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Minor stimulation of soil carbon storage by nitrogen addition: A meta-analysis

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ABSTRACT

It is a well-established concept that nitrogen (N) limits plant growth and ecosystem production. However, whether N limits land carbon (C) sequestration – particularly in soil, the largest pool in the land – remains highly controversial. We conducted a meta-analysis to synthesize 257 studies published in the literature with 512 paired comparisons to quantify the changes of ecosystem C processes in response to N addition. Our results show that N addition significantly increased aboveground, belowground, and litter C pools by 35.7, 23.0, and 20.9%, respectively, across all the studies. Despite the substantial increases in C inputs from vegetation to soil system, N addition resulted in no significant change in C storage of both organic horizon and mineral soil in forests and grasslands, but a significant 3.5% increase in agricultural ecosystems, largely due to less contribution from aboveground production and increases in DOC and soil respiration. Thus, N stimulation of C storage primarily occurred in plant pools but little in soil pools. Moreover, N-induced change in soil C storage was positively related to changes in belowground production but not to those in aboveground growth. Our global synthesis also suggests that earth system models need to treat soil C inputs from aboveground and belowground sources differentially for soil C sequestration in response to N deposition and fertilization.

1. Introduction

Atmospheric nitrogen (N) deposition, primarily from fossil fuel combustion and artificial fertilizer application (Davidson, 2009), has increased three- to five-fold over the last century (IPCC, 2007) and presently adds more than 200 Tg each year, largely to terrestrial ecosystems (Galloway et al., 2008), which exceeds the annual N input from natural sources (EPA, 2008). Global annual N deposition rates are projected to increase by a factor of 2.5 by the end of the century (Lamarque et al., 2005). The carbon (C) and N cycles are highly coupled in terrestrial ecosystems as the basis of biogeochemical cycles and energy flows (Rastetter and Shaver, 1992; Tateno and Chapin, 1997; Cleveland and Liptzin, 2007). Terrestrial ecosystems sequester nearly 30% of anthropogenic C emissions, offering the most effective yet natural means to climate change mitigation (Le Quere et al., 2009). Nitrogen deposition and rising atmospheric CO_2 concentration have been suggested to be major mechanisms underlying terrestrial ecosystem C sequestration (Schimel et al., 2001; IPCC, 2007). A recent analysis of eddy-flux and biomass accumulation data in temperate and boreal forests in western Europe and the United States also suggests a strong positive correlation of net C sequestration with N deposition (Magnani et al., 2007).

However, how N regulates C cycle–climate feedbacks is largely uncertain, which is a critical issue in model projections of future states of climate and ecosystems (Hungate et al., 2003; Thornton et al., 2007; Sokolov et al., 2008; Thornton et al., 2009). Earth system models that do not incorporate C–N interactions usually predict strong land C sequestration due to CO_2 fertilization, but a positive feedback was commonly simulated under climate warming that triggers biologically mediated C release and leads to a warmer climate (Cox et al., 2000; Friedlingstein et al., 2006; Plattner et al., 2008). In contrast, the earth system models with N processes simulate weakened CO_2 fertilization, enhanced warming effects on N availability and C sequestration, and a negative land C–climate feedback (Thornton et al., 2007; Sokolov et al., 2008). To develop robust earth system models with fully coupled N–C–climate interactions, we urgently need process-level knowledge on N regulations of C sequestration in land ecosystems (Reay et al., 2008).

N addition usually stimulates plant growth, resulting in increased C storage in plant pools in most ecosystems (Vitousek and Howarth, 1991; Vitousek, 2004; LeBauer and Treseder, 2008). Whether the increased plant growth can lead to net C storage in

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soil – the largest pool in terrestrial ecosystems – is still highly controversial. N fertilization significantly stimulated soil C gain in some ecosystems (Hyvönen et al., 2008; Pregitzer et al., 2008) but substantial loss in other ecosystems (Neff et al., 2002; Mack et al., 2004; Khan et al., 2007). The controversy is unlikely to be effectively resolved by studies at individual sites due to complex interactions and high spatial variability of various competing processes. It is necessary to synthesize results across studies to reveal a central tendency and identify broad-scale patterns of N-induced changes in soil C sequestration.

To help extrapolate results from individual studies to inform regional and global modeling studies, we conducted a meta-analysis, which has the potential to reveal a central tendency of diverse results from different experimental sites (Hedges et al., 1999). Furthermore, how responses of vegetation processes (i.e., aboveground, belowground, and litter production) to N addition contribute to N-induced changes in soil C storages is largely unclear, especially at the global scale. Several studies have shown that soil C storage was significantly correlated with the quantity of belowground organic matter inputs, but not with aboveground input (Balesdent and Balabane, 1996; Norby et al., 2004; Russell et al., 2007). However, most of modeling studies assumed that soil C dynamics equally depend on both belowground and aboveground primary production (Parton et al., 1987; Potter et al., 1993; Luo and Reynolds, 1999; McGuire et al., 2000; Shao et al., 2007). It is yet to be examined what controls soil C content, primarily aboveground, or belowground biomass, or both, at ecosystem and regional scales.

In this study, 257 experimental studies were synthesized to examine responses of soil C pools to N addition either as fertilization or mimic of deposition (i.e., spray N fertilizer solution) and investigate the potential mechanism for how ecosystem C pools and fluxes regulate N-induced changes in soil C pools. The ecosystem C pools and fluxes considered in the analysis include leaf, shoot, root, litter, microbial biomass C (MBC), dissolved organic C (DOC), O horizon soil, and mineral soil, soil respiration (Rs), and C mineralization (C-min). The meta-analysis was used to address the following three questions. First, to what extent were soil C storage altered by N addition globally? Second, how did ecosystem C processes respond to N addition? Third, what are potential mechanisms for N-induced changes in soil C pools?

2. Methods

2.1. Data sources

In this meta-analysis, we reviewed more than 2000 published papers on N fertilization and/or deposition studies searched from Web of Science® (1900–2008) and chose 257 of them for this analysis (Supplementary materials, Text S1) according to the following criteria: (i) Experiments in which N fertilizers were directly added to plots in the field and at least one of our selected variables (i.e., C pools in leaf, shoot, root, litter, microbe, organic horizon, mineral soil, and dissolved organic C, and C fluxes: C mineralization, and soil respiration) were included whereas reviews, modeling, greenhouse experiments, and descriptive N deposition studies without controls were excluded. (ii) Treatment and control plots at the beginning of experiments had similar species composition and soil properties. For those crop rotation experiments, the selected data should have the same tillage management, crop species and rotation sequences. (iii) The N application rates, experiment durations and soil depths were clearly indicated. Measurements were made at the same temporal and spatial scales. Experiments shorter than 1 year were excluded to avoid short-term noise. (iv) Terrestrial ecosystems were included whereas freshwater and marine ecosystems were excluded from the study. (v) The means, standard deviations or standard errors and samples sizes of our chosen variables were directly reported or could be calculated from the chosen papers. The 257 studies were distributed mostly in North America and Europe (Fig. 1).

