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Effects of climate warming on carbon fluxes in grasslands— A global meta-analysis

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Abstract

Climate warming will affect terrestrial ecosystems in many ways, and warming-induced changes in terrestrial carbon (C) cycling could accelerate or slow future warming. So far, warming experiments have shown a wide range of C flux responses, across and within biome types. However, past meta-analyses of C flux responses have lacked sufficient sample size to discern relative responses for a given biome type. For instance grasslands contribute greatly to global terrestrial C fluxes, and to date grassland warming experiments provide the opportunity to evaluate concurrent responses of both plant and soil C fluxes. Here, we compiled data from 70 sites (in total 622 observations) to evaluate the response of C fluxes to experimental warming across three grassland types (cold, temperate, and semi-arid), warming methods, and short (≤3 years) and longer-term (>3 years) experiment lengths. Overall, our meta-analysis revealed that experimental warming stimulated C fluxes in grassland ecosystems with regard to both plant production (e.g., net primary productivity (NPP) 15.4%; aboveground NPP (ANPP) by 7.6%, belowground NPP (BNPP) by 11.6%) and soil respiration (Rs) (9.5%). However, the magnitude of C flux stimulation varied significantly across cold, temperate and semi-arid grasslands, in that responses for most C fluxes were larger in cold than temperate or semi-arid ecosystems. In semi-arid and temperate grasslands, ecosystem respiration (Reco) was more sensitive to warming than gross primary productivity (GPP), while the opposite was observed for cold grasslands, where warming produced a net increase in whole-ecosystem C storage. However, the stimulatory effect of warming on ANPP and Rs observed in short-term studies (≤3 years) in both cold and temperate grasslands disappeared in longer-term experiments (>3 years). These results highlight the importance of conducting long-term warming experiments, and in examining responses across a wide range of climate.

KEYWORDS

carbon fluxes, climate warming, global, grassland, meta-analysis

1 | INTRODUCTION

Due to the accumulation of carbon dioxide (CO_2) and other greenhouse gases in the atmosphere, global surface temperatures are projected to increase by 1.0–3.7°C by the end of 21th century relative to the period of 1986–2005 (Collins et al., 2013). The terrestrial biosphere-atmosphere exchange of C is approximately 120 Pg C year^{-1} and, as is every biological process, this exchange is highly temperature sensitive (e.g., Piao et al., 2013; Reichstein et al., 2005). Given the vast carbon (C) stocks in vegetation (450–650 Pg C) and soils (1,500–2,400 Pg C), even small changes in C fluxes due to global warming will have a tremendous effect on atmospheric CO_2 concentrations and, in turn, on future climate (Ciais et al., 2013). In a recent coupled model inter-comparison study (CMIP5), future climate change alone was found to reduce the land carbon uptake by on average 58.4 ± 28.5 Pg C per 1°C temperature increase (over 140 years of simulation) caused by both increased ecosystem respiration as well as reduced photosynthesis (Arora et al., 2013). However, the CMIP5 results show that Earth System Models produce widely differing projections of vegetation and soil C dynamics in response to warming and often poorly fit observations (Carvalhais et al., 2014; Luo et al., 2016).

Grasslands cover approximately 30% of the Earth's land surface, and they store approximately 10%–30% of global soil C (Booker, Huntsinger, Bartolome, Sayre, & Stewart, 2013; Scurlock & Hall, 1998). Interannual variations in the global terrestrial C sink appear to be dominated by semi-arid ecosystems and grasslands and their sensitivity to variations in temperature and precipitation (Ahlstrom et al., 2015; Poulter et al., 2014). Therefore, responses of grassland C fluxes to climate warming can play a large role in driving changes in global C cycling (e.g., Ahlstrom et al., 2015; Parton, Scurlock, Ojima, Schimel, & Hall, 1995). However, reported responses of grassland C cycling to warming experiments have produced inconsistent results, including positive (Ganjurjav et al., 2015; Peng et al., 2014; Sekine, Yoshitake, Tomotsune, Masuda, & Koizumi, 2013), negative (Niu et al., 2008; Phillips, Gregg, & Wilson, 2011), or no effects (Pendall et al., 2013; Wu, Dijkstra, Koch, Peñuelas, & Hungate, 2011). These divergent responses could be due to several factors, such as: (a) variations in initial climate conditions, (b) differing temperature sensitivities of various C cycle processes, (c) differences in the duration of warming treatments, as well as (d) differences in experimental warming methods.

Initial climate conditions should mediate grassland response to warming due to limitation of C cycle processes by temperature and moisture conditions. For example, grasslands in cold areas might be more sensitive to warming, because they typically have larger soil organic carbon stocks that could be vulnerable to decomposition (e.g., Crowther et al., 2016) and because decomposition typically increases with temperature (e.g., Davidson & Janssens, 2006). Low temperatures can limit plant primary production through both direct constraints on growth rates and indirectly by slowing rate of soil nitrogen (N) supply to plants (e.g., Bai et al., 2013; Liu et al., 2017; Wu, Dijkstra, Koch, & Hungate, 2012). Plant growth in cold or temperate grasslands can also be stimulated by lengthening of the growing season (e.g., Wan, Hui, Wallace, & Luo, 2005). In semi-arid grasslands, water availability is a primary driver for carbon exchange (Jiang et al., 2012; Wilcox et al., 2017). Warming-induced drought can reduce both gross primary production (GPP) and ecosystem respiration (Reco) (Maestre et al., 2015; Sharkhuu et al., 2013; Xu et al., 2013). However, currently available meta-analyses of warming experiments include C flux responses from relatively few grassland sites (Rustad et al., 2001, $n \le 6$; Wu et al., 2011, $n \le 10$; Lu et al., 2013, $n \le 16$), and have not distinguished among different grassland types, i.e., cold, temperate and semi-arid grasslands, which differ markedly with regard to climate, vegetation and soil properties.

Warming can affect various ecosystem C fluxes differently. For example, warming increased GPP but not Reco in a meadow grassland in Tibet, producing a large increase in net ecosystem exchange (NEE) (Chen et al., 2017). In other cases, such as for a short-grass prairie in Oklahoma, USA, warming suppressed both GPP and Reco in parallel, yielding no effect on NEE (Xu et al., 2016). In contrast to forest warming experiments which typically manipulate only soil temperatures, grassland warming experiments usually increase temperatures for both plants and soils, which makes grassland experiments particularly valuable for examining concurrent responses to warming of GPP and Reco as well as their net balance, NEE. Nonetheless, even within grasslands, variations in warming methods could contribute to variations in C flux responses to warming.

