-limited forest types. In this context, we found that above litter production declined only in boreal forests while fine roots production declined in boreal and temperate forests (Fig. 3a and b). These findings are supported by previous studies that reported that elevated N addition usually decreases fine roots and microbial biomass (Frey et al., 2014; Janssens et al., 2010).

Similarly to C input, our meta-analysis showed that N addition enhanced C output in N-limited forest ecosystem types by 6% and 7% for boreal and temperate forests, respectively (Fig. 3a and b). In comparison, it inhibited C output in the N-rich forest ecosystem, which declined on average by 30% and 10% for subtropical and tropical forests, respectively (Fig. 3c and d) in concordance with several previous studies meta-analyses (Janssens et al., 2010; Tian et al., 2018). Janssens et al. (2010), by assessing 36 nitrogen-manipulation studies in forest ecosystems, reported a decline by 15% of Rh under N enrichment, in line with our reported average decline in Rh of 12% under N addition (Fig. 3b). We observed that Rs and Rh had a positive response to N enrichment only in N-limited forest ecosystem types (Fig. 3a and b), suggesting that N availability in an ecosystem is the main factor influencing C output response to N addition. However, in individual studies, N addition has contrasting effects on forest C output. Several studies have shown that N addition negatively affected Rs in boreal forests (Olsson et al., 2005) and subtropical forests (Mo et al., 2008). In contrast, an increase of Rs in boreal and temperate forests was demonstrated by Hasselquist et al. (2012) and Bowden et al. (2004). Several factors, such as the differences in forest age, tree species, forest productivity, soil characteristics, and flora composition, can explain these discrepancies (Hyvönen et al., 2008; Pregitzer et al., 2008). It could also be due to alterations in age, quantity, and quality of aboveground litter inputs. Although our meta-analysis indicated that C input showed greater response than C output in boreal and subtropical forests (Fig. 3a and c), the reverse effect has been observed in temperate and tropical forests (Fig. 3d and d). We did not explore the effect of N enrichment on detritus C pools, microbial and root respiration due to data limitations, which added additional uncertainty on the net C flux response under N addition.

Moreover, Rs changes were demonstrated to correlate negatively with the magnitude of SOC (Table S2). To explain these trends, we need to invoke 3 main mechanisms: (i) N enrichment leads to the loss of soil C as CO_2 to the atmosphere; (ii) C loss through respiration, erosion, and leaching; and (iii) upsurge the probability that N saturation hypotheses do occur (Janssens et al., 2010). Our results support this assertion, which reported a reduction in soil C:N ratios (Fig. S2). Also, Rs showed a more significant increase in N-limited ecosystems (boreal and temperate forests) than those in N-rich (subtropical and tropical forests)(Fig. 3) indicating that Rs plays a significant role in forest C sequestration.

4.3. Impacts of N fertilizer rates, forest types, and depth layers on soil carbon sequestration

Apart from differences between forest types, the impacts on N addition on soil carbon sequestration were also affected by rate, duration, type of N fertilizer, and the ambient N deposition level. Although a previous study reported a minor contribution of N deposition to forest carbon sequestration (Schulte-Uebbing et al.). Our results highlight that C dynamics significantly increased at the low N application level (<30 kg N ha^{-1} yr^{-1}) (Fig. 3), implying that biological activity often results in an increase and is more sensitive and in low amounts of nitrogen. This result is also supported by Yu et al. (2020), who reported that SOC accumulation rates in response to 14 years of N addition were 1.5 ± 0.1 Mg ha^{-1} yr^{-1}, 1.3 ± 0.4 Mg ha^{-1} yr^{-1}, and 0.9 ± 0.3 Mg ha^{-1} yr^{-1} for low (50 kg N ha^{-1} yr^{-1}), medium (100 kg N ha^{-1} yr^{-1}) and high N addition (150 kg N ha^{-1} yr^{-1}).