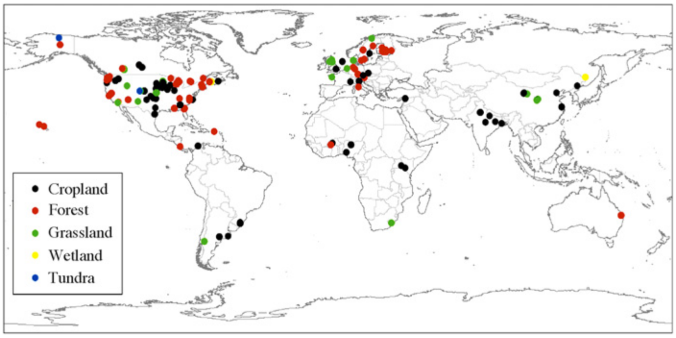

Fig. 1. Global distribution of N addition experiments included in this meta-analysis. Most studies have been conducted in the North America and Europe.

If more than one level of N addition were conducted at the same experiment, measurements from different N application rates were considered independent observations to evaluate the central tendency of the N addition effects on C dynamics (Curtis and Wang, 1998; Liu and Greaver, 2009). If more than one measurement on different temporal scales of the chosen variables were presented from the same experiment, we extracted measurement data from the latest sampling (Treseder, 2008). Detailed information about the sites, biomes, locations, and data sets is presented in Table S1. In addition, we separated the database into two sub-databases for agricultural and non-agricultural ecosystems, respectively, to compare the effects of human disturbance and ecosystems types on the responses of ecosystem C cycles to N additions. Furthermore, the non-agricultural ecosystems included forests, grasslands (including hay meadows and pastures), and others (deserts, tundra and wetlands). Data on mean annual temperature (MAT) and mean annual precipitation (MAP) at the study sites were either extracted from the published papers or, in the case that it was not reported in the paper, from the global data base at http://www.worldclim.org/ with latitude and longitude coordinates.

Data were extracted from 257 published experimental studies (Table S1), including leaf C pool, aboveground plant C pool (i.e., shoot), belowground plant C pool (i.e., root), litter C pool, microbial biomass C (MBC), dissolved organic C (DOC), organic horizon C pool (O horizon), soil C pool (SCP), soil respiration (Rs), and C mineralization (C-Min) for this analysis. Whenever available, data of root:shoot ratio (R:S), soil pH, and bulk density (BD) were also considered. Of 257 studies, 89 reported soil C concentrations. Since this meta-analysis study did not find significant effects of N fertilization on soil bulk density (Fig. 2), response ratios of soil C concentrations in response to N fertilization were used to represent changes in soil C pool sizes. Category variables were ecosystem types (croplands, forests, grasslands, wetlands, tundra, and deserts) and fertilizer types (NH_4^+, NO_3^-, NH_4NO_3, and urea). Forcing and environmental variables included soil depths (0–50 cm), N application rates (0.33–74 g N m^{-2} yr^{-1}), cumulative N amounts, study durations (1–45 years), MAT, MAP, and latitude.

2.2. Analysis

We followed the methods used by Hedges et al. (1999), Luo et al. (2006), and Liao et al. (2008) to evaluate the responses of ecosystem C processes to N additions. A response ratio (RR, the ratio of the mean value of a concerned variable in N fertilization treatment to that in control) is used here as an index of the magnitude of N addition effect (Hedges et al., 1999; Luo et al., 2006; Liao et al.,

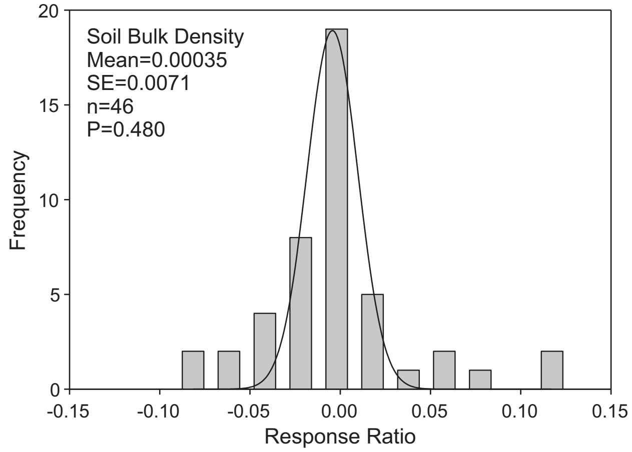

Fig. 2. Effects of N addition on soil bulk density. N addition did not cause statistically significant differences in soil bulk density ($P = 0.480$).

2008). We calculated response ratio (RR) (Hedges et al., 1999) to indicate effects of N addition by

$$\mathrm{RR} = \ln \frac{\overline{X_t}}{\overline{X_c}} = \ln\left(\overline{X_t}\right) - \ln\left(\overline{X_c}\right) \tag{1}$$

where $\overline{X_t}$ and $\overline{X_c}$ are means in the treatment and control groups, respectively. Its variance (v) is estimated by

$$v = \frac{s_t^2}{n_t \overline{X_t}^2} + \frac{s_c^2}{n_c \overline{X_c}^2} \tag{2}$$

where n_t and n_c are the sample sizes for the treatment and control groups, respectively; s_t and s_c are the standard deviations for the treatment and control groups, respectively.

The mean of response ratio (RR_{++}) is calculated from RR of individual pair comparison between N treatment and control, RR_{ij} ($i = 1, 2, \ldots, m$; $j = 1, 2, \ldots, k_i$). Here m is the number of groups (e.g., different facilities or ecosystem types), k_i is the number of comparisons in the ith group. The calculation of mean response ratios was done by

$$\mathrm{RR}_{++} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{k_i} w_{ij}\mathrm{RR}_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{k_i} w_{ij}} \tag{3}$$

with the standard error as:

$$s(\mathrm{RR}_{++}) = \sqrt{\frac{1}{\sum_{i=1}^{m}\sum_{j=1}^{k_i} w_{ij}}} \tag{4}$$

where w_{ij} is the weighting factor and is estimated by

$$w_{ij} = \frac{1}{v} \tag{5}$$

In this way, studies with greater precision (i.e., lower v) were given greater weights to compute mean response ratio (RR_{++}) so that the precision of the combined estimate and the power of the tests increased (Gurevitch and Hedges, 1999). We used t-test to examine whether or not the response ratio in the N treatment was significantly different from that in control.

We also plotted frequency distributions of RR to display variability among individual studies. The frequency distributions were assumed to follow normal distributions and fitted by a Gaussian function (i.e., normal distribution):

$$y = a \exp\left[-\frac{(x-\mu)^2}{2\sigma^2}\right] \tag{6}$$

where x is RR, y is the frequency (i.e., number of RR values), a is a coefficient showing the expected number of RR values at $x = \mu$, μ and σ are mean and variance of the frequency distributions of RR, respectively, and e is the base of exponent. We used the Sigma Plot software for fitting of the normal functions. We also conducted simple and multivariate correlation analyses to examine relationships of response ratio of soil C pool with environmental and biogeochemical variables.