The stimulatory effect of warming on grassland C fluxes might only be transient. That is, initial responses to warming can be modulated over longer timescales by nutrient limitation, as demonstrated for a subalpine grassland in the Pyrenees, Spain (Sebastià, 2007), and by changes in plant species composition, as observed in a Mediterranean grassland in California (Zavaleta et al., 2003). Elsewhere, experimental warming initially increased aboveground net primary productivity (ANPP) across four grasslands in the western U.S., but this stimulation steadily diminished over 9 years of warming as plant species composition changed and enhanced N losses constrained plant growth (Wu et al., 2012). In central France, warming initially stimulated ANPP relative to controls, then suppressed it during the second through fourth years of measurement, as plant functional types changed and became more nitrogen limited (Cantarel, Bloor, & Soussana, 2013). However, past meta-analyses of terrestrial ecosystem responses to warming have focused on short-term responses (≤3 years) (Rustad et al., 2001; Wu et al., 2011), or used the data from the latest year of warming without considering the effects of the warming duration and the interannual variability therein (Lu et al., 2013). This complexity, together with differences in climate, vegetation and soil conditions, makes it challenging to predict changes in grassland C cycle fluxes to future climate warming.

We conducted a comprehensive meta-analysis using data from 70 grassland sites (in total 622 observations from 87 publications) to (a) investigate how different grassland C fluxes respond to warming, overall, and for three different grassland types (cold, temperate, and semi-arid grasslands) and by plant functional type; (b) elucidate the relative sensitivities of GPP and Reco to warming; (c) examine whether warming responses differ between short (≤3 year) and longer (>3 year) timescales and (d) evaluate whether different warming approaches affect C flux responses.

We expected that cold-region grasslands would have larger positive responses to warming by overcoming cold-limitation to growth and decomposition processes. By contrast, we expected that semi-arid grasslands would have smaller or negative responses due to intensification of moisture limitation to these processes. We examined the relative warming responses for paired GPP and Reco measurements, a comparison not conducted by prior meta-analyses, to discern which processes were most sensitive to warming. We expected that stimulation of C cycle processes in short-term studies would diminish over the longer term, as fast-turnover C and N pools equilibrate and plant and soil microbial species composition shift and acclimate to warmer conditions. In addition, we assessed whether observed differences in warming responses were affected by plant functional type or by experimental warming method.

2 | MATERIAL AND METHODS

2.1 | Data collection

Studies included in this meta-analysis (1980–2017) were collected by using the *Web of Science* and *Google Scholar* for the following combinations of key words: (a) experimental warming (OR climate change OR elevated temperature OR translocation) AND (b) biomass production (OR C fluxes OR NEE OR GPP OR respiration OR biogeochemical process) AND (c) grasslands (OR meadow OR steppe OR savanna OR pasture OR grass prairie). Studies were included only if they report on (a) control and warming treatments; (b) provide mean, standard deviation (or standard error) and sample size for respective C fluxes; and (c) C fluxes at least measured for one growing season. Compiled C fluxes were gross primary productivity (GPP), aboveground (ANPP), below ground (BNPP) and net primary productivity (NPP = ANPP+BNPP or GPP-plant respiration) all representing ecosystem carbon gain. Further variables, representing ecosystems C losses, were ecosystem (Reco) and soil respiration (Rs = belowground autotrophic + heterotrophic), as well as NEE (GPP-Reco) resulting from the balance of ecosystem C gains and losses. Note, all carbon fluxes are presented with a positive sign. An increase in NEE is accordingly an increase in net ecosystem carbon storage (C gain). Multiple levels of warming magnitude and different grassland species at one site were considered as independent measurements. If required, data were extracted from figures using SigmaScan Pro 5. In addition to C fluxes, we also collected from original papers site-related information such as geographical location (Figure 1), plant functional type, mean annual temperature (MAT) and mean annual precipitation (MAP) as well as warming method and experimental length.

Following these criteria, 622 observations from 70 different sites were included in this meta-analysis. Studies geographically

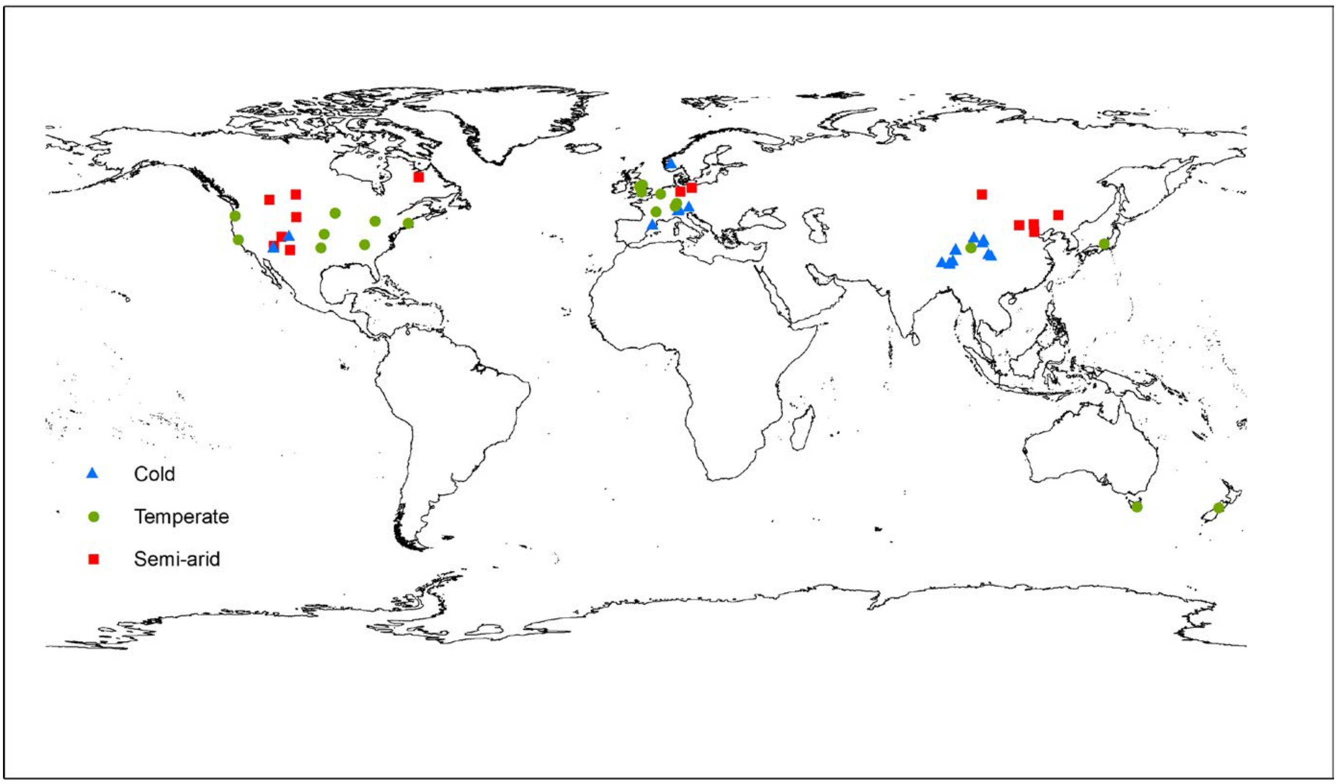

FIGURE 1 Global distribution of grassland sites included in the meta-analysis (n = 70) [Colour figure can be viewed at wileyonlinelibrary.com]

