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REGULAR ARTICLE

New soil carbon sequestration with nitrogen enrichment: a meta-analysis

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Abstract
Background and aims Through agriculture and industry, humans are increasing the deposition and availability of nitrogen (N) in ecosystems worldwide. Carbon (C) isotope tracers provide useful insights into soil C dynamics, as they allow to study soil C pools of different ages. We evaluated to what extent N enrichment affects soil C dynamics in experiments that applied C isotope tracers.
Methods Using meta-analysis, we synthesized data from 35 published papers. We made a distinction between "new C" and "old C" stocks, i.e., soil C derived from plant C input since the start of the isotopic enrichment, or unlabeled, pre-existing soil C.
Results Averaged across studies, N addition increased new soil C stocks (+30.3%), total soil C stocks (+6.1%) and soil C input proxies (+30.7%). Although N addition had no overall, average, effect on old soil C stocks and old soil C respiration, old soil C stocks increased with the amount of N added and respiration of old soil C declined. Nitrogen-induced effects on new soil C and soil C input both decreased with the amount of extraneous N added in control treatments.
Conclusion Although our findings require additional confirmation from long-term field experiments, our analysis provides isotopic evidence that N addition stimulates soil C storage both by increasing soil C input and (at high N rates) by decreasing decomposition of old soil C. Furthermore, we demonstrate that the widely reported saturating response of plant growth to N enrichment also applies to new soil C storage.

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Introduction

By burning fossil fuel and applying artificial fertilizer to cropland, humans have increased atmospheric N deposition three- to five-fold over the last century (IPCC 2007; Bouwman et al. 2013; Lamarque et al. 2013). Global N deposition rates are projected to increase by 2.5 times or more by the end of this century (Reay et al. 2008), and much of this N will be deposited in terrestrial ecosystems. Because plant growth is typically limited by N availability (LeBauer and Treseder 2008; Bai et al. 2010; Wright 2019) and N limits the CO_2 fertilization on plant biomass (Terrer et al. 2019), increasing N deposition rates are widely expected to stimulate ecosystem C storage (Reay et al. 2008; Janssens et al. 2010; Chen et al. 2018). However, it is still unclear to what extent N additions affect soil C stocks. Soils store about twice as much C as the atmosphere and form a large natural source of CO_2 (Eswaran et al. 1993). Thus, soil C responses to N enrichment could play a key role in determining future trajectories of atmospheric CO_2 concentrations (Dijkstra et al. 2004; Loisel et al. 2019).

The size of the soil C pool is determined by the balance between soil C input – mostly from plant litter and roots (e.g., exudates and allocation to mycorrhizal fungi) – and soil C output through the decomposition of soil organic matter (Trumbore 1997; Jastrow et al. 2007). By stimulating plant growth and litter production, N input from anthropogenic sources can increase soil C stocks through the enhancement of C inputs (e.g., Gong et al. 2012; Tian and Niu 2015). However, in some cases N enrichment stimulates soil C input without increasing soil C stocks (Mack et al. 2004; Allison et al. 2010) and vice versa (Pregitzer et al. 2008), suggesting that N-induced changes in decomposition (i.e., soil C output) affect soil C storage as well (Janssens et al. 2010). Indeed, N additions can decrease the activity of lignin-modifying enzymes (Chen et al. 2018) and N-induced decreases in soil pH can decrease decomposition rates (e.g. Zhou et al. 2017); both these responses would stimulate soil C storage.

Because most N enrichment experiments do not directly measure the fate of newly added plant litter vs. native soil organic matter, they provide limited mechanistic insight in the processes underlying soil C sequestration (Cardon et al. 2001). However, the dynamics of these two different C pools can be studied through isotopic labeling, in which the isotopic signature of soil C inputs differ from pre-existing soil C (from now on referred to as “old soil C”). This approach enables us to determine the amount of soil C derived from old soil C versus “new soil C” (i.e., cumulative plant inputs since labeling began) (Keith et al. 1986; Balesdent et al. 1987). Similarly, by analysing the isotopic composition of total soil CO_2 respiration in labeling experiments, we can quantify the decomposition of old soil C (Rochette et al. 1999).

The response of soil C storage to N addition varies with environmental conditions and between ecosystems. For instance, field experiments suggest that N enrichment generally does not alter soil C stocks in grasslands (Lu et al. 2011), but stimulates soil C sequestration in temperate, tropical, subtropical and boreal forests (Janssens et al. 2010; Cusack et al. 2011; Frey et al. 2014; Maaroufi et al. 2019). Furthermore, N enrichment reduced litter decomposition in N-rich ecosystems, but not in N-limited ecosystems (Chen et al. 2015). Effects of N also depend on litter quality; whereas N addition typically stimulates the decomposition of labile C, it slows down the decomposition of recalcitrant C (Fog 1988; Talbot and Treseder 2012; Chen et al. 2018).

Because N enrichment studies cover a wide range of ecosystem types and environmental conditions, deriving a global response to N enrichment from individual experiments is challenging. Moreover, high spatial variability in soil C stocks and low replication mean that individual experiments often lack the statistical power to detect changes in soil C dynamics (Hungate et al. 1995). A quantitative synthesis of results across multiple studies can overcome both these problems. Thus, we used meta-analysis to synthesize studies that applied isotopic labeling to evaluate the impacts of N enrichment on new and old soil C. By synthesizing these data, we aimed to identify the main factors determining new and old soil C stocks with N enrichment, thereby increasing mechanistic insight into the processes underlying soil C storage. We hypothesized that N addition stimulates soil C storage both by increasing plant growth and new soil C storage, and by reducing the decomposition of old soil C.

Methods

Data collection

We used Web of Science (Thompson Reuters) to search for studies published before March 2020 that employed an isotopic C tracer to study the effect of N enrichment on soil C dynamics. We used the search terms "nitrogen", "soil AND carbon" and "isotop* OR label*" for article topic.

To be included in our dataset, studies had to meet the following criteria. First, studies had to include at least two N treatments ("control" & "high N"), with N addition rates (kg N ha^{-1} yr^{-1}) for both treatments clearly indicated. Second, to distinguish "new soil C" and "old soil C", C labeling should be applied to create a difference in the isotopic composition of plants and soils. There are two ways to achieve this goal: (1) growing plants under isotopically labeled CO_2 (i.e., $^{13}CO_2$ or $^{14}CO_2$); (2) growing C_3 plants on soils that developed under C_4 vegetation, or vice versa. C_3 plants discriminate more strongly against ^{13}C than C_4 plants because of differences in the photosynthetic pathway, thereby creating differences in the ^{13}C isotopic composition of plant biomass and soil organic matter input (Farquhar et al. 1989). Thus, in both approaches, new soil C derived from plants will differ from native (i.e., unlabeled) soil C. Third, we only considered studies that applied continuous labeling, usually from the first leaf emergence to sampling time, to ensure that the total amount of new soil C could be determined (Kuzyakov and Domanski 2000). We included both pot- and field-experiments in our analysis. In total we found 35 studies that met our requirements (Table 1).

From each study we extracted data on new, old, and total soil C, and old soil C respiration when these were reported, for both control and high N treatments (Data S1-S5). For studies reporting new soil C stocks, we also extracted data on soil C input proxies (root biomass, or yield data if root biomass was unavailable), following the approach of van Groenigen et al. (2017). To avoid pseudoreplication, we only included the most recent observations from each study in our dataset. We tabulated means, standard deviation and the number of replicates for both control and high N treatments. Missing standard deviations were estimated from the mean coefficient of variation across the dataset (e.g., van Groenigen et al. 2017).