3. Results

The weighted mean response ratio of soil C pool (SCP) across all the 512 pairs of comparisons was 0.0217, which was statistically significant from zero ($P < 0.001$) (Fig. 3A). SCP significantly increased with N addition by a mean RR of 0.0342 ($P < 0.001$) in agricultural ecosystems (Fig. 3B) but did not significantly change with a mean RR of −0.0026 ($P = 0.92$) in non-agricultural ecosystems (Fig. 3C), including grasslands, forests, wetlands, tundra, and

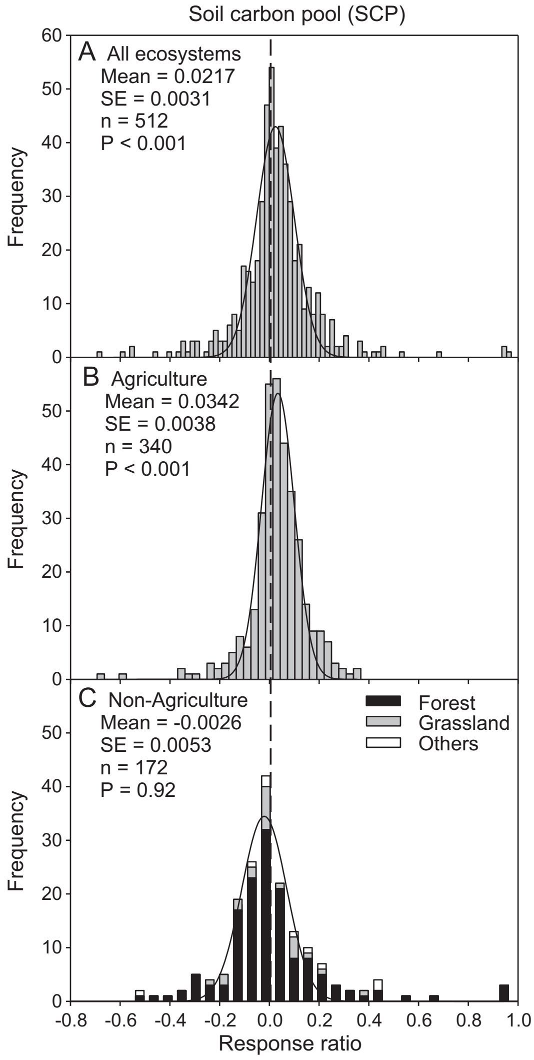

Fig. 3. Frequency distributions of response ratios (RR) of soil carbon pools (SCP) for all (A), agricultural (B), and non-agricultural ecosystems (C). In panel c, the black part of bars indicates data points from forests, the gray part for grasslands, and the white part for other ecosystems (i.e., tundra and wetland). The solid line is the fitted Gaussian (Normal) distribution of frequency data. The vertical lines are drawn at RR = 0. The averaged effects of N addition on soil C storage are statistically significant within agricultural ecosystems (panel b) but not within non-agricultural ecosystems (panel c).

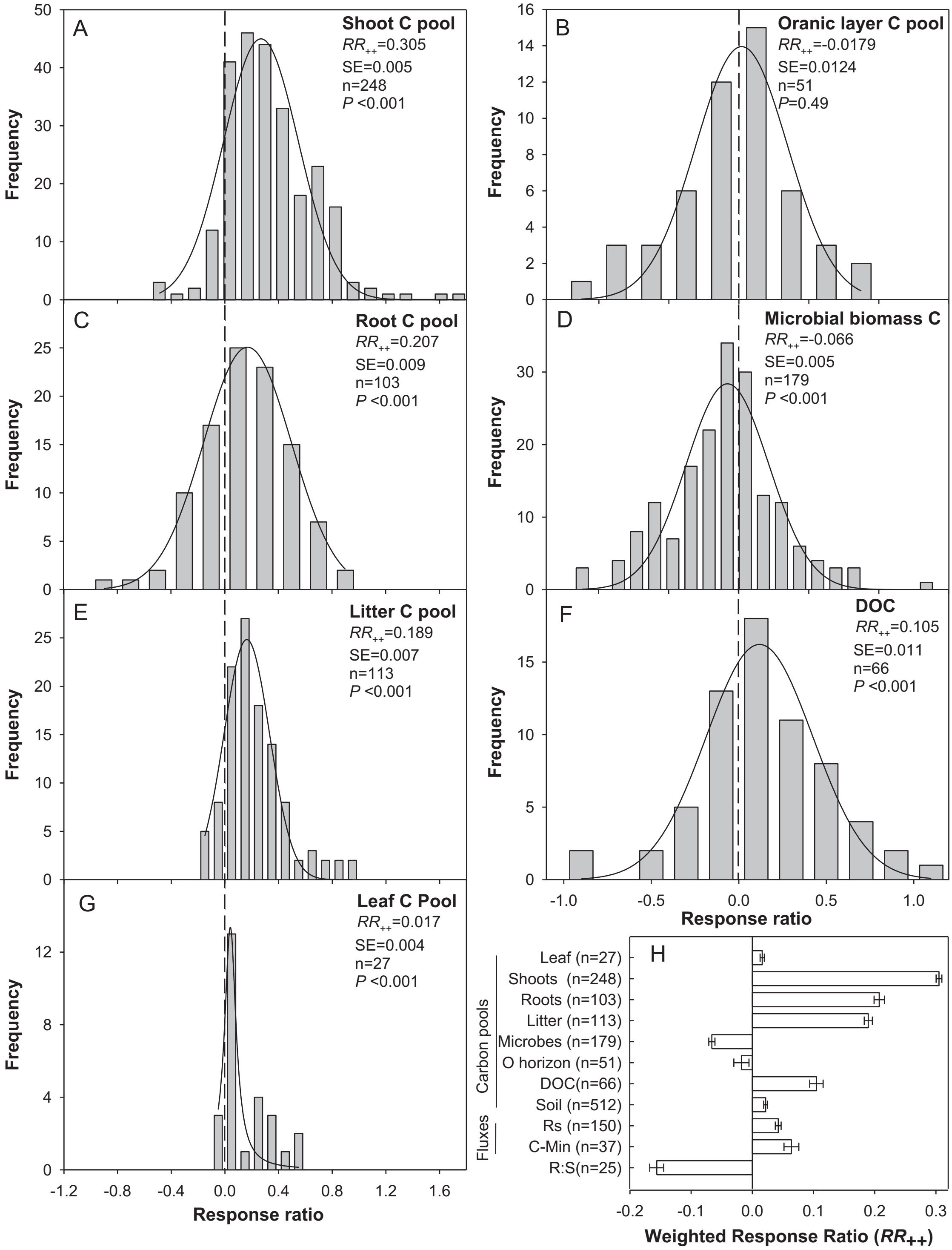

Fig. 4. Frequency distributions of response ratios (RR) of aboveground plant carbon pools (A), organic horizon C pool (B), belowground plant carbon pools (C), microbial biomass C (D), litter C pool (E), dissolved organic C (DOC, F), and leaf C pool (G). Panel H shows weighted response ratio (RR_{++}) of those C pools, two fluxes (Rs: soil respiration, C-min: C mineralization), and root:shoot ratio (R:S) in response to N addition. The solid line is the fitted Gaussian (Normal) distribution of frequency data. The vertical lines were drawn at RR = 0.

deserts. In addition, N-induced changes in SCP varied much more in non-agricultural than agricultural soils. The 95% response ratios of SCP fell within a range from −0.223 (2.5 percentile) to 0.249 (97.5 percentile) in agricultural soils and from −0.407 to 0.674 in non-agricultural soils. In the entire data set, N-induced changes in SCP ranged from the lowest RR of −0.693 (i.e., a 50% reduction) in a 45-year fertilized cropland to the highest of 0.972 (i.e., a 275% increase) in a forest.