covered North America, Europe, Oceania and Asia (Figure 1). Except considering all data (i.e., all grassland) we categorized grasslands into three different types applying the Köppen–Geiger climate classification (Kottek, Grieser, Beck, Rudolf, & Rubel, 2006). The Köppen–Geiger main climate of polar and snow was summarized into "cold," and warm temperate climates were summarized into "temperate" grassland. The Köppen–Geiger arid climate classification is too strict to include the grasslands collected in our literature review, so we classified grasslands as "semi-arid" if the ratio of MAP and mean annual potential evapotranspiration (PET) was <0.5 (UNEP, 1992). PET for each site was taken from WorldClim (http://WorldClim.org).

For experimental warming, various methods were deployed, including environmental chambers (chambers), soil heating cables (heating cables), infrared radiators (IRs), open-top chambers (OTCs) and mesocosm translocation (translocation). Reported periods of experimental warming ranged from 1 to 11 years, with 55% of warming experiments conducted for up to 3 years, 34% of experiments 3–5 years, and 11% lasting longer than 6 years. Across all sites, mean increases of annual soil and air temperatures were 1.8 ± 1.0°C and 2.0°C ± 1.3°C, respectively. Across all studies, warming had a minor influence on mean annual soil water content which decreased only by 2.4% ± 2.0% (Table S1). Grassland plant functional types in this study include forbs, grasses, sedges and mixtures thereof.

2.2 | Meta-analysis

As is common for meta-analyses (Lu et al., 2013; Rustad et al., 2001), in this study we calculated response ratios (RR) to reflect the effects of environmental warming on different grassland C fluxes. RR is defined by the ratio of the mean value of a grassland C flux of the whole experimental period in the warming treatment $\overline{X_e}$ to that in the control treatment $\overline{X_c}$ (Equation 1). Note that we considered the average values of the whole measurement period for each climate variable and C flux. Following Hedges, Gurevitch, and Curtis (1999), the logarithm of RR is used to reduce bias and to ensure a normal sampling distribution.

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

The corresponding variance for each ln RR (v) was calculated as:

$$v = \frac{{s_e}^2}{n_e {X_e}^2} + \frac{{s_c}^2}{n_c {X_c}^2} \tag{2}$$

with n_e and n_c, s_e and s_c representing the sample size and standard deviation in the warming and control treatment, respectively. From this variance and the between study variance σ^2 representing a random effects model, we derived a weighing factor w:

$$w_{ij} = \frac{1}{v + \sigma^2} \tag{3}$$

The weighing factor was used to calculate (using the package *metafor* in *R*) a weighted response ratio (R_{++}) from individual R_{ij} (i = 1, ..., m; j = 1, ..., k_i) by giving greater weight to the studies whose estimates have greater precision reflected by smaller v. Here m represents the number of groups (e.g., grassland type, plant type, warming duration and warming method) and k_i is the number of comparisons in the ith group.

$$\mathrm{RR}_{++} = \frac{\sum_{i=1}^{m}\sum_{j=1}^{ki} wij \ln \mathrm{RR}_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{ki} w_{ij}} \tag{4}$$

The effect of warming was considered significant if the 95% confidence interval (CI) value of RR++ for a variable did not overlap zero, with CI given by

$$95\%\mathrm{CI} = \mathrm{RR}_{++} \pm 1.96 SE(\mathrm{RR}_{++}) \tag{5}$$

with SE calculated following 1999.

$$SE\left(\mathrm{RR}_{++}\right) = \sqrt{\frac{1}{\sum_{i=1}^{m}\sum_{j=1}^{ki} w_{ij}}} \tag{6}$$

The percentage change of a variable was obtained by

$$(e^{RR++} - 1) \times 100 \tag{7}$$

In addition to the above described statistical evaluation (Equations 1–7), meta-regression considering different weights of variables (Thompson & Higgins, 2002; Equation 4) was used to test the relative sensitivity of GPP and Reco to warming, and how C flux responses were influenced by site characteristics (e.g., MAT, MAP; MAP/ETP). To test the effects of warming duration, a multi-level meta-analysis was used (White, Barrett, Jackson, & Higgins, 2012).

3 | RESULTS

3.1 | Effects of experimental warming on grassland C fluxes: overall, and by grassland type

Considering data of all grassland types (i.e. cold, temperate, and semi-arid), experimental warming generally stimulated C fluxes for both assimilation (ANPP, BNPP, GPP and NPP) and dissimilation processes (Reco and Rs) (Figure 2, bottom panel). Across all studies, warming by an average of 2°C increased NPP by 15.4%, ANPP by 7.6%, BNPP by 10.6% and Rs by 9.5% (p < 0.05). In contrast, GPP, Reco and NEE were enhanced by warming but effects were not statistically significant. Sample sizes were smaller for GPP (n = 25 sites), Rs (n = 24), Reco (n = 26) and NEE (n = 20) than the biomass-based productivity measurements (n = 29, 64, and 32 sites for NPP, ANPP, and BNPP, respectively), making it more difficult to detect significant effects of warming on the gas-based C fluxes other than Rs.

Comparing across the three different grassland types, warming affected C fluxes more strongly in cold than in temperate and