Previous studies suggest that plant growth and total soil C storage with N addition depend on ΔN (i.e., the difference in N addition between the control and high N treatments; e.g., Maaroufi et al. 2015), plant type (e.g., Yue et al. 2016), atmospheric CO_2 concentration (van Groenigen et al. 2006), soil N availability (Chen et al. 2015) and soil pH (Nottingham et al. 2015). Similarly, several studies suggest that N fertilizer stimulates plant growth more strongly when it is applied in combination with other nutrients (e.g., Crowther et al. 2019; Elser et al. 2007). Thus, we categorized studies based on these experimental conditions. To account for plant type, we made a distinction between studies on woody species and studies on herbaceous species. We made a distinction between studies that added other nutrients together with N, and studies that did not. Atmospheric CO_2 concentration, soil pH and ΔN were included in our analysis as continuous factors. Our dataset included only 5 studies on woody species, limiting the representativeness of the overall treatment effects for this category.

We used soil C:N ratios as an indicator of initial soil N availability (e.g., Terrer et al. 2019). Because plant growth responses to N addition show a saturating response (Aber et al. 1998), we also included N addition levels in control treatments as a predictor variable. Some pot studies in our dataset applied N fertilizer homogenously throughout the entire soil column by mixing (e.g., Heath et al. 2005). In these cases, we tabulated N addition levels equivalent to the amount of N added to the 0–20 cm layer. Finally, we tabulated information about labeling type (i.e., C_3-C_4, ^{13}C, or ^{14}C), study method (i.e., pot vs. field), clay content (%) and experimental duration (i.e., the natural log of the number of days since the isotopic label was introduced in the experiment).

Meta-analysis

For each study in our dataset, we calculated the response of new soil C stocks, old soil C stocks, total soil C stocks, C input proxies and old soil C respiration to N enrichment. We expressed treatment effects as the natural log of the response ratio (lnR), a metric commonly used in meta-analysis (Hedges et al. 1999; Osenberg et al. 1999):

$$\mathrm{lnR} = ln\left(\frac{V_h}{V_c}\right)$$

Table 1 Overview of N enrichment experiments included in our meta-analysis; responses that were reported in each study are indicated by '●'

Reference	System/species	Plant type	Duration in years[a]	Label[b]	New C	C input proxy[c]	Old C resp.	Old C
Allmaras et al. 2004	*Zea mays*	Herbaceous	13	C_3-C_4	●	● Y		●
Bicharanloo et al. 2019	*Triticum aestivum*	Herbaceous	0.33	^{13}C	●	● RB		●
Billes et al. 1993	*Triticum aestivum*	Herbaceous	0.08	^{14}C	●	● RB		
Bushby et al. 1992	*Panicurn maximum*	Herbaceous	0.24	^{14}C	●	● RB		
Butterly et al. 2015	*Triticum aestivum / Pisum sativum*	Herbaceous	0.46	^{13}C	●	● RB		
Cardon et al. 2001	California grassland	Herbaceous	1.84	C_3-C_4	●	● RB	●	●
Carrillo et al. 2014	*Bouteloua gracilis*	Herbaceous	0.08	^{13}C			●	
Cheng and Johnson 1998	*Triticum aestivum*	Herbaceous	0.08	C_3-C_4			●	
Cotrufo and Gorissen 1997	*Lolium perenne / Agrostis capillaris/ Festuca ovina*	Herbaceous	0.15	^{14}C	●	● RB		
Dijkstra et al. 2004	*Agropyron repens / Bromus inermis / Koeleria cristata / Poa pratensis / Achillea millefolium / Anemone cylindrica / Asclepias tuberosa/ Solidago rigida /Amorpha canescens / Lespedeza capitata / Lupinus perennis / Petalostemum villosum*	Herbaceous	5	^{13}C	●	● RL		●
Ge et al. 2015	*Oryza sativa*	Herbaceous	0.09	^{13}C	●	● RB		
Ge et al. 2017	*Oryza sativa*	Herbaceous	0.05	^{13}C	●	● RB		
Gong et al. 2012	*Zea mays*	Herbaceous	0.24	C_3-C_4	●	● RB	●	●
Hagedorn et al. 2003	*Fagus sylvatica / Picea abies*	Woody	4	^{13}C	●	● RB		●
Haile-Mariam et al. 2000	*Pinus ponderosa*	Woody	0.51	^{13}C	●	● RB		
Heath et al. 2005	*Fagus sylvatica / Quercus rober* *Carpinus betulus /Betual pendula* *Abies alba / Pinus sylvestris*	Woody	1.23	C_3-C_4	●	● RB		●
Hofmann et al. 2009	*Zea mays*	Herbaceous	36	C_3-C_4	●	● Y		●
Hungate et al. 1997	California grassland	Herbaceous	1.51	^{13}C			●	
Kazanski 2017	*Bromus inermus / Agropyron repens*	Herbaceous	0.29	C_3-C_4	●	● RB	●	●
Liljeroth et al. 1990	*Triticum aestivum*	Herbaceous	0.15	^{14}C	●	● RB	●	
Liljeroth et al. 1994	*Triticum aestivum / Zea mays*	Herbaceous	0.16	^{14}C	●	● RB	●	
Paterson et al. 2008	*Lolium perenne*	Herbaceous	0.18	^{13}C			●	
Phillips et al. 2012	*Pinus taeda*	Woody	1	^{13}C	●	● RG		●
Silveira et al. 2013 Liu et al. 2017	*Paspalum notatum / Cynodon dactylon*	Herbaceous	2	C_3-C_4	●	● RB		●
Van der Krift et al. 2001	*Festuca ovina / Anthoxanthum odoratum / Festuca rubra / Holcus lanatus*	Herbaceous	0.19	^{14}C	●	● RB		
Van Ginkel et al. 1997	*Lolium perenne*	Herbaceous	0.21	^{14}C	●	● RB	●	
Van Kessel et al. 2000	*Lolium perenne*	Herbaceous	4	C_3-C_4	●	● RB		●
Van Groenigen et al. 2003 Hebeisen et al. 1997	*Lolium perenne / Trifolium repens*	Herbaceous	9	^{13}C	●	● RB		●
Ventura et al. 2019	*Populus × canadensis Mönch*	Woody	2	C_3-C_4	●	● BNPP		
Wilts et al. 2004	*Zea mays*	Herbaceous	30	C_3-C_4	●	● S		●
Xu et al. 2018	*Triticum aestivum / Lupinus albus*	Herbaceous	0.14	C_3-C_4 / ^{13}C			●	
Zhang et al. 2012	*Zea mays*	Herbaceous	49	C_3-C_4	●	● Y		●
Zhou et al. 2020	*Lycopersicon esculentum*	Herbaceous	0.31	^{13}C	●	● RB	●	●

[a] Number of years during which the soil in the study received isotopically labeled C input

[b] ^{14}C = isotopic labeling by ^{14}C-CO_2; ^{13}C = isotopic labeling by ^{13}C-CO_2; C_3-C_4 = isotopic labeling by using a shift in C_3 vs. C_4 vegetation

[c] RB = root biomass, RG = root growth, RL = root litter, Y = yield, BNPP = belowground net primary productivity, S = stover

with V_h and V_c as the arithmetic mean values of new soil C, old soil C, total soil C, soil C input, and old soil C respiration in the high N and control treatments, respectively. The variance (var) of lnR was calculated as:

$$\text{var} = \frac{SD_h^2}{N_h V_h^2} + \frac{SD_c^2}{N_c V_c^2}$$

with N_h and N_c as the replicate numbers for high N and control treatments, respectively.

