Responses of ecosystem carbon cycle to experimental warming: a meta-analysis

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Abstract. Global warming potentially alters the terrestrial carbon (C) cycle, likely feeding back to further climate warming. However, how the ecosystem C cycle responds and feeds back to warming remains unclear. Here we used a meta-analysis approach to quantify the response ratios of 18 variables of the ecosystem C cycle to experimental warming and evaluated ecosystem C-cycle feedback to climate warming. Our results showed that warming stimulated gross ecosystem photosynthesis (GEP) by 15.7%, net primary production (NPP) by 4.4%, and plant C pools from above- and belowground parts by 6.8% and 7.0%, respectively. Experimental warming accelerated litter mass loss by 6.8%, soil respiration by 9.0%, and dissolved organic C leaching by 12.1%. In addition, the responses of some of those variables to experimental warming differed among the ecosystem types. Our results demonstrated that the stimulation of plant-derived C influx basically offset the increase in warming-induced efflux and resulted in insignificant changes in litter and soil C content, indicating that climate warming may not trigger strong positive C-climate feedback from terrestrial ecosystems. Moreover, the increase in plant C storage together with the slight but not statistically significant decrease of net ecosystem exchange (NEE) across ecosystems suggests that terrestrial ecosystems might be a weak C sink rather than a C source under global climate warming. Our results are also potentially useful for parameterizing and benchmarking land surface models in terms of C cycle responses to climate warming.

Key words: C-climate feedback; C efflux; C influx; C pools; global warming; terrestrial ecosystems.

Introduction

Global warming induced by the buildup of CO_2 and other greenhouse gases in the atmosphere is expected to increase global land surface temperature by 1.1–6.4°C by the end of this century (IPCC 2007). Climate warming may strongly impact C dynamics by altering both the structure (Petchey et al. 1999, Walker et al. 2006) and functioning (Luo et al. 2001, Nemani et al. 2003, Bond-Lamberty and Thomson 2010) of terrestrial ecosystems. An altered ecosystem C cycle may exhibit a positive or negative feedback to global warming, which in turn augments or diminishes warming effects. It is well established that plant growth and net primary production (NPP) are usually limited by water (Chapin et al. 2002), nitrogen availability (Vitousek and Howarth 1991, Lu et al. 2011*a*), and air temperature (Saugier et al. 2001, Lin et al. 2010) in most terrestrial ecosystems. However, it is still uncertain as to whether or not plant C accumulation leads to a positive or negative feedback to climate warming (Cao and Wood-

ward 1998, Cox et al. 2000, Melillo et al. 2002, Davidson and Janssens 2006, Smith and Fang 2010). Therefore, more accurate projections of future C cycling require a fuller understanding of the responses of the ecosystem C cycle to climate warming.

Considering that temperature influences almost all ecosystem biogeochemical processes, such as production (Ciais et al. 2005), decomposition (Melillo et al. 2002, de Dato et al. 2010), and nutrient cycling (Melillo et al. 2011), most of these processes may be potentially affected by climate warming and eventually regulate terrestrial C feedback to climate warming. Terrestrial C-cycle feedback to climate warming is negative if warming results in net C storage in ecosystems but positive if warming leads to net C release from ecosystems (Luo 2007, Luo et al. 2009). Current coupled C-climate models all predict a positive feedback between terrestrial C cycle and climate warming due to decreased net primary production (NPP) and/or increased respiratory C release under climate warming (Friedlingstein et al. 2006). Those modeling predictions offer interesting hypotheses on future states of ecosystems and climate, which have to be carefully examined through manipulative experiments (Moorcroft 2006, Luo et al. 2011). Although extensive individual studies have investigated

warming effects on ecosystem processes, especially in low-stature ecosystems (e.g., grasslands and tundra), how the C-cycle feedbacks to warming remain elusive (Ciais et al. 2005, Beier et al. 2009, Luo et al. 2009). Data integration or meta-analysis is a useful approach to combining available data from different sources to examine terrestrial C-cycle feedback to global warming with a unified view.

Previous studies have shown that many ecosystem biogeochemical processes are significantly affected by temperature manipulations. For example, experimental warming significantly increases leaf and ecosystem photosynthesis, aboveground NPP, and biomass accumulation as well as soil respiration (Rustad et al. 2001, Lin et al. 2010, Wu et al. 2010). Plant phenology, reproduction, physiology, and chemistry are also influenced considerably by climate warming (Arft et al. 1999, Peñuelas and Filella 2001, Dormann and Woodin 2002). Moreover, plant functional types are found to be one of the major determinants of plant biomass under experimentally manipulated warming condition, with woody species experiencing significantly greater stimulation than herbaceous ones (Lin et al. 2010). However, compared to the aboveground C processes, it still remains unclear as to how the belowground C dynamics of ecosystems (e.g., litter decomposition, litter, root and soil C contents, microbial biomass C, and dissolved organic carbon [DOC]) generally responds to experimental warming and what the differences are among biomes/ecosystem types. For instance, soil C content in mineral soil exhibits mixed trends, either increasing (Welker et al. 2004), decreasing (Saleska et al. 2002), or nonsignificant change (Luo et al. 2009) under experimental warming. Responses of microbial biomass C and litter decomposition to manipulative warming are also highly variable (van Meeteren et al. 2008, Andresen et al. 2009, Belay-Tedla et al. 2009, Cheng et al. 2010). Plant root growth and biomass in mineral soil could be significantly stimulated (Andresen et al. 2010) or inhibited (Björk et al. 2007) under elevated temperature. Additionally, in short-term studies which were conducted at the seedling stage or during the early growth stages of tree plants (Usami et al. 2001, Yin et al. 2008), the responses of plant growth from both above- and belowground parts may differ from those observed in natural forests (Rasmussen et al. 2002). The highly mixed results observed in diverse individual studies are unlikely to offer an integrated understanding of warming effects on belowground C dynamics. This greatly limits our ability to probe the ecosystem C-cycle feedbacks to global climate warming. Therefore, a general pattern of ecosystem C dynamics and a comparison among different types in response to experimental warming are necessitated to improve land surface models for the projections of future warming-induced ecological consequences.