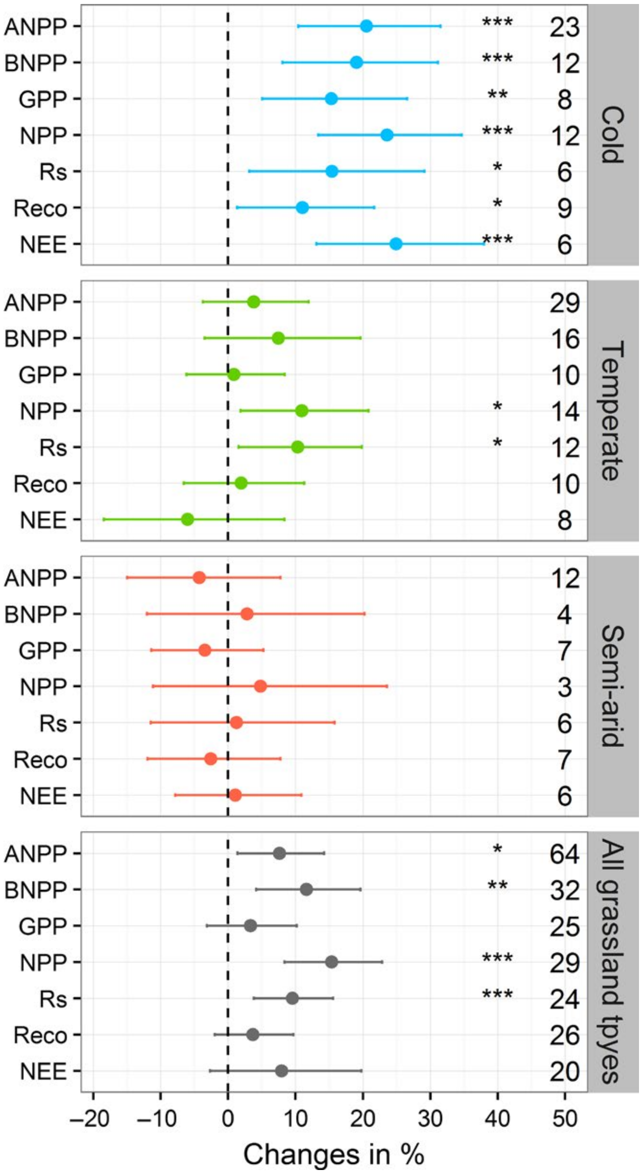

FIGURE 2 Mean percentage changes in main carbon fluxes across different grassland types under warming with 95% CI. Level of significance (p < 0.001: "***"; 0.001 < p < 0.01: "**"; 0.01 < p < 0.05: "*"; 0.05 < p < 0.1: ".") and sample size for each variable is shown on the right. Note that the class of all grassland types includes all data from cold, temperate and semi-arid grasslands [Colour figure can be viewed at wileyonlinelibrary.com]

semi-arid grasslands. In cold grasslands, warming significantly increased ANPP (20.5%), BNPP (19.0%), NPP (23.6%), GPP (15.3%), Reco (11.0%) and Rs (15.4%), while in temperate grasslands, warming significantly increased NPP (11.0%) and Rs (10.3%) solely . Warming did not significantly affect C fluxes in semi-arid grasslands, but this grassland type showed a general tendency of decreasing C fluxes under warming. Due to larger absolute increases in C uptake (GPP) than C release processes (Reco), NEE (net C gain) was significantly increased by 24.9% in cold grasslands due to warming. However warming effects on NEE in temperate (−6.0%) and semi-arid grasslands (1.1%) did not differ significantly from zero (Figure 2).

Correlation analysis of changes in grassland C fluxes with environmental parameters revealed a negative correlation of all grassland carbon fluxes with MAT, indicating a larger change under colder climatic conditions. This correlation was significant for ANPP, GPP, NPP but not for BNPP, Reco, or Rs (Table 1). Correlations of C fluxes with MAP and the ratio of MAP and PET were only significant for BNPP, which showed a negative correlation, indicating an increase in BNPP with drier conditions, perhaps reflecting an adaptation of the root system to water deficits.

To further explore potential impacts of water limitation on grassland carbon fluxes with warming, we used a subset of the compiled data from those with multi-factor experiments investigating changes of single and combined effects of temperature and precipitation. Due to limitations in sample size, we conducted this multi-factorial analysis only for ANPP. Results reveal that ANPP was stimulated by both temperature and precipitation, but the overall highest increase of ANPP was found in the combined treatment of warming and precipitation (Table 2).

3.2 | Differential responses of GPP and Reco to experimental warming

In addition to the overall response ratios for all grassland C fluxes (Figure 2), we selected GPP and Reco, which together determine grassland net ecosystem carbon exchange (NEE) for a more detailed analysis of their relative responses to warming when paired for the same warming experiment. Overall, changes in GPP in response to warming were positively correlated (p < 0.001) with changes in Reco (Figure 3). However, there were different trends for different grassland types, with cold grasslands showing increasing C fluxes with warming (Figure 3a). In

TABLE 1 Regression analysis of Log responses of main carbon fluxes under warming against mean annual temperature (MAT), mean annual precipitation (MAP), and the ratio of MAP to PET (MAP/PET) including all grassland types, with + and – representing direction of slope (m) and P level of significance and n indicating sample size

	ANPP		BNPP		GPP		NPP		Rs		Reco		NEE	
	m	P/*n*	m	P/*n*	m	P/*n*	m	P/*n*	m	P/*n*	m	P/*n*	m	P
MAT	-	**0.02/63**	-	0.09/32	-	**0.02/24**	-	**0.04/29**	-	0.70/24	-	0.14/25	-	0.09/19
MAP	+	0.96/56	-	**0.04/26**	+	0.43/24	-	0.14/23	+	0.55/23	+	0.39/25	+	0.47/19
MAP/PET	-	0.96/56	-	**0.04/26**	+	0.77/24	-	0.08/23	+	0.59/24	+	0.88/25	-	0.56/19

Bold indicates significant (p<0.05) regressions.

TABLE 2 Mean percentage changes in ANPP with warming (W); increased precipitation (P+, or both warming and increased precipitation (WP+), along with level of significance ($p < 0.001$: "***"; $0.001 < p < 0.01$: "**"; $0.01 < p < 0.05$: "*"; $0.05 < p < 0.1$; n.s. not significant; n.a. not analyzed)

Treatment	W	P+	WP+
Cold	n.s.	n.a.	n.s.
Temperate	16.9***	10.1*	11.7**
Semi-arid	n.s.	n.s.	31.8***
All grassland types	14.3***	13.8***	15.1***

Note. that the class of all grassland types includes all data from cold, temperate and semi-arid grasslands.

