Global Change Biology celebrating 20 years

Global Change Biology (2014) **20**, 2332–2343, doi: 10.1111/gcb.12490

Different responses of soil respiration and its components to nitrogen addition among biomes: a meta-analysis

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Abstract

Anthropogenic activities have increased nitrogen (N) deposition by threefold to fivefold over the last century, which may considerably affect soil respiration (*Rs*). Although numerous individual studies and a few meta-analyses have been conducted, it remains controversial as to how N addition affects *Rs* and its components [i.e., autotrophic (*Ra*) and heterotrophic respiration (*Rh*)]. To reconcile the difference, we conducted a comprehensive meta-analysis of 295 published studies to examine the responses of *Rs* and its components to N addition in terrestrial ecosystems. We also assessed variations in their responses in relation to ecosystem types, environmental conditions, and experimental duration (DUR). Our results show that N addition significantly increased *Rs* by 2.0% across all biomes but decreased by 1.44% in forests and increased by 7.84% and 12.4% in grasslands and croplands, respectively ($P < 0.05$). The differences may largely result from diverse responses of *Ra* to N addition among biomes with more stimulation of *Ra* in croplands and grasslands compared with no significant change in forests. *Rh* exhibited a similar negative response to N addition among biomes except that in croplands, tropical and boreal forests. Methods of partitioning *Rs* did not induce significant differences in the responses of *Ra* or *Rh* to N addition, except that *Ra* from root exclusion and component integration methods exhibited the opposite responses in temperate forests. The response ratios (*RR*) of *Rs* to N addition were positively correlated with mean annual temperature (MAT), with being more significant when MAT was less than 15 °C, but negatively with DUR. In addition, the responses of *Rs* and its components to N addition largely resulted from the changes in root and microbial biomass and soil C content as indicated by correlation analysis. The response patterns of *Rs* to N addition as revealed in this study can be benchmarks for future modeling and experimental studies.

Keywords: autotrophic respiration, experimental duration, heterotrophic respiration, mean annual temperature, nitrogen fertilization, soil respiration

Received 15 May 2013; revised version received 10 November 2013 and accepted 21 November 2013

Introduction

Anthropogenic activities, such as fossil fuel combustion and application of artificial nitrogen (N)- based fertilizers, have increased atmospheric N deposition by threefold to fivefold over the past century (IPCC, 2007). Nitrogen deposition has been considered as one major component of global change and is predicted to increase in the future (Galloway, 1998; Lamarque *et al.*, 2005). The widespread N enrichment in the atmosphere and soil has considerably altered regional and global environments and affected terrestrial carbon (C) cycle (Schlesinger & Andrews, 2000; Luo *et al.*, 2006; Reay *et al.*, 2008), which is projected to change the trajectory of future climate change through climate-C cycle feedback (Melillo *et al.*, 2002; Luo, 2007; Luo *et al.*, 2009).

Soil respiration (*Rs*) represents CO_2 release through the soil surface from microbial/heterotrophic respiration (*Rh*) during organic matter and litter decomposition and root/autotrophic respiration (*Ra*) in live roots and their symbionts (Boone *et al.*, 1998; Luo & Zhou, 2006; Schindlbacher *et al.*, 2009). As the second largest C flux between the atmosphere and terrestrial ecosystems with a range from 68 to 98 Pg C yr^{-1} (Raich & Schlesinger, 1992; Raich *et al.*, 2002; Bond-Lamberty & Thomson, 2010), *Rs* plays a vital role in regulating atmospheric CO_2 concentration and climatic dynamics in the Earth system (Luo & Zhou, 2006). The rates of *Rs* are affected largely by major global change factors (e.g.,

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increased N deposition and elevated CO_2, Cardon *et al.*, 2001; Bowden *et al.*, 2004; Deng *et al.*, 2010). Therefore, understanding the responses of *Rs* and its components to global change is urgently needed for projecting climate change in the future.

Numerous studies have investigated the responses of *Rs* and C–N interactions to experimental N deposition. However, the effects of simulated N deposition on *Rs* and its components (i.e., *Ra* and *Rh*) remain controversial due to the differences of biome types, environmental conditions, and experimental methods (Craine *et al.*, 2001; Moscatelli *et al.*, 2008; Xu & Wan, 2008). Among individual studies, *Rs* significantly increased in some studies (e.g., Allison *et al.*, 2008; Xu & Wan, 2008; Han *et al.*, 2012), but substantially decreased or remained unchanged in others (e.g., Illeris *et al.*, 2003; Ding *et al.*, 2007; Mo *et al.*, 2008) in response to N addition. The controversy is unlikely to be resolved by these individual studies due to the different interactions of ecosystem C processes and high spatiotemporal variability of *Rs* responses to N addition.

Recently, three meta-analyses related to effects of N addition on *Rs* (i.e., Janssens *et al.*, 2010; Liu & Greaver, 2010; Lu *et al.*, 2011) have been conducted. Two of them mainly emphasized the central tendency of soil C pool (SCP) and associated C processes under N addition (Liu & Greaver, 2010; Lu *et al.*, 2011), while the other by Janssens *et al.* (2010) only examined the responses of *Rs* to N addition in temperate forests. The results among three meta-analyses varied largely due to data sets compiled for the different biomes. For instance, N addition decreased *Rs* by 17% in temperate forests due to the shift of microbial community composition (Janssens *et al.*, 2010) but did not alter it in nonagriculture biomes in Liu & Greaver (2010). If croplands were taken into account, *Rs* showed a significant positive response to N addition (Lu *et al.*, 2011). Therefore, it is necessary to compile all available data for different biomes to synthesize results from individual studies to reveal biome-scale patterns of N-induced changes in *Rs* and its components and to identify the major drivers for responses of *Rs* to N addition.

The effects of N addition on *Rs* are determined by the respective responses of the two components (i.e., *Ra* and *Rh*) as mentioned previously. It is, however, difficult to separate two components due to technical difficulties and complex interactions between root exudates and microbial decomposition (e.g., rhizosphere primng effects, Hanson *et al.*, 2000; Schindlbacher *et al.*, 2009; Kuzyakov & Gavrichkova, 2010). Although Janssens *et al.* (2010) have evaluated different responses of *Rh* and *Ra* to N addition in temperate forests, it is poorly understood in other biomes. Furthermore, whether or not methods of partitioning *Rs* affect their respective responses of *Ra* and *Rh* to N addition is still unclear. This may constrain the understanding of mechanisms underlying the responses of *Rs* to N addition. In addition, the C releases through *Ra* or *Rh* are indicated to associate with some C pools, such as root biomass, soil organic C (SOC), and microbial biomass C (MBC) (Haynes & Gower, 1995; Phillips & Fahey, 2007). How the responses of these pools to N addition affect those of *Rs* and its components needs to be further addressed.