We examined major processes that potentially regulate the changes in SCP in response to N addition. Our analysis showed that, across all the studies, C storage in leaf, shoots, roots, litter, and dissolved organic C (DOC) significantly increased with N addition by mean RRs of 0.017, 0.305, 0.207, 0.189, and 0.105 ($P < 0.001$), respectively (Fig. 4A, C, E, F, and G), while microbial biomass C (MBC) significantly decreased by a mean RR of 0.066 ($P < 0.001$) and O horizon C pool did not change with N addition (Fig. 4B and D). Soil

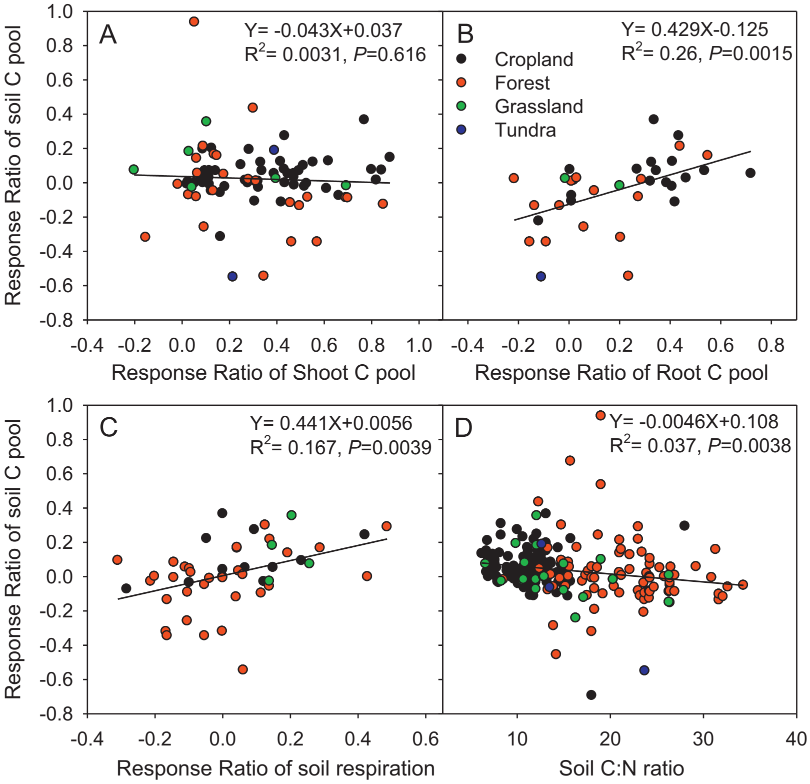

Fig. 5. Relationships of response ratios (RR) of soil C pool with RR of aboveground plant carbon pools (A), belowground plant carbon pools (B), RR of soil respiration (C), and soil C:N (D). N-induced changes in soil C sink were positively correlated with changes in belowground plant growth and soil respiration but decreased with soil C:N. N stimulated aboveground plant growth does not significantly contribute to changes in soil C sink. The significant correlation between the response ratio of soil C pool and soil C:N ratio is more due to differences among ecosystem types having different means than variations within each group.

respiration and C mineralization also significantly increased with N addition by means of 0.042 and 0.064, respectively ($P < 0.001$, Fig. 4H). Interestingly, the RRs of C storages in response to N addition steadily decreased from shoots to roots, litter, DOC, and soil (Fig. 4H). N-induced changes in most variables were larger in agricultural than in non-agricultural ecosystems except microbial biomass C and C mineralization (Table 1).

The N-induced changes in root C pools were significantly correlated with changes in SCP ($P = 0.002$) across all studies (Fig. 5B) and within forest sites ($P = 0.022$) (Table 2). Their relationship was marginally significant at the P level of 0.077 within croplands and could not be evaluated for grasslands due to too few data points. However, N-induced increases in shoot C pools were not significantly correlated with changes in SCP ($P = 0.616$) across all studies (Fig. 5A), within forests ($P = 0.147$), or within grasslands ($P = 0.50$), and marginally significant within croplands ($P = 0.083$) (Tables 2 and 3). Soil C storage was partially controlled by respiratory C release via microbial decomposition. N-induced changes in soil respiration were significantly correlated with changes in SCP across all studies ($P = 0.004$) (Fig. 5C) and within forests but not within croplands and grasslands (Table 2). In addition, N-induced changes in soil C pools were significantly and negatively correlated with soil C:N ratio across all studies among different ecosystems types ($P = 0.004$) (Fig. 5D). Note that the explanatory powers of the regression results (R^2) are relatively low within each ecosystem (Table 2), which indicates large noise and a high degree of subjective uncertainty associated with other processes.

The responses of C pools and fluxes to N fertilization may vary with ecosystem types and fertilizers. For the 10 variables of C pools and fluxes evaluated in this study, the absolute values of 8 RR_{++} were lower for forests than for croplands, grasslands, and others (i.e., tundra and wetland, Fig. 6A). The rest of the RR_{++} values in forests were larger than those of croplands and grasslands. The absolute RR_{++} values of microbial biomass C, O horizon soil C, DOC, and root C pools with N addition were larger for fertilizer $NH_4{}^+$ than for others ($NO_3{}^-$, NH_4NO_3, and urea), when the RR_{++} values of other C pools and flux were similar (Fig. 6B).

Environmental and/or forcing factors also influenced the responses of ecosystem C storage to N addition. Our meta-analysis suggested that MAP or experimental duration was not significantly correlated with N-induced changes in SCP across all the studies or within individual ecosystem types (Tables 2 and 3). N-induced changes in SCP, however, significantly increased with latitude, N application rates, and cumulative N amounts but decreased with

Table 1

Percentage of change $[(e^{RR_{++}} - 1) \times 100\%]$ of 10 variables in agricultural and non-agricultural ecosystems related to ecosystem C processes in response to N additions.

Variables	Agriculture		Non-agriculture	
	Percent of change	*N*	Percent of change	*N*
Carbon pool				
Leaf	17.26 ± 5.96	2	1.57 ± 0.35	25
Shoots	43.16 ± 0.67	102	28.49 ± 0.67	146
Roots	31.09 ± 1.56	26	19.75 ± 1.02	77
Litter	37.90 ± 0.96	56	7.01 ± 0.92	57
Microbes	−2.20 ± 0.74	86	−9.80 ± 0.68	93
O horizon	–	–	−1.77 ± 1.24	51
DOC	17.85 ± 1.66	25	5.91 ± 1.48	41
Soil	3.48 ± 0.38	340	−0.26 ± 0.53	172
Carbon flux				
Rs	16.13 ± 1.18	26	2.17 ± 0.52	124
C-min	5.96 ± 1.30	32	11.23 ± 3.55	5

Note: DOC, dissolved organic carbon; Rs, soil respiration; and C-min: carbon mineralization. Non-agriculture includes grasslands, forests, wetlands, tundra, and deserts.

