Title

Impacts of drying–wetting cycles on rhizosphere respiration and soil organic matter decomposition

Authors

Zhu, Biao

Cheng, Weixin

Publication Date

2013-08-01

DOI

10.1016/j.soilbio.2013.03.027

Peer reviewed

Soil Biology & Biochemistry 63 (2013) 89–96

Contents lists available at SciVerse ScienceDirect

Soil Biology & Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Impacts of drying–wetting cycles on rhizosphere respiration and soil organic matter decomposition

Biao Zhu [a,b,*], Weixin Cheng [a,c]

[a] Department of Environmental Studies, University of California, Santa Cruz, CA 95064, USA
[b] Earth Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, CA 94720, USA
[c] State Key Laboratory of Forest and Soil Ecology, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110164, China

ARTICLE INFO

Article history:
Received 22 November 2012
Received in revised form
22 March 2013
Accepted 25 March 2013
Available online 12 April 2013

Keywords:
Drying–wetting
Rhizosphere respiration
C mineralization
Net N mineralization
Rhizosphere priming effect
Rhizodeposition

ABSTRACT

Drying–wetting cycles influence both soil organic matter (SOM) decomposition and rhizosphere processes. Rhizosphere processes also affect SOM decomposition through rhizosphere priming. However, little is known about how drying–wetting cycles regulate SOM decomposition with rhizosphere priming, because most previous studies incubated root-free soils and omitted the rhizosphere effect. To investigate the effect of drying–wetting cycles on SOM decomposition in the presence of plants, we grew sunflower (*Helianthus annuus*) and soybean (*Glycine max*) in a sandy loam soil under the treatments of either constant moisture or 12 drying–wetting cycles, and used a continuous ^{13}C-labeling method to partition soil respiration into rhizosphere respiration and SOM decomposition. We found that compared to the constantly-moist treatment, the severe drying–wetting cycles in soils planted with sunflower significantly reduced shoot biomass (32%), root biomass (52%), rhizosphere respiration (29%), and SOM decomposition (22%), while the moderate drying–wetting cycles in soils planted with soybean did not significantly affect these variables. Moreover, SOM decomposition rates in the planted treatment subjected to constantly-moist or drying–wetting conditions were significantly higher compared with the constantly-moist unplanted treatment, indicating a positive rhizosphere priming effect under both soil moisture regimes. However, drying–wetting reduced the rhizosphere priming of sunflower (69% versus 33%) likely due to lower plant biomass and rhizodeposition, but produced similar rhizosphere priming of soybean (82% versus 85%). Overall, drying–wetting cycles significantly modulated rhizosphere respiration and SOM decomposition, with the magnitude depending on soil drying intensity and plant growth performance.

Published by Elsevier Ltd.

1. Introduction

Soil moisture is a key factor affecting microbial activity and soil organic matter (SOM) decomposition (Moyano et al., 2013). Surface soils often undergo gradual drying by evapotranspiration followed by rapid wetting as a result of precipitation or irrigation. These drying–wetting cycles can influence soil aggregation (Denef et al., 2001; Cosentino et al., 2006), microbial activity and community structure (Gordon et al., 2008; Tiemann and Billings, 2011; Evans and Wallenstein, 2012), and C and N mineralization (Birch, 1958; Fierer and Schimel, 2003; Borken and Matzner, 2009). In the coming decades, many soils will likely be subjected to more frequent and intense drying–wetting cycles (Huntington, 2006), which can impact SOM decomposition and its feedback to climate change.

Soil CO_2 efflux is a large component of the global carbon cycle and plays a significant role in the feedback between the carbon cycle and climate change (Heimann and Reichstein, 2008). Field studies have observed large soil CO_2 efflux after rewetting of dry soils using eddy covariance techniques and soil respiration chambers (Jarvis et al., 2007). Following the early work of Birch (1958), many lab incubations of root-free soils (e.g. Fierer and Schimel, 2003; Xiang et al., 2008; Guo et al., 2012) have been used to investigate the impact of drying–wetting on microbial stress–response physiology (Schimel et al., 2007) and microbial decomposition of SOM (Borken and Matzner, 2009). However, soil CO_2 efflux in natural ecosystems consists of two components—microbial decomposition of native SOM, and rhizosphere respiration by roots and associated microbes using root-derived substrates which is omitted in previous root-free soil incubation studies. Most

* Corresponding author. Earth Sciences Division, Lawrence Berkeley National Laboratory, Berkeley, CA 94720, USA. Tel.: +1 831 331 3627.
E-mail address: biaozhu@gmail.com (B. Zhu).

0038-0717/$ – see front matter Published by Elsevier Ltd.
http://dx.doi.org/10.1016/j.soilbio.2013.03.027

microbes live in the rhizosphere and their activities are affected by the presence of plants. Thus predicting the realistic impact of drying–wetting cycles on SOM decomposition should account for plant–microbe interactions.

Increasing evidence suggests that root-derived substrate input to the soil (i.e. rhizodeposition) can increase SOM decomposition up to 3-fold (Cheng et al., 2003; Zhu and Cheng, 2011a), a similar magnitude of soil temperature and moisture effects on SOM decomposition. Although the mechanisms for this rhizosphere priming effect (defined as a change in SOM decomposition by root-derived carbon input) are not completely understood (Kuzyakov, 2002; Cheng and Kuzyakov, 2005; Kuzyakov, 2010), plant biomass and rhizodeposit quantity (Dijkstra et al., 2006; Dijkstra and Cheng, 2007a) have been shown to control the magnitude of rhizosphere priming effect. Increased soil moisture increases the rhizosphere priming effect (Niklaus and Falloon, 2006; Dijkstra and Cheng, 2007b), but the effect of drying–wetting cycles on rhizosphere priming has not been studied. Soil drying–wetting cycles may control the magnitude of rhizosphere priming by affecting plant biomass and rhizodeposit quantity. Moreover, soil drying intensity induced by plant transpiration rate can impact plant growth and rhizodeposit quantity, further affecting rhizosphere priming and the responses of SOM decomposition to drying–wetting cycles.

Here we investigated the impact of drying–wetting cycles on rhizosphere respiration and SOM decomposition in a 68-day greenhouse experiment. We partitioned cumulative soil respiration during an entire drying–wetting cycle into rhizosphere respiration and SOM decomposition using a continuous ^{13}C-labeling technique (Cheng and Dijkstra, 2007), estimated cumulative net N mineralization during the whole experimental period using an N-budgeting method (Cheng, 2009), and calculated rhizosphere priming effect as the difference in SOM decomposition between the planted treatment and the unplanted treatment (Kuzyakov, 2002; Cheng and Kuzyakov, 2005). Given that the intensity of drying can affect cumulative C and N mineralization in root-free soils (Borken and Matzner, 2009; Unger et al., 2010), we used two plant species with different transpiration rates to simulate two drying–wetting regimes. Sunflower (*Helianthus annuus* L.) has relatively high transpiration rate and causes severe soil drying, while soybean (*Glycine max* L. Merr.) has relatively low transpiration rate and leads to moderate soil drying. We hypothesize the severe drying–wetting in soils planted with sunflower significantly reduces rhizosphere respiration, SOM decomposition, cumulative net N mineralization and the rhizosphere priming effect, while the moderate drying–wetting in soils planted with soybean has little or no effect on these variables.