As the responses of *Rs* to warming and elevated CO_2 are greater in the first several years than in later years largely due to ecosystem acclimation and/or adaptation (Rustad *et al.*, 2001; Søe *et al.*, 2004; Lu *et al.*, 2013), the responses of *Rs* to N addition may be also time-dependent. We thus hypothesized that experimental duration would significantly affect the response ratios of *Rs* to N addition [*RR* (*Rs*)] due to the potential acclimation of plants and/or soil microbes (Hopkins & Hüner, 1995). In addition, climatic conditions [including latitude (LAT), mean annual temperature (MAT), and mean annual precipitation (MAP)] in individual studies may also affect the responses of *Rs* to N addition due to the constraints of prevailing climatic factors on biological activities (e.g., microbial or root activity, extracellular enzymatic activity, Bardgett & Wardle, 2010).

This study aims to assess the responses of *Rs* and its components (*Ra* and *Rh*) to N addition in different biomes and to evaluate the global response of *Rs* to N deposition weighted by area and averaged rates of *Rs* in each biome. The spatiotemporal variation of *Rs* responses to N addition with the fertilization regime (e.g., experimental duration) and climate conditions is examined synchronously. Our objectives are to determine (i) how *Rs* and its components (*Ra* and *Rh*) respond to N addition in different biomes; (ii) how the responses of C pools impact the effects of N addition on *Rs*, *Ra*, and *Rh*; and (iii) how environmental variables and experimental duration affect the responses of *Rs* to N addition.

Materials and methods

Data sources

Peer-reviewed journal articles were searched using Web of Science (1900–2012) with the following search term combinations: (nitrogen OR N OR urea OR fertiliz* OR manure OR nitri* OR ammon*) AND (CO_2 OR carbon* OR microb* OR litter OR leaf* OR soil OR plant OR ecosystem) AND (effect* OR respon* OR affect* OR impact* OR increas* OR decreas* OR alter*) NOT (animal* OR medic* OR chemist*). To avoid bias in publication selection, the studies were selected on the basis of the following considerations. (i) Experiments were conducted in the field and had at least one pair of data (under control and treatment), including *carbon (C) pools*: litter, root, microbe, O-horizon soil, bulk soil, and dissolved organic C; *soil C fluxes*: soil respiration (*Rs*) and its components (*Ra* and *Rh*); and *biomass*: root, litter, microbe, and shoot: root ratio; (ii) Fertilization regime was clearly described, which included experimental duration (DUR), forms of N fertilizers, N application rates (Rate), frequency (application times per year, FREQ), and cumulative N amounts in experimental duration (Amount) as well as soil parameters such as soil depth and pH; (iii) Field experiments had been carried out at the same temporal and spatial scales in both control and treatment plots and only chosen when the duration was longer than one growing season; (iv) Initial environmental conditions, species compositions, and soil properties in the control and treatment plots were the same in the studies; (v) Only experiments conducted in terrestrial ecosystems were included; (vi) The means, standard deviations/errors, and samples sizes of variables in the control and treatment groups could be extracted directly from context, tables or digitized graphs. In total, 295 published papers about N fertilization and/or simulated deposition studies were selected from more than 3000 published papers (Data S1).

Meanwhile, environmental variables: latitude, mean annual temperature (MAT), and mean annual precipitation (MAP) were recorded directly from papers or cited papers, or in the case that it was not reported extracted from the data base at http://www.worldclim.org/ using the location information (e.g. latitude and longitude). The studies contained more than one rate of N addition (e.g., Johnson *et al.*, 2000; Chen *et al.*, 2002; Lee & Jose, 2003) or more than one vegetation type (e.g. Priess & Folster, 2001; Lee & Jose, 2003; Bowden *et al.*, 2004) were treated as multiple data points.

Data were extracted from selected papers (Data S1), including soil respiration (*Rs*), soil autotrophic respiration (*Ra*), heterotrophic respiration (*Rh*), soil C pool (SCP), soil organic C (SOC), soil dissolved organic C (DOC), microbial biomass C (MBC), root biomass (RB), fine root biomass (FRB, the diameter was defined as ≤2 mm, few as diameter < 5 mm or <1 mm), and litter mass (LM) (Data S2). To test the differences in responses of C processes to N addition, six types of biomes: tropical forests, temperate forests, boreal forests, croplands, grasslands, and others (deserts, tundras, and wetlands) and five forms of fertilizers (NH_4^+, NO_3^-, NH_4NO_3, urea, and manure) were differentiated in this analysis. Forcing and environmental variables included N application rates (0–74 g N m^{-2} yr^{-1}), frequency of N application per year (1–360 times yr^{-1}), experimental duration (1–45 years), soil depth (0–80 cm), MAT (−10.8–28.3 °C), MAP (82–5578 mm) and latitude (78°S–79°N) (Fig. 1).

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 *Rs* and its components (*Ra* and *Rh*) to N addition. A response ratio (*RR*, natural log of the ratio of the mean value of a concerned variable in N treatment plots to that in control) was used to represent the magnitude of the effects of simulated N deposition as below:

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

where $\overline{X_t}$ and $\overline{X_c}$ are means of the concerned variable in 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 of the concerned variable in treatment and control groups, respectively; S_t and S_c are the standard deviations for the treatment and control groups, respectively. The reciprocal of its variance ($w = \frac{1}{v}$) was considered as the weight of each *RR*, which is consistent with the weighting estimates in Janssens *et al.* (2010) and Lu *et al.* (2011) but different from that in Liu & Greaver (2010) (Table 1). The mean response ratio (RR_{++}) was calculated from *RR* of individual pairwise comparison between treatment and control, RR_{ij} (i = 1, 2,…, m; j = 1, 2,…, k) as below. Here, m is