Table 2

Regression analysis of response ratios (RR) of soil C pool (SCP) against RR of different pools and fluxes and environmental variables in all ecosystems, croplands, forests, and grasslands.

Variable *X*	All ecosystems					Cropland					Forest					Grassland				
	a	*b*	*n*	R^2	*P*	*a*	*b*	*n*	R^2	*P*	*a*	*b*	*n*	R^2	*P*	*a*	*b*	*n*	R^2	*P*
RR(APCP)	0.037	−0.043	84	0.003	0.616	0.0046	0.11	50	0.062	0.083	0.072	−0.32	26	0.086	0.147	0.127	−0.161	6	0.121	0.50
RR(BPCP)	−0.125	**0.429**	36	0.260	0.002	−0.035	0.262	18	0.183	0.077	−0.152	**0.337**	15	0.129	0.022	0.022	−0.194	2	–	–
RR(Rs)	0.020	**0.363**	51	0.11	0.017	0.076	0.286	12	0.154	0.207	−0.006	0.313	35	0.073	0.117	0.032	0.614	4	0.044	0.791
RR(LCP)	0.0077	0.107	52	0.051	0.108	0.039	0.040	38	0.016	0.454	0.015	0.031	11	0.001	0.942	0.068	0.299	2	–	–
DOC	0.018	0.0026	41	~0.00	0.982	−0.023	0.018	21	0.001	0.889	0.106	0.178	12	0.034	0.568	−0.035	−0.059	8	0.012	0.794
Soil C/N	0.108	**−0.005**	227	0.037	0.004	0.095	−0.004	123	0.009	0.306	0.151	−0.006	81	0.028	0.133	0.135	−0.008	20	0.116	0.143
Latitude	−0.037	**0.002**	512	0.013	0.011	−0.012	0.001	340	0.011	0.058	−0.151	**0.004**	143	0.046	0.010	0.041	−0.001	23	0.004	0.762
MAT	0.062	**−0.003**	512	0.017	0.003	0.061	**−0.002**	340	0.016	0.022	0.087	**−0.007**	143	0.054	0.005	−0.035	0.003	23	0.012	0.620
MAP	0.054	~0.00	512	0.007	0.062	0.050	−0.000	340	0.002	0.359	0.051	−0.000	143	0.009	0.271	0.035	−0.000	23	0.011	0.637
Depth	0.048	**−0.001**	512	0.031	<0.01	0.066	**−0.002**	340	0.136	<0.01	−0.006	0.002	143	0.011	0.209	−0.007	0.000	23	0.000	0.957
Rate	0.004	**0.002**	512	0.011	0.019	0.010	**0.002**	340	0.017	0.017	−0.011	0.002	143	0.007	0.308	−0.078	0.008	23	0.100	0.141
Amount	0.014	**<0.01**	512	0.009	0.029	0.019	**0.000**	340	0.016	0.020	−0.002	0.000	143	0.005	0.402	−0.040	0.000	23	0.093	0.156
Duration	0.016	0.001	512	0.004	0.17	0.024	0.001	340	0.004	0.233	−0.002	0.002	143	0.005	0.395	−0.010	0.001	23	0.001	0.879

Note: Correlated variables includes aboveground and belowground plant C pool (APCP and BPCP, respectively), soil respiration (Rs), litter C pool (LCP), dissolved organic C (DOC), soil C:N, latitude, mean annual temperature (MAT), mean annual precipitation (MAP), soil depth (Depth), N application rate (Rate), cumulative N fertilization amount (Amount), and experimental duration (Duration). The regression analysis was based on RR(SCP) = *a* + *bX*, where *X* is the independent variables in the first left column, *a* is the intercept, and *b* is the regression coefficient. *n* is sample size, r^2 is determinant coefficient and *p* is probability of significance of the regression relationship. *b* values in bold are statistically significant from zero.

MAP and soil depth across all studies and within croplands. Within forests, N-induced changes in SCP significantly increased only with latitude but decreased with MAT. No correlations were significant between changes in soil C pools and the environmental and forcing variables in grasslands (Table 2).

Many of those environmental and forcing factors were significantly correlated with each other (Table 3). We used stepwise regression analysis to examine multivariate effects on N-induced changes in soil C pools. Although soil depth, cumulative N amount, and latitude were the three covariates that interactively influenced responses of SCP to N addition, they together explained for only 5% of the variability in response ratios of SCP among all studies (Table 4).

4. Discussion

4.1. *N effects on plant growth vs. soil C storage*

It has been well documented that plant growth is stimulated by N fertilization. For example, recent meta-analyses have consistently shown that aboveground net primary productivity (NPP) and root biomass increased with N addition (LeBauer and Treseder, 2008; Xia and Wan, 2008). Our results also demonstrated that C pools in both aboveground and belowground plant production significantly increased under N addition (Fig. 4A and C), resulting in increased fresh organic C input through plant litterfall and roots to soil. Averaged litter C pools increased by 20.9% in N fertilized treatment in comparison with control (Fig. 4E). The stimulation of litter input and the improvement of litter quality (i.e., decreased litter C:N ratio) under N addition (e.g., Aerts et al., 1995; Matsushima and Chang, 2007) can influence litter decomposition process (Knorr et al., 2005) and then soil C storage.

It has also been shown that plant productivity is usually higher in fertile than infertile soil. For plants distributed across the globe from tropical and temperate forests to alpine tundra and desert, Reich et al. (1997, 1999) found that leaf N content was strongly correlated with photosynthesis and leaf morphology (e.g., leaf lifespan and surface area-to-mass ratio). In N fertilized plots, soil N availability can stimulate plants to produce higher leaf N concentration and then result in higher photosynthetic capacity compared to control plots (Aerts et al., 1995; Gough et al., 2000; Hyvönen et al., 2007). N limitations to plant productivity are regulated by processes such as mineralization, immobilization, and plant physiological adjustments (Reich et al., 2006; LeBauer and Treseder, 2008).

The well-established N limitation is a plant-centric concept, which has recently been applied to ecosystem carbon sequestration. For example, progressive N limitation (PNL) theory predicts that C sequestration in plants and soils with elevated CO_2 as well as other perturbations may be constrained by N availability and supply in many ecosystems (Luo et al., 2004; Gill et al., 2006). However, experimental studies did not carefully examine how N influences soil carbon storage. This study synthesized 257 studies of N fertilization on soil carbon storage at the global scale. Our results indicate that soil carbon did not significantly change in non-agricultural ecosystems in response to N addition, while it increased by 3.5% in agriculture (Fig. 3B and C). Nevertheless, several reviews and meta-analyses showed that N fertilization slightly increased soil C storage in forests with limited sample sizes (Hyvönen et al., 2007; Nave et al., 2009; Janssens et al., 2010).