Our meta-analytical approach was adopted from van Groenigen et al. (2017). Briefly, we analysed our data using a mixed-effects model with the *rma.mv* function in the R package "metafor" (Viechtbauer 2010). Because several studies contributed more than one effect size (e.g. in multifactorial experiments), we included "study" as a random effect. We weighted lnR by the inverse of its variance. Models were fitted according to Knapp and Hartung (2003); 95% confidence intervals (CI) of treatment effects were based on critical values from a t-distribution. Effect sizes were considered significant if their 95% CI did not include zero. We used a Wald test to statistically evaluate differences in treatment effects among categories. The "glmulti" package was used to identify which of the factors described above best predicted treatment effects of N enrichment, following the same approach as Terrer et al. (2016) and van Groenigen et al. (2017). In short, we analysed our data with all possible models that could be constructed using combinations of the experimental factors. Model selection was based on Akaike Information Criterion corrected for small samples (AICc) as criterion. The relative importance value for a particular predictor was equal to the sum of the Akaike weights (probability that a model is the most plausible model) for the models in which the predictor appears. A cut-off of 0.8 was set to differentiate between important and redundant predictors, so that predictors with relative importance near or less than 0.8 are considered unimportant.

Results

Averaged across the entire dataset, N addition significantly stimulated soil C input proxies (+30.7%, $p < 0.001$), new soil C stocks (+30.3%, $p < 0.001$), and total soil C stocks (+6.1%, $p < 0.001$) (Fig. 1). In contrast, N addition did not significantly affect the respiration of old soil C (+0.2%, $p = 0.98$) or old soil C stocks (+1.2%, $p = 0.60$). When we limited our analysis to long-term (i.e., >5 year) studies conducted under field conditions, we found quantitatively similar results for all variables (Fig. S1). Unfortunately, no long-term data were available for old soil C respiration.

Our model selection approach indicated that "Control N" (i.e., N addition level in control treatments) was the most important predictor for N-induced effects on both new soil C stocks and soil C input proxies (Fig. 2a, b). Among all the potential models for the response of new soil C stocks to N additions ("$\ln R_N$"), the model $\ln R_N \sim$ Control N had the lowest AIC value (Table S1). Of all the potential models for the response of C input to N additions ("$\ln R_I$"), the model $\ln R_I \sim$ Control N was the most parsimonious within 2 AIC units (Table S2). Across the entire dataset, $\ln R_N$ and $\ln R_I$ both decreased with increasing control N levels ($p < 0.05$, Fig. 3a, b). Nitrogen-induced changes in soil C input and new soil C stocks were significantly correlated ($p < 0.05$; Fig. S2).

The dataset of N effects on old soil C respiration ($\ln R_{OR}$) only contained pot studies on herbaceous species. Therefore, the model selection approach for this dataset did not include plant type or study method as possible predictors. Model selection indicated that "ΔN" was the most important predictor for $\ln R_{OR}$ (Fig. 4a). The model $\ln R_{OR} \sim \Delta N$ was the most parsimonious model within 2 AIC units (Table S3); $\ln R_{OR}$ decreased by 0.125 units per 100 kg N ha^{-1} yr^{-1} change in ΔN ($p < 0.05$; Fig. 5).

The response of old soil C stocks to N addition ("$\ln R_O$") was best predicted by Control N, ΔN and CO_2 concentration (Fig. 4b). Among all the potential models, the model $\ln R_O \sim$ Control N + ΔN + CO_2 concentration was the most parsimonious model within 2 AIC units (Table S4). Analysing our dataset with this model, the effect of N addition on old soil C stocks increased with ΔN ($p < 0.001$) and atmospheric CO_2 concentrations ($p < 0.001$), but it decreased with control N levels ($p < 0.01$; Fig. 6).

The response of total soil C stocks to N addition ("$\ln R_T$") was best explained by atmospheric CO_2 concentrations (Fig. 4c). Among all the potential models, "$\ln R_T \sim CO_2$ concentration" had the lowest AIC value (Table S5). As with old soil C stocks, the effect of N addition increased with atmospheric CO_2; $\ln R_T$ increased by 0.012 units per 100 ppm change in atmospheric CO_2 concentrations (95% CI: 0.003–0.021; $p < 0.01$).

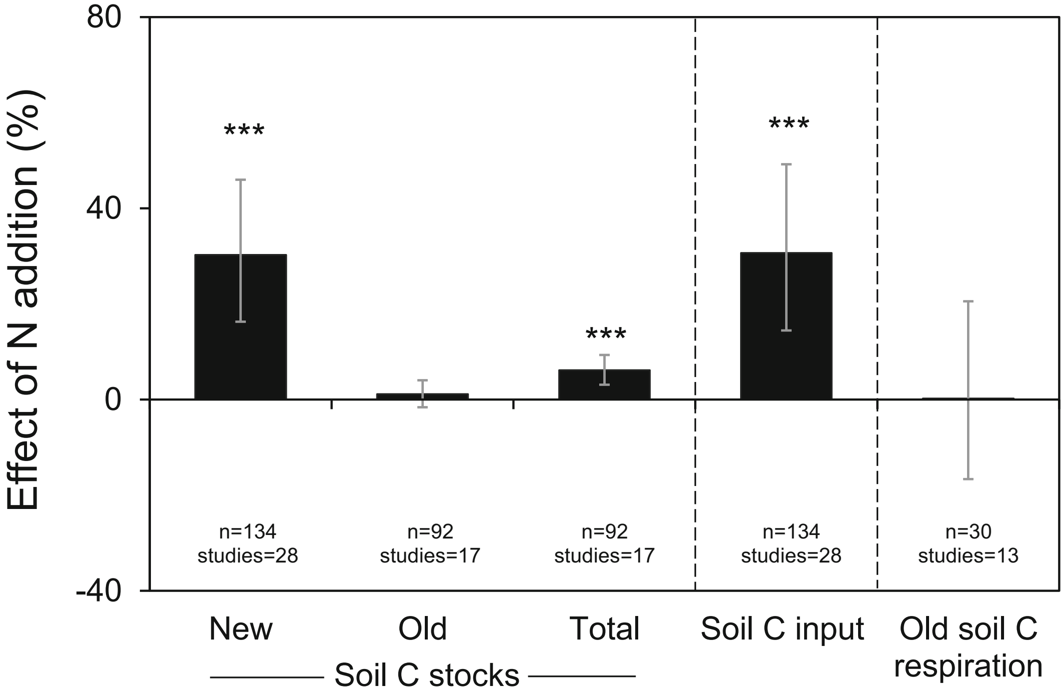


Fig. 1 Results of a meta-analysis on the responses of new soil C stocks, old soil C stocks, total soil C stocks, soil C input proxies and old soil C respiration to N addition. The number of observations (n) and total number of independent studies included in each analysis are displayed below each bar. Error bars indicate 95% confidence intervals. ** and *** indicate significance at $p < 0.01$ and $p < 0.001$, respectively