A meta-analysis, which conducts statistical calculation and comparison to elicit the integrated results of

independent studies (Gurevitch and Hedges 1999), has been increasingly conducted in current global change research. In this study, we compiled data from individual studies under experimental warming across various ecosystems, following the method developed by Hedges et al. (1999), to quantitatively evaluate the central tendency of the warming effects on ecosystem C pools and fluxes. Specifically, this study was aimed to: (1) quantify the responses of C fluxes (C influx and efflux) to experimental warming, (2) investigate the responses of C pool sizes (including plant, litter, microbial biomass, mineral soil, and dissolved organic C) to experimental warming, (3) examine whether ecosystem types and environmental factors influence the responses of ecosystem C fluxes and pools to warming, and (4) evaluate ecosystem C-cycle feedback to climate warming.

METHODS

Data compilation

Publications (Appendix A) that studied C dynamics under experimental warming were collected by searching Web of Science (1900–2010) and China Knowledge Resource Integrated Database (*available online*).[5,6] The compiled database contained 18 variables associated with the C cycle, including C pools, fluxes, and other related parameters in response to experimental warming (Supplement). To avoid publication bias, the following five criteria were set to select the proper observations. (1) Treatments with warming and control were conducted in field experimental studies and at least one of our considered variables was reported. (2) The warming and control plots were established to have the same ecosystem types, dominant plant species, and soil types. The studies with temperature gradients were excluded. (3) The warming method, magnitude, experimental duration, and soil depth were clearly recorded and the measurements of variables in the control and warmed groups were performed at the same temporal and spatial scales. (4) To avoid short-term noise, experiments whose durations were less than one growing season were excluded. (5) The means, standard deviations (or standard errors), and sample sizes of the chosen variables were directly provided or could be calculated from the studies. Most of the 130 studies were conducted in North America and Europe (Appendix B: Fig. B1). Given that meta-analysis requires that the compiled observations should be independent (Hedges et al. 1999), the measurement made for the latest sampling was used if more than one measurement at different times were available from the same study. Also, measurements under different warming magnitudes and ecosystem types were considered as independent observations if more than one warming magnitude or

[5] http://apps.webofknowledge.com/
[6] http://www.cnki.net/

ecosystem type were available from the same study (Liu and Greaver 2009, Lu et al. 2011*b*). Considering that the logarithm of the response ratio (Eq. 1) could only be calculated for observations with positive values, negative net ecosystem exchange (NEE) data (seven of 18 observations) were excluded from this meta-analysis based on the results that relative changes in NEE for negative NEE data were not significantly different from those for all NEE data (Liu and Greaver 2009). Therefore, the exclusion of the negative NEE data may not influence the general pattern of the response of NEE to experimental warming.

The compiled database included C pool (i.e., plant C from above- and belowground parts, litter C, microbial biomass C, soil C, and dissolved organic C [DOC]), C fluxes (i.e., NPP, litter decomposition, and soil respiration), and other related parameters (i.e., soil temperature, soil water content, and soil pH). The plant C pools from above- and belowground parts were determined either by plant biomass or by plant C content. Litter C quantity and quality were described by litter C stock and litter C:N ratio. The soil C pool was determined by soil C content or C storage. C flux data were obtained from the studies that directly reported net photosynthetic rate (NPR, leaf level measurement), gross ecosystem photosynthesis (GEP, ecosystem level measurement), net primary productivity (NPP), the average or cumulative litter mass loss, soil respiration (including autotrophic and heterotrophic respiration), NEE, and ecosystem respiration in response to experimental warming.

Environmental and forcing factors may confound the responses of C dynamics to experimental warming, so the variables were further categorized into four groups: warming method (greenhouse and/or closed chamber, infrared heater, open top chamber (OTC), reflective curtain, soil heating cable), warming magnitude (<1°, 1–3°, >3°C; see Plate 1), experimental duration (0–5, 5–10, >10 yr), and ecosystem type (forest, shrubland, grassland, tundra, wetland). In addition, site location, latitude, soil depth, mean annual temperature (MAT), and mean annual precipitation (MAP) were also obtained in our database. MAT and MAP of each site were either extracted from the publications or, in case it was not described in the publication, from the global database with site location coordinates (*available online*).[7]

Analyses

In this study, we employed a meta-analysis approach and calculated the response ratio (RR) to reflect the effects of experimental warming on terrestrial ecosystem C pools and fluxes. RR is defined as the ratio of the mean value of a given variable in the treatment group ($\bar{X}_t$) to that in the control group ($\bar{X}_c$), and was used as the measure of the warming effect on that corresponding variable (Eq. 1). Thus, RR is an effective index of effect

[7] http://www.worldclim.org/

size for many manipulative experiments, and the logarithm of RR is a suitable measure for meta-analyses as its bias is small and its sampling distribution is approximately normal (Hedges et al. 1999):

$$\ln \mathrm{RR} = \ln(\bar{X}_t/\bar{X}_c) = \ln(\bar{X}_t) - \ln(\bar{X}_c). \quad (1)$$

More specifically, the mean and standard deviation (S) or standard error with sample size of each treatment were extracted to calculate the logarithm of RR, variance (v), weighting factor (w_{ij}), the weighted response ratio (RR_{++}), and the 95% confidence interval (CI) of RR_{++} for the purpose of statistical tests (Eqs. 2–7) (Gurevitch and Hedges 1999, Hedges et al. 1999, Luo et al. 2006). We calculated a weighted response ratio (RR_{++}) from individual RR_{ij} ($i = 1, 2, \ldots, m$; $j = 1, 2, \ldots, k_i$) by giving greater weight to the studies whose estimates have greater precision (smaller v) so that the precision of the combined estimate and the power of the tests can be improved (Gurevitch and Hedges 1999). Here m is the number of groups (e.g., different ecosystem types), k_i is the number of comparisons in the ith group. It should be noted that Eq. 5 may lead to inaccurate estimation when the sample sizes are small (e.g., $n < 5$ per group), and hence a more appropriate SE of RR_{++} is obtained by Eq. 6 (Hedges et al. 1999). The frequency distribution of ln RR is assumed to follow a normal distribution and to be fitted by a Gaussian function (Eq. 8; Luo et al. 2006):

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

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

$$\mathrm{RR}_{++} = \frac{\sum_{i=1}^{m} \sum_{j=1}^{ki} w_{ij} \mathrm{RR}_{ij}}{\sum_{i=1}^{m} \sum_{j=1}^{ki} w_{ij}} \quad (4)$$

$$S(\mathrm{RR}_{++}) = \sqrt{\frac{1}{\sum_{i=1}^{m} \sum_{j=1}^{ki} w_{ij}}} \quad (5)$$

$$S(\mathrm{RR}_{++})$$
$$= \sqrt{\left[\frac{1}{\sum_{j=1}^{k} w_j}\right] \left\{ 1 + 4 \sum_{i=1}^{k} \frac{1}{df_i} \left(\frac{w_{ij}}{w_i}\right)^2 \frac{w_{ij}\left[\left(\sum_{j=1}^{k} w_j\right) - w_{ij}\right]}{\left(\sum_{j=1}^{k} w_j\right)^2} \right\}} \quad (6)$$

$$95\% \text{ CI} = \mathrm{RR}_{++} \pm 1.96 S(\mathrm{RR}_{++}) \quad (7)$$

TABLE 1. Percentage changes of 13 variables related to carbon cycle, environmental variables, and litter C:N ratio in response to experimental warming.