In non-agricultural systems, the return of increased biomass growth to the soil was mainly via the aboveground litterfall. Both litter and organic horizon C: N ratios significantly decreased in response to N addition (Knorr et al., 2005; M. Lu and Y. Luo, unpublished data). Unprotected surface litter and organic horizon soil

Table 3
Correlation analysis of environmental and/or forcing variables with each other for response ratio of SCP [RR(SCP)].

P values of the correlations	Pearson correlation coefficients							
	RR(SCP)	Latitude	MAT	MAP	Duration	Rate	Amount	Depth
RR(SCP)		**0.112**	**−0.128**	−0.078	0.060	**0.106**	**0.096**	**−0.176**
Latitude	0.011		**−0.828**	**−0.399**	0.082	−0.040	0.043	−0.046
MAT	0.004	<0.0001		**0.388**	**−0.121**	−0.017	**−0.102**	**0.134**
MAP	0.078	<0.0001	<0.0001		**−0.076**	0.042	−0.097	**−0.009**
Duration	0.176	0.064	0.006	0.036		0.076	**0.740**	0.018
Rate	0.017	0.366	0.705	0.144	0.089		**0.566**	0.010
Amount	0.031	0.334	0.022	0.360	<0.0001	<0.0001		0.071
Depth	<0.0001	0.300	0.001	0.003	0.693	0.826	0.113	

Note: The environmental/forcing variables are latitude, mean annual temperature (MAT), mean annual precipitation (MAP), experimental duration (Duration), N application rate (Rate), cumulative N fertilization amount (Amount), and soil depth (Depth). The values on up-right side of the diagonal are Pearson correlation coefficients. The values on low-left side of the diagonal are *P* values to indicate statistical significance of the correlation coefficients ($p < 0.05$).

Table 4
Stepwise linear regression of response ratio of soil C pools [RR(SCP)] with cumulative N fertilization amount (Amount), soil depth (Depth), and Latitude.

Equation	R^2	*P*-Value
RR(SCP) = −0.00123 × Soil depth + 0.04715	0.031	<0.0001
RR(SCP) = −0.00128 × Soil depth + 0.00009 × Amount + 0.03275	0.039	<0.0001
RR(SCP) = −0.00125 × Soil depth + 0.00009 × Amount + 0.00142 × Latitude − 0.024800	0.047	<0.0001

Note: The stepwise regression analysis started with all the environmental/forcing variables, which are latitude, mean annual temperature (MAT), mean annual precipitation (MAP), experimental duration (Duration), and N application rate (Rate) in addition to Amount and Depth. All the variables except Amount, Depth, and Latitude were excluded during the analysis, indicating that Amount, Depth, and Latitude were the only three covariates that interactively affected responses of SCP to N addition.

with high substrate quality decomposed quickly and had relatively small impacts on soil organic C (SOC). In addition, N addition decreased plant root: shoot ratio (Fig. 4H). Our regression analyses also showed that N-induced changes in soil C pool were not significantly correlated with changes in aboveground plant growth, but were positively correlated with changes in belowground root growth and soil respiration (Fig. 5A–C). Therefore, root production and turnover are crucial for soil C sequestration when most of plant biomass C enter mineral soil via roots in non-agricultural systems (Trumbore and Gaudinski, 2003). N-induced stimulation of aboveground plant production may not lead to the increase of soil C sequestration (Balesdent and Balabane, 1996; Norby et al., 2004; Russell et al., 2007). Our results challenge the modeling assumption that soil C dynamics equally depend on both belowground and aboveground primary production (Parton et al., 1987; Potter et al., 1993; Luo and Reynolds, 1999; McGuire et al., 2000; Shao et al., 2007). Furthermore, N addition increased soil respiration to counteract increased belowground C input in influencing SOC (Fig. 4H), resulting in increases in SOC in some ecosystems and decreases in others. N-induced stimulation of DOC may also accelerate C leaching to water bodies (Chapin et al., 2002). Thus, the plant-centric concept of N limitation may not fully explain the patterns in C sequestration in terrestrial ecosystems (Luo et al., 2006).

In agricultural soils, the N-induced increases inC influx from both above- and below-ground plant production were higher than

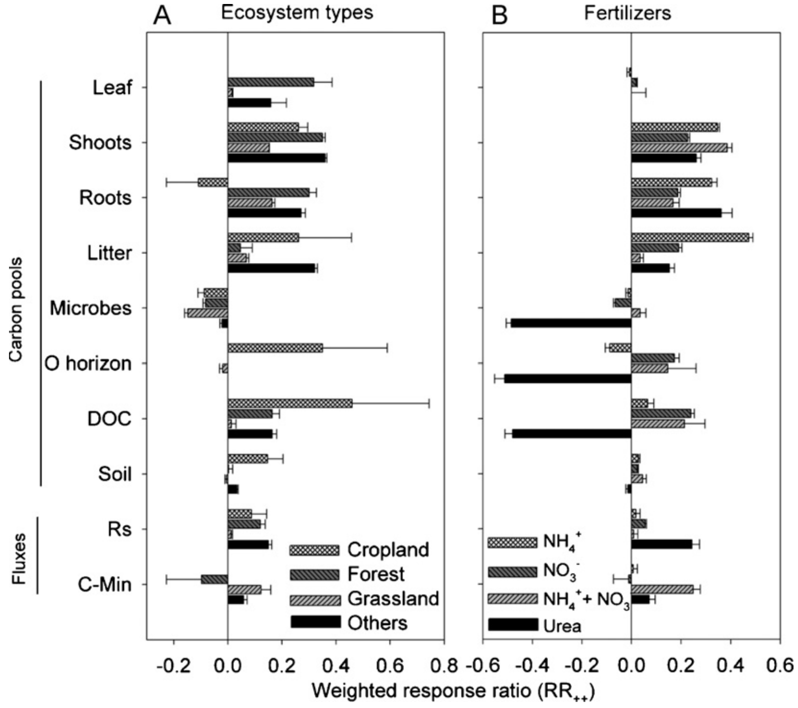

Fig. 6. Weighted response ratios (RR_{++}) of 10 variables related to carbon pools and fluxes in response to N addition with four ecosystem types (cropland, forest, grassland, and others-tundra and wetland) and four fertilizers (NH_4^+, NO_3^-, NH_4NO_3, and urea). Bars represent RR_{++} ± 95% confidence intervals. The vertical lines were drawn at RR = 0. DOC: dissolved organic C, Rs: soil respiration, and C-min: C mineralization.

Table 5
Mean, standard error (SE) and sample size (*n*) of response ratios (RRs) for soil C turnover rate, soil C residence time and soil pH in response to N additions, and the reference/background values in control plots for soil C concentration (%), soil C content (Mg ha^{-1}), and soil C:N ratio in agricultural and non-agricultural ecosystems.