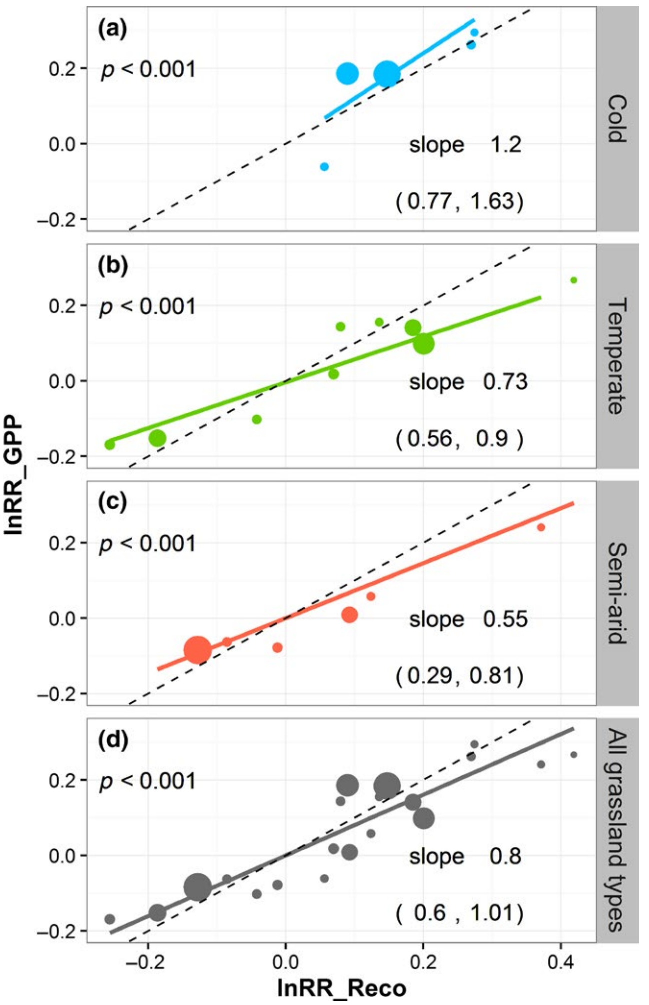

FIGURE 3 Correlation of warming response of GPP and Reco in (a) cold, (b) temperate, (c) semi-arid, and (d) all grassland types (i.e., all data of cold, temperate and semi-arid). Points represent single pairs of data, with different sizes showing different weighting. Colored lines represent best-fit lines obtained from meta-regression, whereas dashed black line represent the 1:1 line. Slope values represent mean values with the 95% confidence interval in brackets (low, high boundary value). Slopes > 1 indicate greater relative change of GPP in response to warming than Reco compared for the same sites [Colour figure can be viewed at wileyonlinelibrary.com]

contrast, semi-arid systems tended to decreasing C fluxes with warming, while temperate grasslands showed responses in both directions. Comparing the magnitude of change of GPP and Reco revealed that GPP was less sensitive to warming than Reco in semi-arid and temperate grasslands, indicated by slopes of 0.55 and 0.73, respectively (Figure 3b,c). The opposite trend, thus a higher stimulation of GPP than Reco (slope of 1.2) was observed in cold grasslands (Figure 3a), resulting likely in increasing NEE in cold and a decreasing NEE in temperate and semi-arid grasslands under warming. To be noted, these opposing effects in different grassland types are missed when comparing GPP and Reco over all sites, a comparison which yields a slope of 0.8 (Figure 3d) and suggests slightly greater sensitivity of Reco than GPP.

3.3 | Plant functional type-specific response of C fluxes to experimental warming

In addition to different grassland types, we also analyzed responses of C fluxes to warming for different plant functional types, i.e., sedges, forb, grass and grass/forb mixtures. As shown in Figure 4, all C fluxes were significantly stimulated (10.5%–24.1%) by warming for sedges ($p < 0.05$), which mainly occur in cold climate conditions. Responses for other plant functional types were not significant, except increases of ANPP (17.4%) and Reco (19.2%) for forb and Rs (10.3%) for forb-grass mixtures. Overall responses of C fluxes to warming were higher in sedges and forbs as compared to grass and grass/forb mixtures.

3.4 | Response of C fluxes depending on experimental warming duration

Reported periods of experimental warming ranged from one to 11 years, with 55% of warming experiments conducted for up to 3 years and 45% lasting longer than 3 years; however, all C fluxes were not measured at all sites, and so we selected the two C fluxes measured most commonly, ANPP and Rs, representing each a process of ecosystem C gain and loss. Still, longer-term responses (>3 years) were associated with much lower sample size, and thus, higher uncertainties (Figure 5). Nonetheless, for both cold and temperate grasslands, warming significantly stimulated ANPP (20.8% and 7.0%, respectively) for experiments ≤3 years, but stimulation was much lower and no longer statistically significant in experiments lasting longer than 3 years. Respiration (Rs) was significantly stimulated only in cold grasslands in short-term experiments, and similar to ANPP, this stimulation was not significant after 3 years of experimental warming. As for the time-averaged comparison (Figure 2), ANPP in semi-arid grassland was not stimulated by warming either in short or in longer-term studies.

3.5 | Relevance and influence of different warming methods on grassland C fluxes

The five most common methods used to simulate climate warming in grassland ecosystems were soil heating cables (cables), environmental chambers (chambers), infrared heaters (IRs), open-top chambers

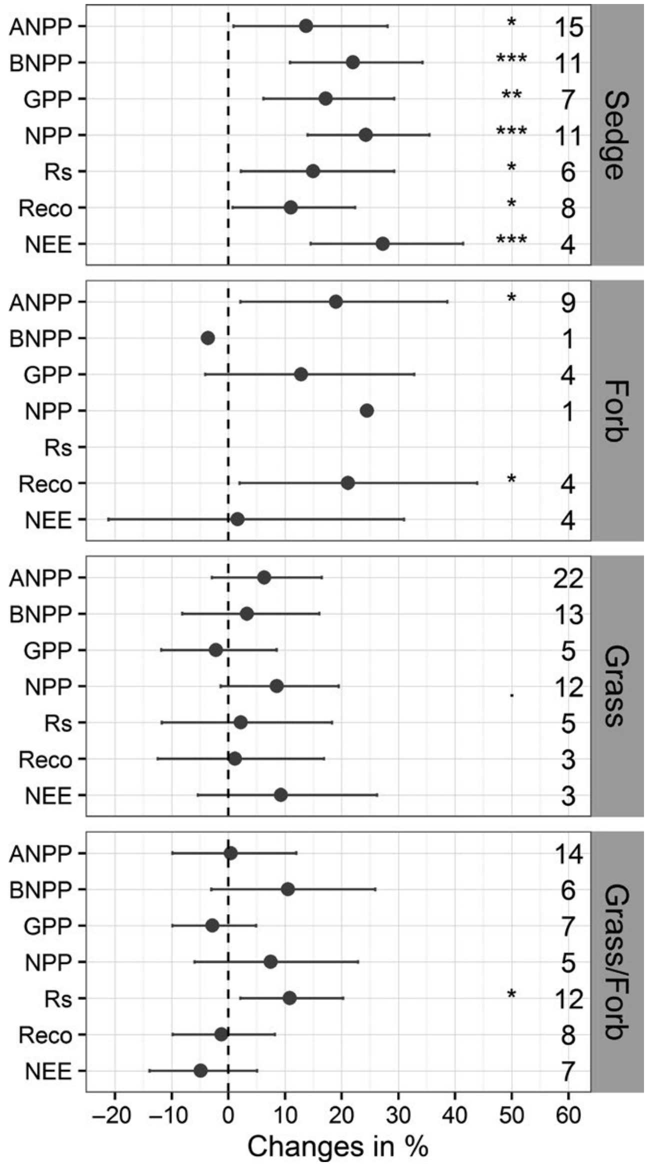

FIGURE 4 Mean percentage changes in main carbon fluxes across different grassland plant functional types under warming with 95% CI. Level of significance ($p < 0.001$: "***"; $0.001 < p < 0.01$: "**"; $0.01 < p < 0.05$: "*"; $0.05 < p < 0.1$: ".") and sample size for each variable is shown on the right