Variable	Percentage change	Sample size (n)
Carbon (C) fluxes		
Net photosynthetic rate	4.50 ± 1.92	15
Gross ecosystem photosynthesis	15.73 ± 2.62	20
Net primary production	4.40 ± 2.05	16
Litter mass loss	6.75 ± 0.78	34
Soil respiration	8.98 ± 1.01	66
Net ecosystem exchange	-3.97 ± 5.08	11
Ecosystem respiration	6.01 ± 1.54	24
Carbon (C) pools		
Plant aboveground part C	6.75 ± 0.75	83
Plant belowground part C	7.03 ± 0.72	67
Litter C	0.82 ± 0.93	20
Microbial biomass C	4.88 ± 1.39	30
Soil C	-1.01 ± 0.78	33
Dissolved organic C	12.08 ± 1.99	13
Environmental variables		
Air temperature	15.67 ± 0.36 ($1.81 \pm 0.16°C$)	45
Soil temperature	10.22 ± 0.52 ($1.33 \pm 0.12°C$)	50
Soil water content	-5.95 ± 0.89 ($-2.67 \pm 0.11\%$)	30
Soil pH	0.09 ± 0.72	11
C:N ratio		
Litter C:N ratio	1.20 ± 0.67	22

Note: Percentage change was calculated as ($e^{RR_{++}} - 1) \times 100\%$; values are means $\pm$ SE. The second set of values (in parentheses) indicates the average increases in air ($\sim1.81° \pm 0.16°C$) and soil temperature ($\sim1.33° \pm 0.12°C$) and decrease in soil water content under the experimental warming treatment in comparison with control groups; these values represent the absolute average changes in environmental variables under warming condition.

$$y = a \exp\left[-\frac{(x - \mu)^2}{2\sigma^2}\right] \qquad (8)$$

where x is the mean of ln RR in an individual interval; y is the frequency in an interval; a is the expected number of ln RR values at $x = \mu$; and μ and σ^2 are the mean and variance of the normal distribution of ln RR, respectively. If the 95% CI value of RR_{++} for a variable does not cover zero, the response of the variable to experimental warming is considered significantly different between the two treatments. Otherwise, the response is considered not to differ significantly. We also used t tests to examine whether or not the RR_{++} of a variable differed significantly among ecosystem types, among warming magnitudes, and among experimental durations. The percentage change of a variable was obtained by the formula: ($e^{RR_{++}} - 1) \times 100\%$. In addition, we also conducted regression analyses to examine the relationships between ln RR and environmental and forcing factors.

RESULTS

The percentage changes of 18 variables related to ecosystem C cycle showed mixed responses to experimental warming (Table 1). Warming largely changed soil properties and environmental variables. For example, soil temperature and inorganic N availability significantly increased by 10.2% and 58.7%, respectively ($P < 0.05$; Appendix B: Fig. B4), while soil water content significantly decreased by 6.0% ($P < 0.05$) under experimental warming. In contrast, the effects of warming on soil pH were insignificant ($P > 0.1$).

