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Similar responses of soil carbon storage to drought and irrigation in terrestrial ecosystems but with contrasting mechanisms: A meta-analysis



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ABSTRACT

Global climate models predict that future precipitation regimes will largely change across the globe due to the intensification of the global water cycle under climate warming, which may generate considerable impacts on ecosystem carbon (C) dynamics. Although substantial manipulative experiments have been conducted to probe the responses of ecosystem C processes to altered precipitation, how soil C storage responds to both drought and irrigation is still unclear across biomes and the globe. A meta-analysis of 179 published studies was carried out to examine responses of soil C storage and associated C fluxes and pools to drought and irrigation. Our results showed that, on average across all biomes, drought and irrigation similarly induced minor increases in soil C pool (SCP) by 1.45% and 1.27%, respectively. However, drought and irrigation oppositely affected both C fluxes and plant C pools as well as in agroecosystems (e.g., croplands and grasslands). The drought-induced increases in root: shoot ratio and decreases in heterotrophic respiration and soil C turnover rate mostly contributed to minor increase in SCP, while an increase in newly fixed C inputs in soil was more important under irrigation. In addition, the relative changes in precipitation intensity in manipulative experiments were positively correlated with response ratios of plant C pool (PCP), net primary production (NPP), microbial biomass C, ecosystem, soil and heterotrophic respiration. The drought-induced responses of SCP exhibited a positive correlation with experimental duration but not under irrigation and for other C pools and fluxes. These results indicate that more attention should be paid to the responses of C allocation and turnover rate to drought and irrigation, which should be incorporated into land surface models to better project effects of altered precipitation on ecosystem C cycling in terrestrial ecosystems.

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1. Introduction

As a consequence of climate change (especially global warming), air circulation and the hydrological cycle have largely been intensified, leading to rapid shifts in precipitation regimes across the globe (IPCC, 2007). For example, global precipitation was

http://dx.doi.org/10.1016/j.agee.2016.04.030 0167-8809/© 2016 Elsevier B.V. All rights reserved. estimated to increase by $7.4\% \pm 2.6\%$ with each 1 °C increment in temperature over the period 1987–2006 (Wentz et al., 2007). Altered precipitation may directly and indirectly affect terrestrial C dynamics and then ecosystem structure and function (Cable et al., 2008), which may impact interactions with other global change drivers (e.g., elevated CO₂, climate warming). The shifts in precipitation regimes (i.e., amount, intensity, and frequency, IPCC, 2007) were suggested to have an even greater impact on ecosystem dynamics than the singular or combined effects of rising atmospheric CO₂ concentration and temperature (Weltzin et al., 2003). Therefore, understanding the responses of ecosystem

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C cycle to precipitation changes is of key importance to accurately project the rate and extent of climate change (Houghton, 2007).

Changes in precipitation not only affects soil physical processes (e.g., water infiltration, runoff, and leaching) but also impacts biotic processes (e.g., plant growth, CO₂ and N₂O production in soil) in ecosystems (Linn and Doran, 1984; Pastor and Post, 1986). Previous studies have mainly focused on precipitation-derived impacts on aboveground C processes, including leaf photosynthesis (e.g., Santiago and Mulkey, 2005), aboveground net primary productivity (NPP, Knapp et al., 2002), and species composition (Fauset et al., 2012). However, their responses to altered precipitation remain controversial among individual studies and biomes (Gerten et al., 2008). For example, aboveground NPP has been demonstrated to increase with mean annual precipitation in arid and semi-arid regions, while to decrease in moist ecosystems (Fay et al., 2003). The underlying mechanisms for the diverse responses of aboveground NPP to precipitation changes may be the different antecedent moisture conditions among the study sites (Yan et al., 2010). In contrast, understanding the responses of belowground C processes to altered precipitation (drought and irrigation) are relatively incomplete, largely due to methodological difficulties for estimating belowground C processes and the complex biotic interactions in soil- root interface (Luo and Zhou, 2006). For example, in a meta-analysis, the limited data (only four points) of belowground NPP made it difficult to evaluate the effects of altered precipitation (Wu et al., 2011), although belowground NPP accounts for more than one-half of NPP, especially in arid and semi-arid ecosystems.

Carbon storage in soil (i.e. soil C pool), the largest terrestrial C pool in the biosphere, is more than that in the atmosphere and vegetation combined (Post et al., 1982; Amundson, 2001) and is predicted to play a significant role in the changing climate (Lal, 2004). Altered precipitation affects soil C stocks by impacting soil C inputs from aboveground and belowground biomass and outputs from soil organic matter (SOM) decomposition (Fröberg et al., 2008). Drought may increase the physical protection of SOM and inhibit the decomposition rates, while irrigation may stimulate both C inputs and SOM decomposition via increased substrate availability (Vasconcelos et al., 2004). Altered water availability has been demonstrated to change the partitioning of photosynthetically assimilated C between shoots and roots (Asch

et al., 2005), and thus influenced C allocation between plants and soil (Gill and Jackson, 2000). Since soil organic C often has a longer C turnover time than plant C pools, C allocation between soil and plants is of importance for forecasting the future global climate (Weltzin et al., 2003). However, how soil C storage and C allocation respond to decreased or increased precipitation (i.e., drought or irrigation) is largely unclear in terrestrial ecosystems, which may limit our mechanistic understanding on the responses of ecosystem C budget to altered precipitation (Houghton, 2007).