Variables	Agriculture			Non-agriculture		
	Mean	SE	*n*	Mean	SE	*n*
RR of soil C turnover rate	−0.046	0.052	11	0.003	0.037	37
RR of soil C residence time	0.046	0.051	11	−0.003	0.032	37
RR of Soil pH	−0.041	0.005	99	−0.034	0.002	102
Soil C concentration (%)	2.05	0.18	167	3.46	0.65	100
Soil C content (Mg ha^{-1})	35.93	2.81	173	52.82	4.09	72
Soil C:N ratio	11.36	0.260	125	19.73	0.60	110

Note: Soil C turnover rates were calculated from Rs/SCP. Soil C residence times were calculated from SCP/Rs. Soil C concentration (%), soil C content, and soil C:N ratio were the reference/background soil properties of agricultural and non-agricultural ecosystems in this meta-analysis. Non-agriculture includes grasslands, forests, wetlands, tundra, and deserts.

that in non-agricultural systems (Table 1). In addition, N fertilization decreased soil C turnover rate or increased residence time in agricultural systems (Table 5). Thus, increased aboveground plant biomass was partially turned into subsoil via plowing where the decomposition rate may be significantly lower than that at the soil surface (Lomander, 2002; Gillabel et al., 2010), resulting in the net soil C accumulation under N addition. In addition, tillage management and the combination of tillage, irrigation and N fertilization may influence soil C sequestration in response to N-induced residue increase (Halvorson et al., 2002; Russell et al., 2009; Sainju et al., 2010). Other syntheses and individual studies have also shown that N addition to agricultural ecosystems typically increased SOC concentration (Jarecki and Lal, 2003; Alvarez, 2005; Lu et al., 2009), particularly when increased biomass was partially returned to soils as crop residues. Furthermore, agricultural soils have a relatively low C:N ratio (<15, Fig. 4D, Booth et al., 2005) and may lead to high N mineralization rates (Barrios et al., 1996) in comparison with non-agricultural soils.

From our meta-analysis, N fertilization significantly increased C inputs from aboveground, belowground, and litter C pools by 35.7, 23.0, and 20.9%, respectively, across all the studies (Fig. 7), which reflect the change in total C input to the soil and is consistent with previous synthesized studies (Hyvönen et al., 2007; LeBauer and Treseder, 2008; Xia and Wan, 2008). However, a decrease in root:shoot ratio under N fertilization (14.5%) resulted in less C allocation to root growth (Fig. 7), and N-stimulated aboveground production may not contribute much to soil C storage (Gale and Cambardella, 2000; Norby et al., 2004; Russell et al., 2009). Thus, direct C input into the soil system, which considerably contributes to soil C storage, is reduced. In addition, increases in litter decomposition (Knorr et al., 2005), soil respiration (4.3%, Fig. 7), and soil C mineralization (6.6%) under N fertilization accelerated C loss, causing less C accumulation in soil C (Fig. 7, see Section 4.2). Furthermore, N fertilization stimulated DOC, resulting in C leaching to ground and surface water (Chapin et al., 2002). Thus, the overall impact of N addition on SOC was relatively small with a 2.2% increase (Fig. 7, Janssens et al., 2010).

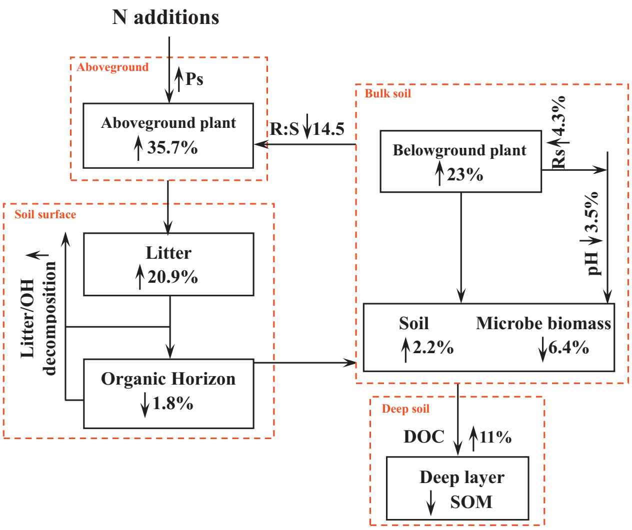

Fig. 7. Potential mechanisms of C processes in response to N additions. SOM: soil organic matter, R:S ratio: root:shoot ratio, OH: organic horizon, and Rs: soil respiration. The short arrows ↑ and ↓ represent increase and decrease in C processes in response to N addition, respectively.

4.2. N effects on C output vs. soil C storage

Any changes in SCP caused by N addition could be counterbalanced by corresponding changes in respiratory C release, particularly in forests. Soil respiration in N addition treatments increased in some studies but decreased in other studies in comparison with that in control (Hobbie, 2000; Trumbore and Gaudinski, 2003; Khan et al., 2007). Our meta-analysis results demonstrated that N additions stimulated soil respiration by 16.1% within agriculture and by 2.2% within non-agricultural ecosystems (Table 1) with an average of 4.3% across all studies (Fig. 7). Soil C mineralization was also enhanced by 6.6% under N addition (Fig. 4H). In addition, the stimulation of DOC by N addition may also accelerate C leaching to ground and surface water (Chapin et al., 2002). The stimulated N-induced C release and leaching counterbalanced the increase of C input via above- and belowground plant biomass growth (Fig. 7). Therefore, the stimulation of C loss and regulation of root:shoot ratio (see Section 4.3) maintained the relative stability of soil C storage.

The chemistry of soil organic matter (SOM) and litter can strongly influence decomposition and soil carbon dynamics. N-induced changes in soil C pools were significantly and negatively correlated with soil C:N ratios across all studies among different ecosystems types ($P = 0.004$) (Fig. 5D). The negative relationship suggests that N addition accelerated decomposition of SOM in high C:N soil but reduced decomposition of SOC in low C:N soil. In high C:N soil (>15, most in non-agriculture), microbial activities are limited by N availability. N addition stimulated microbial decomposition of SOC. In low C:N soil (<15, most in agriculture), however, microbial activities may be repressed by N addition, leading to decreased decomposition of SOC.

Decomposition of SOC in response to N addition involves complex microbial processes (Carreiro et al., 2000; Hobbie, 2000). High concentrations of inorganic N under N fertilization usually accelerate the degradation of easily decomposable litter and may slow the decomposition of recalcitrant litter due to stimulation or repression of different sets of microbial extracellular enzymes (Carreiro et al., 2000). The response of microbial biomass to N fertilization can be strongly correlative to the variety of plant production, fresh C supply and the changes of soil properties (Compton et al., 2004). Our results show negative responses of microbial biomass C (MBC) to N addition (Table 1; Figs. 4D and 7), which was similar to the another meta-analysis study by Treseder (2008). She argued that decreased microbial biomass largely resulted from declines in soil CO_2 emissions with only 17 samples, in which majority of data were from laboratory incubation (76%) and represented heterotrophic respiration. However, our results with 150 samples show that soil respiration (containing autotrophic and heterotrophic respiration) increased by 4.3% in response to N fertilization (Fig. 4H). Several other processes may contribute to the decrease in microbial biomass C in response to N fertilization. First, an increase in soil inorganic N can react with SOM and lead to the accumulation of recalcitrant compounds (Soderstrom et al., 1983; Fog, 1988), which may be toxic to microbial growth under N enrichment (Treseder, 2008; Janssens et al., 2010). Second, N addition significantly decreased soil pH by 3.5% across various ecosystems (Table 5). The soil acidification can result in calcium and magnesium leaching and other corresponding changes in soil physical–chemical properties, which may limit microbial biomass growth (Vitousek et al., 1997; Treseder, 2008). Moreover, N fertilization may result in N saturation and constrain the activities of beta-glucosidase in mineral soil and N fixation, causing the decreases in microbial C acquisition and microbial biomass (DeForest et al., 2004). Thus, decreases in microbial biomass C under N addition may result from declines in soil pH values (Table 5), inhibition of N fixation, soil inorganic N accumulation, and N saturation, but not from the reduction of root biomass and soil respiration (Figs. 4C and H, and 7). These processes can largely influence soil microbial community structure and decrease microbial biomass.