2. Materials and methods

2.1. Experimental setup

Surface (0–30 cm) soils were collected from a farm on the campus of University of California, Santa Cruz. The farm was converted from coastal grassland in 1974 and has been planted with various crops and vegetables such as sunflower, soybean, strawberry and lettuce. The sandy loam soil (Mollisol) had a pH of 5.8 (no carbonate), 10.7 mg C g^{-1} soil, and 1.3 mg N g^{-1} soil. The soil $\delta^{13}C$ was −25.7‰ and $\delta^{15}N$ was 7.5‰. The same soil was used in another experiment (Zhu and Cheng, 2012). The soils were sieved through a 4-mm screen and air-dried before use. A nylon bag filled with 1500 g washed sand was placed at the bottom of each bottom-capped polyvinyl chloride (PVC) pot (diameter 15 cm, height 40 cm, equipped with an inlet tube at the bottom for aeration and CO_2 trapping), and then 8300 g air-dried soil (equal to 8160 g oven-dried soil) was packed into each pot at a bulk density of 1.36 g cm^{-3}.

We used 22 pots in this experiment: 6 pots were unplanted, 8 pots were planted with sunflower (variety Sunbright F1), and 8 pots were planted with soybean (variety Envy). All pots were wetted to 25% (w/w, equivalent of 100% water holding capacity) and pre-incubated in the dark (covered with black plastic sheet) inside the greenhouse for 60 days before sowing. Among the 8 pots planted with sunflower or soybean, 3 pots were maintained at constant soil moisture and 5 pots at varying soil moisture. Therefore, there are five treatments in this experiment: unplanted with constant moisture ($n = 6$), sunflower with constant moisture ($n = 3$), sunflower with varying moisture ($n = 5$), soybean with constant moisture ($n = 3$), and soybean with varying moisture ($n = 5$). We planted five pre-soaked seeds of sunflower or soybean (inoculated with *Bradyrhizobium japonicum*) in the 16 planted pots and thinned to one individual plant per pot after seedling emergence.

We maintained a constant soil moisture of 25% (w/w) in the 6 unplanted pots and 6 planted pots (3 for sunflower and 3 for soybean). In order to achieve such constant soil moisture, we connected each of the 12 pots to a common reservoir of deionized water (a 19-L black bucket, 30 cm diameter, 36 cm height) with black rubber tubing and a solenoid valve (three-way normally open type, Parker Hannifin Corporation, CT). Water level in the bucket was maintained at 10 cm above the bottom of the pots by daily addition. When water was lost through evaporation in unplanted pots or evapotranspiration in planted pots, deionized water from the bucket flowed to the bottom of the pots through the rubber tubing and solenoid valve, and then to the top soil through soil pores due to capillary action. Every 2–3 days, we weighed each of the 12 pots to monitor the moisture content and adjusted it when needed. As a result, soil moisture in these 12 pots remained at approximately 25% (w/w) throughout the experiment.

Soil moisture in the other 10 planted pots (5 for sunflower and 5 for soybean) underwent 12 drying–wetting cycles (Fig. 1A). "Drying" occurred naturally by water loss through evapotranspiration, which gradually intensified from 80 g pot^{-1} day^{-1} initially to 410 g pot^{-1} day^{-1} for sunflower and 290 g pot^{-1} day^{-1} for soybean at the end of the experiment. "Wetting" was achieved by manually adding deionized water from the soil surface. During the first 10 days after planting, we kept soil moisture at 25% by daily watering to help seed germination and seedling growth. During the first 3 drying–wetting cycles (10–30 days after planting), both sunflower and soybean were subjected to moderate drought, and soil moisture varied between 25% and ~16%. Then during the next 8 drying–wetting cycles (30–64 days after planting), sunflower experienced severe periodic droughts (dry down to ~10%), while soybean was exposed to gradually increasing periodic droughts (dry down to 18–14%). During the last drying–wetting cycle when we measured soil respiration (Fig. 1B), soils under both species experienced a similar level of drying–wetting cycle, although the length of the cycle was 3 days for soils under sunflower (64–67 days after planting) and 4 days for soils under soybean (64–68 days after planting), because sunflower had higher biomass and larger transpiration rate than soybean.

Throughout the experiment, air temperature inside the greenhouse was maintained below 28 °C during the day (6 AM–6 PM) by an air conditioner and above 18 °C during the night (6 PM–6 AM) by a heater, and relative air humidity was kept at 50% by a dehumidifier. Supplemental lighting was turned on during cloudy days (light intensity < 800 μmol m^{-2} s^{-1}). To avoid anaerobic conditions in the 22 pots, we forced ambient greenhouse air through each pot for 30 min every 6 h using an aquarium pump controlled by a digital timer. Another timer controlled all solenoid valves connected to the pots of constant moisture treatment. Immediately before each period of aeration the watering connections were closed, and the aeration connections were opened, and right after

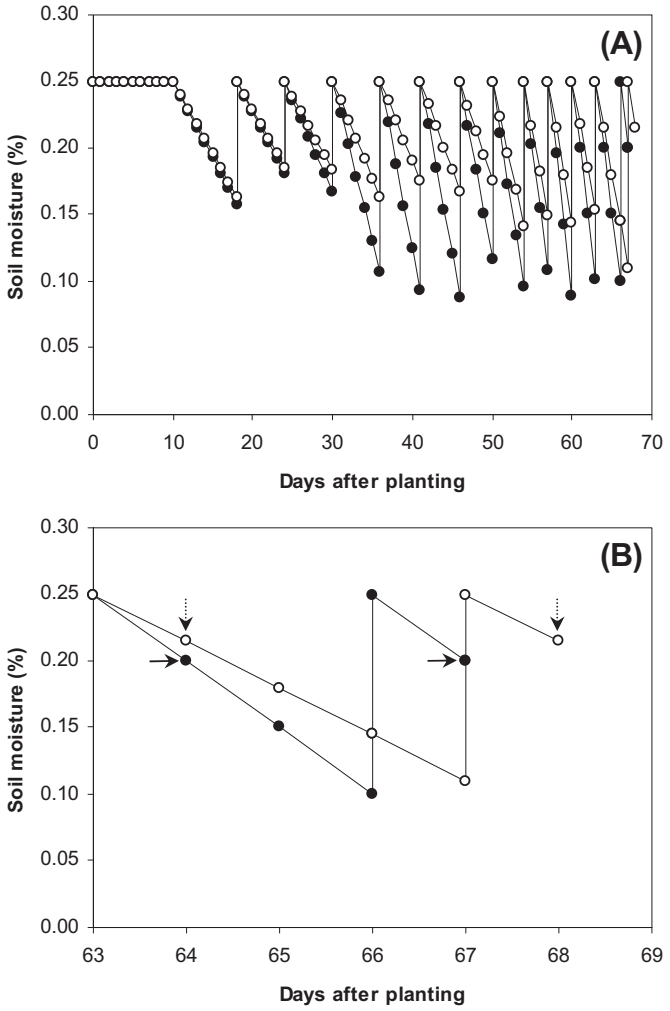

Fig. 1. Gravimetric soil moisture content (w/w, %) during the entire experimental period (A) and during 63–68 days after planting (B) for sunflower-varying treatment (closed circles ●) and soybean-varying treatment (open circles ○). CO_2 trapping was conducted during 64–67 days after planting for sunflower (indicated by the two horizontal arrows) and 64–68 days after planting for soybean (indicated by the two vertical arrows) to cover a complete drying–wetting cycle.

each aeration period, the connections were switched back. This valve system prevented interference between water flow and gas flow to the pot. This gas flow for aeration also helped water move from the bottom to the top of the pot. We randomly relocated the pots once a week to ensure similar growing conditions for the plants.