To better comprehend the effects of altered precipitation on the terrestrial C cycle (especially soil C storage), we conducted a metaanalysis from diverse experimental precipitation changes to quantify a general tendency of the precipitation effects on soil C storage, related C fluxes and pools, C allocation (e.g., root: shoot ratio), and soil C turnover rate. This study focuses on effects of changes in precipitation amount (i.e., irrigation and drought treatments), although the precipitation changes include many aspects of precipitation regimes at the global scale (Alexander et al., 2006; IPCC, 2007). Totally 179 published studies were included to examine the responses of ecosystem C pools and fluxes to drought and/or irrigation before May 2013. The concerned variables in the study mainly included soil and plant C pools, microbial biomass C, and the related C fluxes (e.g., NPP, ecosystem respiration, soil respiration and its components). The metaanalysis was used to address the three following questions. First, to what extent was soil C storage affected by drought and irrigation? Second, what the mechanisms for the responses of soil C storage to drought and irrigation, respectively? Third, how did experimental variables affect the responses of C pools and fluxes to precipitation changes?

2. Materials and methods

2.1. Data sources

Peer-reviewed journal articles related to precipitation manipulation (i.e., drought and/or irrigation) published before May 2013 were searched using Web of Science (1900–2012) with the following search term combinations: (water OR rain* OR precipitation OR moist* OR drought OR dry OR irrigat* OR humid) AND



Fig. 1. Global distribution of manipulative experiments with precipitation changes selected in this meta-analysis. Circular and triangular symbols are sites with drought or irrigation treatments, respectively. Numbers before symbols are actual amount of sites in each biome from 179 papers, in which drought and irrigation treatments were conducted in 111 and 84 studies, respectively, and 16 studies included both of them. Trop. F.: Tropical forests; Tempe F.: Temperate forests; Boreal F.: Boreal forests.

(CO₂ 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* OR shift OR stimulat* OR regulat*). To avoid bias in publication selection, those studies were compiled into a database when the following five criteria were met (Text S1 and Database S1 in Appendix A & B): (i) at least one of the selected variables was measured in both control and treatments with altered precipitation (including drought and/or irrigation) at the same temporal and spatial scales; (ii) the plots under the precipitation treatment had the same ecosystem types, dominant vegetation composition, and environmental conditions as those under the control; (iii) the method, magnitude (absolute amounts or relative changes), and experimental duration of drought or irrigation were clearly indicated; (iv) the duration in the selected experiments should be longer than one growing season to avoid the response noise from short-term precipitation change; and (v) the means, standard deviations/errors, and sample sizes of the chosen variables were reported in papers. It should be noted that, in the studies with multi-factorial experiments including altered precipitation on selected variables, only the data from the control and drought or irrigation treatment were compiled to avoid the interactive effects of other factors on variables. In total, 179 published papers were compiled into the literature database from more than 2000 papers (Text S1, Fig. 1).

Environmental variables, including latitude (45°41′ S–74°30′ N, Fig. 1), mean annual temperature (–11.5 to 28.0 °C), and mean annual precipitation (66.3–4500 mm), were recorded directly from papers or cited papers or, in the case that it was not reported, extracted from the database at http://www.worldclim.org/using the location information (e.g., latitude and longitude). The studies that contained more than one magnitude of precipitation changes (e.g., Fay et al. (2008) and Yahdjian et al. (2006)) or more than one vegetation type (e.g., Casals et al. (2009) and Fiala et al. (2009)) were treated as independent treatments with multiple data points.

Data were extracted from the selected papers (Text S1, Database S1), including soil C pool (SCP), soil dissolved organic C, plant C pool (PCP), aboveground and belowground PCP, fine root biomass, coarse root biomass, microbial biomass C (MBC), litterfall, net photosynthetic rate, net primary production (NPP), aboveground and belowground NPP, ecosystem respiration, soil respiration, root and heterotrophic respiration. Since the diverse methods were used to measure some variables, we recorded the measurement methods for SCP (e.g., dry combustion, Walkley-Black, and weight loss on ignition), MBC (e.g., fumigation extraction, substrateinduced respiration (SIR), and chloroform fumigation-incubation), and DOC (e.g., dry combustion and colorimetric methods) to examine the effects of methods on these variables (Tables S2 and S3). To test the differences in responses of C processes to altered precipitation among biomes, nine types of biomes: tropical, temperate, and boreal forests, shrublands, croplands, grasslands, tundras, deserts, and wetlands, were differentiated in this analysis. Drought or irrigation treatments in wetlands were represented by lower or higher water table. Furthermore, since the more significant responses of C processes to climate changes (e.g., elevated CO₂ and warming) generally occurred in the first several years than in later years (Rustad et al., 2001), the effects of experimental duration on the responses of ecosystem C pools and fluxes were also analyzed in this study. We also examined the response difference among the five types of climate (arid, semiarid, semi-moist, moist, and Mediterranean) according to mean annual precipitation and evapotranspiration in the study sites. The effects of forcing variables included the magnitudes of changes in precipitation (-100 to 300%), experimental duration (1-35 years), and soil depth (5-60 cm) on responses of variables were also examined.