Discussion

New soil C plays a key role in soil C dynamics, since its quantity and quality influence soil C decomposition rates (e.g., De Graaff et al. 2010). The positive correlation between N-effects on new soil C stocks and soil C input proxies suggests that, N-induced changes in new soil C stocks are at least partly driven by changes in soil

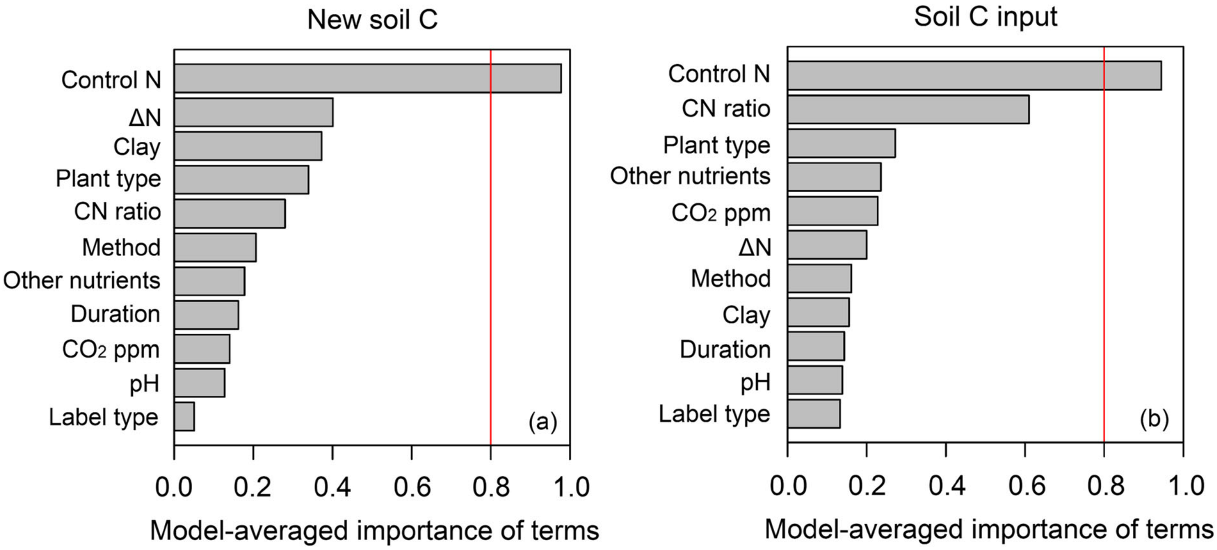


Fig. 2 Model-averaged importance of the predictors of the N-effect on new soil C stocks (**a**) and soil C input proxies (**b**). The importance is based on the sum of Akaike weights derived from model selection using AICc (Akaike's Information Criteria corrected for small samples). See Fig. 1 for the number of observations and independent studies used in each analysis

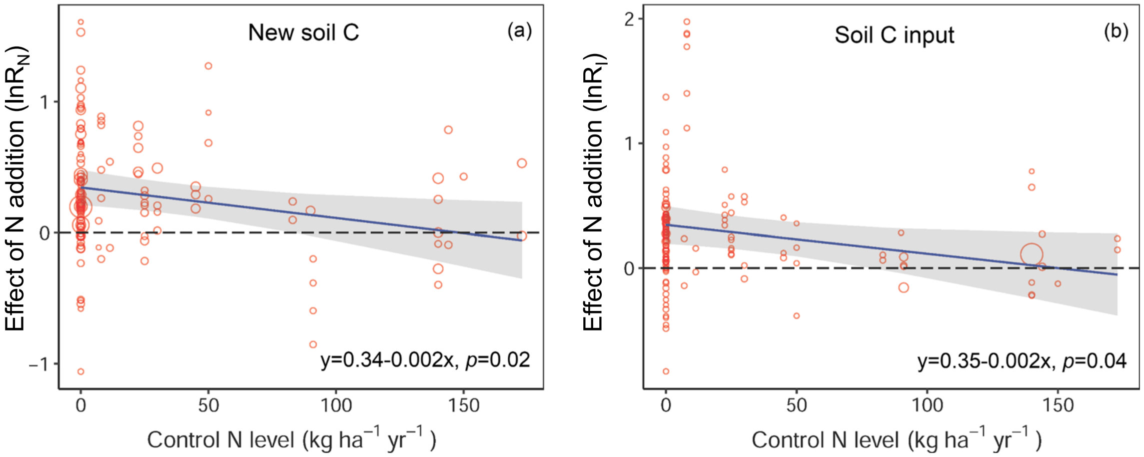


Fig. 3 The relationship between control N levels and treatment effects ($\ln R_N$) on new soil C stocks (**a**) and the relationship between control N levels and treatment effects ($\ln R_I$) on soil C input (**b**). Symbol size represents the weight of each observation in our meta-analysis. See Fig. 1 for the number of observations and independent studies used in each analysis

C input. N-effects on soil C input and new soil C stocks both decreased with increasing control N levels. These findings can probably be explained by saturation of the N enrichment effect (Aber et al. 1998). Adding N to N-rich soils often induces shifts in nutrient limitations of plant growth from N to phosphorus (Vitousek et al. 2010; Penuelas et al. 2013; Deng et al. 2017). Under these conditions, further N addition no longer increases plant growth and may even decrease plant growth when competition dominates plant–microbe relationships (Čapek et al. 2018). Furthermore, high N addition rates tend to decrease soil pH (Tian and Niu 2015), thereby causing a loss of base cations and increasing soluble aluminium concentration, both of which negatively affect plant production (Bowman et al. 2008).

Because N addition promotes plant growth more strongly in N-poor ecosystems (e.g., Chen et al. 2015), we expected N additions to increase new C stocks and plant growth more strongly in experiments with high soil C:N ratios. Yet, treatment effects did not depend on soil C:N ratio for studies in our dataset. One possible explanation for this result is that soil disturbance distorted the relation between soil C:N ratio and soil N availability. Experiments in our analysis inherently involve some level of soil disturbance, such as replacing vegetation (i.e., by using soil that developed under vegetation with a different photosynthetic pathway than that of the experimental vegetation) and transferring soil from the field to pots. Furthermore, some experiments in agricultural systems applied disturbance during the

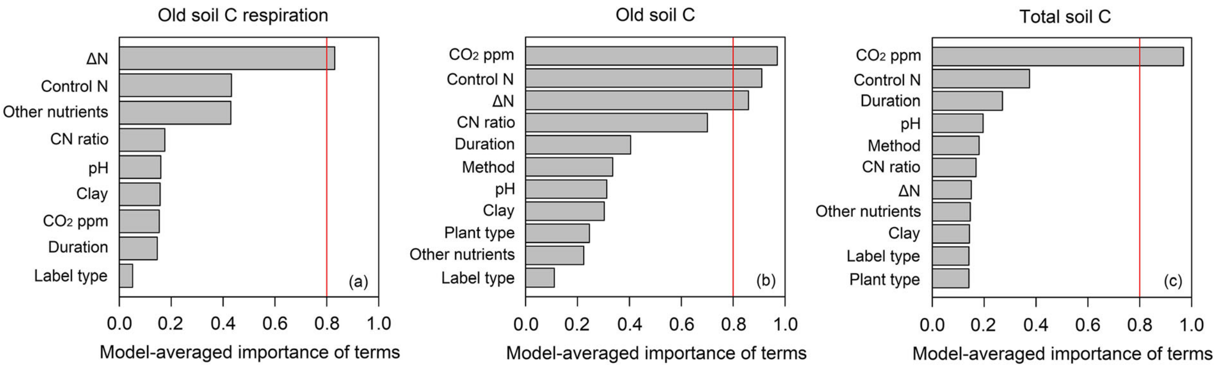


Fig. 4 Model-averaged importance of the predictors of the N-effect on old soil C respiration (**a**) old soil C stocks (**b**) and total soil C stocks (**c**). The importance is based on the sum of Akaike weights derived from model selection using AICc (Akaike's Information Criteria corrected for small samples). See Fig. 1 for the number of observations and independent studies used in each analysis