Plants were continuously labeled with naturally ^{13}C-depleted CO_2 in the greenhouse during the entire experiment. Throughout the experimental period, we maintained a constant CO_2 concentration (400 ± 5 ppm) and $\delta^{13}C$ value (−18.0 ± 0.5‰) inside the greenhouse. Details about this continuous ^{13}C-labeling method can be found in Cheng and Dijkstra (2007) and Pausch et al. (2013).

2.2. Measurements and calculations

During 64–67 days after planting, we chose 3 unplanted pots (randomly) and the 8 sunflower pots for soil respiration measurement followed by destructive sampling. This 3-day period covered a complete drying–wetting cycle for sunflower (Fig. 1B). Similarly, during 64–68 days after planting, the remaining three unplanted pots and the 8 soybean pots were measured and sampled. Both sunflower and soybean were at flowering stage during the CO_2 trapping and harvesting.

We measured soil respiration using a closed-circulation CO_2 trapping system (Cheng et al., 2003). Briefly, we sealed each pot at the base of the plant with non-toxic silicone rubber and first removed CO_2 inside each pot by circulating the isolated air through a soda lime column for 1 h. Then CO_2 produced during the next 72- or 96-h period in each sealed pot was trapped in a 400 ml 0.5 M NaOH solution by periodic air circulation for 30 min at a 6-h interval. Null systems were included to correct for handling errors. For the 6 planted pots of constantly-moist treatment, the solenoid valve-to-water reservoir was closed during the trapping period, and water was added to the pots during the night to compensate for water loss during the day. There is no water loss and thus no need to adjust soil moisture for the 6 unplanted pots of constantly-moist treatment. For the 10 planted pots of drying–wetting treatment, water was added on 66 and 67 days after planting to bring the soil moisture back to 25% (Fig. 1B). The rewetting was timed at the middle of the entire CO_2 trapping period to encompass the whole drying–rewetting cycle.

An aliquot of each NaOH solution was analyzed for total inorganic C using a Shimadzu 5050A TOC analyzer. Another aliquot was precipitated as $SrCO_3$ and analyzed for $\delta^{13}C$ using a PDZ Europa ANCA–GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Harris et al., 1997). The $\delta^{13}C$ values measured in $SrCO_3$ were corrected for minor contamination from carbonate in the NaOH stock solution and from sample handling (Cheng et al., 2003). We separated soil respiration (C_{total}) into SOM decomposition (C_{soil}) and rhizosphere respiration (C_{root}) using a two-source linear mixing model:

$$C_{soil} = C_{total}\left(\delta^{13}C_{root} - \delta^{13}C_{total}\right) \Big/ \left(\delta^{13}C_{root} - \delta^{13}C_{soil}\right) \quad (1)$$

$$C_{root} = C_{total} - C_{soil} \quad (2)$$

where $\delta^{13}C_{root}$ is the $\delta^{13}C$ value of rhizosphere respiration which was calculated based on the $\delta^{13}C$ value of shoot biomass and the ^{13}C fractionation of root-derived CO_2 relative to shoot biomass (1.1‰ for sunflower and 1.3‰ for soybean, Zhu and Cheng, 2011b). $\delta^{13}C_{total}$ is the measured $\delta^{13}C$ value of total respired CO_2, and $\delta^{13}C_{soil}$ is the mean $\delta^{13}C$ value of CO_2 solely from SOM decomposition measured in the unplanted treatment.

Immediately after CO_2 trapping, we harvested plant biomass and separated into shoots and roots. We homogenized the soil after root picking, and took a representative fresh soil sample (400 g) from each pot. Fine roots were removed from soil samples of planted pots by handpicking. Then these soils were prepared (oven-dried, ground, fumigated and/or extracted) for measuring soil moisture, C%, N%, $\delta^{13}C$ and $\delta^{15}N$, microbial biomass C and N, and soil mineral N (NH_4^+ and NO_3^-) within two days.

We measured microbial biomass C and N using the chloroform fumigation–extraction method (Wu et al., 1990). One subsample (50 g) was extracted with 60 ml 0.5 M K_2SO_4 solution, another subsample (50 g) was fumigated by ethanol-free chloroform in the dark for 48 h and then extracted with 60 ml 0.5 M K_2SO_4 solution. The concentration of total organic C in each extract was analyzed using a Shimadzu TOC 5050A analyzer. The concentration of total N in each extract was analyzed by a Lachat QuikChem 8000 auto-analyzer using a persulfate digestion method that oxidizes all N forms to NO_3^- (Cabrera and Beare, 1993). Microbial biomass C and N were calculated as the difference between fumigated and unfumigated samples, adjusted by a proportionality coefficient (0.45) for both C and N (Jenkinson et al., 2004). Soil mineral N was measured using 2 M KCl extraction (50 g soil and 60 ml solution) followed by

measuring NH_4^+ and NO_3^- concentration in the extracts on a Lachat QuikChem 8000 autoanalyzer.

We dried (60 °C and 48 h in an oven), weighed and ground all plant samples (shoots and roots), and dried (105 °C and 48 h in an oven) and ground a subsample of the soil (20 g) from each pot. Ground plant and soil samples were then analyzed for C%, N%, $\delta^{13}C$ and $\delta^{15}N$ using a Carlo Elba 1108 elemental analyzer interfaced to a ThermoFinningan Delta Plus XP isotope ratio mass spectrometer.

2.3. Statistical analyses

For all the variables in Tables 1, 2 and Fig. 2A–C, we used one-way ANOVA (post hoc Tukey test) to compare the means among different treatments. The mean of rhizosphere priming effect (Fig. 2D) was calculated as the difference in mean SOM decomposition rate between the planted treatment and the unplanted treatment. The 95% confidence interval of rhizosphere priming effect (Fig. 2D) was based on the independent-samples *t*-test between SOM decomposition rate in the planted treatment ($n = 3$ or 5) and that in the unplanted treatment ($n = 6$). In order to compare our results with other studies, we also computed rhizosphere priming effect on a relative scale (%), i.e. the difference in SOM decomposition rate between the planted treatment and the unplanted treatment relative to the SOM decomposition rate in the unplanted treatment (Cheng and Kuzyakov, 2005). Linear regression was used to show the relationship between root biomass and CO_2 fluxes (rhizosphere respiration and rhizosphere priming effect) (Fig. 3). We used SPSS 18.0 to perform all statistical analyses and set the significance level at $P < 0.05$.

3. Results

Both sunflower and soybean in the constant moisture treatment did not experience drought. Because of its high transpiration rate, sunflower in the varying moisture treatment periodically experienced a severe drought as indicated by the very low soil moisture (9–11%) and the wilted leaves at the end of the drying period, while soybean in the varying moisture treatment periodically experienced a relatively moderate drought due to its lower transpiration rate. Therefore, sunflower and soybean were exposed to the same frequency but different magnitude of drying–wetting cycles (Fig. 1A).

Shoot, root and total biomass of sunflower were 32–52% lower in the varying moisture treatment than in the constant moisture treatment ($P < 0.05$, Table 1), while the tissue N concentration of sunflower was 44–61% higher in the varying moisture treatment ($P < 0.05$, Table 1). Likely due to the periodic drought stress, the $\delta^{13}C$ values of shoot, root or total plant of sunflower were 1.8‰ higher in the varying moisture treatment ($P < 0.05$, Table 1). In contrast, plant biomass, tissue N concentration and $\delta^{13}C$ value of soybean did not differ significantly between the two moisture treatments (Table 1), likely because the moderate drying was less stressful.