2.2. Data analysis

In this study, we employed a meta-analysis approach according to the methods of Hedges et al. (1999) and Luo et al. (2006) to calculate response ratio (*RR*) of each variables in individual studies to show the effects of drought or irrigation. The *RR* is defined as natural log of the ratio of the mean value of a concerned variable in treatment (drought or irrigation) plots ($\overline{X_t}$) to that in control one ($\overline{X_c}$, Eq. (1)):

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

The variance (ν) of each *RR* was calculated by Eq. (2) using the sample size (n_t and n_c) and standard deviations (S_t and S_c) of the concerned variables in treatment (t) and control groups (c).

$$\nu = \frac{s_t^2}{n_t X_t^2} + \frac{s_c^2}{n_c X_c^2}$$
(2)

The reciprocal of the variance (1/v) was considered as the weight (w) of each *RR*, whereby the values with greater precision were given a greater weight in valuation of the mean response ratio (*RR*₊) in Eq. (3), in which *m* is the number of groups (e.g., ecosystem types), and *k* is the number of comparisons in the *i*th group:

$$RR_{++} = \frac{\sum_{i=1}^{m} \sum_{j=1}^{k} w_{ij} RR_{ij}}{\sum_{i=1}^{m} \sum_{j=1}^{k} w_{ij}}$$
(3)

When the number of data points was larger than 20, the standard error of the RR_{++} was estimated by Eq. (4), which was used to evaluate the significance of RR_{++} by T-test.

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

The 95% confidence interval (95% CI) was calculated as RR_+ \pm 1.96 *S* (RR_{++}). The percentage changes of variables caused by drought or irrigation were measured by [exp (RR_{++}) – 1] × 100%. If the number was lower than 20, we used bootstrapping method by a resampling simulation to obtain the lowest and highest 2.5% values as our CI based on 5000 iterations (Janssens et al., 2010). If the 95% CI did not overlap with zero, a significant response induced by altered precipitation was detected.

The frequency distribution of individual response ratios (*RR*) was tested by Normal-test, and described by a Gaussian function using Eq. (5) in Sigmaplot software (Systat Software Inc., CA, USA):

$$y = \alpha \, \exp\left[-\frac{(x-\mu)^2}{2\sigma^2}\right] \tag{5}$$

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

In order to evaluate the effects of drought and irrigation on soil C turnover rate, we employed a one-pool biogeochemical model of soil C cycling in Eq. (6) (Olson, 1963) with the Bayesian probability inversion and a Markov chain Monte Carlo (MCMC) technique (Xu et al., 2006; McCarthy, 2007), as described in Groenigen et al. (2014):

$$C_t = C_0 \left[\exp(-Kt) \right] + I/K \left[1 - \exp(-Kt) \right]$$
(6)

where *t* is time (year), C_0 is the initial soil C content in a precipitation experiment (g C m⁻²); C_t is soil C content (g C m⁻²) at time *t*; *K* is the decomposition rate constant of soil C (year⁻¹, the

rate at which C leaves the soil system, 1/K is defined as soil C turnover time); *I* is the annual input of C to soil ($g C m^{-2} yr^{-1}$). The data used in the model thus included soil C content, decomposition rate, and soil C input, which were reported with at least two points over time in both the control and treatment groups (Database S2). We used Rs and Rh as proxies for soil C decomposition rate, and applied NPP as the proxy for soil C input. Totally there were 10 studies under drought and 32 studies under irrigation. Modeled Rh (*R*) was estimated by Eq. (7) (Groenigen et al., 2014), where C_m is the modeled SCP based on the model in Eq. (6), C_0 , *I* and *t* are as before.

$$R = (C_m(t_i) - C_0 + I \times t_i)/t_i \tag{7}$$

The modeled effects of drought and irrigation on *I* and *R* were constrained to be within $\pm 15\%$ of their observed effects, respectively (i.e., the ratio of soil C input under drought or irrigation treatment to that in the control, and the ratio of Rh (or Rs) under drought or irrigation treatment to that in control). The responses of *I*, *K*, and the projected equilibrium soil C (Equilibrium C, i.e., I/K, Groenigen et al., 2014) to drought or irrigation were calculated as Eq. (6). We weighted each observed response ratio by the replications in each study (i.e. $n_c \times n_t/(n_c + n_t)$, where n_c and n_t are as before).

The multivariate effects of latitude, mean annual temperature and precipitation, and treatments (including intensity and duration of precipitation changes) on the responses of the selected variables were analyzed by stepwise linear regression. The effects of biome types (i.e., tropical, temperate, and boreal forests, shrublands, croplands, grasslands, tundras, deserts and wetlands), climate types (i.e., arid, semi-arid, semi-moist, moist, and Mediterranean), precipitation treatments (i.e., drought and irrigation), and their interactions on the RR of the concerned variables were tested by ANOVA (Table 1). The three-way interaction among climate, biome, and treatment was not executed due to the limited number of data points as well as the two-way interactions for some variables. To assess the reliability of ANOVA, the Levene's test was applied to the model residuals for the homogeneity of variance across different levels of a certain factor (Table S4, Mopper and Kieber, 2002). For variables with heteroscedasticity, we transformed the RR data (i.e., SCP, PCP, above- and belowground PCP, MBC, NPP, belowground NPP, leaf C pool, net photosynthetic rate, and soil water content) using the arc-tangent function, which largely improved the homogeneity of variance (Tables 1,S5). The correlations between the relative changes in precipitation intensity in manipulative experiments (%) and *RR* of variables were examined by correlation analysis (Fig. 6, SPSS 16.0, SPSS Inc., Chicago, IL, USA). All the statistical analyses were listed in Table S6.

