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Response of soil CO_2 efflux to water manipulation in a tallgrass prairie ecosystem

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Abstract

Although CO_2 efflux plays a critical role in carbon exchange between the biosphere and atmosphere, our understanding of its regulation by soil moisture is rather limited. This study was designed to examine the relationship between soil CO_2 efflux and soil moisture in a natural ecosystem by taking advantage of the historically long drought period from 29 July to 21 September 2000 in the southern Central Great Plain, USA. At the end of August when soil moisture content at the top 50 mm was reduced to less than 50 g kg^{-1} gravimetrically, we applied 8 levels of water treatments (simulated to rainfall of 0, 10, 25, 50, 100, 150, 200, and 300 mm) with three replicates to 24 plots in a Tallgrass Prairie ecosystem in Central Oklahoma, USA. In order to quantify root-free soil CO_2 efflux, we applied the same 8 levels of water treatments to 24 500-mm soil columns using soil from field adjacent to the experimental plots. We characterized dynamic patterns of soil moisture and soil CO_2 efflux over the experimental period of 21 days. Both soil moisture content and CO_2 efflux showed dramatic increases immediately after the water addition, followed by a gradual decline. The time courses in response to water treatments are well described by $Y = Y_0 + ate^{-bt}$, where Y is either soil moisture or CO_2 efflux, t is time, Y_0, a, and b are coefficients. Among the 8 water treatments, the maximal soil CO_2 efflux rate occurred at the 50 mm water level in the field and 100 mm in the root-free soil 1 day after the treatment. The maximal soil CO_2 efflux gradually shifted to higher water levels as the experiment continued. We found the relationship between soil CO_2 efflux and soil moisture using the data from the 21-day experiment was highly scattered, suggesting complex mechanisms determining soil CO_2 efflux by soil moisture.

Introduction

Soil is the largest carbon (C) pool in terrestrial ecosystems (Mielnick and Dugas, 2000), containing approximately 1500 Pg C, which is about twice as much C as in the atmosphere (750 Pg) and three times as much as in the living plants pool (Schlesinger, 1990, 1995; Wang et al., 1999). Any change in soil C content would affect the atmospheric CO_2 concentration and global carbon balance (Schlesinger, 1991; Trumbore et al., 1996). Soil CO_2 efflux (mainly on soil respiration) is the major pathway to release C from the soil to the atmosphere, releasing approximately 68–75 Pg C per year (Raich and Schlesinger, 1992; Raich and Potter, 1995). Quantification of soil CO_2 efflux is critical to our understanding of global C cycling.

Soil CO_2 efflux (sum of degases, root respiration and microbial respiration) has been extensively studied in the past decade (Hanson et al., 1993; Norman et al., 1992). Soil CO_2 efflux rate varies with soil temperature, moisture, root activity, and substrate supply (Davidson et al., 1998). Soil temperature generally stimulates soil CO_2 efflux (Carlyle and Than, 1988; Peterjohn et al., 1993,1994; Raich and Schlesinger, 1992; Simmons et al., 1996). The relationship between temperature and soil CO_2 efflux usually can be described by an exponential equation (Davidson et al., 1998) or an Arrhenius equation (Buchmann, 2000;

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Lloyd and Taylor, 1994). Values of temperature quotient, Q_{10}, of soil CO_2 efflux vary from 1.3 to 5.6 (Chen et al., 2000; Peterjohn et al., 1993,1994; Raich, 1995; Raich and Schlesinger, 1992; Simmons et al., 1996). The variation in Q_{10} is related to soil structure and soil moisture. This temperature sensitivity of soil CO_2 efflux was also reflected in experimental warming studies, where elevated soil temperature resulted in substantial increases in soil CO_2 efflux (Hobbie, 1996; Luo et al., 2001; McGuire et al., 1995; Peterjohn et al., 1993; Rustad et al., 1995).

Soil moisture is another major factor influencing soil CO_2 efflux. Soil CO_2 efflux is usually low in dry soil and increases immediately after rains (Grahammer et al., 1991; Holt et al., 1990). Maximum soil CO_2 efflux was found to occur at -15 kPa (50% water hold-capacity) in humid acrisols and a boreal mor layer (Ilstedt et al., 2000). In moisture excess or waterlogging conditions, soil CO_2 efflux is reduced (Kucera and Kirkham, 1971) because of anaerobic condition and suppression of CO_2 emission. Soil moisture affects soil CO_2 efflux by its direct influence on root and microbial activities, or indirect influences on soil physical and chemical properties (Raich and Schlesinger, 1992; Schimel and Clein, 1991).