The plants were successfully labeled with ^{13}C-depleted CO_2. The $\delta^{13}C$ value of plant C showed the expected ^{13}C-depletion, ranging from −40.6‰ to −38.7‰ in shoots and from −39.2‰ to −37.4‰ in roots for sunflower, and −37.1‰ in shoots and −35.8‰ in roots for soybean (Table 1). The $\delta^{13}C$ value of soil respiration in unplanted pots was −24.5‰ (Table 2), slightly higher than the $\delta^{13}C$ value of bulk soil organic carbon (−25.7‰). Moreover, the $\delta^{13}C$ value of soil respiration was −35.9‰ in sunflower–constant treatment, −34.3‰ in sunflower-varying treatment, −31.0‰ in soybean-constant treatment, and −31.4‰ in soybean-varying treatment (Table 2).

Using the two-source linear mixing model (Eqs. (1) and (2)), we partitioned soil respiration measured during the last drying–wetting cycle (C_{total}, Fig. 2A) into root-derived component (C_{root}, Fig. 2B) and SOM-derived component (C_{soil}, Fig. 2C). Rhizosphere respiration (C_{root}) was significantly lower in sunflower with varying soil moisture treatment than in sunflower with constant soil moisture treatment ($P < 0.05$), while it did not differ significantly between the two soil moisture treatments for soybean ($P > 0.05$, Fig. 2B). Sunflower showed higher rhizosphere respiration than soybean (Fig. 2B), mainly due to its higher root biomass (Table 1) and root N content (data not shown). Indeed, there was a significant positive relationship between rhizosphere respiration rate and root biomass ($R^2 = 0.80$, $P < 0.001$, Fig. 3A) or root N content ($R^2 = 0.76$, $P < 0.001$) across the four planted treatments.

Soil organic matter decomposition (C_{soil}) accounted for 34–36% of soil respiration in the two sunflower treatments and 51–54% of soil respiration in the two soybean treatments. C_{soil} was 22% lower in sunflower-varying treatment than in sunflower-constant treatment ($P < 0.05$), but was similar between the two soybean treatments (Fig. 2C). Unlike the pattern of rhizosphere respiration (Fig. 2B), SOM decomposition in the two soil moisture treatments planted with soybean was similar to that in the sunflower-constant treatment ($P > 0.05$), but was significantly higher than that in the sunflower-varying treatment ($P < 0.05$, Fig. 2C). There was no significant relationship between SOM decomposition rate and root biomass ($R^2 = 0.06$, $P > 0.05$) across the four planted treatments.

Compared to the unplanted control treatment, the presence of plants significantly increased the SOM decomposition rate by 33–85% ($P < 0.05$, Fig. 2C), indicating positive rhizosphere priming effects (C_{primed}, Fig. 2D). C_{primed} was significantly lower in sunflower-varying treatment than in sunflower-constant treatment (33% versus 69% above the unplanted control, $P < 0.05$), while it did not differ significantly between the two soybean treatments (82% versus 85% above the unplanted control, $P > 0.05$). Although sunflower had higher root biomass (Table 1) and higher root N content (data not shown) than soybean, the rhizosphere priming effect of sunflower was similar to or lower than that of soybean (Fig. 2D). A significant positive correlation between rhizosphere priming effect and root biomass was observed for the two sunflower treatments ($R^2 = 0.60$, $P < 0.05$, Fig. 3B) and for the two soybean treatments ($R^2 = 0.55$, $P < 0.05$, Fig. 3B), but not together ($R^2 = 0.05$, $P > 0.05$). The rhizosphere priming effect per unit root biomass was significantly higher in soybean than in sunflower.

Table 1
Plant biomass, $\delta^{13}C$ value, and N concentration of sunflower and soybean harvested at the end of the experiment. Values represent means of three or five replicates with standard errors in parenthesis. Different letters within each column represent significant differences in mean value between the treatments (one-way ANOVA, Tukey test, $P < 0.05$).

Treatment	Biomass (g kg soil^{-1})			$\delta^{13}C$ (‰)			N concentration (%)		
	Shoot	Root	Total	Shoot	Root	Total	Shoot	Root	Total
Sunflower-constant ($n = 3$)	9.33 (0.34) a	2.19 (0.26) a	11.51 (0.14) a	−40.6 (0.3) a	−39.2 (0.3) a	−40.4 (0.3) a	1.06 (0.07) a	1.06 (0.05) a	1.06 (0.05) a
Sunflower-varying ($n = 5$)	6.33 (0.22) b	1.05 (0.04) b	7.38 (0.22) b	−38.7 (0.1) b	−37.4 (0.1) b	−38.6 (0.1) b	1.53 (0.02) b	1.70 (0.04) b	1.56 (0.03) b
Soybean-constant ($n = 3$)	3.41 (0.27) c	0.46 (0.06) c	3.86 (0.33) c	−37.1 (0.3) c	−35.8 (0.3) c	−37.0 (0.3) c	2.82 (0.24) c	2.00 (0.05) c	2.73 (0.21) c
Soybean-varying ($n = 5$)	3.06 (0.17) c	0.48 (0.05) c	3.53 (0.21) c	−37.1 (0.3) c	−35.7 (0.1) c	−36.9 (0.2) c	3.15 (0.32) c	2.12 (0.07) c	3.02 (0.29) c

Table 2
$\delta^{13}C$ value of soil respiration ($\delta^{13}C_{total}$), plant $\delta^{15}N$ value, plant N content, soil mineral N (NH_4^+ and NO_3^-), microbial biomass C (MBC), and microbial biomass N (MBN) measured at the end of the experiment. Cumulative net N mineralization (CNNM) over the 128-day experiment (60-day pre-incubation plus 68-day plant growth) is calculated as the sum of N in plant biomass and in soil mineral N (NH_4^+ and NO_3^-). Values represent means of three to six replicates with standard errors in parenthesis. Different letters within each column represent significant differences in mean value between the treatments (one-way ANOVA, Tukey test, $P < 0.05$).

Treatment	$\delta^{13}C_{total}$ (‰)	Plant $\delta^{15}N$ (‰)	Plant N content (mg N kg soil^{-1})	NH_4^+ (mg N kg soil^{-1})	NO_3^- (mg N kg soil^{-1})	MBC (mg C kg soil^{-1})	MBN (mg N kg soil^{-1})	CNNM (mg N kg soil^{-1})
Unplanted-constant ($n = 6$)	−24.5 (0.3) a			0.7 (0.1) a	114.5 (4.7) a	215.9 (5.2) b	44.1 (2.3) a	115.2 (4.7) a
Sunflower-constant ($n = 3$)	−35.9 (0.2) d	6.2 (0.2) a	121.5 (5.2) a	0.4 (0.1) a	0.0	249.2 (4.6) a	33.3 (1.2) b	122.0 (5.2) a
Sunflower-varying ($n = 5$)	−34.3 (0.2) c	6.2 (0.1) a	114.8 (1.9) a	0.5 (0.1) a	0.5 (0.1) b	220.4 (7.9) b	33.8 (1.1) b	115.7 (1.9) a
Soybean-constant ($n = 3$)	−31.0 (0.5) b	7.5 (0.3) b	104.0 (1.4) a	0.5 (0.1) a	0.7 (0.1) b	207.8 (2.2) bc	37.2 (2.4) ab	105.2 (1.4) a
Soybean-varying ($n = 5$)	−31.4 (0.4) b	6.7 (0.1) a	104.4 (5.5) a	0.6 (0.1) a	1.4 (0.4) b	194.0 (2.7) c	34.7 (0.4) b	106.4 (6.0) a