Responses of C fluxes to experimental warming

The overall effects of experimental warming on ecosystem C fluxes (both C influx and efflux) were found to be stimulative (Table 1). Compared with control groups, the average NPP was significantly enhanced by 4.4% under the warming ones ($P < 0.05$; Fig. 1a). Experimental warming also increased litter mass loss by 6.8% ($P < 0.05$; Fig. 1b), resulting in an acceleration of litter decomposition. Soil respiration was stimulated by 9.0% under manipulative warming, with a 9.4% increase in autotrophic respiration and a 7.5% increase in heterotrophic respiration ($P < 0.05$; Fig. 1c). In addition, ecosystem respiration significantly increased by 6.0% ($P < 0.05$; Fig. 1d), whereas NEE showed an insignificant change ($P > 0.1$; Table 1) in response to experimental warming. Moreover, warming-induced changes in C fluxes showed large variability among the studies, ranging from a minimum ln RR of -0.24 to a maximum of 0.38 in NPP, from -0.20 to 0.44 in litter decomposition, and from -0.45 to 0.50 in soil respiration (Appendix B: Fig. B2).
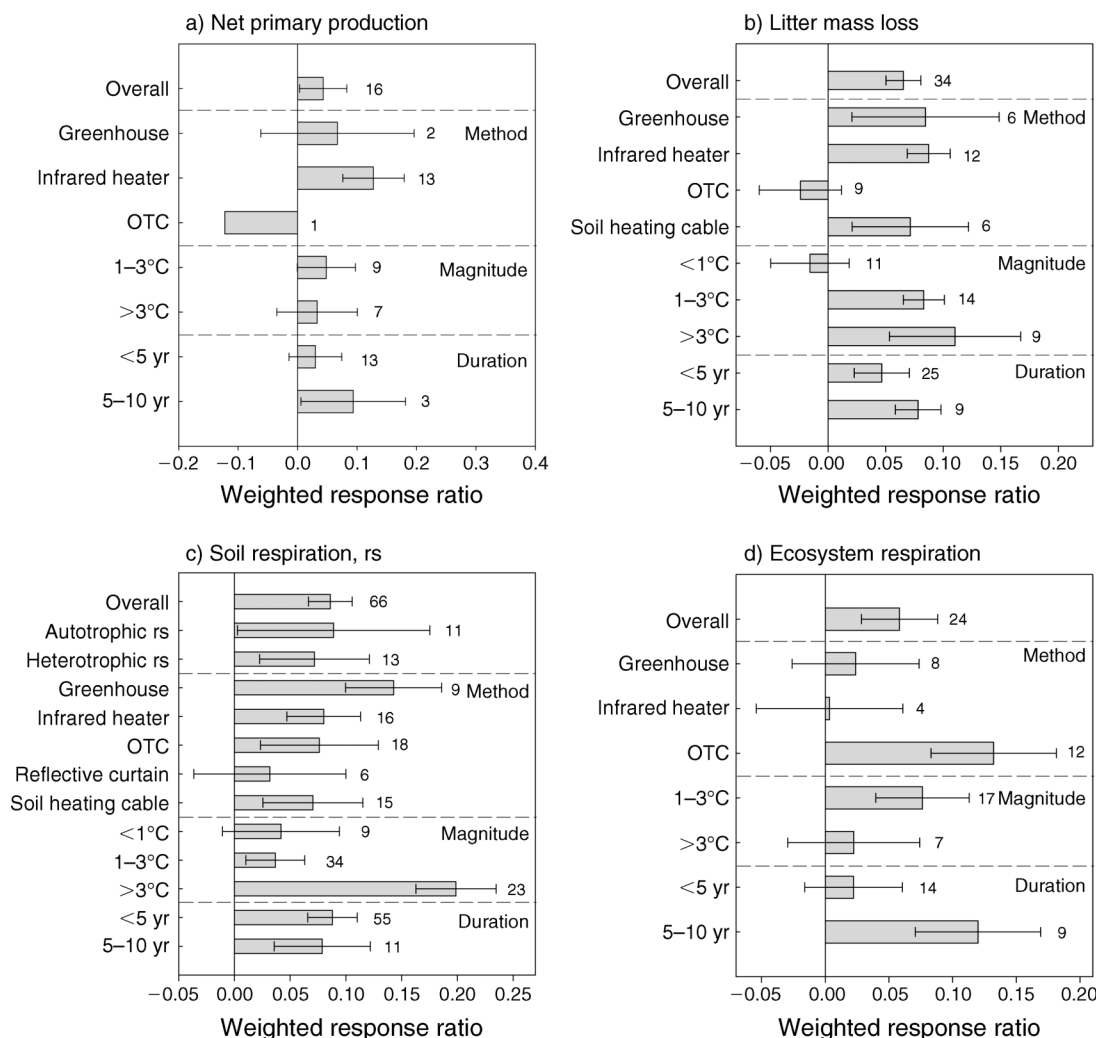
FIG. 1. The weighted response ratios (RR_{++}) for the responses to experimental warming of four variables related to the ecosystem C fluxes: (a) net primary production; (b) litter mass loss; (c) soil respiration; and (d) ecosystem respiration. Bars represent RR_{++} and 95% confidence intervals. The vertical lines are drawn at $\ln RR = 0$. The sample size for each variable is shown next to the bar; OTC stands for open top chamber.

Warming effects on C pools

The plant C contents in above- and belowground parts significantly increased by 6.8% and 7.0%, respectively, under experimental warming ($P < 0.05$; Fig. 2a, b). Warming also significantly enhanced microbial biomass C and dissolved organic C (DOC) by 4.9% and 12.1%, respectively ($P < 0.05$; Fig. 2d, Table 1), while litter C content exhibited only a minor change ($P > 0.1$; Table 1). However, experimental warming had no significant effects on the C pool in mineral soil ($P > 0.1$; Fig. 2c). The warming-induced changes in C pools exhibited great variability among the studies, ranging from a minimum $\ln RR$ of -0.46 to a maximum of 1.02 in the plant C from aboveground part, from -0.96 to 1.47 in the plant C from belowground part, from -1.07 to 0.63 in microbial biomass C, and from -0.47 to 0.62 in mineral soil (Appendix B: Fig. B3).

Factors influencing ecosystem C cycle responses to experimental warming

The litter mass loss and soil respiration significantly increased in both forests and grasslands ($P < 0.05$ for both), but exhibited minor changes in shrublands under warming condition ($P > 0.1$; Fig. 3a–c). Experimental warming significantly enhanced plant C pools from both above- and belowground parts in forests, grasslands, and wetlands ($P < 0.05$; Fig. 3a, b, e). However, plant C pool from belowground part in tundra decreased in the warming treatment ($P < 0.05$; Fig. 3d). In addition, soil C storage was not significantly affected by elevated
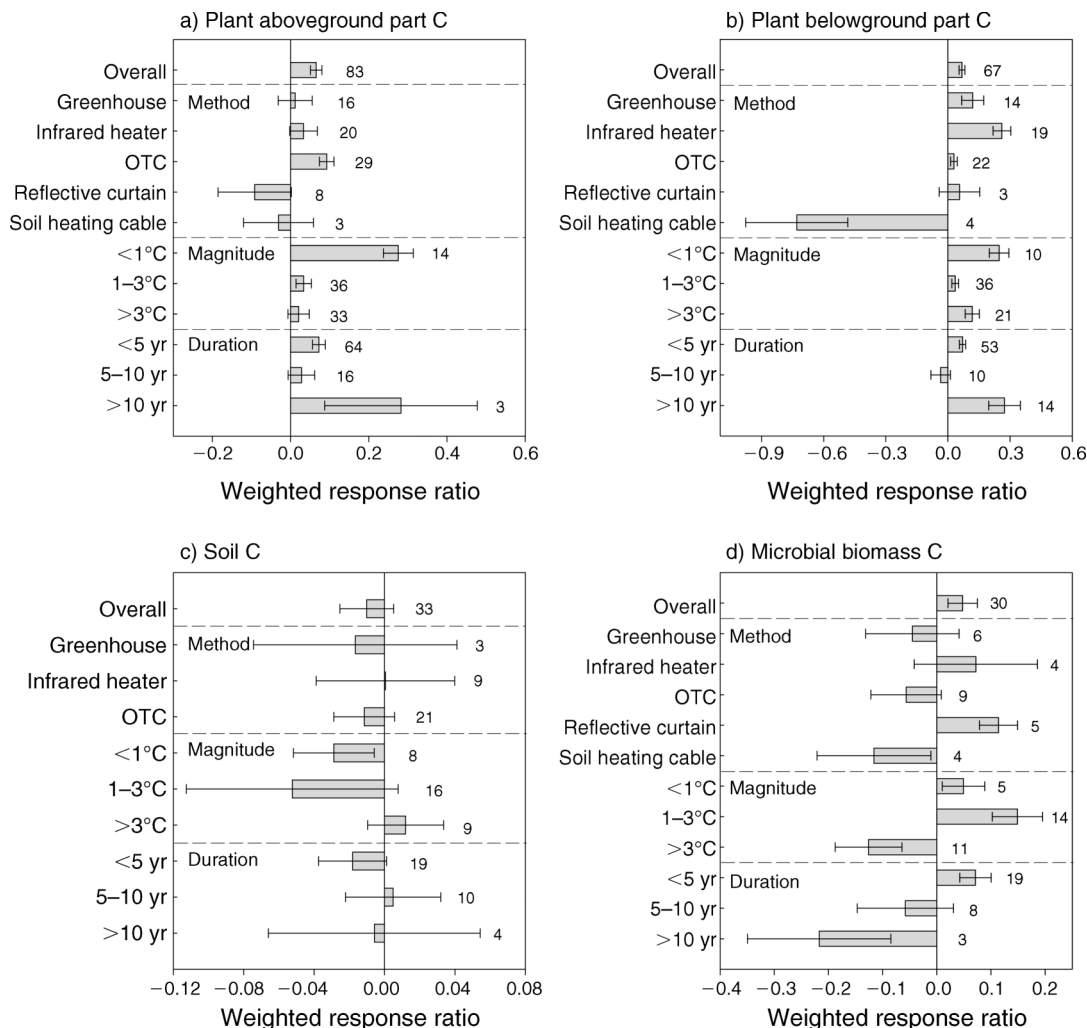
FIG. 2. The weighted response ratios (RR_{++}) for the responses to experimental warming of four variables related to the ecosystem C pools: (a) plant aboveground part C; (b) plant belowground part C; (c) soil C; and (d) microbial biomass C. Bars represent RR_{++} and 95% confidence intervals. The vertical lines are drawn at ln RR = 0. The sample size for each variable is shown next to the bar.