Modeling predictions of ecosystem C cycling require both temperature and moisture functions of soil CO_2 efflux. Luo et al. (2001) recently reported the acclimatization of soil respiration to warming in a tall grass prairie. Our understanding of the relationship between soil moisture and CO_2 efflux is greatly limited. Most of the studies on the moisture-CO_2 efflux relationships are based on observations of seasonal variation (Luo et al., 1996; Mielnick and Dugas, 2000) or along spatial gradients (Davidson et al., 1998) in water content. While the observations are directly obtained from natural ecosystems without disturbance of soil structure and plant growth, such a relationship is usually confounded by other environmental factors due to considerable seasonal and spatial variations in soil temperature and root and microbial activities. To understand how soil moisture affects soil CO_2 efflux, it is imperative to conduct experiments that manipulate soil moisture alone while keeping soil temperature and other biological and environmental conditions relatively unaffected.

The objective of this study was to characterize dynamic patterns of soil CO_2 efflux in response to water additions to soil. We took the advantage of a historically long drought period in 2000 in the southern Great Plains, USA. During the period when soil became extremely dry, we manipulated soil moisture content by applying 0, 10, 25, 50, 100, 150, 200, and 300 mm (simulated to yearly rainfall) of water to 24 plots with three replicates. Then we monitored the changes in soil moisture content and soil surface CO_2 efflux for an entire drying cycle of 21 days. During the experimental period, soil CO_2 efflux experienced dramatic changes when the dry soil was wetted while soil temperature was relatively constant. Such a field experiment is not only cost-effective but also has the potential to identify an independent effect of moisture on soil CO_2 efflux by minimizing interactions between temperature and moisture in influencing soil CO_2 efflux. We also did a replicated experiment with 24 columns with root-free soil in the laboratory to exclude root effects on soil CO_2 efflux during the water experiment.

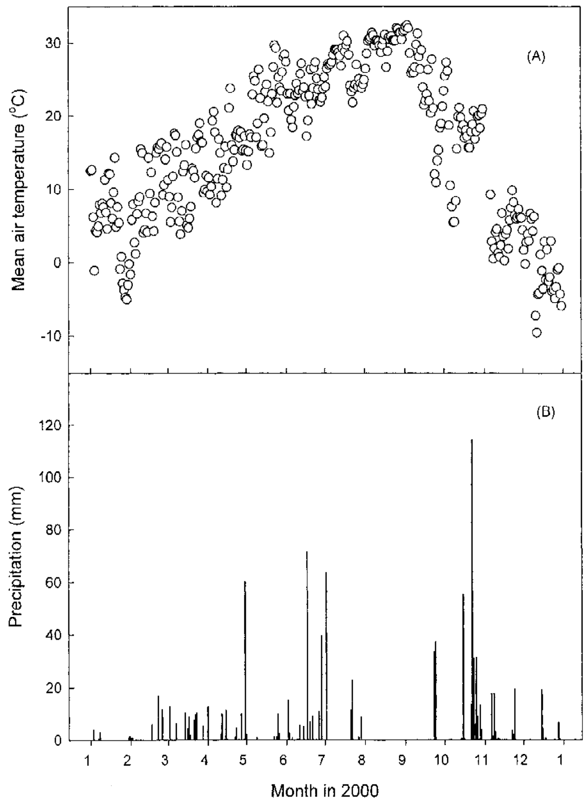

Figure 1. Daily mean air temperature (A) and precipitation (B) in year 2000 at experimental site, which is 3 km east of Norman campus, the Univeristy of Oklahoma, USA. There is a long dry period without precipitation from 29 July to 22 September 2000 (B).

Materials and methods

Field experimental site

The field study was conducted on a Tallgrass Prairie ecosystem, 3 km east of the University of Oklahoma, Norman campus, USA (Lat 35.2° N, Lon 97.4° W). The soil was Vernon clay loam and vegetation is dominated by *Panicum virgatum*, *Schizachyrium scoparium*, *Andropogon gerardii*, *Sorghastrum nutans*, *Ambrosia psilostachyia*, *Xanthocephalum texanum*, *Bromus japonicus*, and *Eragrostis* spp. The daily mean air temperature ranged from −9.5 to 32.4 °C in 2000 (Figure 1A) with a long dry period without precipitation from 29 July to 22 September 2000 (Figure 1B). Soil water content at the top 50 mm decreased to approximately 50 g kg^{-1} by the end of August. We conducted a water experiment so that responses of soil CO_2 efflux to different water levels could be characterized. No precipitation occurred during the field experimental period from 1 to 22 September.

In the experiment, we used a random block design with three blocks as replicates, having 1.0 m spaces between blocks. In each block, eight 0.5 m×0.5 m plots were randomly arranged with 1.0 m spaces between spots. Eight levels of water amount, which simulated rainfall of 0 (control), 10, 25, 50, 100, 150, 200, and 300 mm, were applied to each plot in one block. Water was first pumped into a tank from a pond close to the experimental site and then sprayed into the plot using hand sprinklers. Treatments with simulated rainfall of 10, 25, 50, and 100 mm were finished in the morning of September 2, 2000 while treatments with 150, 200, and 300 mm water began in the afternoon of September 1 and were finished in the afternoon of September 2, 2000 to minimize lateral movement of water. Before the beginning of water treatments, a PVC soil collar (8000 mm^2 in area and 5 mm in height) was installed in the center of each plot, usually 20 mm above ground, for measurement of soil CO_2 efflux.