After 68 days of plant growth and soil incubation plus 60 days of pre-incubation, soil NH_4^+ (0.4–0.7 mg N kg soil^{-1}) did not differ among the five treatments, while soil NO_3^- was only 0–1.4 mg N kg soil^{-1} in the four planted treatments, but was 115 mg N kg soil^{-1} in the unplanted treatment (Table 2) due to the lack of plant uptake. Total N content in plant biomass was 115–122 mg N kg soil^{-1} in the two sunflower treatments, and was 104 mg N kg soil^{-1} in the two soybean treatments. The $\delta^{15}N$ value of soybean was not depleted compared to the reference plant (sunflower) (Table 2), indicating negligible amount of N fixed by the soybean-*Bradyrhizobium* symbiosis. Therefore, we estimated cumulative net N mineralized from soil throughout the 128-day experiment as the sum of soil mineral N and plant N uptake (plant biomass N) measured at the end of this experiment. Although we did not measure initial soil mineral N at the beginning of pre-incubation, and ignored the potential gaseous losses of mineralized N through denitrification (which should be negligible because of frequent soil aeration), the comparison of cumulative net N mineralization among treatments should still be robust. Despite the difference in soil C mineralization measured during the last drying–wetting cycle (Fig. 2C), we observed no significant difference in cumulative net N mineralization among the five treatments ($P > 0.05$, Table 2). Moreover, microbial biomass C (MBC) ranged from 194 to 249 mg C kg soil^{-1}, and microbial biomass N (MBN) ranged from 33.3 to

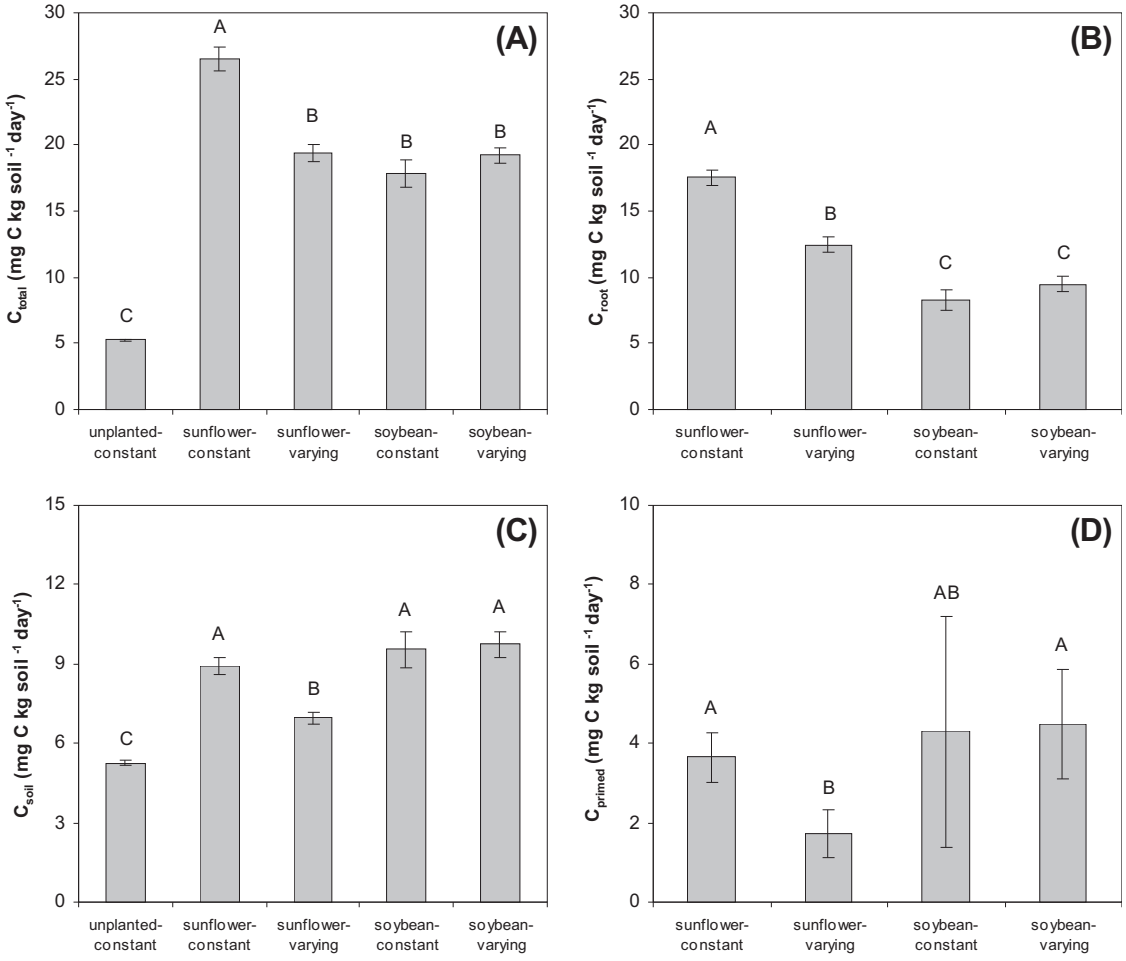

Fig. 2. Soil respiration (A), rhizosphere respiration (B), SOM decomposition (C) and rhizosphere priming effect (D) for the unplanted treatment and four planted treatments. Error bars represent standard errors of the mean in A–C and 95% confidence interval in D. Different letters in each figure represent significant differences in mean value between the treatments (A–C: one-way ANOVA, Tukey test, $P < 0.05$; D: comparing 95% confidence interval, $P < 0.05$).

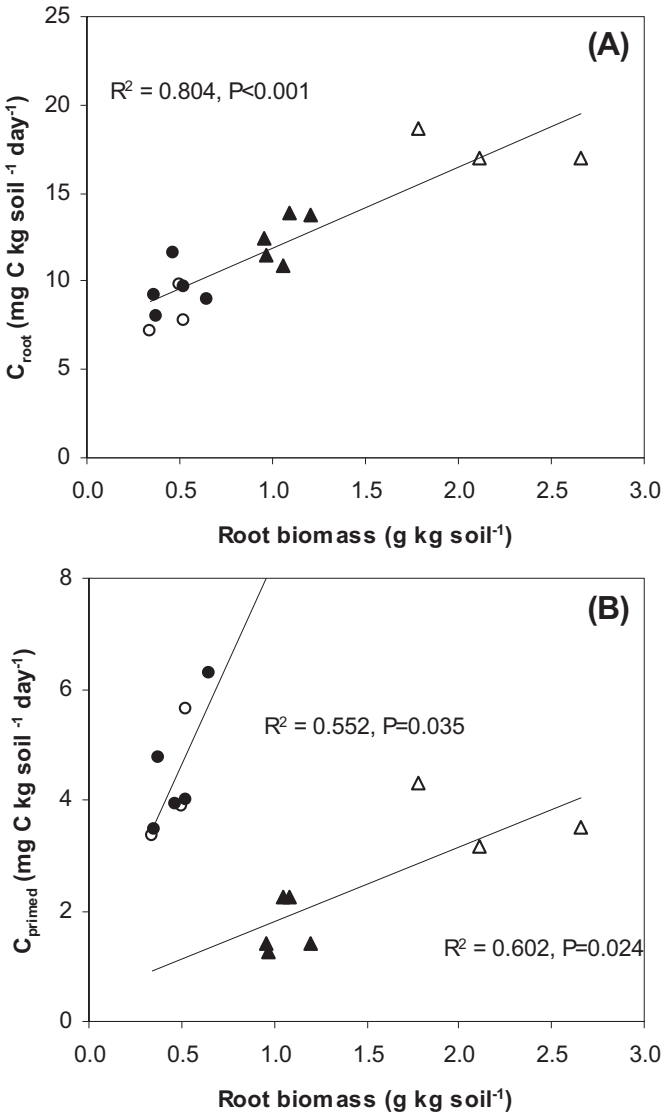

Fig. 3. (A) Relationship between rhizosphere respiration (C_{root}) and root biomass; and (B) Relationship between rhizosphere priming effect (C_{primed}) and root biomass across the four treatments with plants. Open triangles (△) represent sunflower-constant treatment, filled triangles (▲) represent sunflower-varying treatment, open circles (○) represent soybean-constant treatment, and filled circles (●) represent soybean-varying treatment.