3. Results

3.1. The effects of drought and irrigation on soil and plant C pools

Across all biomes, both drought and irrigation induced similarly positive effects on soil carbon pool (SCP), but had opposite effects on plant C pool (PCP) (Figs. 2, 3 a–d, Table S1). Specifically, drought and irrigation increased SCP by 1.45% and 1.27%, respectively, while drought significantly decreased PCP by 25.1% and irrigation increased it by 34.4% (Figs. 2 and 3, Table S1). Drought and irrigation also triggered opposite responses of above- and belowground PCP, and microbial biomass C (MBC, Fig. 2). Drought significantly decreased aboveground NPP, belowground PCP, and MBC by 25.7%, 31.4% and 28.2%, while irrigation stimulated them by 25.5%, 15.4% and 42.2%, respectively (Figs. 2 and 3, Table S1). In addition, irrigation significantly increased leaf C pool and soil dissolved organic C, while drought induced a significant depression on leaf C pool (Table S1).

3.2. The effects of drought and irrigation on C fluxes and soil C turnover rate

The effects of drought and irrigation on ecosystem C inputs, including net primary production (NPP), aboveground NPP and belowground NPP (Figs. 2 and 3), were opposite as well as leaf net photosynthetic rate (Table S1). NPP, aboveground and belowground NPP were all significantly inhibited by drought and stimulated by irrigation except belowground NPP in temperate forests with no irrigation-induced change (Fig. 3). Similarly, drought and irrigation had opposite effects on CO₂ outflux (Figs. 2 and 3, Table S1). The former decreased ecosystem, soil, root, and heterotrophic respiration by 18.1%, 15.7%, 23.8%, and 34.7%, while

Table 1

Results of ANOVA showing the F values and levels of significance for the effects of climate types (Clim., i.e., arid, semi-arid, semi-moist, moist, and Mediterranean), biome types (Biom., including tropical forests, temperate forests, boreal forests, shrublands, croplands, grasslands, tundras, deserts and wetlands), and treatment types (Treat., i.e., drought and irrigation) on variables related to soil conditions, carbon pools and fluxes. The sample sizes of response ratio of all variables in ANOVA were listed in Fig. S7.

Variables	Clim.	Biom.	Treat.	Clim. × Biom.	$Biom. \times Treat.$	Clim. × Treat.
Soil C pool (SCP)	0.55 ^{ns}	0.26 ^{ns}	0.69 ^{ns}	0.23 ^{ns}	-	0.19 ^{ns}
Plant C pool (PCP)	6.03 ** (0.0018)	6.42 **** (0.000092)	7.03 [*] (0.012)	23.47 *** (0.00002)	-	2.77 ^{ns}
Aboveground plant C pool (APCP)	8.441 ^{***} (0.000047)	14 ^{***} (0.0000000)	5.72 [*] (0.019)	0.12 ^{ns}	7.42 *** (0.00099)	9.62 **** (0.00015)
Belowground plant C pool (BPCP)	5.14 ^{**} (0.0029)	4.99 ^{***} (0.00027)	17.91 ** (0.000071)	0.018 ^{ns}	3.92 ^{ns}	8.63 **** (0.00046)
Microbial biomass C (MBC)	9.775 ^{***} (0.00014)	3.134 [*] (0.03)	11.33** (0.0022)		-	-
Net primary production (NPP)	0.78 ^{ns}	-	13.29 ^{**} (0.0015)	-	-	-
Aboveground NPP (ANPP)	6.02 ** (0.00092)	2.38 ^{ns}	12.60** (0.00064)	-	-	4.99 * (0.028)
Belowground NPP (BNPP)	0.334 ^{ns}	0.09 ^{ns}	9.87 ** (0.0063)	-	-	0.74 ^{ns}
Ecosystem respiration (Re)	2.70 ^{ns}	0.05 ^{ns}	27.17 **** (0.000036)	-	-	-
Soil respiration (Rs)	13.08 *** (0.000000010)	0.98 ^{ns}	30.62 ^{***} (0.00000022)	5.48 ^{****} (0.000056)	5.46 ^{***} (0.0016)	2.50 ^{ns}
Leaf C pool	1.35 ^{ns}	0.86 ^{ns}	11.32** (0.0083)	-	-	-
Leaf net photosynthetic rate (Pn)	12.29 **** (0.0000000)	1.87 ^{ns}	18.05 ^{***} (0.000084)	1.61 ^{ns}	-	0.24 ^{ns}
Soil water content (SWC)	29.63 *** (0.0000000)	19.30 **** (0.0000000)	127.00**** (0.0000000)	1.15 ^{ns}	2.32 ^{ns}	1.12 ^{ns}
Water use efficiency (WUE) ^a	2.23 ^{ns}	2.34 ^{ns}	-	-	-	-
Root: shoot ratio ^b	13.47 *** (0.0001)	13.59*** (0.00053)	1.39 ^{ns}	-	-	-
Leaf mass per area (LMA)	1.53 ^{ns}	6.63 ^{****} (0.00047)	3.00 ^{ns}	-	-	-
Leaf area index (LAI)	0.12 ^{ns}	-	5.41 [*] (0.049)	-	-	-

The values in brackets are significance. ^{ns}sig. > 0.05; ^{*}sig. < 0.05; ^{**}sig. < 0.01; ^{***}sig. < 0.001.