Laboratory experiment

Soil was collected from the adjacent area of the field experimental site for studying CO_2 efflux in response to water treatments in root-free soil. In order to create relative uniform soil columns, we ground soil and sieved with mesh of 10 mm. Large roots were removed by sieving and fine roots were removed manually. We put 4662 g soil in each of the 24 polyvinyl chloride tubes (PVC, 8000 mm^2 in area and 500 mm in length) with cap at the bottom. The PVC tubes were placed outside the greenhouse at the Univeristy of Oklahoma Norman campus in August 30. The 24 PVC tubes were randomly arranged with three blocks as replicates as in the field experiment. Eight levels of simulated rainfall with 0, 10, 25, 50, 100, 150, 200, and 300 mm were applied to each tube in a block. Water treatments were done in September 4. No water was leaked out of the PVC tubes except for the treatment with 300 mm.

Soil CO_2 efflux measurements

Soil CO_2 efflux was measured using a LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, Nebraska, USA) attached with a LI-6400-09 soil CO_2 flux chamber. To avoid extremely high temperatures at noon, measurements were made in the morning (8:00–10:00 am) in the field and both in the morning and the afternoon (5:00–8:00 pm) for the root-free soil tubes. The soil chamber was placed on the PVC collars in the field or PVC tubes in the laboratory. We programmed LI-6400 such that each measurement was taken according to the change in CO_2 concentration in the chamber. One datum point was taken in each measurement. We also adjusted chamber volume according to the collar height above the soil surface. Soil temperature was measured at the 50-mm depth with thermocouple connected to LI-6400.

Soil moisture and plant biomass measurements

Soil moisture in the field was measured gravimetrically at 1 day before, day 1, 3, 5, 7, 10, 15, and 20 after the water treatments. Soil samples of 20–30 g at surface 0–50 mm were taken in each plot and put in glass jars. Soil samples were dried at oven at 105 °C for 48 h. Soil moisture was calculated as:

$$\text{Soil moisture } (g\ kg^{-1}) = \frac{W1 - W2}{W2} \times 1000, \quad (1)$$

where W_1 was the sample weight before dried and W_2 is the sample weight after dried.

By the end of the experiment, we harvested aboveground biomass and took soil cores for measurements of root biomass. Since no significant differences in both aboveground and belowground biomass were found between water treatments, data are not presented in the paper.

Data analysis

Effects of time and water treatments were determined by analysis of variance according to the general linear model procedure of Statistical Analysis System (SAS Inc., Cary NC, USA). Variation was partitioned into date, water, their interactions, and block.

For the laboratory experiment with root-free soil, we combined two data sets of soil CO_2 efflux collected in morning and afternoon of the same days, using

$$R = R_0 Q_{10}^{(T-T_0)/10}, \tag{2}$$

where R is measured soil CO_2 efflux, T is measured soil temperature; R_0 and T_0 are reference soil CO_2 efflux and soil temperature. In this study, R_0 and T_0 were set to soil CO_2 efflux at 25 °C (R_{25}) and 25 °C, respectively. Two unknown variables, R_{25} and Q_{10}, in a specific day were calculated from Equation (2) using measured R and T in the morning and in the the afternoon of the same day.

In the field experiment, soil temperature at 50 mm depth varied for several degrees during the experimental period. In an attempt to eliminate temperature effects, we made the corrections using Equation (2). Surprisingly, we found that corrected soil CO_2 efflux showed more variability, making it more difficult for the time-course analysis than the original data sets. Therefore, we decided to conduct the time-course analysis on the original data.

Time courses of soil CO_2 efflux and soil moisture were quantitatively described by:

$$Y = Y_0 + ate^{-bt}, \tag{3}$$

where Y is soil CO_2 efflux or soil moisture, Y_0 is soil CO_2 efflux or soil moisture before water treatment, t is time, and a and b are coefficients. Y_0, a, and b were estimated from measured time courses of soil CO_2 efflux or moisture using the SAS program (SAS company, Cary, NC).

Results

Soil temperature and soil moisture in the field

Soil temperature measured at depth of 50 mm in the morning (08:00–10:00) was 30.0 °C at the beginning of the experiment and 25.2 °C at the end of the experiment (Figure 2). No significant differences were found among water treatments.

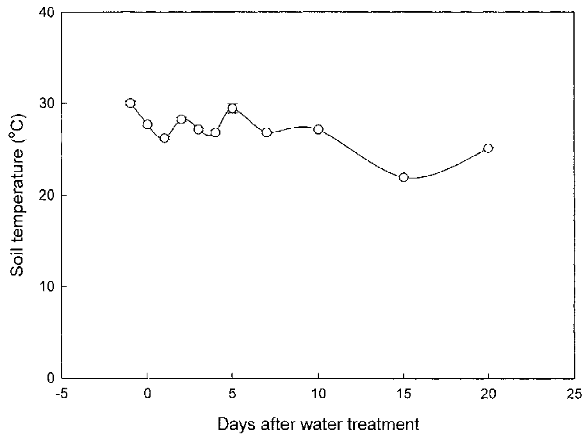

Figure 2. Soil temperature at 50 mm depth in the field in the morning (8.00–10.00) during water treatment periods. Data were the average of soil temperature of 24 plots in each day and shown as mean ±SE.