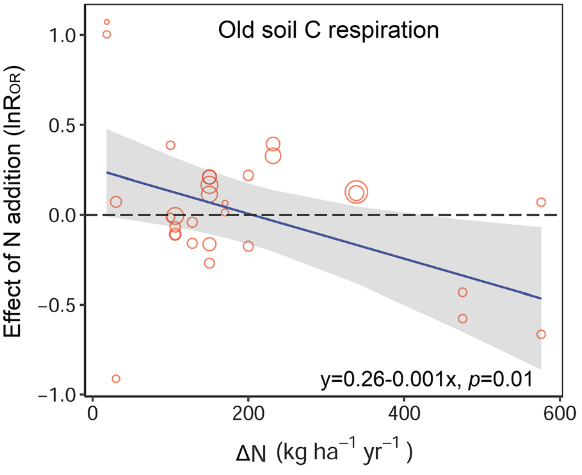


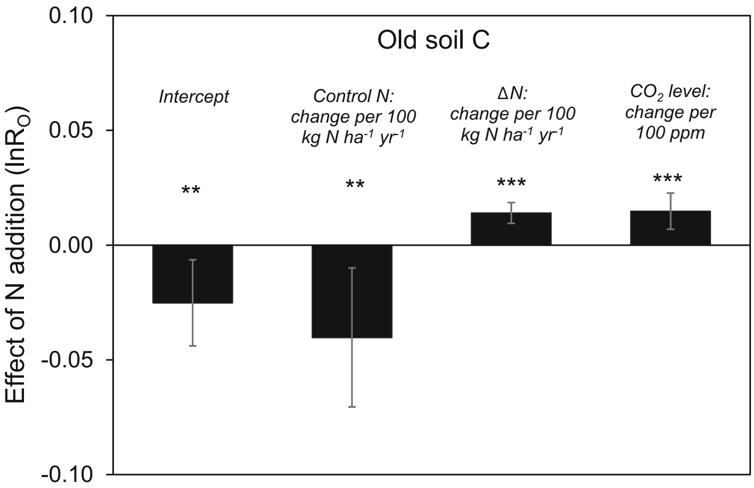
Fig. 5 The relationship between N addition levels (ΔN) and treatment effects on old soil C respiration ($\ln R_{OR}$). Symbol size represents the weight of each paired observation in our meta-analysis. The analysis is based on 30 observations, derived from 13 independent studies

experiment in the form of tillage operations. When soil disturbance breaks up aggregates, physically protected soil organic matter becomes available to microbes, stimulating organic matter decomposition and increasing nutrient availability (e.g., Kristensen et al. 2000). Thus, soil disturbance may have contributed to the relatively high variation in treatment effects on new soil C and soil C input in our dataset.

The central role of control N levels in determining the potential of N-induced new soil C storage has important implications for soils both in agricultural and natural ecosystems. Soil C sequestration in agricultural systems has been widely suggested as a main mechanism to reduce anthropogenic CO_2 emissions and slow down climate change (e.g., Minasny et al. 2017). Our results suggest that N additions to agricultural soils that previously received little or no additional N could contribute to these efforts. In contrast, further N additions to agricultural systems that already receive substantial amounts of fertilizer N are unlikely to stimulate new soil C storage. Soil emissions of N_2O strongly increase when fertilizer N rates exceed crop N uptake (e.g., van Groenigen et al. 2010), suggesting that further N additions in these systems might even work counterproductive in terms of greenhouse gas mitigation. Less intensively managed ecosystems on the other hand typically receive low amounts of N input, mostly through atmospheric N deposition. Thus, our results suggest that future increases in atmospheric N deposition will lead to net soil C sequestration in these systems.

Although N addition on average did not affect old soil C contents or old soil C respiration, $\ln R_O$ increased and $\ln R_{OR}$ decreased with ΔN. We speculate that these results reflect the various mechanisms through which N additions can affect old soil C respiration. N additions can stimulate decomposition of native soil organic matter indirectly by increasing plant growth and labile C inputs which act as substrate for soil microbes (e.g. Paterson et al. 2008). On the other hand, N additions can have direct negative effects on lignin-modifying enzymes (Chen et al. 2018), and N-induced decreases in soil pH may decrease decomposition rates (e.g. Zhou et al. 2017). In the absence of plants, N additions typically decrease microbial respiration (Fog 1988; Janssens et al. 2010), suggesting that negative effects of N additions on soil microbial activity dominate when N rates exceed plant N uptake, i.e. at high ΔN. This

Fig. 6 Results of a meta-analysis on the response of old soil C stocks to N addition ($\ln R_O$), based on a model that includes Control N levels, ΔN and atmospheric CO_2 level as moderators. Intercept represents the $\ln R_O$ for Control N and ΔN at 0 kg N ha^{-1} yr^{-1} and atmospheric CO_2 level at 400 ppm. The analysis is based on 92 observations, derived from 17 independent studies. Error bars indicate 95% confidence intervals. **,*** indicate significance at $p < 0.01$ and $p < 0.001$, respectively



interpretation is consistent with several studies indicating that N additions decrease soil respiration more strongly at high N addition rates (e.g. Janssens et al. 2010).

The positive relation between atmospheric CO_2 concentration and $\ln R_O$ corroborates studies suggesting that N enrichment reduces old soil C decomposition under elevated CO_2 (e.g. Cardon et al. 2001; Cheng and Johnson 1998). It is also consistent with a recent meta-analysis showing that N additions tend to increase old soil C stocks under elevated CO_2 (van Groenigen et al. 2017). This result might be explained by N additions reducing CO_2-induced priming of soil organic matter by alleviating N limitation of plant growth. Indeed, several studies show that elevated CO_2 stimulates decomposition of old soil organic matter, thereby releasing N to support plant productivity (e.g. Cheng 1999; Langley et al. 2009). CO_2-induced priming occurs mostly in N limited ecosystems (Dijkstra et al. 2013; Terrer et al. 2018), possibly explaining why N addition reduces CO_2-induced decomposition of old C.

Three limitations of our analysis must be noted. Most importantly, our dataset includes relatively few long-term studies under field conditions. For instance, the longest experiment on woody species lasted 6 years, a relatively short period to measure treatment effects on long-living plants. Unfortunately, the subset of long-term field studies is too small for our model selection approach. However, the few long-term field studies that directly tested the impact of important model predictors largely support our findings. For instance, Wilts et al. (2004) found that in a 29 yr old experiment, average new soil C stocks increased with N addition, and $\ln R_N$ decreased with increased control N levels. In a study with relatively high control N levels (140 kg N ha^{-1} yr^{-1}) and high ΔN values (420 kg N ha^{-1} yr^{-1}), van Groenigen et al. (2003) found that N addition tended to decrease new soil C stocks and increase old soil C stocks. However, individual studies are limited by high spatial variability in soil C stocks and the effects described above were not significant. Clearly, more long-term studies are needed to determine whether the factors affecting N-induced soil C storage change over time. Spatial variability in soil C stocks can be reduced by planting communities on homogenized soils (e.g. Cardon et al. 2001; van Kessel et al. 2000), and statistical sensitivity to detect treatment effects might also be improved by increasing the difference in isotopic signature between newly fixed and old C pools (Ogle and Pendall 2015), or by combining isotopic labeling with physical soil fractionation techniques (e.g., Dijkstra et al. 2004).