4.3. Broad-scale mechanisms of N regulation of soil C sequestration

Our analysis suggests two broad-scale mechanisms underlying minor changes in soil carbon storage in response to N fertilization. First, N addition alters plant allocation and stimulated more plant aboveground (35.7%) than belowground (23.0%) biomass growth (Fig. 4A *vs.* C). Shifted plant biomass allocation implies that N additions may stimulate aboveground competition of plants for light and photosynthesis but decrease root competition for nutrients availability (Tilman, 1987; Suding et al., 2005). N fertilization usually reduced root: shoot ratio (Fig. 4H). The stimulated plant growth is proportionally less allocated to root growth, which is critical for soil carbon formation. Thus, direct carbon input into the soil system via root litter was relatively less than that via surface litter. In addition, N-induced substantial increases in aboveground plant C stock were not correlated with N-induced change in soil C storage whereas N-induced changes in belowground C stock was significantly and positively correlated with that in soil C storage. Some individual studies have also shown that SOC storage was significantly correlated with the quantity of belowground organic matter inputs, but not with aboveground input (Balesdent and Balabane, 1996; Gale and Cambardella, 2000; Norby et al., 2004; Russell et al., 2007, 2009; Zhou et al., 2009). Therefore, N-stimulated aboveground production may not contribute much to soil C storage.

Second, N addition significantly stimulated soil respiratory C loss as predominantly regulated by soil C:N ratio. C storage tends to decrease in soil with high C:N soils of forests and grasslands (>15) but increase in low C:N soil of croplands (<15) in response to N addition. This is because N fertilization generally stimulated soil C decomposition in high C:N soil where microbial activities are limited by N availability, and decreased SOC decomposition in low C:N soil where microbial activities may be repressed by N addition. Nevertheless, mechanisms underlying responses of microbial decomposition to N addition are complex (Carreiro et al., 2000; Hobbie, 2000; Waldrop et al., 2004) and yet to be carefully explored.

4.4. Synergistic effects of rising CO_2 and N deposition

Soil N availability may gradually constrain the capability of terrestrial ecosystems to sequester carbon in long-lived plant biomass and SOM under elevated CO_2, which plays a critical role in regulating future climate change (Luo et al., 2004). According to the progressive N limitation (PNL) concept, elevated CO_2 alone may not be sustainable into the future to sequester atmospheric CO_2. Our meta-analysis results also showed that N addition alone, on average, resulted in only minor stimulation of soil C storage (Fig. 3A). However, N deposition and rising atmospheric CO_2 concentration may synergistically stimulate soil C sequestration.

Exposure to elevated CO_2 levels usually enhanced net soil C storage when N fertilization was applied (Reich et al., 2006; Hungate et al., 2009). In addition, the response of C sequestration in woody biomass of forests to increased atmospheric CO_2 depends on soil fertility, in particular N (Oren et al., 2001). Since most forests with high C:N ratios are N-limited (Fig. 5D), assessment of future carbon sequestration under elevated CO_2 should consider the limitations imposed by soil N, as well as interactions with N deposition. On the contrary, CO_2 stimulation of ecosystem C storage is generally accompanied by the net N accumulation (Luo et al., 2006) via increased fixation, decreased losses, and/or increased uptake from deep soil. Similarly, N accrues in ecosystems as C pools build up during succession over tens and hundreds of years (Vitousek, 2004; Davidson et al., 2007; Yang and Luo, 2010), largely because C storage in organic compounds is associated with N sequestration. In contrast, N addition alone, as shown in this and many other studies, did not press directional changes in soil C storage, particularly in forest and grassland soils, as it did on plant growth.

4.5. Implications for earth system modeling

This study also revealed key mechanisms underlying C and N interactions, which are imperative for development and improvement of earth system models. For example, N addition strongly regulated plant carbon allocation more to aboveground than belowground systems (Table 1 and Fig. 4A *vs.* C). However, N-induced substantial increases in aboveground plant production, in general, did not contribute to soil C storage yet belowground production did (Fig. 5A *vs.* B). Accordingly, earth system models need to simulate plant C allocation dynamically and to treat soil C input from aboveground and belowground sources differentially in order to realistically estimate C sequestration potential in soil in response to N deposition and fertilization.

C:N ratio is a dominant factor that regulates N effects on microbial decomposition of litter and soil organic matter (Fig. 5D). As a result, C storage tends to decrease in soil with high C:N soils of forests and grasslands but increase in low C:N soil of croplands in response to N addition. The differential responses of ecosystems with different C:N ratios to N deposition and fertilization should be incorporated into earth system models to simulate soil C dynamics. Our study is among the first global syntheses that identify broad-scale patterns and mechanisms to help extrapolate results from individual studies to inform regional and global modeling.

5. Conclusion

Our meta-analysis results show that N addition significantly increased above- and below-ground plant C stocks, litter C pool, DOC, and soil respiration while it decreased microbial biomass C. In summary, four subsystems, i.e., aboveground plant subsystem, litter-organic horizon subsystem, belowground plant-soil subsystem, and deep soil subsystem, could be elicited to describe how N addition regulates key processes of C cycle in terrestrial ecosystems (Fig. 7). Although N addition resulted in substantial increases in C input to soil systems, there was only a minor N-induced stimulation of increase of 2.2% in soil C storage across all ecosystems ($P < 0.001$), with a 3.48% increase in agricultural ecosystems ($P < 0.001$) and a non-significant change in non-agricultural ecosystems (−0.26%, $P = 0.92$, Fig. 3). Thus, N stimulation of C storage primarily occurs in plant pools but little in soil pools. Two key mechanisms may contribute to the lack of N-induced stimulation in soil C storage. First, N addition altered plant allocation, with more to aboveground than belowground growth. Thus, direct C input into soil via root litter was relatively decreased compared to that via surface litter. In addition, N-induced change in soil C storage was not correlated with N-induced substantial increases in aboveground plant growth whereas significantly and positively correlated with that in belowground plant growth. Therefore, aboveground biomass does not contribute much to soil carbon storage. Second, N addition significantly stimulated soil respiratory C loss, which is predominantly regulated by soil C:N ratio. C storage tends to decrease in soil with high C:N ratio of forests and grasslands but increase in low C:N soil of croplands in response to N addition. Those broad-scale patterns identified by our global synthesis suggest that earth system models need to simulate dynamic plant C allocation and differentially treat soil C input from aboveground and belowground sources to lower estimates of C sequestration potential in soil in response to N deposition and fertilization.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.agee.2010.12.010.

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