Soil moisture content in the field at top 50 mm was approximate 50 g kg^{-1} at the beginning of the experiment and decreased slightly through the experimental period in the control plots (Figure 3). In other plots, soil moisture content increased right after water additions followed by gradual declines. The increases in soil moisture content were positively related to water amount added, being 150 g kg^{-1} with 10 mm water addition and 320 g kg^{-1} with 300 mm water addition 1 day after treatments. Soil moisture content decreased to the control level 5 days after the addition of 10 mm and 25 mm water, 7 days with 50 mm and 100 mm, 10 days with 150 mm, and 15 days with 200 and 300 mm water additions (Figure 3). The time course of soil moisture content in response to water additions can be well described by Equation (3). Coefficient Y_0, which represents pretreatment soil water content, has relatively constant values among treatments whereas coefficients a and b decreased with the increase of water levels (Figure 3).

Soil CO_2 in the field

Soil CO_2 efflux significantly varied with water levels, dates, and blocks in both field and laboratory experiments (P<0.05). However, the interactions were nonsignificant at P<0.05 in the field study and significant at P<0.05 in the laboratory study (Table 1).

In the control plots (0 mm water), soil CO_2 efflux gradually decreased from 2.2 to 0.2 μmol m^{-2} s^{-1} during the experimental period (Figure 4). Water additions stimulated soil CO_2 efflux in all the seven

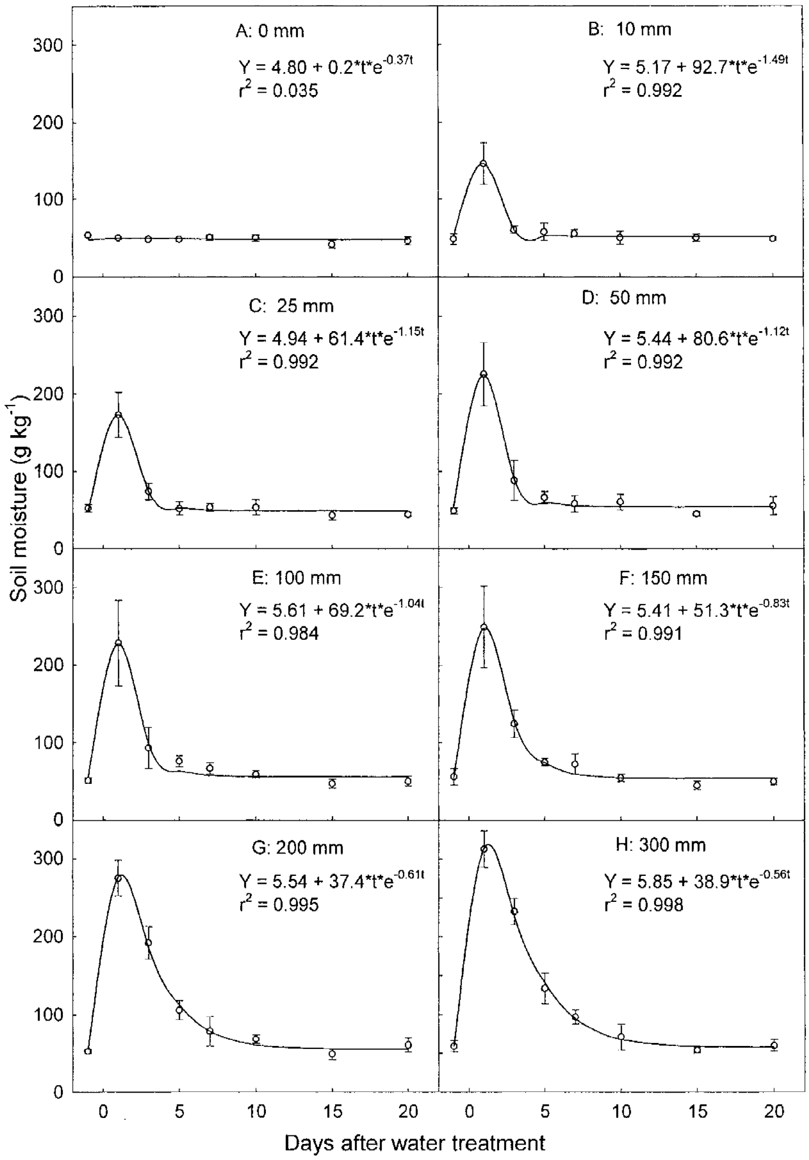

Figure 3. Time course of soil moisture in the field as affected by different levels of water treatment. Open circles were the measured data and shown as mean ±SE. Curves were the equation $Y = Y_0 + ate^{-bt}$ to describe experimental data. Water level was shown at each panel.