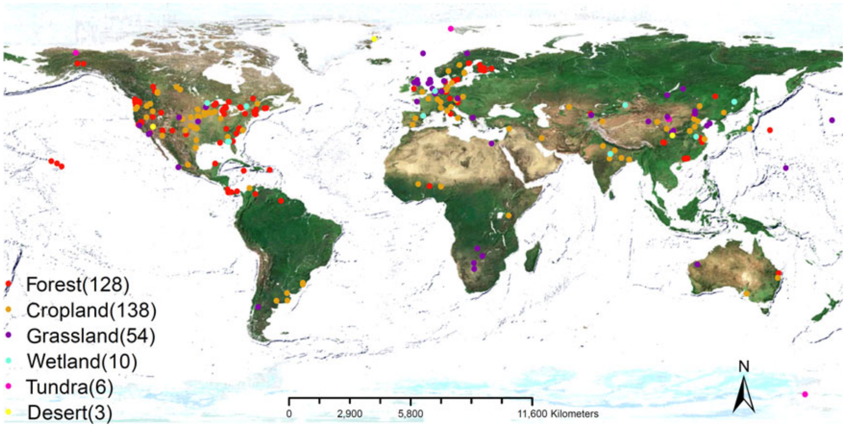

Fig. 1 Global distribution of N addition experiments selected in this meta-analysis. Numbers in parentheses is the actual number of sites in each biome from 295 papers.

the number of groups (e.g., ecosystem types), and k is the number of comparisons in the ith group.

$$RR_{++} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{k} W_{ij}RR_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{k} W_{ij}} \tag{3}$$

The standard error of RR_{++} was estimated by

$$s(RR_{++}) = \sqrt{\frac{1}{\sum_{i=1}^{m}\sum_{j=1}^{k} W_{ij}}} \tag{4}$$

Considering the differences of area and average rates of *Rs* among biomes, we incorporated the area weights and averaged *Rs* in each biome into a new estimation for global response of *Rs* to N addition. The global terrestrial [*RR* (R_S)] was calculated by

$$\text{Global terrestrial}[RR(Rs)] = \ln\left[\frac{\sum_{j=1}^{m} W_{aj}Rs_jE_j}{\sum_{j=1}^{m} W_{aj}Rs_j}\right] \tag{5}$$

where E_j = exp (RR_{++}) in each biome, m is the number of biome types, W_{aj} is the area weight of each biome in total area from Whittake & Likens (1973); and R_{Sj} is the averaged rate of *Rs* calculated from the data in control groups in each biome.

Multiple comparisons were used to examine the differences in distribution of *RR* (*Rs*) data among biomes in our meta-analysis (i.e., tropical forests, temperate forests, boreal forests, croplands, grasslands, and others) and those in the same biome among different meta-analyses (i.e. Janssens *et al.*, 2010; Liu & Greaver, 2010; Lu *et al.*, 2011; and this study). If the number of data points used for assessing RR_{++} of a concerned variable was larger than 20, we calculated 95% confidence interval (CI) as $RR_{++} \pm 1.96\ S\ (RR_{++})$. When the number was lower than 20, we used bootstrapping method to obtain the lowest and highest 2.5% values as our bootstrap confidence based on 5000 iterations (Adams *et al.*, 1997; Janssens *et al.*, 2010). In case, the 95% CI did not overlap with zero, a significant N-induced response was considered. The percentage changes of variables caused by N addition were measured by [exp (RR_{++})−1] × 100%. The frequency distribution of individual response ratio (*RR*) was tested by Normal-test and described by a Gaussian function using equation (6) in SigmaPlot software (Systat Software Inc., CA, USA).

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

where x is *RR* of *Rs*; y is the frequency (i.e., number of *RR* values); α is a coefficient showing the expected number of *RR* values at $x = \mu$; and μ and σ are mean and variance of the frequency distributions of *RR*, respectively.

The effects of biome types, forms of fertilizers and their interactions on the *RR* of variables were examined by UNIANOVA. The correlations of *RR* among different variables were examined by correlation analysis. The multivariate effects of environmental conditions and fertilization regime on *RR* (*Rs*) were analyzed by stepwise regression.

Table 1 Stepwise linear regression of response ratio of soil respiration [*RR* (*Rs*)] with environmental conditions and N-fertilization regimes, including latitude(LAT), mean annual temperature (MAT), mean annual precipitation (MAP), experimental duration (DUR), and N application rate (Rate), frequency of N application per year (FREQ) and cumulative N amount in experimental duration (Amount). Only four variables: MAT, DUR, MAP, and FREQ were selected in the analysis of stepwise linear regression, indicating that the only four covariates interactively affected responses of *Rs* to N addition and MAT was the most important factor

Equation	R^2	*P*-value
RR (*Rs*) = 0.010MAT-0.151	0.126	<0.001
RR (*Rs*) = 0.010MAT-0.003DUR-0.130	0.146	<0.001
RR (*Rs*) = 0.013MAT-0.004DUR-0.000039MAP-0.112	0.159	<0.001
RR (*Rs*) = 0.013MAT-0.004DUR-0.000038MAP-0.00046FREQ-0.113	0.169	<0.001

Results

Effects of N addition on Rs and its components

Despite of the different types of biomes addressed in the previous three meta-analyses (Table S1), their distribution of individual response ratios of *Rs* [*RR* (*Rs*)] in each biome did not display the significant difference compared with that in our study (Fig. S1). Our results show that the weighted response ratio of *Rs* [RR_{++} (*Rs*)] across all the biomes with 257 pairs of comparisons was 0.019 ± 0.004 ($P < 0.01$, Figs 2a and d). When the area and averaged rate of *Rs* in each biome were taken into account in terms of weight, the global terrestrial RR_{++} (*Rs*) increased to 0.025 ± 0.008 (Fig. 2d, $P < 0.01$), which was slightly higher than the weighted *RR* (*Rs*). The *Rs* in forests (including tropical, temperate, and boreal) decreased by 1.44% under N addition ($P < 0.05$), while it increased by 7.84% and 12.41% in grasslands and croplands, respectively ($P < 0.01$, Figs 2a and d). The 95% response ratios of *Rs* fell within a range from −0.628 (2.5 percentile) to 0.321 (97.5 percentile) in forests, −0.284 to 0.614 in croplands, and −0.379 to 0.839 in grasslands. Among forests, N addition significantly decreased *Rs* by 16.00% and 2.66% in boreal and tropical forests ($P < 0.05$), respectively, but did not affect *Rs* in temperate forests.