temperature in grasslands, shrublands, and tundra ($P > 0.1$) but slightly decreased in forests ($P < 0.05$; Fig. 3).

Responses of ecosystem C flux to experimental warming (e.g., NPP, litter mass loss, soil respiration, and ecosystem respiration) were not dependent on the methods of greenhouse, infrared heater, and soil heating cable ($P > 0.1$; Fig. 1). However, the OTC warming method reduced NPP and caused a minor stimulation of litter decomposition (Fig. 1a, b). No significant difference was found in the response of soil C content to warming by greenhouse, infrared heater, and OTC ($P > 0.1$; Fig. 2c), while direct soil heating by cables significantly decreased root C and microbial biomass C ($P < 0.05$; Fig. 2b, d).

An increase in warming magnitude from low (<1°C) to high temperature (>3°C) resulted in greater increases in litter mass loss and soil respiration ($P < 0.05$; Fig. 1b, c). However, the change in plant C from above-

ground part at low magnitude was higher than those at medium and high magnitudes ($P < 0.05$; Fig. 2a). Warming magnitude did not significantly affect the responses of plant C from belowground part and soil C content to experimental warming ($P > 0.1$; Appendix B: Table B1), while low and medium warming magnitudes significantly increased microbial biomass C but high magnitude decreased microbial biomass C ($P < 0.05$; Fig. 2d).

The duration did not influence the changes in soil respiration and ecosystem respiration in the warming experiments ($P > 0.1$; Appendix B: Table B1). However, the net C accumulation in plant C pool from belowground part tended to increase more in the long-term (>10 yr) studies than in short- and medium-term ones ($P < 0.05$; Fig. 2b). Both experimental duration and environmental factors had no significant effects on the
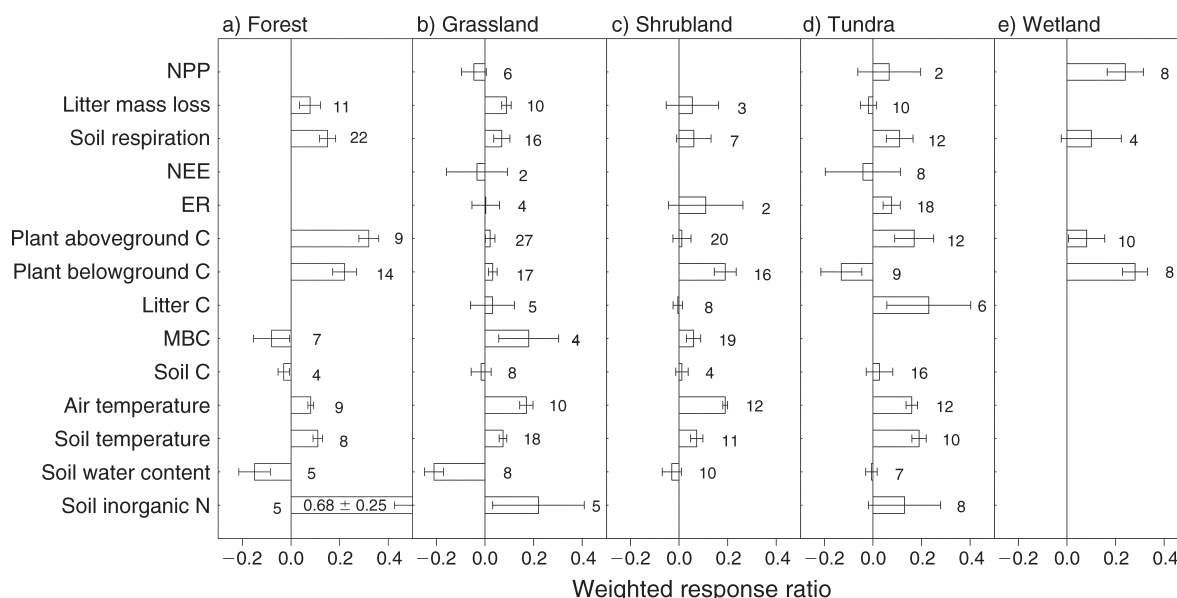
FIG. 3. The weighted response ratios (RR_{++}) for the responses to experimental warming of 14 variables related to the ecosystem C cycle across ecosystem types: (a) forest; (b) grassland; (c) shrubland; (d) tundra; and (e) wetland. Bars represent RR_{++} and 95% confidence intervals. The vertical lines are drawn at $\ln RR = 0$. The sample size for each variable is shown next to the bar. Abbreviations are: NPP, net primary production; NEE, net ecosystem exchange; ER, ecosystem respiration; and MBC, microbial biomass C.

change in soil C pool ($P > 0.1$; Fig. 2c; Appendix B: Table B1).