Table 1. Analysis of variance for soil CO_2 efflux as affected by different water treatments, data of measurements, and blocks in the field and lab study

Source of variation	Field study		Lab study	
	df	CO_2 efflux	df	CO_2 efflux
Date	10	**	9	**
Water	7	**	7	**
Block	2	**	2	**
Date*Water	68	NS	63	**

NS, *, and ** represented nonsignificant, or significant at P<0.05, and 0.01, respectively.

treatments. In response to water additions, soil CO_2 efflux increased immediately, reached a peak, and then gradually decreased. Comparison among seven levels of treatments indicated that the peak soil CO_2 efflux was highest (approximately 8 μmol m^{-2} s^{-1}) with 10 and 50 mm water additions and lowest (4 μmol m^{-2} s^{-1}) with 150 mm addition. The high peaks of soil CO_2 efflux with 10 and 50 mm water additions were likely caused by soil degassing when CO_2 highly concentrated air in soil pores were replaced by water. In

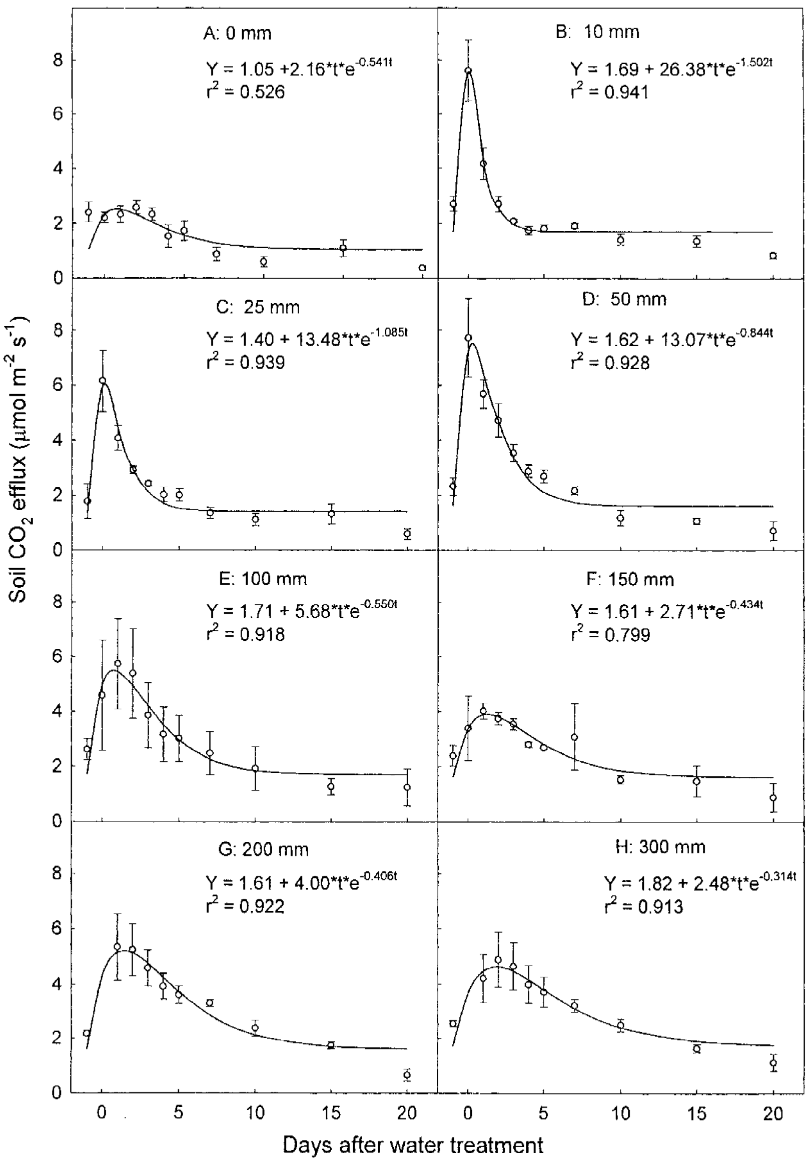

Figure 4. Time course of soil CO_2 efflux in the field as affected by different levels of water treatment. Open circles were the measured data and shown as mean ±SE. Curves were the equation $Y = Y_0 + ate^{-bt}$ to describe experimental data. Water level was shown at each panel.

the three treatments with 150, 200, and 300 mm water additions, it took one full day for soil to absorb the additional water while measurement of soil CO_2 efflux in field was not practical. It is likely that we missed the time window to capture the active degassing phase of gas exchange, resulting in the observation of low peaks of soil CO_2 efflux. To quantify the effect of degassing on soil CO_2 efflux, we need to conduct other experiments, mostly likely in the laboratory, with fully sealed soil columns to allow continuous measurements of soil CO_2 efflux.