On average, N addition significantly stimulated autotrophic respiration (*Ra*) by 22.38% ($P < 0.05$) but reduced heterotrophic respiration (*Rh*) by 12.79% ($P < 0.01$, Figs 2e and f) across all studies. The weighted response ratios of *Ra* [RR_{++} (*Ra*)] were significantly different among the biomes ($P < 0.05$, Fig. 2e). N addition did not significantly affect *Ra* in forests, while croplands and grasslands displayed posi-

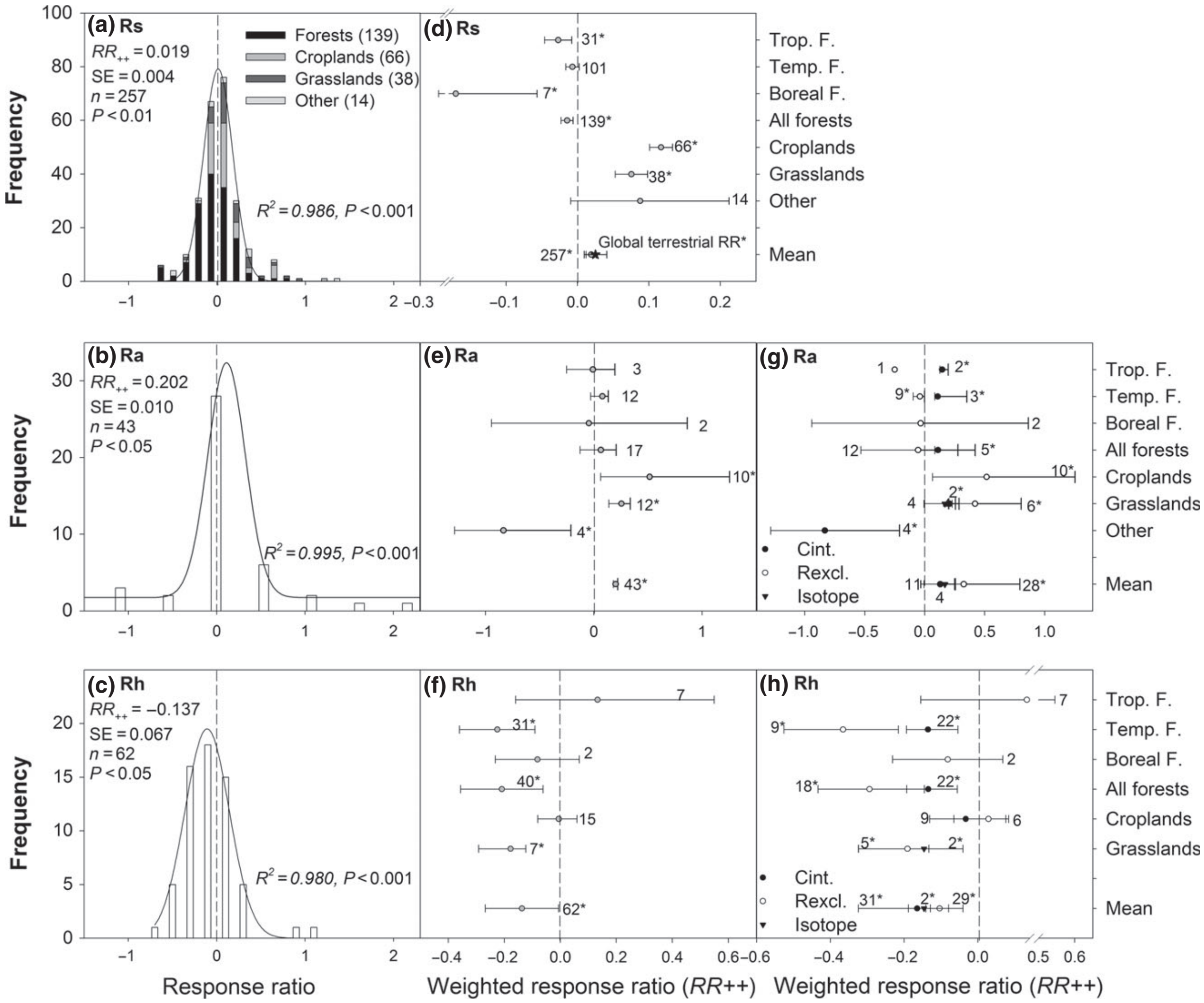

Fig. 2 Frequency distributions of response ratios (*RR*) of soil respiration (*Rs*, panel a), autotrophic respiration (*Ra*, panel b), and heterotrophic respiration (*Rh*, panel c) in all biomes. The values of R2 and P in the lower right of panels a, b, and c were the results of Gaussian regression. The *P* value of normal distribution test of [*RR* (*Rs*)], [*RR* (*Ra*)] and [*RR* (*Rh*)] were 0.1089, 0.8623, and 0.8001, respectively. Biomes in panel A were separated into forests, croplands, grasslands, and others. Panels d, e, and f show weighted response ratios (RR_{++}) of Rs (d), *Ra* (e), and *Rh* (f) in different biomes. Panels g and h show (RR_{++}) of *Ra* (g) and *Rh* (h) from different methods: component integration (Cint.), root exclusion (Rexcl.), and isotopic approaches (Isotope), which were based on the separation methods in Hanson et al. (2000). The symbol in panel D represent global terrestrial [RR_{++} (*Rs*)] to N addition weighted by the area and mean Rs in each biome. The numbers above the symbols in panels d, e, f, g, and h were the amount of data points, symbols * after the number indicated statistical significance ($P < 0.05$). If the number of data points is lower than 20, we calculated the confidence interval (CI) using bootstrapping approach (5000 iterations). If the number is larger than 20, we calculated CI based on (RR_{++}) and [*S* (RR_{++})]. The error bars indicated 95% CI. If it did not overlap with zero, a significant N -induced response was considered. Trop. F.: Tropical forests; Temp. F.: Temperate forests; Boreal F.: Boreal forests.

tive responses of *Ra* and wetlands had negative one. By contrast, *Rh* exhibited relatively consistent negative responses under N addition among biomes except for croplands, tropical and boreal forests with nonsignificant changes (Fig. 2f). Methods of partitioning *Rs* (i.e., component integration, root exclusion, and isotopic approaches) did not induce significant differences in the responses of *Ra* or *Rh* to N addition (Figs 2g and h), except that *Ra* from root exclusion and component integration showed the opposite responses in temperate forests (Fig. 2g).