44.1 mg N kg soil^{-1} among the five treatments and was reduced by the presence of plants (Table 2). Compared to the constantly-moist treatment, drying–wetting decreased MBC (but not MBN) in pots planted with sunflower ($P < 0.05$, Table 2), but had no significant effect on MBC or MBN in pots planted with soybean ($P > 0.05$, Table 2).

4. Discussion

The impact of drying–wetting on soil C mineralization has been studied extensively in both lab and field conditions (Borken and Matzner, 2009; Moyano et al., 2013). However, lab studies often incubated root-free soils and omitted the rhizosphere effect, while field studies rarely separated soil-derived CO_2 from root-derived CO_2 by isotopic techniques. Therefore, we are still unclear about how plants affect the responses of soil C mineralization to drying–wetting cycles. In this study, we showed that soil drying–wetting had a negative or neutral effect on soil C mineralization and rhizosphere priming, depending on soil drying intensity and plant growth performance. This clearly shows that drying–wetting cycles can modulate soil C dynamics through rhizosphere processes.

4.1. Do drying–wetting cycles stimulate cumulative soil C and N mineralization?

As far as we know, this is the first measurement of cumulative soil C mineralization under the presence of plants during a complete drying–wetting cycle. Compared with soils planted with sunflower or soybean and kept constantly moist, soils planted with sunflower and subjected to severe drying–wetting released 22% less SOM-derived CO_2, while soils planted with soybean and subjected to moderate drying–wetting released the same amount of SOM-derived CO_2 (Fig. 2C). Two possible mechanisms may explain this decline in soil C mineralization by drying–wetting in the sunflower treatment: (1) after 3 moderate and 8 severe drying–wetting cycles, the flush of soil C mineralization after wetting was not much higher compared with the constantly-moist soil, because frequent drying and wetting diminished the wetting flushes due to limitation of accessible soil organic mater pool (Xiang et al., 2008; Evans and Wallenstein, 2012); and (2) drying–wetting significantly reduced sunflower shoot (32%) and root biomass (52%), which likely led to lower plant C inputs to the soil (rhizodeposition), less microbial biomass and activity (Table 2), and smaller rhizosphere priming effect (discussed in more detail in 4.3 section). Moreover, we found similar C mineralization in soils planted with soybean between a constantly-moist treatment and a moderate drying–wetting treatment. This may be related to the less severe drought experienced by soybean due to its relatively low transpiration rate (or drying rate), which did not significantly impact plant biomass, rhizodeposition, microbial biomass and activity, and rhizosphere priming effect (discussed in more detail in 4.3 section).

We also used an N-budgeting method (Cheng, 2009; Zhu and Cheng, 2012) to estimate cumulative net N mineralization during the entire experimental period. We found that drying–wetting had no effect on cumulative net N mineralization in soils planted with sunflower or soybean. Soils planted with sunflower and unplanted control soils both showed higher, but not significant, rates of cumulative net N mineralization than soils planted with soybean (Table 2). The cumulative net N mineralization rate is difficult to measure in the field because accurately quantifying plant N uptake and all N losses to the environment is nearly impossible. Laboratory studies using root-free soils have found mixed effects of drying–wetting on cumulative net N mineralization, ranging from inhibition (Pulleman and Tietema, 1999; Mikha et al., 2005; Muhr et al., 2010) to stimulation (Miller et al., 2005; Gordon et al., 2008; Xiang et al., 2008), depending on factors such as soil type, experimental setup, and measurement method (Borken and Matzner, 2009). As the presence of plants could affect soil gross and net N mineralization through rhizosphere processes (Frank and Groffman, 2009), future studies should use approaches to measure soil N cycling in intact plant communities to better predict soil N availability in a changing environment.

It should be noted that the effect of drying–wetting severity is associated with the effect of species identity on the cumulative soil C/N mineralization. Sunflower induced severe drying–wetting cycles on soils due to its high transpiration rate, while soybean induced moderate drying–wetting cycles on soils due to its relatively lower transpiration rate. Therefore, the different impacts of drying–wetting on soil C/N mineralization (Fig. 2 and Table 2) are attributed to both the different soil drying intensity and the associated different plant growth performances.

4.2. Do drying–wetting cycles impact rhizosphere respiration and SOM decomposition to the same extent?

We used a novel continuous ^{13}C-labeling method to partition soil respiration and found that rhizosphere respiration and SOM decomposition showed similar responses to drying–wetting cycles. Compared to the constant soil moisture treatment, drying–wetting cycles did not significantly affect the proportion of SOM decomposition to soil respiration (34% vs. 36% in sunflower, and 54% vs. 51% in soybean) when the entire drying–wetting cycle was included. Previous studies tend to show that microbial respiration is more responsive to short-term dynamics in soil moisture than rhizosphere respiration. For example, Carbone et al. (2011) showed that root respiration was more responsive to seasonal changes in soil moisture, while microbial respiration dominated the response to episodic wetting in a Mediterranean pine forest, using a natural abundance ^{14}C method for source partitioning. Other studies using isotopic (Unger et al., 2010; Casals et al., 2011) or non-isotopic (Liu et al., 2002; Yan et al., 2010) methods for source partitioning also found similar results. Rhizosphere respiration is dependent on substrate input from recent photosynthesis (Högberg et al., 2001; Kuzyakov and Cheng, 2001), which should be less affected by short-term soil moisture dynamics. Microbial respiration, however, is determined by available biomass or non-biomass sources of soil organic carbon, which can increase after rewetting due to various mechanisms (Wu and Brookes, 2005; Xiang et al., 2008; Borken and Matzner, 2009; Navarro-Garćia et al., 2012). In this study, the severe drying–wetting reduced microbial and rhizosphere respiration to a similar extent in the sunflower treatment, and the moderate drying–wetting did not affect either component in the soybean treatment. Differences in experimental designs and methods (e.g. cumulative flux during the entire drying–wetting cycle vs. short-term flux during the dry or wet period) might contribute to the different results between this greenhouse study and previous studies.

4.3. Do drying–wetting cycles affect rhizosphere priming effect?

Due to technical challenges to remove water from the unplanted soils at the same rate as the evapotranspiration rate in the planted soils without unintended effect on soil temperature and CO_2 trapping during respiration measurement, we did not include an unplanted, varying-moisture treatment. Therefore, our calculation of rhizosphere priming effect for the two planted, varying-moisture treatments is different from the common definition (i.e. change in SOM decomposition between bulk soil and rhizosphere soil under the same temperature and moisture conditions, Kuzyakov, 2002; Cheng and Kuzyakov, 2005). Given that previous studies on rhizosphere priming are often conducted on well-watered soils to maintain the same moisture as in the unplanted control treatment (Kuzyakov, 2010), and that most soils are naturally exposed to drying–wetting cycles induced by evapotranspiration and precipitation/irrigation, comparing SOM decomposition in a planted, varying-moisture treatment with that in an unplanted, constant-moisture treatment provides useful information on soil C/N dynamics.