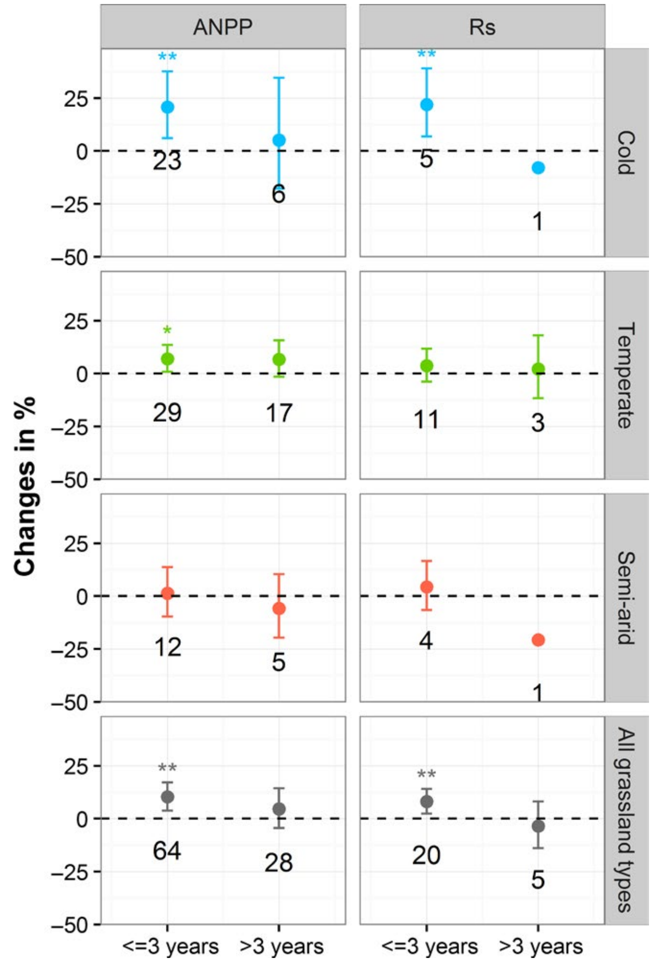

FIGURE 5 Mean percentage changes in ANPP (left) and Rs (right) for different grassland types (rows) in the short (≤3 years) and longer-term (>3 years) warming experiments with 95% CI, above which, significance code ($p < 0.001$: "***"; $0.001 < p < 0.01$: "**"; $0.01 < p < 0.05$: "*"; $0.05 < p < 0.1$: ".") for each warming period was shown. Note that the class of all grassland types includes all data from cold, temperate and semi-arid grasslands [Colour figure can be viewed at wileyonlinelibrary.com]

(OTCs) and translocation. IRs (e.g., n for ANPP = 26) and OTCs (n for ANPP = 24) were most used, while cables, chambers and translocation were applied far less (n for ANPP = 3–7 each). The use of methods was not evenly distributed across grassland types, but instead was rather type specific. IRs and OTCs were used mainly in temperate and cold grasslands, respectively. For semi-arid grasslands, we found a mixture of IRs, OTCs and translocation. Overall, the strongest and most significant warming effects on C fluxes were reported for OTCs (Figure 6). As these are mainly used in cold grasslands, which also showed the highest sensitivity to warming, it remains unclear if and to what extend this response could be related to the OTCs warming method or to other conditions in these grasslands. Due to the specific dominance of OTCs and IRs for cold and temperate grasslands, respectively, and the overall low sampling size of other methods (cables, chambers and translocations), a detailed cross- method comparison within one grassland type was not possible.

4 | DISCUSSION

4.1 | Variation in grassland C flux responses to warming

Including a large number of grassland warming experiments from a total of 70 sites, this study showed that warming by an average of 2°C increased various grassland C fluxes (n = 20–64) by 3.3%–15.4% (Figure 2). Another meta-analysis across multiple ecosystem types compiled by Lu et al. (2013) reported few significant warming-induced changes in grassland C fluxes, including a small, nonsignificant suppression of NPP (n = 6), a significant stimulation of Rs (n = 16),

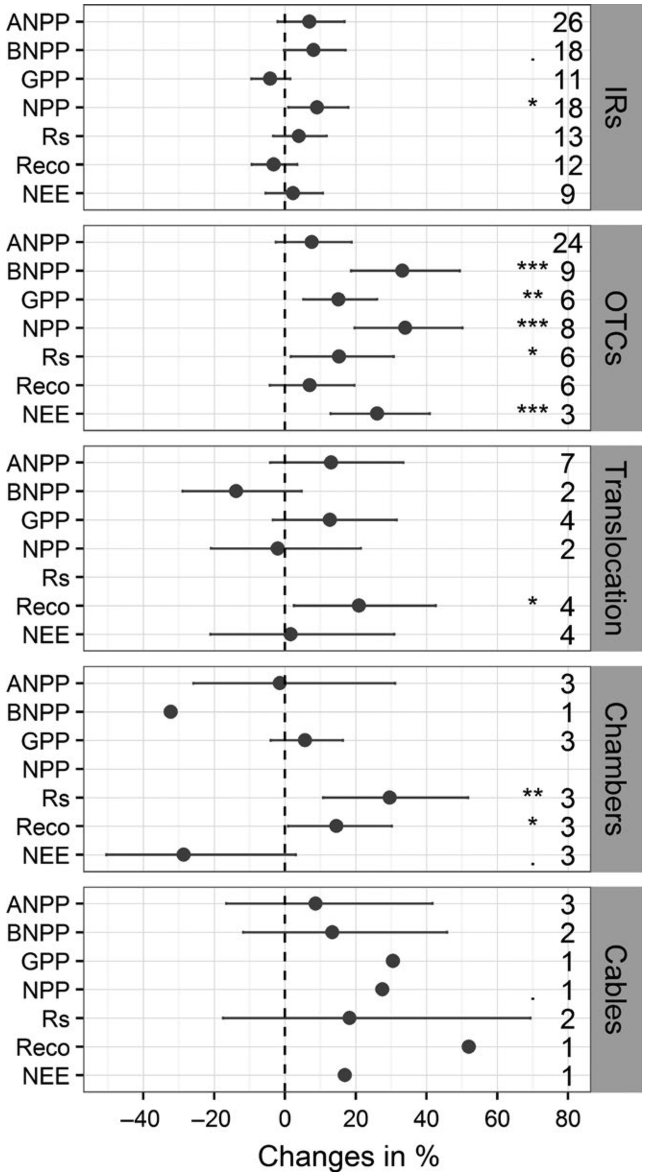

FIGURE 6 Percentage changes in main carbon fluxes with different warming methods across different biomes with 95% CI. Level of significance ($p < 0.001$: "***"; $0.001 < p < 0.01$: "**"; $0.01 < p < 0.05$: "*"; $0.05 < p < 0.1$: ".") and sample size for each variable is show on the right