Our results are also in agreement with results from 15 long-term (14–30 years) experiments in Sweden and Finland, where C sequestration per unit of N applied was higher at low application rates (30–50 kg N ha^{-1} yr^{-1}) than at high application rates (50–200 kg N ha^{-1} yr^{-1}) (Hyvönen et al., 2008). The impact of N form was significant and negative in subtropical forests (Fig. 3c). In contrast, it was positive and significant only for urea in temperate forests (Fig. 3b). Our meta-analysis showed that a reduction of ambient N deposition results in low carbon sequestration in forest soils. Our findings showed that C dynamics were a positive and strong correlation with N application time (Table S3), particularly in short-term application (<1 year), implying that the effect of short duration is related to low N application levels. Taking all evidence into account, our meta-analysis found that N-limited forest ecosystems are a predominant net global forest C sink and that N addition substantially stimulated belowground soil C sequestration, particularly at low- N addition levels. At the same time, there are indications that the effects are reduced with the duration of the additions.

5. Conclusions

Our meta-analysis showed that on average, N enrichment enhanced soil C pools and inhibited C fluxes (input and output) in Chinese forests. N addition increased soil C dynamics in N-limited compared to N-rich forest systems. Specifically N addition increased C pools (MBC, TC, SOC, and DOC) by 17%, 10%, and 4% in boreal, temperate, and tropical forests but slightly decreased in subtropical forests (-0.34%). Thereby overcompensating C input (litter inputs and fine roots) reductions occurring in temperate (-11%), subtropical (-18.6%), and tropical forests (-18.8%), although being already positive for boreal forests (+10%). Whereas N addition significantly increased C output by +6 and +7% in boreal and temperate forests while it decreased by -30 and 40% in subtropical and tropical forests. The C dynamics response was more sensitive in N-limited than N-rich (e.g., subtropical forests) ecosystems. Hence, the response of C dynamics in a nitrogen-saturated ecosystem differs radically from one that is nitrogen limited. Overall N deposition enhanced soil C sequestration (C pools) at below 30 kg N ha^{-1} yr^{-1} and short period

(<1 year) of time. This implies that in (large) parts of China, which are currently characterized by short-level and short-term elevated N deposition levels.

Declaration of competing interest

The authors declare that they have no known competing financial interests.

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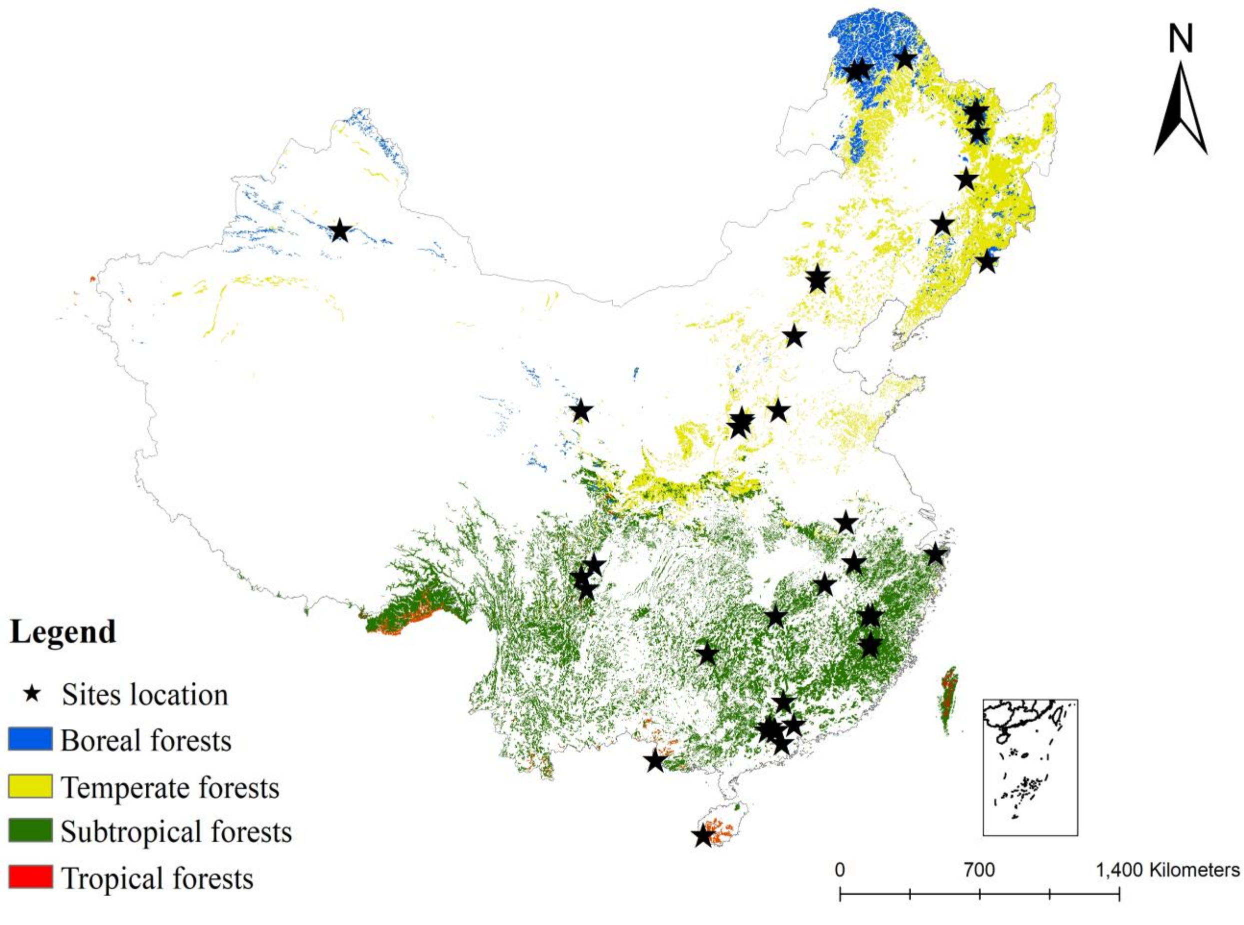