Control of N addition on Rs

The response ratios of *Rs* [*RR* (*Rs*)] across all the studies were significantly correlated with climatic conditions including mean annual temperature (MAT), mean annual precipitation (MAP), and latitude (LAT) (Table S2). However, only MAT and MAP were accepted by the best regression model as well as two forcing variables, frequency of N application per year (FREQ), and experimental duration (DUR) (Table 1). Their relative contributions to *RR* (*Rs*) were 0.466, −0.143, −0.105 and −0.167 for MAT, MAP, FREQ, and DUR, respectively. When MAT was less than or equal to 15 °C with the exclusion of the data from tropical forests, the positive correlation between MAT and *RR* (R_S) to N addition was more significant ($R^2 = 0.15$, Fig. 3b). The second most significant factor responsible for the *RR* (*Rs*) was DUR. The *RR* (*Rs*) exhibited a downward trend with increasing DUR across all types of biomes ($R^2 = 0.033$, $P = 0.010$), and the most significant correlation between *RR* (*Rs*) and DUR was found in forests (Fig. 3a, Table 1).

Meanwhile, FREQ and MAP also affected the *RR* (*Rs*) to some extent. Associated responses of soil organic C (SOC) and belowground biomass [e.g., microbial biomass C (MBC), root biomass (RB), and fine root biomass (FRB, only in forests and croplands)] under N addition all displayed significant correlations with *RR* (*Rs*) ($P < 0.01$, Figs 4a–d). The responses of MBC and RB to N addition exhibited a significant correlation with *RR* (*Rh*) and *RR* (*Ra*), respectively (Figs 4d and f). However, the rate of N addition (Rate) did not correlate with *RR* (*Rs*) for all types of biomes (Fig. 5, Table 1), and even, in the individual studies with multiple rates of N addition, *RR* (*Rs*) showed diverse patterns with increasing Rate (Fig. S2).

Discussion

Responses of Rs and its components to N addition in different biomes

N deposition affected soil respiration (*Rs*) and its components (*Ra* and *Rh*) with different magnitudes and even directions in a large number of individual studies (Luo & Zhou, 2006; Allison *et al.*, 2008; Mo *et al.*, 2008). Using a meta-analysis approach, we found that the mean *Rs* was slightly stimulated by N addition compared with the controls across all the biomes ($P < 0.01$, Figs 2a and b), which was similar to the results from Lu *et al.* (2011) and Liu & Greaver (2010) with all biomes and non-agricultural ecosystems, respectively. However, in temperate forests, our results showed less negative effect of N addition on *Rs* compared with that from Janssens *et al.* (2010), which may partly result from the differences of data samples (101 vs. 57) and the inclusion of few tropical and boreal forests in the later (e.g., Allison *et al.*, 2008).

Different biomes exhibited diverse responses of *Rs* to N addition (Fig. 2d). The negative responses of *Rs* to N addition in forests, especially in tropical and boreal forests, significantly differed from the positive responses in grasslands and croplands (Fig. 2d). The difference can be interpreted by the synthesized responses of *Ra* and *Rh* to N addition. N addition significantly increased *Ra* in croplands and grasslands, while did not affect it in forests (Fig. 2e). Responses of *Ra* to N addition were closely correlated with changes in root biomass (RB, Fig. 4f). In water-limited grasslands (Lauenroth *et al.*, 1978), plants often allocate a greater proportion of newly assimilated products to roots with a larger root/shoot ratio (Mokany *et al.*, 2006) compared with that in forests (Evans, 1989; Ripullone *et al.*, 2003), resulting in the less negative response of root C/N to N addition in grasslands (−0.145 ± 0.023) compared with that in forests (−0.360 ± 0.020, Fig. S3). Under N addition, the photosynthesis often significantly increased, which may induce greater demand for water and/or other nutrients in grasslands (Poorter & Nagel, 2000; Zhou *et al.*, 2009), and then more organic matter and energy were invested to roots for maintaining soil/root water transport and mineral absorption compared with those in forests (Hogberg *et al.*, 2001; Mokany *et al.*,

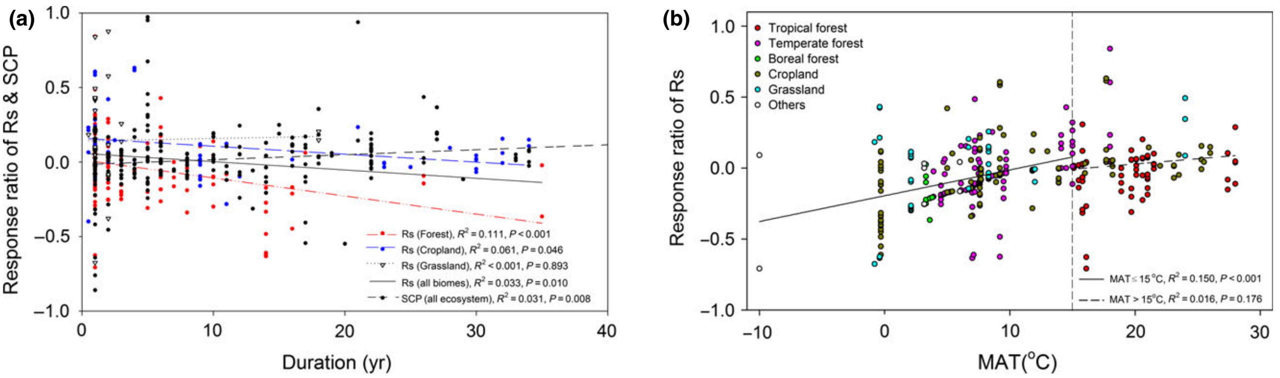

Fig. 3 Relationships of response ratios (*RR*) of soil respiration (*Rs*) or soil carbon pool (SCP) with experimental duration of N addition (Duration, panel a) and mean annual temperature (MAT, panel b).