and no change in NEE ($n = 2$). Compared to other meta-analyses of warming experiments (Lu et al., 2013; Rustad et al., 2001; Wu et al., 2011), our results included a much larger sample size for grassland ecosystems. This allowed both greater statistical power to discern warming responses for the general grassland biome (i.e., class of all grassland types), as well as a first-time analysis specifically for different grassland types, i.e., cold, temperate, and semi-arid, characterized by differences in climate, soil, and vegetation properties.

In our study, the changes in C fluxes under warming differed across cold, temperate, and semi-arid grasslands. These differences corresponded with differences in MAT and plant functional type rather than differences in precipitation (Table 1, Figure 4). In line with previous meta-analyses across multiple terrestrial ecosystems (Lu et al., 2013; Rustad et al., 2001; Wang et al., 2014), our study also reported that warming-induced changes in ANPP, NPP, NEE and GPP were negatively correlated with MAT (Table 1), which indicated higher sensitivity of C fluxes to warming of grassland ecosystems in colder environments.

Differences in warming method and plant functional type largely covaried with grassland type, making it difficult to identify whether the observed differences in C flux responses to warming were necessarily attributable to these climate-defined grassland types. That is, OTCs were the main approach used for warming experiments in cold grasslands, IRs dominated the warming experiments in temperate grasslands, and sample sizes of experiments using alternative methods were too small to allow comparison of methods within either grassland type. However, both warming methods produced a similar amount of air and soil warming, factors which should be the main driver of the observed changes in ecosystem C fluxes. Similarly, greater C flux responses to warming were observed in sedge-dominated ecosystems relative to other types of grassland (Figure 4), but this plant functional type occurred only in cold grasslands, and so it is not apparent whether the temperature sensitivity of C fluxes in this grassland type was due to its plant composition or to covarying soil and climate factors.

Cold grasslands were expected to be generally more limited by temperature than by water compared to semi-arid and temperate grasslands, and should benefit the most from longer snow-free and growing seasons associated with warming (e.g., Price, Waser, Ecology, & Jun, 1998). In addition, warming is likely to increase the microbial decomposition of soil organic matter (e.g., Crowther et al., 2016, Cheng et al., 2017) and N mineralization (e.g., Bai et al., 2013; Liu et al., 2017; Rustad et al., 2001), thus alleviating nutrient limitations and stimulating plant N uptake, particularly for cold grassland soils, which are characterized by the highest SOC contents. Only in cold grasslands did the responses of Rs, ANPP and BNPP significantly increase with warming magnitude (Table S1), suggesting that neither heat stress nor nutrient limitation of plant growth was confounding warming effects in these ecosystems.

In contrast to cold grasslands, C cycling in semi-arid grasslands was expected to be primarily water-limited rather than temperature limited (Sharkhuu et al., 2013). Ecosystem C fluxes can be constrained by the suppression of plant physiological activity through warming-induced atmospheric and soil water deficits (Niu et al., 2008). In addition, previous studies have reported that, in semi-arid grasslands, warming leads to heat stress of microbial processes (De Dato et al., 2008; Sardans, Peñuelas, & Estiarte, 2008); thus, nutrient turnover and availability are negatively affected (Fu, Shen, Zhang, & Zhou, 2012; Maestre et al., 2015) along with ecosystem C exchange in these semi-arid grasslands (Liu, Zhang, & Wan, 2009; Zong et al., 2013). Results from our analysis of multi-factorial experiments (Table 2) showed that the combination of warming and water additions mostly increased ANPP in semi-arid grassland, which demonstrated that soil moisture likely constrains the response of ANPP to warming in this grassland type.

TABLE 3 Effects of warming by on average 2°C on global grassland ecosystem C fluxes (GPP, Reco and NEE) either by considering different biome types (method A) or by averaging across biome types (method B)

Biome	GPP[a] (tC ha year^{-1})	Percentage change (%)	Area[b] (km^2)	Warming effect[c] (MtC year^{-1})	Factor[d]
Cold	14.2	15.3	3,005,023	652.6	
Temperate	27.1	0.8	7,147,700	163.7	
Semi-arid	16.5	−3.4	11,710,797	−663.8	
Total				152.5	
Cross-biome Average	20.0	3.3	21,863,520	1,442.3	9.5
Biome	Reco[a] (tC ha year^{-1})	Percentage change (%)	Area[b] (km^2)	Warming effect[c] (MtC year^{-1})	Factor[d]
Cold	12.1	11.0	3,005,023	400.4	
Temperate	15.3	2.0	7,147,700	214.0	
Semi-arid	7.4	−2.6	11,710,797	−222.7	
Total				391.7	
Cross-biome Average	12.0	3.7	21,863,520	974.0	2.5
Biome	NEE[a] (tC ha year^{-1})	Percentage change (%)	Area[b] (km^2)	Warming effect[c] (MtC year^{-1})	Factor[d]
Cold	7.8	24.9	3,005,023	585.0	
Temperate	5.1	−6.0	7,147,700	−216.5	
Semi-arid	7.8	1.1	11,710,797	99.0	
Total				467.5	
Cross-biome Average	6.7	7.9	21,863,520	1,155.6	2.5

[a]Ecosystem C fluxes (GPP, Reco and NEE) is average value of the studies included in this meta-analysis. [b]Area of each biome is derived from distribution mapping of world grassland types (Dixon et al., 2014). [c]Warming effect (MtC year^{-1}) = C fluxes (tC ha year^{-1}) × Percentage change (%) × Area (km^2) ÷ 10^6. [d]Factor = warming effect (Method B)/warming effect (Method A).

In temperate grasslands, warming stimulated both NPP and Rs, though the magnitude of these responses were smaller than in cold grasslands. That is, temperate grasslands showed only half the enhancement for NPP (11% vs. 23%) and two-thirds the enhancement for Rs (10% vs. 15%) as observed for cold grasslands (Figure 2). Limitations by water or nutrients may partly offset the potentially stimulatory effects of warming on both assimilatory and dissimilatory C exchange processes in temperate grasslands.