The variables in italic were arc-tangent transformed before the ANOVA.

^a ANOVA was conducted within the treatment type of drought.

^b the effects of climate and biome was conducted within the treatment type of drought, the effect of treatment was analyzed within semi-arid grasslands, in which the irrigation experiments were only carried out.



Fig. 2. Potential mechanisms of similar responses of soil carbon pool (SCP) to drought (a) and irrigation (b). SWC: soil water content, PCP: plant carbon pool, APCP: aboveground plant carbon pool, BPCP: belowground carbo pool, MBC: microbial biomass carbon, DOC: dissolved organic carbon, Pn: leaf net photosynthetic rate, NPP: net primary production, ANPP: aboveground NPP, BNPP: belowground NPP, Re: ecosystem respiration, Rs: soil respiration, Rr: root respiration, Rh: heterotrophic respiration, WUE: water use efficiency, Root:shoot: root:shoot ratio, LMA: leaf mass per area, LAI: leaf area index. The short arrows \uparrow and \downarrow represent increase and decrease respectively in response to precipitation changes (drought or irrigation).

the latter enhanced them by 25.6%, 21.9%, 10.3%, and 23.0%, respectively (Figs. 2 and 3, Table S1).

Based on the data with at least two points over time under drought (10 groups) and irrigation (32 groups) treatments (Database S2) and a one-pool biogeochemical model, drought was estimated to significantly decrease both soil C input and decomposition rate constant (Fig. 4a), while irrigation was to increase them (Fig. 4b). Compared to the effects of irrigation on soil C input and decomposition rate constant, drought induced more inhibition in decomposition rate constant than soil C input (Fig. 4), which potentially caused the minor increase in SCP as well as decrease in soil C turnover rate.

3.3. Factors influencing C cycle responses to drought and irrigation

Among the environmental and forcing variables, mean annual temperature (MAT), intensity of precipitation change (Intensity) and experimental duration (Duration) were accepted by the best regression model for the response ratios (*RRs*) of PCP; MAT, Intensity and Latitude for the *RRs* of aboveground NPP; Intensity and Duration for the *RRs* of aboveground PCP; and only Intensity and mean annual precipitation (MAP) for the *RRs* of belowground PCP and MBC to drought (Table S8). Under irrigation, Intensity, MAP and Latitude were accepted by the best regression model for the *RRs* of SCP, ecosystem and root respiration, respectively (Table S8). MAT



Fig. 3. Weighted response ratio (*RR*₊₊) of soil carbon pool (SCP, a and b), plant C pool (PCP, c and d), aboveground and below-ground plant C pool (APCP, BPCP, e and f), microbial C pool (MBC, g and h), net primary production (NPP, i and j) and aboveground net primary production (ANPP, k and l), belowground NPP (BNPP, m and n), ecosystem respiration (*Re*, a and p), soil respiration (*Rs*, q and r) and its two components: root respiration (*Rr*, s and t), and soil heterotrophic respiration (*Rh*, u and v), to drought (a, c, e, g, i, k, m, o, q, s, and u) and irrigation treatments (b, d, f, h, j, l, n, p, r, t and v) in each biome. The error bars indicated 95% CI. Trop. F.: Tropical forests; Temp. F.: Temperate forests;



Fig. 4. Weighted response ratio (*RR*₊₊) of modeled soil C input (*Input*), soil C turnover rate (*K*,), and projected equilibrium soil C (Equilibrium C) to drought (a) and irrigation treatments (b). The results in drought and irrigation treatments are based on 10 and 32 studies, respectively (Database S2). Response ratios were weighted by replicates. The error bars indicated 95% CI. If it did not overlap with zero, a significant response induced by altered precipitation was considered.

had a significantly positive correlation with *RR* (SCP) in response to irrigation and a negative correlation with *RR* (PCP) to drought (Table S9). Biome type affected the responses of PCP, aboveground and belowground PCP, MBC, soil water content, root: shoot ratio and leaf mass per area, while climate type significantly affected responses of PCP, aboveground and belowground PCP, MBC, aboveground NPP, soil respiration, net photosynthetic rate, soil water content, and root: shoot ratio (Fig. 5, Table 1). A significant interaction between the different climate and biome types was

found on the responses of PCP and soil respiration. Treatments and biome types exhibited a significant interaction on response ratios of aboveground PCP and soil respiration Rs to altered precipitation, while interaction between treatments and climate types occurred in responses of aboveground and belowground PCP, and ANPP (Table 1).

The relative changes in precipitation intensity in manipulative experiments also displayed significant correlations with response ratios (*RRs*) of most C pools (PCP, aboveground and belowground



Fig. 5. Weighted response ratio (*RR*₊₊) of aboveground plant C pool (APCP, a and b), aboveground net primary production (ANPP, c and d), Leaf net photosynthetic rate (Pn, e and f), soil respiration (Rs, g and h), and root/shoot ratio (R/S, i and j) to drought (a, c, e, g and i) and irrigation (b, d, f, h and j) in different climate types, arid, semi-arid, semi-moist, moist, and Mediterranean.