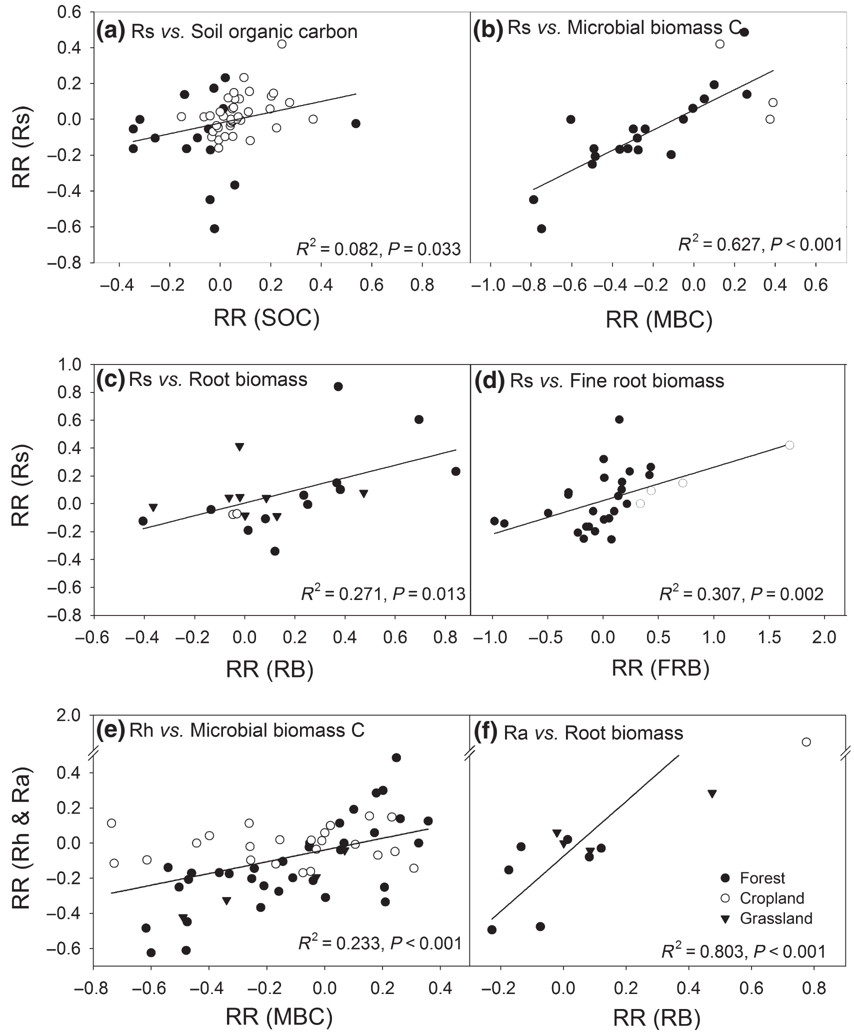

Fig. 4 Relationships of response ratio (*RR*) of soil respiration (*Rs*) with RR of soil organic carbon pool (SOC, panel a), microbial biomass C (MBC, panel b), root biomass (RB, panel c) and fine root mass (FRB, panel d), and the relationships of *RR* of soil heterotrophic respiration (*Rh*) with *RR* (MBC) (e), and *RR* of soil autotrophic respiration (*Ra*) with *RR* (RB) (f), respectively, in forests, croplands and grasslands.

2006; Wang *et al.*, 2007; Schindlbacher *et al.*, 2009). The largest negative response of *Ra* was found in wetlands (other in Fig. 2e), because a lower root/shoot ratio induced by N addition suppressed whole-root oxygen consumption, resulting in a significant depression of *Ra* (Nakamura *et al.*, 2010).

In contrast, N addition induced relatively consistent negative responses of *Rh* to N addition among biomes except no significant responses in croplands, tropical and boreal forests (Fig. 2f). N-induced decrease in *Rh* may arise from an array of inhibitions for microbial decomposition through the change in fundamental gene expression (e.g. reduced expression of ligninolytic genes, Edwards *et al.*, 2011), shift in community composition (Gallo *et al.*, 2004; Zak *et al.*, 2011) and decrease in microbial biomass (Treseder, 2008; Lu *et al.*, 2011). Meanwhile, N addition probably depresses ‘microbial N mining’ process whereby some microbes use labile substrates to require N from decomposition of recalcitrant organic matter at low-N availability (Fontaine *et al.*, 2003; Michel & Matzner, 2003; Craine *et al.*, 2007). In addition, most studies have found that litter decomposition was often inhibited by current N addition rate (commonly >5 kg N ha^{-1} yr^{-1}, Carreiro *et al.*, 2000; Gallo *et al.*, 2004; Knorr *et al.*, 2005) through compositional shifts in saprotrophic microbial communities (e.g., a decrease in fungal/bacterial ratio, Gallo *et al.*, 2004) and change in enzyme activity (e.g., a lower lignin-degrading enzyme production, Frey *et al.*, 2004). Although aboveground litter mass and quality (e.g., the

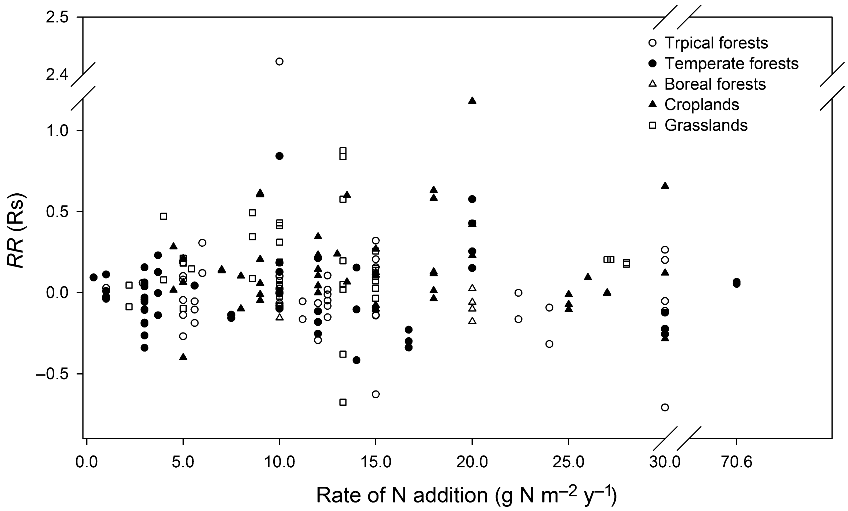

Fig. 5 The relationship between rates of N addition and response ratios (*RR*) of soil respiration (*Rs*).

significant decreases of C/N ratio, especially in forests and croplands in Fig. S3) increased significantly under N addition ($P < 0.05$), the decrease in microbial biomass might largely limit litter decomposition and then *Rh* and SOM turnover in most biomes (Berg & Meentemeyer, 2002; Xiao *et al.*, 2007). In croplands, the removal of aboveground biomass might decrease C inputs to soil, while soil tillage might stimulate decomposition of belowground litter and soil organic matter (SOM) (Reicosky, 1997; Reicosky *et al.*, 1997; Baker *et al.*, 2007), probably resulting in no change in *Rh* by N addition, although microbial biomass decreased (Lu *et al.*, 2011). Thus, compared with the similar responses of *Rh* to N addition among different biomes (Fig. 2f), the diverse responses of *Rs* depended on that of *Ra* to a greater extent (Figs 2d and e).