Second, our dataset only includes studies evaluating the effect of N enrichment as a single factor. However, terrestrial ecosystems are currently exposed to multiple types of environmental change, and these changes are likely to interact. For instance, rising levels of atmospheric CO_2 stimulate plant growth and soil C storage, especially when combined with N additions (van Groenigen et al. 2006; Terrer et al. 2018). Thus, under future atmospheric CO_2 concentrations, N saturation of plant growth and soil C storage may occur at higher N rates than under current CO_2 levels.

Finally, our analysis does not include any studies conducted in the tropics. Because plant productivity in the tropics is usually limited by both N and P, plants growth responses to N enrichment may saturate at relatively low levels (Wright 2019). Thus, the potential for N-induced C sequestration might be smaller in tropical soils than in temperate soils. Together, these three limitations underline the need for more long-term, multi-factor global change experiments on a wider range of ecosystems to study the fate of future soil C stocks.

In summary, our analysis indicates that the response of soil C dynamics to N addition depends on numerous environmental factors and varies strongly between experiments. However, our results suggest that N enrichment increases new soil C stocks substantially. Nitrogen-induced increases in new soil C sequestration are strongest in ecosystems receiving low amounts of N, indicating that the positive effect of N deposition on soil C storage likely diminishes with continuous N enrichment. Furthermore, we found that decomposition of old soil C decreased at high N addition levels. Thus, we provide isotopic evidence that N addition can stimulate soil C storage both by increasing soil C input and by decreasing decomposition rates. These results suggest that to improve prediction of future soil C storage with N enrichment, changes in soil C input and decomposition should both be considered, along with temporal changes in soil N status.

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References

Aber J, McDowell W, Nadelhoffer K, Magill A, Berntson G, Kamakea M, McNulty S, Currie W, Rustad L, Fernandez I (1998) Nitrogen saturation in temperate forest ecosystems: hypotheses revisited. BioScience 48(11):921–934

Allison SD, Gartner TB, Mack MC, McGuire K, Treseder K (2010) Nitrogen alters carbon dynamics during early succession in boreal forest. Soil Biol Biochem 42:1157–1164

Allmaras RR, Linden DR, Clapp CE (2004) Corn-residue transformations into root and soil carbon as related to nitrogen, tillage, and Stover management. Soil Sci Soc Am J 68:1366–1375

Bai Y, Wu J, Clark CM et al (2010) Trade-offs and thresholds in the effects of nitrogen addition on biodiversity and ecosystem functioning: evidence from inner Mongolia grasslands. Glob Chang Biol 16:358–372

Balesdent J, Mariotti A, Guillet B (1987) Natural 13C abundance as a tracer for studies of soil organic matter dynamics. Soil Biol Biochem 19:25–30

Bicharanloo B, Shirvan MB, Keitel C, Dijkstra FA (2019) Nitrogen and phosphorus availability affect wheat carbon allocation pathways: rhizodeposition and mycorrhizal symbiosis. Soil Research

Billes G, Rouhier H, Bottner P (1993) Modifications of the carbon and nitrogen allocations in the plant (*Triticum aestivum* L.) soil system in response to increased atmospheric CO_2 concentration. Plant Soil 157:215–225

Bouwman L, Goldewijk KK, Van Der Hoek KW et al (2013) Exploring global changes in nitrogen and phosphorus cycles in agriculture induced by livestock production over the 1900–2050 period. Proc Natl Acad Sci U S A 110(52): 20882–20887

Bowman WD, Cleveland CC, Halada Ĺ, Hreško J, Baron JS (2008) Negative impact of nitrogen deposition on soil buffering capacity. Nat Geosci 1:767–770

Bushby HVA, Vallis I, Myers RJK (1992) Dynamics of C in a pasture grass (*Panicum maximum* var. Trichoglume)—soil system. Soil Biol Biochem 24:381–387

Butterly CR, Armstrong R, Chen D, Tang C (2015) Carbon and nitrogen partitioning of wheat and field pea grown with two nitrogen levels under elevated CO_2. Plant Soil 391:367–382

Čapek P, Manzoni S, Kaštovská E, Wild B, Diáková K, Bárta J, Schnecker J, Biasi C, Martikainen PJ, Alves RJE, Guggenberger G, Gentsch N, Hugelius G, Palmtag J, Mikutta R, Shibistova O, Urich T, Schleper C, Richter A, Šantrůčková H (2018) A plant–microbe interaction framework explaining nutrient effects on primary production. Nat Ecol Evol 2:1588–1596

Cardon ZG, Hungate BA, Cambardella CA, Chapin FS III, Field CB, Holland EA, Mooney HA (2001) Contrasting effects of elevated CO_2 on old and new soil carbon pools. Soil Biol Biochem 33:365–373

Carrillo Y, Dijkstra FA, Pendall E, LeCain D, Tucker C (2014) Plant rhizosphere influence on microbial C metabolism: the role of elevated CO_2, N availability and root stoichiometry. Biogeochemistry 117:229–240

Chen H, Li D, Gurmesa GA, Yu G, Li L, Zhang W, Fang H, Mo J (2015) Effects of nitrogen deposition on carbon cycle in terrestrial ecosystems of China: a meta-analysis. Environ Pollut 206:352–360

Chen J, Luo Y, van Groenigen KJ et al (2018) A keystone microbial enzyme for nitrogen control of soil carbon storage. Sci Adv 4:eaaq1689

Cheng W, Johnson DW (1998) Elevated CO_2, rhizosphere processes, and soil organic matter decomposition. Plant Soil 202:167–174

Cheng W (1999) Rhizosphere feedbacks in elevated CO_2. Tree Physiol 19:313–320

Cotrufo MF, Gorissen A (1997) Elevated CO_2 enhances belowground C allocation in three perennial grass species at different levels of N availability. New Phytol 137:421–431

Crowther TW, Riggs C, Lind EM, Borer ET, Seabloom EW, Hobbie SE, Wubs J, Adler PB, Firn J, Gherardi L, Hagenah N, Hofmockel KS, Knops JMH, McCulley RL, MacDougall AS, Peri PL, Prober SM, Stevens CJ, Routh D (2019) Sensitivity of global soil carbon stocks to combined nutrient enrichment. Ecol Lett 22(6):936–945

Cusack DF, Silver WL, Torn MS, McDowell WH (2011) Effects of nitrogen additions on above-and belowground carbon dynamics in two tropical forests. Biogeochemistry 104: 203–225

De Graaff MA, Classen AT, Castro HF, Schadt CW (2010) Labile soil carbon inputs mediate the soil microbial community composition and plant residue decomposition rates. New Phytol 188:1055–1064

Deng Q, Hui D, Dennis S, Reddy KC (2017) Responses of terrestrial ecosystem phosphorus cycling to nitrogen addition: a meta-analysis. Glob Ecol Biogeogr 26:713–728