PCP, fine root biomass, and MBC), and C fluxes (NPP, aboveground and belowground NPP, ecosystem respiration, soil and heterotrophic respiration, Fig. 6, P < 0.05). The frequency distribution of *RR* (SCP, PCP and soil respiration) to precipitation changes (including drought and irrigation) did not change with experimental duration, while drought-induced *RR* (SCP) displayed a positive correlation with duration (Fig. S3).

4. Discussion

4.1. Differential effects of altered precipitation on soil C storage vs. plant growth

Altered precipitation may affect plant growth and soil C storage differently, which impacts the fate of terrestrial C storage due to the different C turnover rates in plants and soil (Hyvönen et al., 2007). In our meta-analysis, drought and irrigation induced opposite effects on plant C pool (PCP, negative vs. positive, respectively) as expected (Figs. 2 and 3, Table S1). The opposite responses of PCP to drought and irrigation may be largely attributed to the positive relationship between changes in aboveground NPP and precipitation (Fig. 2, Knapp et al., 2008). Specially, in the drier sites, an increased supply of water effectively

relieves water stresses in both plants and soil organisms, promoting plant nutrient absorption and growth, and vice versa under drought (Kramer, 1969). However, both drought and irrigation induced similarly minor increases in soil C pool (SCP, Figs. 2, 3 a,b, Table S1), which was considerably different from the increasing trend across the precipitation gradients, especially in non-hydric sites (Post et al., 1982). Irrigation-induced increase in SCP may be ascribed to significant stimulation of plant-derived C, which is transferred to the soil through litterfall (Table S1) and root turnover, especially in arid and semiarid lands with high root: shoot ratio (Entry et al., 2002). In contrast, drought-induced depression of SOM decomposition (i.e., a decreased heterotrophic respiration, Figs. 2 and 3, Table S1), shift of C allocation to the belowground (e.g., increased root: shoot ratio, Fig. 5i, Table S1), and decrease in soil C turnover rate may be the principal mechanisms for minor increase in soil C storage (Post et al., 1982).

Under drought condition, soil water deficit may limit the mobility of both microbes and soluble organic matter, since microbes use the water films in macropores as channels to move and absorb substrates from the flowing water in the soil system (Chapin and Matson, 2011). The physical disconnection between microbes and soil organic matter (SOM) thus inhibited microbial biomass (Fig. 3) as well as the activity of extracellular enzymes



Fig. 6. The effects of manipulative precipitation changes (% change compared with control) on response ratio (RR) of plant C pool (PCP, a); aboveground plant C pool (APCP, b), belowground plant C pool (BPCP, c), fine root biomass (FRB, d), microbial biomass C (MBC, e), net primary production (NPP, f), aboveground NPP (ANPP, g) and belowground NPP (BNPP, h), ecosystem respiration (Re, i), soil respiration (Rs, j), and heterotrophic respiration (Rh, k).

(e.g., urease, protease, and β -glucosidase, Sardans and Peñuelas, 2005), resulting in the decrease in SOM decomposition (i.e., a decreased Rh in Figs. 2, 3 u, Table S1, Fontaine and Barot, 2005). Furthermore, the drought-induced inhibition of plant photosynthesis decreased plant nutrient demands to regulate microbial activities for C and N mineralization (Fig. 2, Table S1, Cheng et al., 2012).

Plants tend to allocate more biomass to roots to improve the acquisition of belowground resource under drought condition (i.e., an increased root: shoot ratio, Figs. 2 and 5, Table S1), so the impact of drought on belowground NPP would be less significant than that on aboveground one (Fig. 2a, Table S1, Crawford et al., 2000). Although root mortality has been indicated to increase under drought, a greater proportion of newly-assimilated C was allocated to and deposited in the roots in comparison to that in the shoots (Warembourg and Paul, 1973), with a relatively lower construction costs than other tissues (Chapin and Matson, 2011). The greater proportion of photosynthetic products allocated to the belowground also potentially increased the incorporation of root-borne organic substances into soil microorganisms and SOM under drought (Kuzyakov and Domanski, 2000). Meanwhile, drought-induced decreases in soil C input and soil C turnover rate together also slightly increased soil C accumulation (Amundson, 2001).

4.2. Opposite effects of drought and irrigation on C fluxes

Soil moisture is well known in affecting both photosynthesis and respiration, and then C inputs and outputs in plants and soil (Flexas et al., 2006). In this study, drought and irrigation caused negative and positive effects on C fluxes, respectively, including leaf net photosynthetic rate, NPP, aboveground and belowground NPP, ecosystem respiration, soil respiration and its two components (root and heterotrophic respiration, Figs. 2 and 3, Table S1).

Due to the tight coupling between C and water cycles, precipitation-induced changes in soil water availability simultaneously caused shifts in leaf stomatal conductance, chlorophyll, and leaf mass per area (LMA, Fig. 2, Table S1, Alberte et al., 1977), and then affected net photosynthetic rate and plant respiration (Limousin et al., 2013). Under the long-term drought or irrigation condition, plant community structure may also change largely (Langley and hungate, 2014). However, soil microbial community composition may shift in hours or days in response to change in soil water due to rapid microbial turnover rate (Clark et al., 2009), altering soil C retention and plant-available nutrients (Lundquist et al., 1999). These regulations progressively determined the opposite responses of C fluxes to drought and irrigation in most biomes (Fig. 3), but some exceptions existed in unique environments. For example, ecosystem respiration in tundra exhibited a significant increase in response to drought (Fig. 3). Since tundra soils are often water-saturated, a drought-induced decline in water table introduced more oxygen into previously anaerobic soil and then accelerated the rate of microbial decomposition (Oberbauer et al., 1992).