After it reached the peak, soil CO_2 efflux gradually decreased. The decrease was faster at the lower water levels and slower at higher water levels (Figure 4). With 10 mm and 25 mm water additions, soil CO_2 efflux decreased to 50% of its peak value in 2 and 3 days, respectively. With 50, 100, 150, 200, and 300 mm water additions, soil CO_2 efflux decreased to 50% of its peak value in 4, 7, 10, 9, and 13 days, respectively. The time courses of soil CO_2 efflux at different water levels are well described by Equation (3). As shown in each subfigure of Figure 4, the coefficient

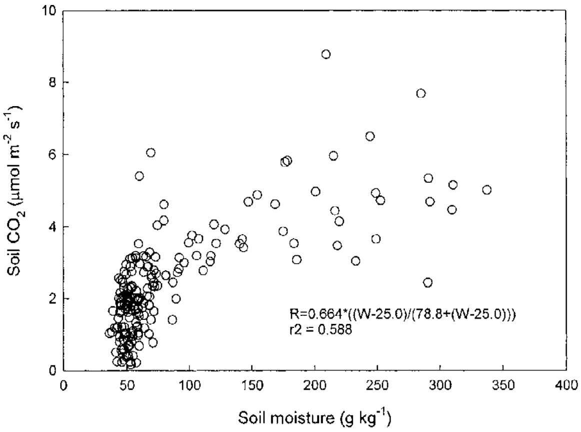

Figure 5 Relationship between soil moisture and soil CO_2 efflux in the field at different water treatment. The relationship is quantitatively described by $R = 0.664^*((W - 25.0)/(78.8 + (W - 25.0)))$ with a determinant coefficient $r^2 = 0.589$. R is soil CO_2 efflux and W is soil moisture.

Y_0, which is the pretreatment soil CO_2 efflux, was relatively constant among treatments. Coefficients a and b were the highest with the 10 mm water addition and decreased with the increase of water levels to the lowest at 300 mm water level. Coefficient a describes how fast the soil CO_2 efflux increases right after water addition. Coefficient b describes how fast the soil CO_2 efflux declines after it reaches the peak. The decreases in coefficients a and b with levels of water addition indicate that soil CO_2 efflux increased slowly before it reached the peak and decreased slowly, too, after it reached the peak in response to water addition.

Relationship between soil moisture and soil CO_2 efflux

Individual data points of soil CO_2 efflux and soil moisture measured on 24 plots over the 21-days experimental period were plotted to examine their relationships (Figure 5). Although only soil moisture content was manipulated in the study with a relatively constant soil temperature over the experimental period, the relationship between soil CO_2 efflux and moisture is highly scattered, possibly due to soil degassing, inhibition of CO_2 diffusion by submerge, and other complex factors in the rhizosphere. In general, soil CO_2 efflux increased with soil water availability. Their relationship is quantitatively described by $R = 0.664 \times \frac{W-25.0}{7.88+(W-25.0)}$ with a determinant coefficient $r^2 = 0.588$ (Figure 5), where R is soil CO_2 efflux and W is soil moisture.

CO_2 efflux from root-free soil columns in the laboratory study

Similar to the field experiment, soil CO_2 efflux in the constructed root-free soil columns was consistently low in the control (0 mm water addition) during experiment period (Figure 6A). With water additions, soil CO_2 efflux in the laboratory study showed a similar pattern as in the field study, with an immediate increase right after water treatment followed by gradual decreases (Figure 6B–H). The peak value of soil CO_2 efflux occurred in day 1 after the treatment of 10, 25, 50, and 100 mm water, day 3 with 150 mm, and day 4 with 200 and 300 mm water additions. The soil CO_2 efflux was not significantly different between the 150 and 200 mm water treatments 5 days after the experiment and among the 150, 200, and 300 mm water treatments 10 days after the experiment.

The time courses of soil CO_2 efflux in response to water additions to the root-free soil columns were also quantitatively described by equation 3 with parameter values presented in each subfigures of Figure 6. The coefficient a is the highest with the 100 mm water addition, indicating the sharpest increase right after water addition. The coefficient a is small with the 200 and 300 mm water addition. The coefficient b, which indicates how fast the soil CO_2 efflux decreases after it reached its peak, is the highest with the 10 mm water addition and the lowest with the 300 mm water addition.