DISCUSSION

C influx and C storage in plants

Experimental warming stimulated plant growth from both above- and belowground parts, leading to increased plant C pools (Fig. 2). The net C accumulation in plants could be attributed to the enhanced NPP under warming condition. Changes in soil N availability (Vitousek and Howarth 1991) and plant phenology (Luo et al. 2009) in response to warming may be the key factors that result in increased NPP in terrestrial ecosystems. The overall response of net N mineralization to warming was significantly accelerated by 31.2%, resulting in an increase of soil inorganic N by 58.7%, i.e., a 50.5% rise in the NH_4^+ pool and a 55% rise in the NO_3^- pool ($P < 0.05$; Appendix B: Fig. B4), although some experiments showed a decrease in N mineralization under warming treatments (Rustad et al. 2001). The warming-induced significant increase in soil N availability may enhance plant N uptake, which in turn increases leaf N content and plant photosynthesis, and eventually stimulate shoot and root growth (Beier et al. 2009, Lu et al. 2011a). In addition, experimental warming can substantially alter plant phenology, including earlier leaf bud burst, advanced flowering (Arft et al. 1999), prolonged growing season (Sherry et al. 2007), and shifted species composition (Peñuelas et al. 2007), which may enhance plant growth and NPP (Peñuelas and Filella 2001, Luo et al. 2009). Our synthesized results are

consistent with those from other meta-analyses that focused on the response of aboveground plant growth to warming (Rustad et al. 2001, Lin et al. 2010, Wu et al. 2011) and are supported by gradient analysis (Raich et al. 1997), common garden (Oleksyn et al. 1998), and other alternative warming studies (Woodward 1992).

C efflux and C pools in litter and soil

C effluxes in terrestrial ecosystems (e.g., litter decomposition, soil respiration, and DOC leaching) were stimulated by experimental warming (Fig. 1, Table 1). It is well known that decomposition processes are governed by physical environments, substrate quality and quantity, and composition and activities of the decomposers (Swift et al. 1979). Experimental warming significantly increased mean air and soil temperature by 1.8° and 1.3°C, respectively, but did not affect litter quality (expressed as litter C:N ratio; Table 1). Warming-induced increases in air and soil temperature and fresh C supply from plant above- and belowground parts might have enhanced microbial growth and activities, resulting in a 4.9% increase in microbial biomass C, and thus accelerated litter decomposition (Wardle 1992). Stimulated litter decomposition might have weakened the increase in litter C influx from plant biomass, leading to minor change in the litter C pool (Fig. 1, Table 1).

Soil respiration and its components (i.e., autotrophic and heterotrophic respiration) may be affected directly and indirectly by experimental warming through influencing substrate supply and environmental factors (e.g.,

temperature, soil moisture and oxygen, nitrogen availability, and soil pH). Previous studies by various approaches such as meta-analysis (Rustad et al. 2001, Wu et al. 2011), synthetic analyses along MAT (or latitude) gradient (Lloyd and Taylor 1994), mesocosm experiments (Lin et al. 1999), and laboratory incubation (Flanagan and Veum 1974) suggest that experimental warming can significantly accelerate soil respiration within a given range of temperature (e.g., 4–32°C; Kesik et al. 2006). Our meta-analysis results show that experimental warming largely stimulated soil respiration, likely resulting from the warming-induced increases in soil temperature, NPP, fresh C input from litterfall, and microbial biomass C as well as enhanced root growth and root C content (Luo and Zhou 2006).

By contrast, warming did not significantly alter the C pools in litter and mineral soil ($P > 0.1$; Fig. 2, Table 1). First, the undetectable change in belowground C pools (e.g., litter C, soil C storage) under warming condition likely results from the fact that the enhanced litter decomposition and soil respiration roughly offsets the warming-induced increases in plant-derived C influx. Second, the large C pool in soil may conceal its smaller response to experimental warming compared with the plant C pool (Batjes 1996). Third, it is difficult to detect the change in soil C under experimental warming in the short-term duration of manipulative experiments (most <5 yr; Fig. 2c), although the change in soil C is biogeochemically significant (Hungate et al. 2009). In addition, the increase in DOC concentration caused by experimental warming may accelerate C leaching to deeper soil and eventually to water bodies (Chapin et al. 2002).

Responses of C dynamics across ecosystem types

The responses of C dynamics to warming may differ considerably among ecosystem types. The results obtained in this synthesis show that experimental warming significantly increased both plant C pools from both above- and belowground parts in forests, grasslands, and wetlands ($P < 0.05$; Fig. 3a, b, e). However, the warming-induced plant C accumulation was significantly higher in forests than that in grasslands ($P < 0.05$; Fig. 3a, b). The highest plant C increase in response to warming was plant C pool from aboveground parts in forests (Fig. 3a), possibly resulting from the highest increase in soil inorganic N (Fig. 3a) and its positive effect on plant growth (Vitousek and Howarth 1991, Lu et al. 2011b). Moreover, due to the methodological difficulties, most studies were conducted at seedling stage or during the early growth stages of forest plants rather than with natural forest plants (Rasmussen et al. 2002). Compared with the tree plants in natural forests, tree seedlings/saplings had the higher temperature sensitivity due to the fast growth of seedling and the increase in sapling carbohydrate reservoir under warming condition (Usami et al. 2001). For example, *Quercus myrsinaefolia* (Usami et al. 2001), *Picea asperata*, and

Abies faxoniana (Yin et al. 2008) may drive the overall pattern and lead to the strong response to warming in this meta-analysis. However, plant C from belowground part in tundra showed a significant decrease under warming condition (Fig. 3d), which might have been caused by the warming-induced amelioration in nutrient conditions and shift of tundra plant community from graminoid plants to moss, and a resultant emphasis on plant C allocation to aboveground parts (Friedlingstein et al. 1999, Sjögersten et al. 2008). Warming significantly increased litter decomposition in forests and grasslands ($P < 0.05$; Fig. 3a, b), but did not significantly change in shrublands and tundra ($P > 0.1$; Fig. 3c, d). The warming-induced increase in plant growth from aboveground parts and undetectable change in litter mass loss may increase aboveground litter C accumulation and enhance its pool size in tundra ($P < 0.05$; Fig. 3d). Compared to other ecosystem types, forests experienced the highest increase in soil respiration, which might lead to the slight but significant decrease of soil C (Fig. 3a). However, even in forests, the responses of C cycle to experimental warming may be different among boreal, temperate, and tropical forests. Unfortunately, to our knowledge, no warming experiments were conducted in tropical forests. Future research is highly needed for understanding critical feedback processes in tropical forests.