Relationships of RR (Rs) with associated C pools

In spite of different effects of N addition on belowground C pools among biomes (Lu *et al.*, 2011), the responses of SOC, microbial biomass C, root and fine root biomass to N addition all displayed significant positive correlations with the response ratio (*RR*) of *Rs* (Fig. 4). It is generally believed that *Ra* mainly results from respiratory CO_2 release of roots, which is used for root growth and maintenance. *Rh* is largely from litter and SOC decomposition due to microbial activities. Therefore, root/fine root biomass is often closely correlated with *Ra* (Fig. 4f, Lee & Jose, 2003; Zhu *et al.*, 2009), while soil microbial biomass, SOC, and litter mass are widely demonstrated to tightly relate with *Rh* (Fig. 4e, Yoshitake *et al.*, 2007; Iqbal *et al.*, 2010), inducing their significant correlations with *Rs* (Fig. 4, Haynes & Gower, 1995; Phillips & Fahey, 2007).

Spatial variation of Rs responses to N addition affected by MAT

Our results showed that when MAT was less than 15 °C, *RR* (*Rs*) had a more significant positive correlation with MAT ($R^2 = 0.15$, Fig. 4b), but the correlation was not significant when MAT was higher than 15 °C, in which the data were mainly from tropical forests (Fig. 4b). Nitrogen addition usually stimulates plant production in most terrestrial ecosystems (Reich *et al.*, 1995; Lu *et al.*, 2011), increasing organic matter input to soil and hence the stimulation of *Rs* (Davidson *et al.*, 2004). However, tropical forests are often P-limited rather than N-limited (Davidson *et al.*, 2004; Bardgett & Wardle, 2010) as well as some temperate forests in high MAT (Ouyang *et al.*, 2008; Liu *et al.*, 2010), resulting in insignificant correlation between *RR* (*Rs*) and MAT.

The temperature sensitivity of *Rs* in the treatment group of N addition in these N-limited biomes was significantly higher (the weighted response ratio of Q_{10} was 0.051 ± 0.018, $P < 0.05$, $N = 21$) than that in the control (also see Deng *et al.*, 2009; Ding *et al.*, 2010; Jin *et al.*, 2010). If we use the formula ($Rs = R_0\, e^{bt}$) to estimate temperature sensitivity of *Rs* and assume that R_0 is equal under both treatment and control groups, *RR* (*Rs*) should be $(b_n - b_c) \times t$, Where b_n and b_c are temperature sensitivity in the treatment and control groups, and *t* is MAT. Nitrogen addition therefore stimulates CO_2 release from soil with larger MAT in biomes at the low range of MAT (Waldrop & Firestone, 2004; Von Luetzow & Koegel-Knabner, 2009). Moreover, MAT, as one of most important environmental variables, can explain a significant part of the observed variability in annual *Rs* on a global scale (Bond-Lamberty & Thomson, 2010). Thus, N addition may amplify the spatial variability of *Rs* largely affected by MAT, resulting in the positive relationship between MAT and *RR* (*Rs*), especially in those areas at the low range of MAT.

Temporal variation of Rs responses to N addition affected by fertilization regime

Fertilization regime (e.g., forms of N fertilizers and experimental duration) has widely been demonstrated to affect plant performance and soil microbial activities (Hossain *et al*., 1995; Kautz *et al*., 2004). Despite of plant preferences for specific forms of N fertilizers in different biomes (Harrison *et al*., 2007), N forms did not significantly influence the responses of *Rs* to N addition across all the biomes (data not shown, also see Liu & Greaver, 2010; Lu *et al*., 2011), which may be ascribed to the ability of converting one form of reactive N to another in soil (Galloway, 1998). Furthermore, the rates of N addition (Rate) also exhibited no significant correlation with *RR* (*Rs*) (Fig. 5), which may result from the effects of confounding factors among study sites, such as precipitation levels, soil physical conditions, and plant species compositions (Braun *et al*., 1999; Bobbink *et al*., 2010). For example, soil may leak a large amount of N out of the system and weaken its effects on *Rs*, especially at high levels of N addition, under high precipitation, and/or at high-porosity soils (Sifola & Postiglione, 2003; Harpole *et al*., 2007).

Both experimental duration (DUR) and the frequency of N addition per year (FREQ), however, significantly affected the *RR* (*Rs*) across all the biomes with a larger effect on *RR* (*Rs*) for DUR than FREQ (Fig. 3a, Table 1). Nitrogen addition commonly stimulates plant growth initially (Hogberg *et al*., 2006) and hence C input to soil, resulting in significant increase in *Ra* and then *Rs* (Figs 2d and e). Under long-term N addition, the increase in *Rs* may be depressed gradually (Nohrstedt, 2001), likely due to the changes in microbial community structure (Treseder, 2008) and soil conditions (e.g., decreased soil pH and exchangeable base cation and increased exchangeable Al, Hogberg *et al*., 2001; Phoenix *et al*., 2012). Interestingly, the trends of *RR* (*Rs*) with increasing DUR were different among biomes (Fig. 3a), probably caused by the difference of management practice (Merino *et al*., 2004). For example, aboveground biomass in croplands and grasslands was often removed due to harvest or grazing, resulting in their slower decrease or no change of *RR* (*Rs*) with DUR in comparison with that in forests (Fig. 3a).

Limitations of experimental methods

Although the meta-analysis provides a statistical evaluation of the central tendency of ecosystem processes with the weighted response ratios across experiments, the overall effects of N addition on *Rs* and its components (*Ra* and *Rh*) may be synthesized with large uncertainties due to the inherent limitations of the methodologies used in such analysis and/or of experimental manipulations. First, most experiments of N addition compiled in our meta-analysis applied spray of N solution to the floor of ecosystems to simulate N deposition, particularly in forests, but neglected natural N deposition in the canopy, where N retention occurs and influences the canopy processes (Gaige *et al*., 2007). In addition, current levels of N addition were much higher than natural deposition (Gaudnik *et al*., 2011). Therefore, the evaluation of the effects of N addition may be biased to some extent, especially for forests. Some of new approaches need to be exploited to simulate realistic N deposition (e.g., spraying N solution from above the canopy by helicopter and towers) in the future study.