Discussion

This study has, for the first time to our knowledge, characterized dynamic patterns of soil CO_2 efflux in response to water additions both in a natural ecosystem and root-free soil columns. After water treatments, soil CO_2 efflux first increased to reach a peak, and then gradually declined (Figure 4 and 6). The peak soil CO_2 efflux varied with water levels. It was high with less water addition and low with more water addition, probably resulted from degassing. The decline in soil CO_2 efflux following its peak is fast with the low water addition and slow with the high water addition. The time courses of soil CO_2 efflux in response to water addition can be well described by a nonlinear function as in Equation (3). The equation was used to estimate time to reach the maximal soil CO_2 efflux, the maximal CO_2 efflux, time when soil CO_2 efflux decreases to 50% of the maximal values. Time when

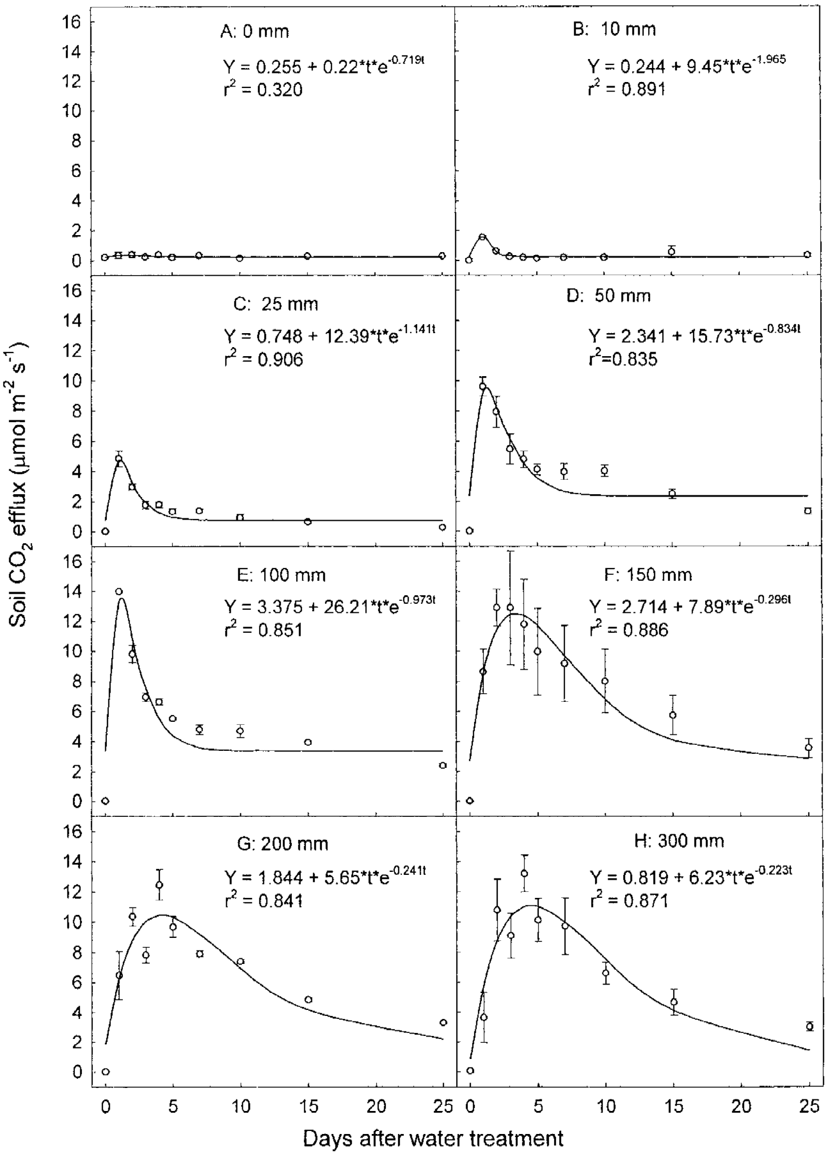

Figure 6 Time course of soil CO_2 efflux of root-free soil column as affected by different levels of water treatment. Open circles were the measured data and shown as mean ±SE. Curves were the equation $Y = Y_0 + ate^{-bt}$ to describe experimental data. Water level was shown at each panel.

soil CO_2 efflux decreases to 50% of the maximal values was the shortest with the lowest amount of water addition and longest with the highest amount of water addition (Figures 4 and 6).

The dynamic patterns of soil CO_2 efflux in response to water addition are affected by multiple factors in rhizosphere carbon processes. When soil is in a dry condition, soil CO_2 efflux is low due to the low microbial activity (Lund and Goksøyr, 1980; Pietikäinen et al., 1999; Schnürer et al., 1986) and inhibition of root CO_2 efflux (Burton et al., 1998; Maier and Kress, 1998). Once water is applied to dry soil, it could trigger a few mechanisms affecting soil CO_2 efflux with different response times. First, additional water fills soil pores and replace CO_2 highly concentrated air, resulting in degassing. Degassing is the fastest response, usually happens within minutes of water applications, and may last up to a few hours. In the strict sense, degassing should not be considered as soil CO_2 efflux. But it is a release of stored CO_2

from past microbial and plant CO_2 efflux. Second, addition of water to an extremely dry soil activates microbe activity, resulting in an increase of soil CO_2 efflux. The activation of microbe activity might take several hours to days (Gliński and Stepniewski, 1985). Third, addition of water within the duration of our experiment also activates CO_2 efflux in living roots through an increase in-specific root CO_2 efflux and an increase in root growth. It has been shown that it takes 7 days for desert plants to initial new root growth after rewet (Huang and Nobel, 1993). Although there was no significant difference in either aboveground or belowground biomass among the water treatment levels at the end of our experiment, we did observe substantial visual difference in foliage greenness among plots with different water additions. The greener foliage is presumably associated with more root activities.