Fig. 1. Distribution of N enrichment experiments included in this meta-analysis (boreal forest, subtropical forest, temperate forest, tropical forest).

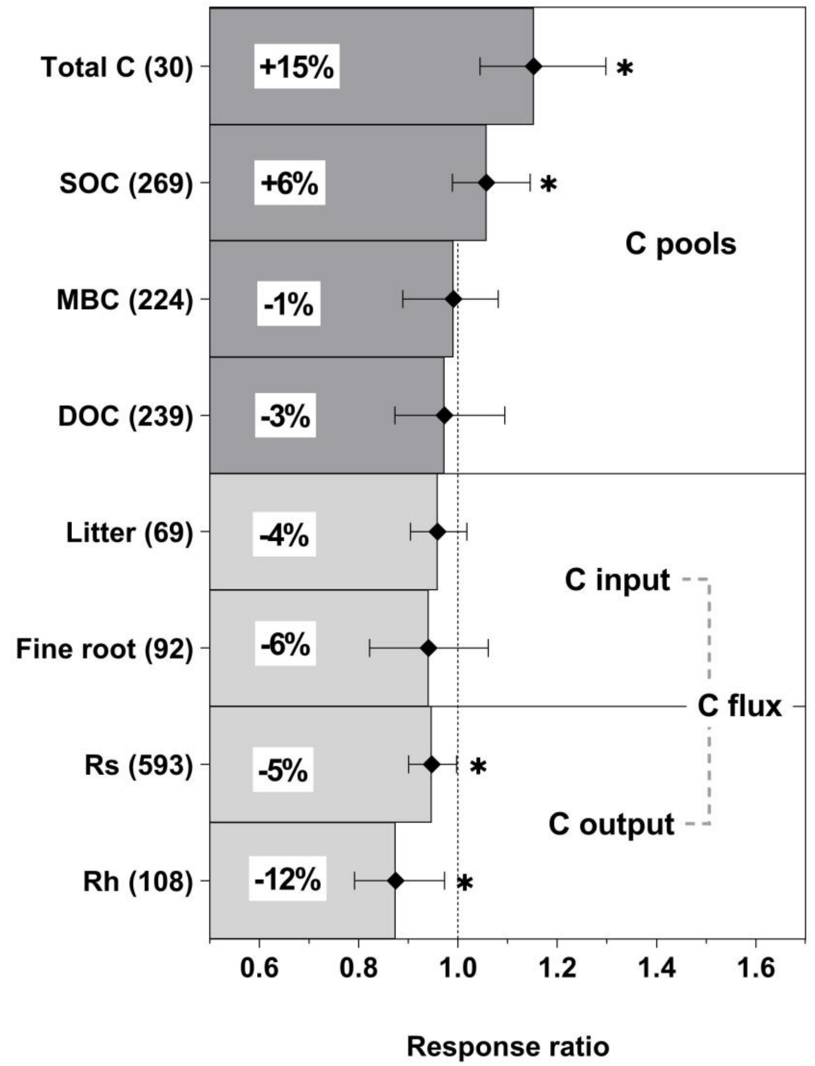

Fig. 2. Estimation of the changes in belowground C budget of forest ecosystem in China under N addition. SOC: soil organic carbon; DOC: dissolved organic carbon; MBC: microbial biomass carbon; Rh: heterotrophic respiration; Rs: soil respiration. *correlation is significant at the 0.05 level.

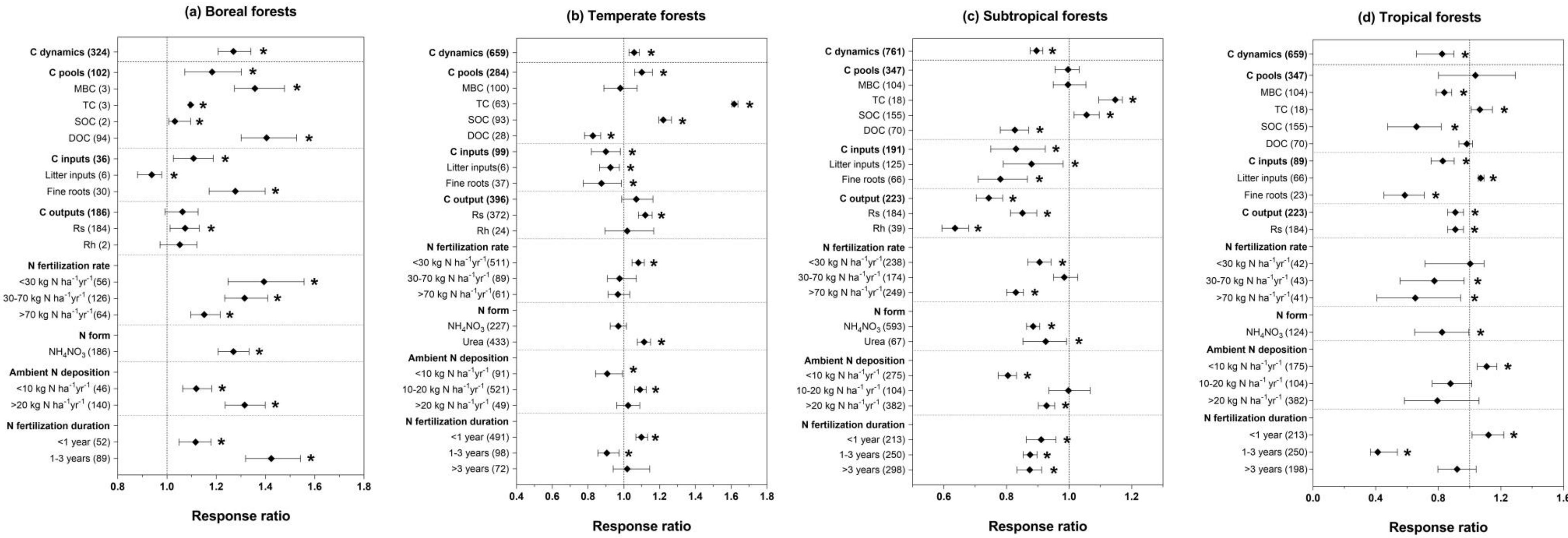

Fig. 3. Effects of N enrichment on C dynamics among forest types: borel forests (a), temperate forests (b), subtropical forests (c) and tropicals forests (d). MBC: Microbial biomass carbon, TC: total carbon, SOC: soil organic carbon, DOC: dissolved organic carbon, Rs: soil respiration ; Rh: heterotrophic respiration. Black bars represent 95% confidence intervals. The different letters in parentheses represent the number of observations. The dashed vertical line was drawn at a mean effect size of 1. *Correlation is significant at the 0.05 level.