Dijkstra FA, Hobbie SE, Knops JM, Reich PB (2004) Nitrogen deposition and plant species interact to influence soil carbon stabilization. Ecol Lett 7:1192–1198

Dijkstra FA, Carrillo Y, Pendall E, Morgan JA (2013) Rhizosphere priming: a nutrient perspective. Front Microbiol 4:216

Elser JJ, Bracken ME, Cleland EE et al (2007) Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol Lett 10: 1135–1142

Eswaran H, Van Den Berg E, Reich P (1993) Organic carbon in soils of the world. Soil Sci Soc Am J 57:192–194

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annu Rev Plant Biol 40: 503–537

Fog K (1988) The effect of added nitrogen on the rate of decomposition of organic matter. Biol Rev 63:433–462

Frey SD, Ollinger S, Nadelhoffer K, Bowden R, Brzostek E, Burton A, Caldwell BA, Crow S, Goodale CL, Grandy AS, Finzi A, Kramer MG, Lajtha K, LeMoine J, Martin M, McDowell WH, Minocha R, Sadowsky JJ, Templer PH, Wickings K (2014) Chronic nitrogen additions suppress decomposition and sequester soil carbon in temperate forests. Biogeochemistry 121:305–316

Ge T, Liu C, Yuan H, Zhao Z, Wu X, Zhu Z, Brookes P, Wu J (2015) Tracking the photosynthesized carbon input into soil organic carbon pools in a rice soil fertilized with nitrogen. Plant Soil 392:17–25

Ge T, Li B, Zhu Z, Hu Y, Yuan H, Dorodnikov M, Jones DL, Wu J, Kuzyakov Y (2017) Rice rhizodeposition and its utilization by microbial groups depends on N fertilization. Biol Fertil Soils 53:37–48

Gong W, Yan X, Wang J (2012) The effect of chemical fertilizer on soil organic carbon renewal and CO_2 emission—a pot experiment with maize. Plant Soil 353:85–94

Hagedorn F, Spinnler D, Siegwolf R (2003) Increased N deposition retards mineralization of old soil organic matter. Soil Biol Biochem 35:1683–1692

Haile-Mariam S, Cheng W, Johnson DW, Ball JT, Paul EA (2000) Use of carbon-13 and carbon-14 to measure the effects of carbon dioxide and nitrogen fertilization on carbon dynamics in ponderosa pine. Soil Sci Soc Am J 64:1984–1993

Heath J, Ayres E, Possell M, Bardgett RD, Black HI, Grant H, Ineson P, Kerstiens G (2005) Rising atmospheric CO_2 reduces sequestration of root-derived soil carbon. Science 309: 1711–1713

Hebeisen T, Lüscher A, Zanetti S et al (1997) Growth response of Trifolium repens L. and Lolium perenne L. as monocultures and bi-species mixture to free air CO_2 enrichment and management. Glob Chang Biol 3(2):149–160

Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156

Hofmann A, Heim A, Gioacchini P, Miltner A, Gehre M, Schmidt MWI (2009) Mineral fertilization did not affect decay of old lignin and SOC in a ^{13}C-labeled arable soil over 36 years. Biogeosciences 6:1139–1148

Hungate BA, Jackson RB, Field CB, Chapin FS III (1995) Detecting changes in soil carbon in CO_2 enrichment experiments. Plant Soil 187:135–145

Hungate BA, Holland EA, Jackson RB, Chapin FS III, Mooney HA, Field CB (1997) The fate of carbon in grasslands under carbon dioxide enrichment. Nature 388:576–579

IPCC (2007) Climate change 2007: the physical science basis. Cambridge University Press, Cambridge

Janssens IA, Dieleman W, Luyssaert S, Subke JA, Reichstein M, Ceulemans R, Ciais P, Dolman AJ, Grace J, Matteucci G, Papale D, Piao SL, Schulze ED, Tang J, Law BE (2010) Reduction of forest soil respiration in response to nitrogen deposition. Nat Geosci 3:315–322

Jastrow JD, Amonette JE, Bailey VL (2007) Mechanisms controlling soil carbon turnover and their potential application for enhancing carbon sequestration. Clim Chang 80:5–23

Kazanski C (2017) Soil carbon cycling responses to elevated CO_2 and nitrogen addition. Doctoral dissertation, University of Minnesota, Minneapolis, United States

Keith H, Oades JM, Martin JK (1986) Input of carbon to soil from wheat plants. Soil Biol Biochem 18:445–449

Knapp G, Hartung J (2003) Improved tests for a random effects meta-regression with a single covariate. Stat Med 22:2693–2710

Kristensen HL, McCarty GW, Meisinger JJ (2000) Effects of soil structure disturbance on mineralization of organic soil nitrogen. Soil Sci Soc Am J 64(1):371–378

Kuzyakov Y, Domanski G (2000) Carbon input by plants into the soil. Review J Plant Nutr Soil Sci 163:421–431

Lamarque JF, Dentener F, McConnell J, Ro CU, Shaw M, Vet R, Bergmann D, Cameron-Smith P, Dalsoren S, Doherty R, Faluvegi G (2013) Multi-model mean nitrogen and sulfur deposition from the atmospheric chemistry and climate model intercomparison project (ACCMIP): evaluation of historical and projected future. Atmos Chem Phys 13(LLNL-JRNL-644459):7997–8018

Langley JA, McKinley DC, Wolf AA, Hungate BA, Drake BG, Megonigal JP (2009) Priming depletes soil carbon and releases nitrogen in a scrub-oak ecosystem exposed to elevated CO_2. Soil Biol Biochem 41:54–60

LeBauer DS, Treseder KK (2008) Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89:371–379

Liljeroth E, Van Veen JA, Miller HJ (1990) Assimilate translocation to the rhizosphere of two wheat lines and subsequent utilization by rhizosphere microorganisms at two soil nitrogen concentrations. Soil Biol Biochem 22:1015–1021

Liljeroth E, Kuikman P, Van Veen JA (1994) Carbon translocation to the rhizosphere of maize and wheat and influence on the turnover of native soil organic matter at different soil nitrogen levels. Plant Soil 161:233–240

Liu K, Sollenberger LE, Silveira ML, Vendramini J, Newman YC (2017) Nutrient pools in bermudagrass swards fertilized at different nitrogen levels. Crop Sci 57:525–533

Loisel J, Connors JPC, Hugelius G, Harden JW, Morgan CL (2019) Soils can help mitigate CO_2 emissions, despite the challenges. Proc Natl Acad Sci 116:10211–10212

Lu M, Zhou X, Luo Y, Yang Y, Fang C, Chen J, Li B (2011) Minor stimulation of soil carbon storage by nitrogen addition: a meta-analysis. Agric Ecosyst Environ 140(1–2):234–244

Maaroufi NI, Nordin A, Hasselquist NJ, Bach LH, Palmqvist K, Gundale MJ (2015) Anthropogenic nitrogen deposition enhances carbon sequestration in boreal soils. Glob Chang Biol 21:3169–3180

Maaroufi NI, Nordin A, Palmqvist K, Hasselquist NJ, Forsmark B, Rosenstock NP, Wallander H, Gundale MJ (2019) Anthropogenic nitrogen enrichment enhances soil carbon accumulation by impacting saprotrophs rather than ectomycorrhizal fungal activity. Glob Chang Biol 25:2900–2914