Characterization of the dynamic patterns of soil CO_2 efflux in response to water addition represents a critical step toward mechanistic understanding of soil carbon fluxes. Although its relationships with soil temperature and moisture can be empirically described, soil CO_2 efflux remains the most unknown process in predicting ecosystem productivity (Grace and Rayment, 2000; Schulze et al., 2000; Valentini et al., 2000). In order to understand mechanisms controlling soil CO_2 efflux, we have to experimentally probe various processes and then use models to integrate our knowledge on individual processes together to predict responses of soil CO_2 efflux to environmental changes. Toward to that end, more experiments are needed to manipulate one or two environmental and/or biological factors while other factors are kept under control.

Although the air temperature was relative constant during experiment period, soil temperature at 50 mm depth still varied for about 8 °C (Figure 2). As the values of Q_{10} for soil CO_2 efflux vary from 1.3 to 5.6 (Chen et al., 2000; Peterjohn et al., 1993, 1994; Raich, 1995; Raich and Schlesinger, 1992; Simmons et al., 1996), soil CO_2 efflux can change from 23% (when Q_{10} is 1.3) to 297% (when Q_{10} is 5.6). In the lab study, we avoid this variation by calculating the measured soil CO_2 efflux into its value at 25 °C. In the field study, we use the original data because we failed to elimination temperature effects by using Equation (2). However, the times courses of soil CO_2 efflux in the field study fit Equation (3) the same as in the lab study. This result suggested that Q10 in the field study be relative lower.

In the previous study, the relationship between soil CO_2 efflux (or soil respiration) and soil moisture fit linear functions (Leiros et al., 1999), exponential and logarithmic (Davidson et al., 1998; Orchard and Cook, 1983). In this study, despite little biomass difference among various treatment plots and relatively constant temperature during the experimental period, the relationship between soil CO_2 efflux and soil moisture is highly scattered (Figure 5). The scattered relationship is contrary to our original hypothesis that soil CO_2 efflux would be highly correlated with soil moisture when temperature is kept constant and there is no difference in plant biomass among treatment plots. This scattered relationship also suggests complex mechanisms regulating soil CO_2 efflux. Indeed, those data points with high CO_2 efflux at low soil moisture are largely associated with degassing right after water additions with low levels of water treatments. Those data points with low CO_2 efflux at high soil moisture are from plots with large amounts of water additions, presumably resulting from inhibition of gaseous movement in water-saturated soil soon after treatments. Nonetheless, the relationship between soil CO_2 efflux and soil moisture can be reasonably described by an asymptotic function within the moisture range achieved in this experiment.

Root-free soil columns were originally designed to exclude possible complications of different root activities among water treatments. During our experimental period, no apparent differences were observed in root biomass and its effects on soil CO_2 efflux. Comparison between the two data sets, however, indicates that CO_2 efflux from the root-free soil columns was higher than that from the field at each water level through the whole period of the water experiment. This is contrary to our original hypothesis that the CO_2 efflux of root-free soil is lower than that of field soil. This contradiction may relate to the process of preparing root-free soil column, at which we ground the soil from the field. It has been known for decades that soil disturbance stimulates microbial activities and then nitrogen mineralization and nitrification (Birch and Friend, 1956; Birch, 1958). Johnson et al., (1995) have recently shown that soil disturbance during potting resulted in soil solution NO_3^- concentrations that are orders of magnitude greater than those typically observed in the field. The observed higher soil CO_2 efflux in the root-free soil columns than in the field in this study indicates that the increment in soil microbial activity due to disturbance is more than the total root CO_2 efflux. The latter could accounts for more than

50% of soil CO_2 efflux (Macfaden, 1970). Nonetheless, measurements from the root-free soil columns confirmed the dynamic patterns of soil CO_2 efflux observed in the field following watering.

In summary, our water manipulation resembles different amounts of rainfall, which is a common phenomenon in the natural world. In spite of the fact that soil CO_2 efflux has been suggested to vary greatly within a drying cycle (Norman et al., 1992), dynamic patterns of soil CO_2 efflux in response to rainfall have not been well characterized in natural ecosystems. This study systematically observed time courses of soil CO_2 efflux in response to 8 water treatments within a drying cycle while air temperature was relatively constant over the period and plant biomass was similar among treatments. In addition, we have successfully used a nonlinear equation (Equation (3)) to describe the time courses. The equation can be highly useful for modeling studies to estimate annual carbon budget that accounts for dynamic variation in soil CO_2 efflux between rainfall events. Furthermore, scattered relationships between observed soil CO_2 efflux and moisture suggest complex mechanisms regulating soil carbon processes, which warrant rigorous research in future.

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