In addition to C input, soil C turnover rate is another key factor in determining C storage capacity in soil (Yan et al., 2014). Using a one-pool biogeochemical model (Olson, 1963), drought was estimated to decrease soil C input and decomposition rate constant (i.e., an increase in soil C turnover time) while irrigation was indicated to increase them (Fig. 4). Relative to the effects of irrigation, drought induced more inhibition in decomposition rate constant than soil C input and then decreased soil C turnover rate (Fig. 4), which potentially determined the minor increase in SCP under drought. Under the irrigation condition, the increase in soil C turnover rate (or decreases in soil C turnover time) may be constrained gradually by increased oxygen limitations in soil (Van Veen et al., 1991), resulting in a similar increase in SCP for all experiments.

4.3. Factors affecting responses of C pools and fluxes to drought and irrigation

Changes in precipitation regimes (e.g., rainfall amount and timing) have widely been demonstrated to affect plant performance and soil microbial activities significantly (Yuan et al., 2003). In our study, most of C fluxes and plant C pools showed the positive correlations between their responses and the relative changes in precipitation intensity in manipulative experiments (Fig. 6). Water limitation often occurs in non-hydric ecosystems, especially in the growing season, due to seasonal and interannual variability in the distribution of precipitation (Rodriguez-Iturbe et al., 2001). The increase in soil water availability under irrigation stimulated C influxes (e.g., NPP, aboveground and belowground NPP) more than C effluxes (e.g., soil and heterotrophic respiration), causing significant increases in fast-turnover C pools (e.g., PCP, aboveground PCP, belowground PCP, fine root biomass and microbial biomass C, in Fig. 6, Luo et al., 2004), and vice versa under drought. However, SCP and coarse root biomass, which are generally characterized with a relatively slower C turnover rate and lower sensitivity to transient disturbance (Gill and Jackson, 2000), did not exhibit significant relationships between their responses and the relative magnitudes of altered precipitation in the short-term (Fig. 6).

Since time is crucial for biotic acclimation under disturbance (Dale et al., 2001), experimental duration may impact the responses of ecosystem C processes to altered precipitation. In order to avoid the noise from short-term manipulation of precipitation, the transient effects of precipitation changes (<one growing season) were eliminated in this study. Our results showed that the response ratio (*RR*) of SCP, PCP and soil respiration to precipitation changes all did not change significantly with experimental duration (\geq one years, Fig. 7). However, the drought-induced *RR* (SCP) exhibited a positive correlation with duration (Fig. S3a). Under drought condition, plant acclimation or adaptation to deficient water supply may largely contribute to the unchanged trend of PCP with experimental duration (Hopkins and

Hüner, 1995). In the long term, plants have developed multiple mechanisms (e.g., non-photochemical chlorophyll fluorescence quenching, hydraulic conductivity, root size and depth, and wateruse efficiency, Table 1) to protect photosynthetic apparatus against water stress and to sustain plant resistance and acclimation to drought (Beier et al., 2012). Although irrigation could relieve the hydraulic pressure in plant-soil system, plant production and microbial activity might be more limited by light and nutrients (Huxman et al., 2004), which may progressively constrain the positive responses to irrigation and remained constant with increasing duration. Under long-term drought, the effects on soil respiration from inhibition of microbial activity and acclimation of plant community may counteract each other (Yordanov et al., 2000), leading to no significant changes in *RR* of soil respiration (Fig. 7), but a positive correlation between *RR*(SCP) and duration (Fig. S3a). The insignificant change in soil C storage with duration under irrigation may be explained by the increased loses of dissolved organic C (Oh et al., 2013), and increased soil C input by plants (Fig. 7b).

The conditions of the study sites, including latitude, mean annual temperature (MAT), mean annual precipitation (MAP), and soil moisture, may also affect the ecophysiological characteristics in different biomes (e.g., the dominant life-form and plant functional types, Arnold, 1955), and then impact the responses of C fluxes and pools to precipitation changes. For example, the response of SCP to irrigation exhibited a significant positive correlation with MAT (Table S9, Baker et al., 1992), while droughtinduced changes in PCP displayed a significant negative correlation with MAT (Table S9). In addition, climate types (i.e. arid, semi-arid, semi-moist, moist, and Mediterranean) also influenced the response ratios of some variables (e.g., aboveground PCP, aboveground NPP, soil respiration, net photosynthetic rate, and root: shoot ratio) to altered precipitation (Fig. 5). For example, in arid and semi-arid biomes, which experienced the long-term water stress, plants have evolved a series of constitutive and adaptive traits for dehydration avoidance (Chaves et al., 2003), resulting in no changes in net photosynthetic rate and aboveground PCP under



Fig. 7. The effects of experimental durations in precipitation changes on response ratio of soil carbon pool (SCP, a and b), plant carbon pool (PCP, c) and soil respiration (Rs, d). In panel b, 1: one year; <5: longer than one year but shorter than 5 years; 5–10: within 5–10 years; >10: longer than 10 years.

drought. In moist biomes, plants generally have a greater sensitivity to drought stress (Reddy et al., 2004), causing significant decreases in net photosynthetic rate and aboveground NPP (Fig. 5).