If we extrapolate these C flux responses globally, consideration of grassland type-specific responses yields markedly smaller responses than extrapolation of the mean response for the whole grassland biome. That is, due to the differences in the effect sizes (Figure 2) and areas (Dixon, Faber-Langendoen, Josse, Morrison, & Loucks, 2014) for different grassland types, global upscaling of mean (all grassland types) effects of warming on GPP, Reco and NEE results in overestimates of warming effects by 9.5, 2.5 and 2.5 times, respectively, compared to grassland type-specific warming responses and global coverage (Table 3).

4.2 | Relative sensitivities of different C fluxes to warming

Analysis based on simultaneously paired measurements of different ecosystem response variables can facilitate the evaluation of their relative sensitivities to manipulation (e.g., Xia et al., 2018). Comparing the relative sensitivities of GPP and Reco (Figure 3) is particularly important as their balance determines NEE, or ecosystem net C gain or loss. This comparison has not been conducted in previous meta-analyses of warming studies. Our analysis showed that GPP was less sensitive than Reco in response to warming, in semi-arid and temperate grasslands, while GPP trended toward greater sensitivity than Reco in cold grasslands (Figure 3). The different theoretical kinetic sensitivities of GPP and Reco may explain this contrasting response: at lower temperatures (i.e., cold grasslands), GPP should be more responsive to warming than Reco, while the reverse should occur at warmer temperatures (Luo, 2007; Niu et al., 2012). For cold grasslands, these warming responses of greater increases in GPP relative to Reco in paired samples are consistent with the overall effects of increasing NEE (Figure 2), indicating that the net effect of warming in these ecosystems is to increase carbon storage. This result is especially important given concerns over potential warming-induced destabilization of large soil C stores in cold ecosystems (e.g., Crowther et al., 2016). Smaller responses by GPP to warming than Reco for temperate and semi-arid grasslands could ultimately produce C losses, unless soil moisture or nutrients constrains the magnitude of both C fluxes in these ecosystems, as appears to be the dominant NEE responses in these grassland types (Figure 2). These results are related to mean soil and air temperature increase of 1.8 ± 1.0°C and 2.0°C ± 1.3°C, respectively, which is representative for COP 21/24 targets (following max. RCP4.5 scenario) but also points out that more severe temperature increases as generally predicted by RCP6.0 and RCP8.5 scenarios (IPCC, 2014) and particularly for cold grasslands, i.e. located at high latitude or high elevation (Pepin, Bradley, & Diaz, 2015), are hardly covered by current climate warming experiments.

4.3 | Diminishing responses to warming over time

Previous meta-analyses usually calculated response ratios by using values of C flux changes presented for the last year of the warming experiment; thus, these studies neglected potential changes over longer time periods (Lu et al., 2013; Rustad et al., 2001; Wu et al., 2011). However, our results show that in the first three years of warming experiments, ANPP and Rs greatly increase in both cold and temperate grasslands, while the response weakens in longer-term studies (Figure 5). Thus, conclusions drawn from short-term experiments should be regarded with caution, as they likely overestimate warming-induced C flux changes. There are mainly two mechanisms that can explain the diminishing effects of warming on C fluxes over time. First, warming can stimulate ANPP and Rs by enhancing plant litter and soil organic matter decomposition and N mineralization (Bai et al., 2013; Liu et al., 2017; Rustad et al., 2001), and thus providing more nutrients for plant growth. However, over longer time periods, accelerated decomposition and increased plant N uptake may decrease soil organic C and N pools as a new ecosystem balance is approached. In other cases, warming has been shown to increase N losses, ultimately reducing N availability for plant growth (e.g., Wu et al., 2012). Thus, ANPP can be increasingly limited by reduced N availability, thereby limiting or even reversing the initial response (Cantarel et al., 2013; Wu et al., 2012; Yoshitake et al., 2015). Second, changes in microbial and plant composition or even loss of grassland species are likely to occur after long-term warming. For example, fungi with higher temperature tolerance and forbs with deeper roots are more competitive under warming-induced drought and limited N availability conditions (Patton, Dong, Nyren, & Nyren, 2007; Xia, Niu, & Wan, 2009). Shifts in the microbial community with variable C use efficiency have been shown to reduce the temperature sensitivity of heterotrophic respiration (Zhou et al., 2011), which directly influences the C exchange of grassland ecosystems. Similar shifts in soil microbial C use efficiency, community structure, and Rs are also seen in a multi-decade soil warming experiment in a temperate forest (Melillo et al., 2017).

In contrast to our study, past meta-analyses of experiments across a range of terrestrial ecosystems did not detect statistically significant temporal changes in the response to warming of ANPP (Lin, Xia, & Wan, 2010; Rustad et al., 2001) or Rs (Lu et al., 2013; Rustad et al., 2001; Wu et al., 2011). This lack of statistical significance may result from the heterogeneity of site-level responses, smaller sample sizes, or averaging of responses among different grassland types. Our analysis for grasslands found that on average, both NPP and Rs increased with warming in the short-term (≤3) but not over the longer-term (>3) (Figure 6). Ultimately, long-term responses will determine the feedbacks of terrestrial ecosystems to the global C cycle (e.g., Piao et al., 2013), and so assessments reporting large short-term increases in production or decomposition in response to experimental warming should be treated with caution.

Our analyses show that experimental warming stimulates C fluxes in grassland ecosystems in regard to both C uptake and respiration. We also show that the response of C fluxes to warming strongly varies across the different grassland types, with higher warming responses in cold than in temperate and semi-arid grasslands. Cold systems also showed greater sensitivity of GPP to warming than Reco, while the converse occurred in temperate and semi-arid grassland. However, this meta-analysis also demonstrates that so far warming experiments in tropical and subtropical grasslands are highly underrepresented in the literature, even though they contribute 30% to the global terrestrial net primary productivity and store 15% of the world´s carbon. However, warming studies might be much more complex since ecosystem carbon stocks and fluxes highly depend on the extent of tree cover (Grace, San José, Meir, Miranda, & Montes, 2006).

Our finding that the initial stimulatory effects of warming on C fluxes weakened over time, even in cold grasslands, broadly contradicts responses of many ecosystem models, which typically predict that both production and decomposition increase with temperature in cold-limited ecosystems (Piao et al., 2013). This result calls for more long-term warming experiments and C flux measurements to better constrain warming effects on ecosystem C processes. Specific attention should also be given to shifts in plant and microbial community structures due to warming as these responses may only occur at decadal time scales (e.g., Melillo et al., 2017) but do ultimately determine the temperature responses of C fluxes at the ecosystem and global scales.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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