Second, the differences of the methods to partition *Rs* into two components (*Ra* and *Rh*, e.g., component integration, root exclusion, and isotopic labeling approaches, Hanson *et al*., 2000) may also lead to some uncertainties in assessing the responses of *Ra* and *Rh* to N addition. For example, component integration with laboratory incubation excludes the constraints of environmental conditions (e.g., precipitation) and their potential interactions with SOC decomposition, which probably induce a less significant inhibition of *Rh* under N addition (Fig. 2h, Risk *et al*., 2008). In addition, the mean responses of *Ra* to N addition in tropical and temperate forests from component integration (Cint.) were positive compared with those from root exclusion (Rexcl.) with a negative one (Fig. 2g). In tropical forests, there were only one point for Rexcl and two points for Cint. Caution should be made to compare their results due to the data limitation (Figs 2g–h). In temperate forests, *Rh* from Rexcl were directly measured and often overestimated, resulting in underestimation of *Ra*, which was subtracted from *Rs*. For Cint method, researchers often directly measured the specific rate of roots and root biomass to calculate the rate of *Ra* (Luo & Zhou, 2006). N-induced increase in root biomass (35.23% ± 2.96%) may cause a greater estimation of RR_{++} (*Ra*) in temperate forests. With less soil and root disturbance, isotope approaches are more appropriate to separate *Ra* and *Rh* from *Rs*, although the cost is relatively high (Hanson *et al*., 2000).

Implications for land surface models and future experiments

Our results from the meta-analysis of 295 individual studies may provide some insights into how soil respiration (*Rs*) and its components respond to atmospheric N deposition. Thus, our study will offers recommendations for development and improvement of land surface models as well as design of manipulative experiments in the future, at least in three aspects. First, the effects of N addition on *Rs* and its components (i.e., *Ra* and *Rh*) were different among biomes with diverse magnitudes and even directions (Fig. 3). The mean responses of *Rs* and its components to N addition in each biome (i.e., weighted response ratios) can be generalized for modeling to provide the useful information to compare with the modeled response to natural N deposition (Piao *et al*., 2013). However, in current land surface models, the responses of ecosystem C processes to N deposition are considered to be consistent among biomes (Lamarque *et al*., 2005). Although the modeling results provide global-scale responses to N deposition, no much information on ecosystem-scale responses is offered. Thus, future land surface models need to differentially treat the effects of atmospheric N deposition in different biomes to forecast the feedback of terrestrial ecosystems to N deposition.

Second, the response ratios of *Rs* [*RR* (*Rs*)] to N addition were positively correlated with MAT at spatial scale at the low range (≤15 °C) but did not exhibit significant correlation with MAT in warmer biomes (>15 °C, Fig. 3b). Furthermore, the sites with suitable climate for plant growth commonly endure high human population and have a relatively higher anthropogenic N fertilization. As a consequence, the natural N deposition may increase in the future (Janssens *et al*., 2010). The spatial difference in *RR* (*Rs*) and natural level of N deposition indicates the necessity of conducting transect studies of experimental N deposition along the MAT gradient to carefully examine the effects of N addition, when other environmental variables (e.g. precipitation and soil) do not affect the interpretation of spatial patterns (Jenny, 1980; Austin & Sala, 2002). Additionally, the relationships can be incorporated into land surface models to improve the prediction about N-regulated feedback of ecosystem C cycle to climate system if they are validated in transect and other studies.

Third, the responses of *Rs* to N addition [*RR* (*Rs*)] were negatively correlated with experimental duration at temporal scales (Fig. 5a). It is generally granted that the long-term experiments with lower level of N addition may better reflect the effects of natural N deposition. Those studies with long-term N addition (up to 35 years), however, may also endure other environmental changes (e.g., temperature, CO_2 concentration, and precipitation, Ollinger *et al*., 2002; Pregitzer *et al*., 2008). Thus, current estimations on effects of N addition may, to a certain degree, be confounded by other multiple environmental factors. Although some short-term (<10 years, e.g. Johnson *et al*., 1997; Norby *et al*., 2000; Villar-Salvador *et al*., 2013) two- or three-factor experiments have been conducted, well-designed long-term experiments with multiple global change factors (e.g., elevated CO_2, warming, and altered precipitation) are necessary to better capture complex interactive processes and to provide inputs and validation for theoretical and model development.

Acknowledgements

The authors thank the three anonymous reviewers for their insightful comments and suggestions. This research was financially supported by the National Natural Science Foundation of China (Grant No. 31070407, 31370489), the Program for Professor of Special Appointment (Eastern Scholar) at Shanghai Institutions of Higher Learning, 2012 Shanghai Pujiang Program (12PJ1401400), and 'Thousand Young Talents' Program in China.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Data S1. The list of 295 papers from which the data were extracted for this meta-analysis.
Data S2. Logarithm of *RR* (ln*RR*) and weighting factor (w_{ij}, in parentheses) of 13 variables extracted from each of the papers.
Figure S1. Distribution of response ratios of soil respiration [*Ln* (Rs_t/Rs_c)] in previous meta-analyses (i.e., Janssens *et al.*, 2010; Liu & Greaver, 2010; Lu *et al.*, 2011) and this meta-analysis in different biomes. The data distributions in this analysis displayed nonsignificant difference from those in the previous studies (i.e., Janssens *et al.*, 2010; Liu & Greaver, 2010; Lu *et al.*, 2011) in same biomes. The lowercase letters indicate statistically significant differences of data distribution among the biomes in this meta-analysis, showing that data distribution in tropical and temperate forests was significantly different from that in croplands and grasslands.
Figure S2. Response ratios (*RR*) of *Rs* (a and b) and *Rh* (c and d) under different rates of N addition in multilevel studies. In individual studies, the patterns of *RR* (R_S) were inconsistent with increasing levels of N addition. (Red: the sites exhibited a larger *RR* (*Rs*) in higher levels than that in lower one, blue: the sites were a smaller *RR* (*Rs*) in higher levels than that in lower one, black: the sites were the largest *RR* (*Rs*) in middle levels of N addition).
Figure S3. Weighted response ratios (RR_{++}) of C:N ratio (C/N) in soil (soil C/N, a), aboveground biomass (aboveground biomass C/N, b), litter mass (litter C/N, c), root biomass (root C/N, d) and microbial biomass (microbial C/N, e) in forests, croplands and grasslands.
Table S1. Summary of three recent meta-analyses on the effects of N addition on soil respiration (*Rs*).
Table S2. Correlation analysis among environmental conditions [including latitude (LAT), mean annual temperature (MAT), mean annual precipitation (MAP)], N-fertilization regimes [including experimental duration (DUR), N application rate (Rate), frequency of N application per year (FREQ), and cumulative N amount in experimental duration (Amount)], and response ratio of *Rs* [*RR* (*Rs*)]. Correlation coefficients are presented in the upper-right triangle and *P* values in the lower left triangle.