Mack MC, Schuur EA, Bret-Harte MS, Shaver GR, Chapin FS III (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. Nature 431:440–443

Minasny B, Malone BP, McBratney AB et al (2017) Soil carbon 4 per mille. Geoderma 292:59–86

Nottingham AT, Turner BL, Stott AW, Tanner EV (2015) Nitrogen and phosphorus constrain labile and stable carbon turnover in lowland tropical forest soils. Soil Biol Biochem 80:26–33

Ogle K, Pendall E (2015) Isotope partitioning of soil respiration: a Bayesian solution to accommodate multiple sources of variability. J Geophys Res Biogeosci 120:221–236

Osenberg CW, Sarnelle O, Cooper SD, Holt RD (1999) Resolving ecological questions through meta-analysis: goals, metrics, and models. Ecology 80:1105–1117

Paterson E, Thornton B, Midwood AJ, Osborne SM, Sim A, Millard P (2008) Atmospheric CO_2 enrichment and nutrient additions to planted soil increase mineralisation of soil organic matter, but do not alter microbial utilisation of plant- and soil C-sources. Soil Biol Biochem 40:2434–2440

Penuelas J, Poulter B, Sardans J et al (2013) Human-induced nitrogen–phosphorus imbalances alter natural and managed ecosystems across the globe. Nat Commun 4:2934

Phillips RP, Meier IC, Bernhardt ES, Grandy AS, Wickings K, Finzi AC (2012) Roots and fungi accelerate carbon and nitrogen cycling in forests exposed to elevated CO_2. Ecol Lett 15:1042–1049

Pregitzer KS, Burton AJ, Zak DR, Talhelm AF (2008) Simulated chronic nitrogen deposition increases carbon storage in northern temperate forests. Glob Chang Biol 14:142–153

Reay DS, Dentener F, Smith P, Grace J, Feely RA (2008) Global nitrogen deposition and carbon sinks. Nat Geosci 1:430–437

Rochette P, Flanagan LB, Gregorich EG (1999) Separating soil respiration into plant and soil components using analyses of the natural abundance of carbon-13. Soil Sci Soc Am J 63: 1207–1213

Silveira ML, Liu K, Sollenberger LE, Follett RF, Vendramini JM (2013) Short-term effects of grazing intensity and nitrogen fertilization on soil organic carbon pools under perennial grass pastures in the southeastern USA. Soil Biol Biochem 58:42–49

Talbot JM, Treseder KK (2012) Interactions among lignin, cellulose, and nitrogen drive litter chemistry–decay relationships. Ecology 93:345–354

Terrer C, Vicca S, Hungate BA, Phillips RP, Prentice IC (2016) Mycorrhizal association as a primary control of the CO_2 fertilization effect. Science 353:72–74

Terrer C, Vicca S, Stocker BD, Hungate BA, Phillips RP, Reich PB, Finzi AC, Prentice IC (2018) Ecosystem responses to elevated CO_2 governed by plant–soil interactions and the cost of nitrogen acquisition. New Phytol 217:507–522

Terrer C, Jackson RB, Prentice IC, Keenan TF, Kaiser C, Vicca S, Fisher JB, Reich PB, Stocker BD, Hungate BA, Peñuelas J, McCallum I, Soudzilovskaia NA, Cernusak LA, Talhelm AF, van Sundert K, Piao S, Newton PCD, Hovenden MJ, Blumenthal DM, Liu YY, Müller C, Winter K, Field CB, Viechtbauer W, van Lissa CJ, Hoosbeek MR, Watanabe M, Koike T, Leshyk VO, Polley HW, Franklin O (2019) Nitrogen and phosphorus constrain the CO_2 fertilization of global plant biomass. Nat Clim Chang 9:684–689

Tian D, Niu S (2015) A global analysis of soil acidification caused by nitrogen addition. Environ Res Lett 10:024019

Trumbore SE (1997) Potential responses of soil organic carbon to global environmental change. Proc Natl Acad Sci U S A 94: 8284–8291

Van der Krift TA, Kuikman PJ, Möller F, Berendse F (2001) Plant species and nutritional-mediated control over rhizodeposition and root decomposition. Plant Soil 228:191–200

Van Ginkel JH, Gorissen A, Van Veen JA (1997) Carbon and nitrogen allocation in Lolium perenne in response to elevated atmospheric CO_2 with emphasis on soil carbon dynamics. Plant Soil 188:299–308

Van Groenigen KJ, Six J, Harris D, Blum H, van Kessel C (2003) Soil ^{13}C-^{15}N dynamics in an N_2-fixing clover system under long-term exposure to elevated atmospheric CO_2. Glob Chang Biol 9:1751–1762

Van Groenigen KJ, Six J, Hungate BA, de Graaff MA, Van Breemen N, van Kessel C (2006) Element interactions limit soil carbon storage. Proc Natl Acad Sci U S A 103:6571–6574

Van Groenigen JW, Velthof GL, Oenema O, van Groenigen KJ, van Kessel C (2010) Towards an agronomic assessment of N_2O emissions: a case study for arable crops. Eur J Soil Sci 61:903–913

Van Groenigen KJ, Osenberg CW, Terrer C et al (2017) Faster turnover of new soil carbon inputs under increased atmospheric CO_2. Glob Chang Biol 23:4420–4429

Van Kessel C, Horwath WR, Hartwig U, Harris D, Lüscher A (2000) Net soil carbon input under ambient and elevated CO_2 concentrations: isotopic evidence after 4 years. Glob Chang Biol 6:435–444

Ventura M, Panzacchi P, Muzzi E, Magnani F, Tonon G (2019) Carbon balance and soil carbon input in a poplar short rotation coppice plantation as affected by nitrogen and wood ash application. New For 50(6):969–990

Viechtbauer W (2010) Metafor: meta-analysis package for R. R package version, 2010, 1-0

Vitousek PM, Porder S, Houlton BZ, Chadwick OA (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen–phosphorus interactions. Ecol Appl 20:5–15

Wilts AR, Reicosky DC, Allmaras RR, Clapp CE (2004) Long-term corn residue effects. Soil Sci Soc Am J 68:1342–1351

Wright SJ (2019) Plant responses to nutrient addition experiments conducted in tropical forests. Ecol Monogr:1382

Xu Q, Wang X, Tang C (2018) The effects of elevated CO_2 and nitrogen availability on rhizosphere priming of soil organic matter under wheat and white lupin. Plant Soil 425:375–387

Yue K, Peng Y, Peng C, Yang W, Peng X, Wu F (2016) Stimulation of terrestrial ecosystem carbon storage by nitrogen addition: a meta-analysis. Sci Rep 6:19895

Zhang B, Yang X, Drury CF, Reynolds WD, He H, Zhang X (2012) Effects of 49 years of fertilization on the distribution and accumulation of soil carbon under corn cultivation. Can J Soil Sci 92:835–839

Zhou Z, Wang C, Zheng M, Jiang L, Luo Y (2017) Patterns and mechanisms of responses by soil microbial communities to nitrogen addition. Soil Biol Biochem 115:433–441

Zhou J, Zang H, Loeppmann S, Gube M, Kuzyakov Y, Pausch J (2020) Arbuscular mycorrhiza enhances rhizodeposition and reduces the rhizosphere priming effect on the decomposition of soil organic matter. Soil Biol Biochem 140:107641