4.4. Experimental limitations in precipitation changes

Plant growth and development are closely linked with rainfall regime and/or regional soil moisture dynamics (Franklin, 1995). and then affect soil C sequestration. Global manipulative experiments with altered precipitation include changes in the magnitude of precipitation, rainfall timing, temporal and spatial variability, and/or extreme precipitation events. It is noted that the magnitude of precipitation in this study was only employed to probe the quantified effects of altered precipitation on terrestrial C cycles because of the temporal and spatial complexities of precipitation in diverse individual studies. In addition, due to soil moisture autocorrelation in antecedent and current conditions and landatmosphere interaction, manipulative changes in soil moisture may subsequently trigger shifts of local evaporation and runoff (Seneviratne et al., 2006) and consequently affect precipitation regimes in both control and treatment groups. Meanwhile, altered precipitation may affect soil temperature through changing soil water status and shading of manipulative equipment, which may confound the effects of water condition on the C cycle to some degree (Luo et al., 2008). However, these effects may be minor based on our field data (data not shown) and others (Gimbel et al., 2015: Wu et al., 2011).

Since the scenarios of future precipitation changes in many specific geographic regions remain ambiguous (Weltzin et al., 2003), the current single simulation of precipitation may not be necessarily in accord with realistic future conditions (Christensen and Christensen, 2003). Therefore, although the meta-analysis provides a statistical evaluation of the central tendency of C pools and fluxes in terrestrial ecosystems with the weighted response ratios across experiments, caution should be taken to apply them in forecasting future climate scenarios due to the inherent limitations of experimental manipulations and/or the methodologies used in such analysis (Beier et al., 2012).

4.5. Implications for land surface models and future experiments

Our results from the meta-analysis of 179 individual studies may provide some insights as to how terrestrial ecosystems respond to altered precipitation (drought and irrigation), and offer suggestions for development and improvement of land surface models as well as design of manipulative experiments in the future. First, both drought and irrigation induced a similarly minor stimulation on soil C storage, although they oppositely affected plant C pools and ecosystem C fluxes (Figs. 2 and 3, Table S1). The drought-induced increase in soil C storage largely resulted from the increases in root: shoot ratio and the decrease in SOC decomposition rate and soil C turnover rate (Figs. 2-4, Table S1), while irrigation-induced increase in plant-derived substrate inputs similarly caused soil C accumulation, although microbial decomposition was stimulated simultaneously. However, in current land surface models (e.g., Top-down Representation of Interactive Foliage and Flora Including Dynamics (TRIFFID) terrestrial ecosystem model and Lund-Potsdam-Jena dynamic (LPJ) model), the positive relationships between MAP and ecosystem C pools (plant and soil) have often been applied to simulate their responses to altered precipitation (Cowling and Shin, 2006). Although those results provided reasonable global-scale responses to irrigation, it was doubtful whether they can reflect the actual responses of soil C dynamic to drought. Therefore, future land surface models may need to incorporate the changes in C allocation, SOC decomposition, and C turnover time or rate into the responses of ecosystem C processes to altered precipitation to forecast the feedback of terrestrial ecosystems to climate change.

Second, the response ratios of most C pools and fluxes to altered precipitation were positively correlated with the relative changes in precipitation, but not with soil C storage (Fig. 6). Across precipitation experiments, different manipulation-imposed stresses (often from -50% to 50%) made it difficult to compare the responses of ecosystem processes to changes in water availability (Vicca et al., 2012). Future studies should follow a common metric that characterizes the actual treatment to design manipulative experiments carefully and to make their results comparable, which may be easily used in development and improvement of land surface models. Third, the responses of ecosystem C processes to altered precipitation did not vary significantly over time (Fig. 7). Although the short-term experiments have been found to be problematic for providing information about the long-term consequences of precipitation changes (Beier et al., 2012), the responses of PCP to altered precipitation in the short-term duration were not significantly different from those in the long-term experiments as well as soil respiration (Fig. 7). This implies that the short-term experiments in precipitation changes also offer some useful information for predicting the longterm consequences of plant C pools and soil C fluxes.

5. Conclusion

Altered precipitation regimes will largely affect key ecosystem processes, such as plant productivity and SOC decomposition in terrestrial ecosystems. Our meta-analysis found that, at a global scale, drought-induced soil water deficit resulted in negative responses of NPP (including aboveground and belowground NPP), plant C pools (aboveground and belowground), MBC, soil respiration and its components, while irrigation induced positive responses of these variables conversely. Interestingly, soil C storage displayed similar positive responses to both drought and irrigation. Agroecosystems (i.e., croplands and grasslands) also showed the similar responses. The responses of soil C storage to altered precipitation are determined by the balance between C input and output. Minor increase in SCP caused by drought could be interpreted by increases in root: shoot ratio, and decreases in heterotrophic respiration and soil C turnover rate, while an increase in newly fixed C inputs in soil was important under irrigation. The responses of C allocation and turnover time should be incorporated into land surface models to project the feedback of ecosystem C cycle to precipitation changes in terrestrial ecosystem.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2016.04.030.

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