Factors influencing the response of C cycle to warming

Environmental (e.g., latitude, MAT, and MAP) and forcing factors (e.g., warming method, warming magnitude, and experimental duration) may potentially influence the responses of ecosystem C fluxes and pools to experimental warming, since we extracted data from diverse manipulative experiments at a global scale. Direct soil warming by heating cables may directly accentuate soil water evaporation, which may in turn largely decrease soil moisture and inhibit microbial biomass and dehydrogenase activities (Arnold et al. 1999). In addition, higher soil temperature by heating cables (e.g., 3°C) may enhance root mortality and result in a decline in root number and biomass compared to other warming methods (Edwards et al. 2004). The increase in warming magnitude from $<1°$ to $>3°C$ resulted in greater stimulation in litter mass loss and soil respiration (Fig. 1b, c), largely driven by its positive effects on decomposition processes (Schuur et al. 2001). However, no significant difference of litter decomposition was found between medium (1–3°C) and high (3°C) warming magnitudes. Such a response suggests that temperature sensitivity of microbes may decline at high temperatures or microbes themselves may be acclimatized to high temperatures (Luo et al. 2001, Melillo et al. 2002). The response of microbial biomass C to different warming magnitudes also showed that microbial growth increased from $<1°$ to 1–3°C, but could be inhibited at higher temperatures ($>3°C$; Fig. 2d). However, experimental duration did not impact the responses of NPP
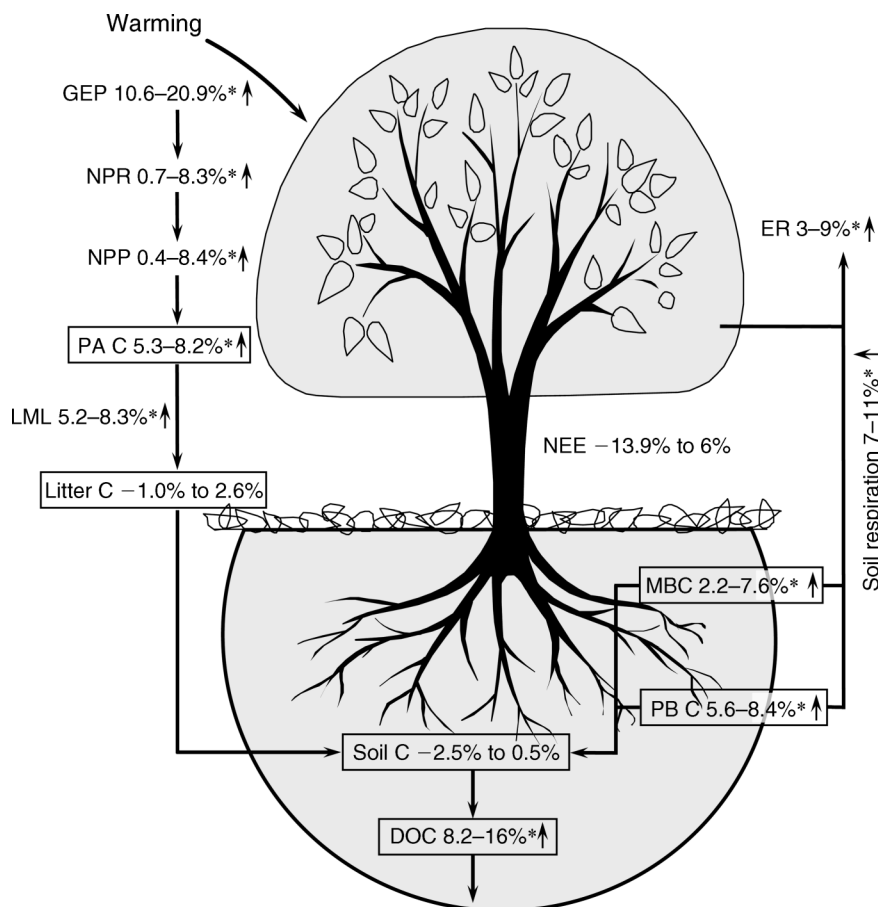
FIG. 4. The responses of ecosystem C cycle to experimental warming with the changes imposed across all warming experiments. The upward arrows are positive response and increase to warming; the downward arrows are negative response and decrease to warming. Asterisks indicate statistical significance. Abbreviations are: GEP, gross ecosystem photosynthesis; NPR, net photosynthesis rate; NPP, net primary production; LML, litter mass loss; NEE, net ecosystem exchange; and ER, ecosystem respiration. C pools are presented in closed panels: PA C, plant aboveground part C; PB C, plant belowground part C; MBC, microbial biomass C; and DOC, dissolved organic C. Numbers indicate the 95% confidence interval of RR_{++}.

* $P < 0.05$.

and soil respiration to experimental warming ($P > 0.1$; Fig. 1; Appendix B: Table B1).

The warming-induced changes in soil respiration, plant C from belowground parts, and soil C pool did not show any statistically significant correlations with environmental and forcing factors, while the changes in plant C pool from aboveground parts had negative correlations with MAT (Appendix B: Table B1). The results indicate that the responses of plant C pool from aboveground part to experimental warming were more sensitive at higher latitudes at which the annual temperature is lower (Root et al. 2003), but the pattern was not applicable to belowground C dynamics. Given that all experimental sites in this meta-analysis are located at middle to high latitudes (25.9°–78.9° N or S; Appendix B: Fig. B1), more research needs to be conducted in the ecosystems at lower latitudes (e.g., tropical forests, savannas) in future manipulative warming studies.