The response of priming effect to soil moisture dynamics was little studied (Kuzyakov, 2010). Two previous studies have showed an increase in priming effect with increasing soil moisture (Niklaus and Falloon, 2006; Dijkstra and Cheng, 2007b). In this study, compared with the constantly-moist treatment, the severe drying–wetting reduced rhizosphere priming effect of sunflower from 69% to 33%, while the moderate drying–wetting did not impact rhizosphere priming effect of soybean (85% vs. 82%). As previous studies have found a positive correlation between rhizosphere priming effect and plant biomass (Dijkstra et al., 2006) or the amount of rhizodeposition (Dijkstra and Cheng, 2007a), it is likely that the severe drying–wetting reduced biomass and presumably rhizodeposition of sunflower (Table 1), which led to lower microbial activities (Table 2), and thus weaker rhizosphere priming effect; whereas the moderate drying–wetting had no effect on biomass or rhizodeposition of soybean, which resulted in similar level of microbial activities, and accordingly similar magnitude of rhizosphere priming effect. The positive correlation between rhizosphere priming effect and root biomass for both sunflower and soybean (Fig. 3B) seems to support this mechanism, although more evidence from direct measurement of the amount and composition of rhizodeposition and the activity of soil microbes (e.g. soil extracellular enzyme activity) are needed in future studies. Nevertheless, it appears that the impact of soil drying–wetting cycles on rhizosphere priming effect may be indirectly mediated by the response of plant growth to the water conditions and subsequently plant C inputs to the soil (i.e. rhizodeposition).

4.4. Implications for the responses of soil CO_2 efflux to moisture dynamics

Our results indicate that soil moisture dynamics or drying–wetting cycles can impact plant–soil interactions (i.e. rhizosphere priming effect) and soil CO_2 efflux. Many lab incubation studies have shown that soil moisture dynamics can significantly affect CO_2 efflux from root-free soils (Borken and Matzner, 2009; Moyano et al., 2012). This study and two recent studies (Niklaus and Falloon, 2006; Dijkstra and Cheng, 2007b) provide further evidence that soil moisture content and dynamics exert significant control of rhizosphere priming effect and thus CO_2 efflux from soils under the presence of plants. Furthermore, most of the previous studies on rhizosphere priming effects are conducted in greenhouse or growth chamber where soil moisture is kept constant in both planted and unplanted treatments by frequent watering (Cheng and Kuzyakov, 2005; Kuzyakov, 2010). The results of these studies should not be directly applied to field ecosystems because they normally expose to drying–wetting cycles. This study shows that the rhizosphere priming effect of sunflower under drying–wetting conditions is lower than that under constantly wet conditions, implying that future increases in drought in some ecosystems may reduce soil carbon loss through its indirect effect on plant growth and rhizosphere priming. This indirect effect of drying–wetting on soil C dynamics through rhizosphere priming should be further explored, particularly in field settings, and be incorporated into ecosystem models to improve the prediction of the response of soil carbon storage and nutrient availability to future changes in precipitation.

5. Conclusions

Our results showed a clear impact of drying–wetting cycles on rhizosphere respiration and soil C mineralization. The severe drying–wetting regime inherent with sunflower plants reduced plant biomass, rhizosphere respiration and SOM decomposition, while the moderate drying–wetting regime associated with soybean plants did not significantly affect these variables. Cumulative net N mineralization during the entire experimental period was not affected by drying–wetting in soils planted with either sunflower or soybean. The autotrophic and heterotrophic component of soil respiration measured during a complete drying–wetting cycle showed similar proportional responses to drying–wetting. Moreover, the presence of plants significantly increased SOM decomposition rate, resulting in notable positive rhizosphere priming. This rhizosphere priming effect was reduced by the severe drying–

wetting of soils planted with sunflower, but was not affected by the moderate drying–wetting of soils planted with soybean. Overall, our results indicate that drying–wetting cycles can impact rhizosphere respiration and SOM decomposition. Thus, future changes in precipitation and evapotranspiration can impact soil moisture dynamics and the release of C from soils.

Acknowledgments

We thank Ching-Yu Huang, Amy Concilio and Linda Luong for laboratory assistance, Joy Matthews and Dyke Andreasen for isotope analysis, and two anonymous reviewers and Caitlin Prices for insightful comments that significantly improved this manuscript. This study was supported by grants from the National Research Initiative of the U.S. Department of Agriculture's Cooperative State Research, Education and Extension Service, the U.S. Department of Energy's Office of Science through the Midwestern Regional Center of the National Institute for Climatic Change Research at Michigan Technological University, and the Kearney Foundation of Soil Science, and summer research awards from the Department of Environmental Studies, University of California, Santa Cruz.