Carbon-cycle feedbacks to climate warming

Warming-induced plant and ecosystem responses, primarily through respiration, soil trace gases, and evapotranspiration (Lukac et al. 2010), together with changes in microbial biomass and activities in association with SOM decomposition under warming condition (Bardgett et al. 2008), potentially have strong feedbacks to atmospheric CO_2 concentration and global climate change. Most global models have predicted a C loss from SOM and/or a decrease in NPP, resulting in a positive feedback to climate warming (Cao and Woodward 1998, Cox et al. 2000, Friedlingstein et al. 2006). However, our synthesized results show that both ecosystem C influx and efflux were stimulated by experimental warming. Specifically, the stimulation of soil respiration and DOC leaching may roughly offset the increase of plant-derived C influx, leading to insignificant change in soil C and NEE (Fig. 4). This suggests that warming might not trigger strong positive

PLATE 1. A 4°C warming experiment by infrared heaters in a tallgrass prairie established in Oklahoma, USA. Photo credit: Y. Luo.

C-cycle feedback to climate warming from terrestrial ecosystems. Moreover, the warming-induced acceleration of C influx and efflux, together with minor changes in litter C, soil C, and NEE, implies that ecosystem C turnover rate may increase (i.e., C residence time may decrease), but ecosystem C storage could remain stable under the future warmer conditions. Our meta-analysis suggests that future ecosystem and climate models need to consider certain C processes and the reduced C residence time (or increased C turnover rate), and distinguish acceleration of ecosystem C flux and minor stimulation of soil C storage for future C dynamic projections under global climate warming. Recently, Shilong Piao et al. used our meta-analysis results to evaluate the model performance for NPP sensitivity to climate variability and found the inconsistency of the temperature sensitivity of NPP between models and field warming experiments (S. L. Piao et al., *unpublished manuscript*).

Uncertainty analysis

Although the meta-analysis provides a statistical approach to calculate the weighted response ratios across experiments and sites, the overall effects of climate warming on ecosystem C balance may be synthesized with large uncertainties due to the inherent limitations of the methodologies used in such analyses and/or of experimental manipulations. First, the compiled database comes mainly from temperature-sensitive regions and/or low-stature ecosystems (e.g., grasslands and tundra) due to their strong responses and manipulative feasibility (Arft et al. 1999, Rustad et al. 2001), while data from many other regions have not been reported or fewer studies were conducted for one reason or another (e.g., forest ecosystems, especially tropical forests). Thus, the lack of sufficient studies from some critical regions may influence the evaluation of the integrated response of terrestrial ecosystems to global climate warming.

Second, although soil C storage and NEE exhibited insignificant changes in this meta-analysis, it still might be difficult to precisely close the ecosystem C budget by comparing the percentage changes in different fluxes and pools under experimental warming, which were drawn from different ecosystems and may not reflect the actual ecosystem C gain or loss. This is because the warming-induced changes in C pools and fluxes depended on their initial amount. In addition, it is difficult to detect the change of soil C (as the largest reservoir of organic C in terrestrial ecosystems) in the current duration of manipulative experiments, although such change is biogeochemically significant for C fluxes under warming condition (Hungate et al. 2009). Thus, it would make large uncertainties through estimating the actual C

balance by comparing the percentage changes of the C pools and fluxes.

Third, the differences of the methods used and measurements made among individual experiments may also lead to uncertainties. For example, the changes in both GEP and ER under experimental warming caused the change in NEE, which may not reflect the C sink or source across a range of ecosystems due to the differences of data sources and sample sizes for these three fluxes. In addition, GEP, ER, and NEE, which are often measured during the growing season, may not actually represent the annual values (Johnson et al. 2000). Moreover, direct soil warming by heating cables may inhibit microbial biomass and increase root mortality, resulting in reduced root biomass compared to other warming methods, which may influence the overall patterns of belowground processes in relation to warming. Thus, in the future studies, an ecologically relevant metric needs to be used for the comparisons of warming manipulation effects so that the applied warming treatments as well the warming magnitude can be reflected, as suggested for the studies of precipitation manipulations (Vicca et al. 2012).

Fourth, our analysis used the weighting factors and weighted response ratios from different experiments to evaluate the warming effects across ecosystems or sites (Eqs. 3–4), which may also lead to uncertainties. In the meta-analysis, the experimental results with lower variance may often up weight the weighting, while those with higher variance may down weight the weighting. To examine the weighting effects on the overall patterns, we plotted frequency distributions of ln RR to display variability among individual studies (Appendix B: Figs. B2 and B3). The central tendencies of the variables (unweighted mean values) are close to the corresponding weighted response ratios (Appendix B: Figs. B2 and B3; Table 1), indicating that investigations with high or low variance may not influence the overall patterns in the meta-analysis.

Conclusions

Our results indicate that although soil respiration and DOC leaching are enhanced under warming condition, the stimulation of plant-derived C influx may offset the increase of warming-induced efflux and result in insignificant changes in litter and soil C content, indicating that climate warming may not trigger strong positive carbon-climate feedbacks from terrestrial ecosystems. Furthermore, the increase of C storage in plants together with the slight but not statistically significant decrease of net ecosystem exchange (NEE) across ecosystems suggests that terrestrial ecosystems might be a weak C sink rather than C source under future climate warming. The warming-induced increases in plant growth and net C accumulation in both plant above- and belowground parts did not lead to any significant changes in litter and soil C storage. The warming-induced C loss in three efflux processes (i.e.,

litter decomposition, soil respiration, and deep layer DOC leaching) counterbalances the increase in photosynthetic C influx under experimental warming, likely resulting from the increase in ecosystem C turnover rate. In addition, our results indicate that the warming-induced changes in soil C pool exhibit no significant correlations with environmental (i.e., latitude, MAT, and MAP) and forcing factors (i.e., warming magnitude and experimental duration), but the responses of some variables (i.e., litter mass loss and root C) to warming treatment vary among ecosystem types. The average responses of ecosystem C fluxes and pools to experimental warming as revealed by this synthesis could be potentially useful for parameterizing and benchmarking land surface models for better understanding C-cycle feedbacks to climate warming.

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SUPPLEMENTAL MATERIAL

Appendix A

Full reference list for studies considered in the Supplement for this meta-analysis (*Ecological Archives* E094-063-A1).

Appendix B

Global distribution of manipulative warming experiments, and the frequency distributions of the natural logarithm of response ratios (ln RR) for C fluxes and pools included in this meta-analysis (*Ecological Archives* E094-063-A2).

Supplement

Logarithm of response ratio (ln RR) and weighting factor (w_{ij}) of 18 variables extracted from studies used in the meta-analysis (*Ecological Archives* E094-063-S1).