References

Birch, H.F., 1958. The effect of soil drying on humus decomposition and nitrogen availability. Plant and Soil 10, 9–31.
Borken, W., Matzner, G., 2009. Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Global Change Biology 15, 808–824.
Cabrera, M.L., Beare, M.H., 1993. Alkaline persulfate oxidation for determining total nitrogen in microbial biomass extracts. Soil Science Society of America Journal 57, 1007–1012.
Carbone, M.S., Still, C.J., Ambrose, A.R., Dawson, T.E., Williams, A.P., Boot, C.M., Schaeffer, S.M., Schimel, J.P., 2011. Seasonal and episodic moisture controls on plant and microbial contributions to soil respiration. Oecologia 167, 265–278.
Casals, P., Lopez–Sangil, L., Carrara, A., Gimeno, C., Nogués, S., 2011. Autotrophic and heterotrophic contributions to short–term soil CO_2 efflux following simulated summer precipitation pulses in a Mediterranean dehesa. Global Biogeochemical Cycles 25, GB3012. http://dx.doi.org/10.1029/2010GB003973.
Cheng, W.X., 2009. Rhizosphere priming effects: its functional relationships with microbial turnover, evapotranspiration, and C–N budgets. Soil Biology & Biochemistry 41, 1795–1801.
Cheng, W.X., Dijkstra, F.A., 2007. Theoretical proof and empirical confirmation of a continuous labeling method using naturally ^{13}C–depleted carbon dioxide. Journal of Integrative Plant Biology 49, 401–407.
Cheng, W.X., Johnson, D.W., Fu, S.L., 2003. Rhizosphere effects on decomposition: controls of plant species, phenology, and fertilization. Soil Science Society of America Journal 67, 1418–1427.
Cheng, W.X., Kuzyakov, Y., 2005. Root effects on soil organic matter decomposition. In: Zobel, R.W., Wright, S.F. (Eds.), Roots and Soil Management: Interactions Between Roots and the Soil. Agronomy Monograph No. 48. ASA–CSSA–SSSA, Madison, pp. 119–143.
Cosentino, D., Chenu, C., Bissonnais, Y.L., 2006. Aggregate stability and microbial community dynamics under drying–wetting cycles in a silt loam soil. Soil Biology & Biochemistry 38, 2053–2062.
Denef, K., Six, J., Bossuyt, H., Frey, S.D., Elliott, E.T., Merckx, R., Paustian, K., 2001. Influence of dry–wet cycles on the interrelationship between aggregate, particulate organic matter, and microbial community dynamics. Soil Biology & Biochemistry 33, 1599–1611.
Dijkstra, F.A., Cheng, W.X., 2007a. Interactions between soil and tree roots accelerate long–term soil carbon decomposition. Ecology Letters 10, 1047–1053.
Dijkstra, F.A., Cheng, W.X., 2007b. Moisture modulates rhizosphere effects on C decomposition in two different soil types. Soil Biology & Biochemistry 39, 2264–2274.
Dijkstra, F.A., Cheng, W.X., Johnson, D.W., 2006. Plant biomass influences rhizosphere priming effects on soil organic matter decomposition in two differently managed soils. Soil Biology & Biochemistry 38, 2519–2526.
Evans, S.E., Wallenstein, M.D., 2012. Soil microbial community responses to drying and rewetting stress: does historical precipitation regime matter? Biogeochemistry 109, 101–116.
Fierer, N., Schimel, J.P., 2003. Effects of drying–rewetting frequency on soil carbon and nitrogen transformations. Soil Biology & Biochemistry 34, 777–787.
Frank, D.A., Groffman, P.M., 2009. Plant rhizospheric N processes: what we don't know and why we should care. Ecology 90, 1512–1519.
Gordon, H., Haygarth, P.M., Bardgett, R.D., 2008. Drying and rewetting effects on soil microbial community composition and nutrient leaching. Soil Biology & Biochemistry 40, 302–311.
Guo, X.B., Drury, C.F., Yang, X.M., Reynolds, W.D., Zhang, R.D., 2012. Impacts of wet–dry cycles and a range of constant water contents on carbon mineralization in soils under three cropping treatments. Soil Science Society of America Journal 76, 485–493.
Harris, D., Porter, L.K., Paul, E.A., 1997. Continuous flow isotope ratio mass spectrometry of carbon dioxide trapped as strontium carbonate. Communications in Soil Science and Plant Analysis 28, 747–757.
Heimann, M., Reichstein, M., 2008. Terrestrial ecosystem carbon dynamics and climate feedbacks. Nature 451, 289–292.
Högberg, P., Nordgren, A., Buchmann, N., Taylor, A.F.S., Ekblad, A., Högberg, M.N., Nyberg, G., Ottosson–Löfvenius, M., Read, D.J., 2001. Large–scale forest girdling shows that current photosynthesis drives soil respiration. Nature 4111, 789–792.
Huntington, T.G., 2006. Evidence for intensification of the global water cycle: review and synthesis. Journal of Hydrology 319, 83–95.
Jarvis, P., Rey, A., Petsikos, C., Wingate, L., Rayment, M., Pereira, J., Banza, J., David, J., Miglietta, F., Borghetti, M., Manca, G., Valentini, R., 2007. Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the "Birch effect". Tree Physiology 27, 929–940.
Jenkinson, D.S., Brookes, P.C., Powlson, D.S., 2004. Measuring soil microbial biomass. Soil Biology & Biochemistry 36, 5–7.
Kuzyakov, Y., 2002. Review: factors affecting rhizosphere priming effects. Journal of Plant Nutrition and Soil Science 165, 382–396.
Kuzyakov, Y., 2010. Priming effects: interactions between living and dead organic matter. Soil Biology & Biochemistry 42, 1363–1371.
Kuzyakov, Y., Cheng, W.X., 2001. Photosynthesis controls of rhizosphere respiration and organic matter decomposition. Soil Biology & Biochemistry 33, 1915–1925.
Liu, X.Z., Wan, S.Q., Su, B., Hui, D.F., Luo, Y.Q., 2002. Response of soil CO_2 efflux to water manipulation in a tallgrass prairie ecosystem. Plant and Soil 240, 213–223.
Mikha, M.M., Rice, C.W., Milliken, G.A., 2005. Carbon and nitrogen mineralization as affected by drying and wetting cycles. Soil Biology & Biochemistry 37, 339–347.
Miller, A.E., Schimel, J.P., Meixner, T., Sickman, J.O., Melack, J.M., 2005. Episodic rewetting enhanced carbon and nitrogen release from chaparral soils. Soil Biology & Biochemistry 37, 2195–2204.
Moyano, F.E., Manzoni, S., Chenu, C., 2013. Responses of soil heterotrophic respiration to moisture availability: an exploration of processes and models. Soil Biology & Biochemistry 59, 72–85.
Moyano, F.E., Vasilyeva, N., Bouckaert, L., Cook, F., Craine, J., Curiel Yuste, J., Don, A., Epron, D., Formanek, Franzluebbers, A., Ilstedt, U., Kätterer, T., Orchard, V., Reichstein, M., Rey, A., Ruamps, L., Subke, J.-A., Thomsen, I.K., Chenu, C., 2012. The moisture response of soil heterotrophic respiration: interaction with soil properties. Biogeosciences 9, 1173–1182.
Muhr, J., Franke, J., Borken, W., 2010. Drying–rewetting events reduce C and N losses from a Norway spruce forest floor. Soil Biology & Biochemistry 42, 1303–1312.
Navarro-Garćia, F., Casermeiro, M.Á., Schimel, J.P., 2012. When structure means conservation: effect of aggregate structure in controlling microbial responses to rewetting events. Soil Biology & Biochemistry 44, 1–8.
Niklaus, P.A., Falloon, P., 2006. Estimating soil carbon sequestration under elevated CO_2 by combining carbon isotope labelling with soil carbon cycle modeling. Global Change Biology 12, 1909–1921.
Pausch, J., Zhu, B., Kuzyakov, Y., Cheng, W.X., 2013. Plant inter–species effects on rhizosphere priming of soil organic matter decomposition. Soil Biology & Biochemistry 57, 91–99.
Pulleman, M., Tietema, A., 1999. Microbial C and N transformations during drying and rewetting of coniferous forest floor material. Soil Biology & Biochemistry 31, 275–285.
Schimel, J., Balser, T.C., Wallenstein, M., 2007. Microbial stress–response physiology and its implications for ecosystem function. Ecology 88, 1386–1394.
Tiemann, L.K., Billings, S.A., 2011. Changes in variability of soil moisture alter microbial community C and N resource use. Soil Biology & Biochemistry 43, 1837–1847.
Unger, S., Máguas, C., Pereira, J.S., David, T.S., Werner, C., 2010. The influence of precipitation pulses on soil respiration – assessing the "Birch effect" by stable carbon isotopes. Soil Biology & Biochemistry 42, 1800–1810.
Wu, J., Brookes, P.C., 2005. The proportional mineralization of microbial biomass and organic matter caused by air–drying and rewetting of a grassland soil. Soil Biology & Biochemistry 37, 507–515.
Wu, J., Joergensen, R.G., Pommerening, B., Chaussod, R., Brookes, P.C., 1990. Measurement of soil microbial biomass C by fumigation-extraction – an automated procedure. Soil Biology & Biochemistry 22, 1167–1169.
Xiang, S.R., Doyle, A., Holden, P.A., Schimel, J.P., 2008. Drying and rewetting effects on C an N mineralization and microbial activity in surface and subsurface California grassland soils. Soil Biology & Biochemistry 40, 2281–2289.
Yan, L.M., Chen, S.P., Huang, J.H., Lin, G.H., 2010. Differential responses of auto– and heterotrophic soil respiration to water and nitrogen addition in a semiarid temperate steppe. Global Change Biology 16, 2345–2357.
Zhu, B., Cheng, W.X., 2011a. Rhizosphere priming effect increases the temperature sensitivity of soil organic matter decomposition. Global Change Biology 17, 2172–2183.
Zhu, B., Cheng, W.X., 2011b. ^{13}C isotope fractionation during rhizosphere respiration of C_3 and C_4 plants. Plant and Soil 342, 277–287.
Zhu, B., Cheng, W.X., 2012. Nodulated soybean enhances rhizosphere priming effects on soil organic matter decomposition more than non–nodulated soybean. Soil Biology & Biochemistry 51, 56–65.