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Precipitation events reduce soil respiration in a coastal wetland based on four-year continuous field measurements

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ABSTRACT

Coastal wetlands are considered as a significant sink for global carbon because their organic-rich soils. Given exposed to shallow water tables, water from groundwater is transported upward to the root zone through capillary rise, thus soil moisture in coastal wetlands is relatively high even when there is no precipitation. We expected that as precipitation occurred, the soils in coastal wetlands might become quickly saturated and lead to the development of anoxic conditions. We further hypothesized that such anoxic conditions might decrease soil respiration by limiting oxygen availability and biological activities of roots and microorganisms. Based on continuous automated soil respiration data collected in a coastal wetland in the Yellow River Delta over 4 years (2012–2015), the results showed that on the annual scale, cumulative soil respiration was 317, 321, 231, and 274 $g\,C\,m^{-2}\,yr^{-1}$ for 2012, 2013, 2014, and 2015, respectively, with an average of 286 $g\,C\,m^{-2}\,yr^{-1}$. The rate of soil respiration increased exponentially with soil temperature during each year and its two seasons (growing season and non-growing season). In addition, soil respiration was significantly related to soil moisture during the growing season, but was not affected by soil moisture during the non-growing season. After each precipitation event, soil respiration was significantly negatively correlated with soil moisture under different initial soil water contents. There was a significant positive correlation between changes in soil respiration and changes in soil moisture following precipitation events. Moreover, the increase of soil moisture following precipitation events changed the temperature response of soil respiration. Our study indicated that precipitation events could decrease soil respiration by increasing soil moisture and inducing anoxic conditions in the coastal wetland. Therefore, we speculate that the continuation of decreasing precipitation and increasing temperature trends in the Yellow River Delta may increase soil carbon losses in the coastal wetland due to the increase in soil respiration.

1. Introduction

Changes in precipitation event size or frequency can alter soil moisture to influence soil respiration in a variety of ecosystems (Batson et al., 2015; Vidon et al., 2016). However, the effects of precipitation events on soil respiration are variable and ecosystem-dependent, and have no definite conclusion (Jiang et al., 2013; Zhang et al., 2015). Numerous previous studies have addressed that soil respiration typically quickly increases following precipitation events after periods of dryness (often called “Birch effect”), especially in arid and semi-arid regions (McIntyre et al., 2009; Bowling et al., 2011; Yan et al., 2014; Rey et al., 2017). The enhancement of CO_2 release can constitute a substantial portion of annual soil respiration (Wu and Lee, 2011; Waring and Powers, 2016), which might have potential important consequences for soil carbon (C) stocks (Wang et al., 2015; Rey et al., 2017). However, opposing results indicated that soil respiration was depressed by precipitation events in temperate and subtropical forests (Wang et al., 2012; Liu et al., 2014). Similarly, decreasing soil moisture levels by precipitation reduction increased CO_2 fluxes to the atmosphere in tropical rain forests (Cleveland et al., 2010; Zhang et al., 2015). In addition, a recent observation suggested that rainfall could result in absorption of atmospheric CO_2 by soils in a desert (Fa et al., 2015). Given that precipitation events may influence soil respiration with widely varying uncertainty, it is imperative to determine the

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response of soil respiration to precipitation event in order to precisely predict soil C balance.

These contradictory results about precipitation effects on soil respiration may be due to differences in seasonal climate variation and soil conditions, especially initial soil moisture condition (Shi et al., 2011; Wu and Lee, 2011; Yoon et al., 2014; Rey et al., 2017). Under dry soil conditions, increasing soil moisture following precipitation during the transition from dry to wet soil conditions is accompanied by increasing soil respiration (Shi et al., 2011; Liu et al., 2014; Rey et al., 2017), which may be attributable to water-driven increases in microbial biomass and activity, root respiration following enhanced photosynthesis, and degassing of soil pore space CO_2 (Nielsen and Ball, 2015). However, under humid soil conditions, as precipitation occurs, soil becomes saturated or flooded with a subsequent continuous increase in soil moisture, which limits the diffusion of O_2, and reduces microbial activity and CO_2 production (Jimenez et al., 2012; McNicol and Silver, 2014; Vidon et al., 2016). Therefore, the direction and magnitude of the soil respiration induced by precipitation may be controlled by initial soil moisture and precipitation size and frequency. Since relatively modest changes in the quantity or timing of precipitation may have disproportionately large impacts on annual soil respiration (Wang et al., 2015; Waring and Powers, 2016; Rey et al., 2017), accurately quantifying soil respiration response to precipitation events is essential to understand soil C balance dynamics. In addition, considering that globally precipitation patterns have been predicted to change with increasing intra-annual variability and more frequent extremes (IPCC, 2013), rainfall events may become even more important in the near future (Rey et al., 2017).

Coastal wetlands are considered as significant sink for global C and contributors to global “blue carbon” resources (Laffoley and Grimsditch, 2009; Livesley and Andrusiak, 2012), with high primary productivity, a low soil organic matter decomposition rate, a low CH_4 generation rate, and the ability to trap and bury significant amounts of allochthonus C (Mcleod et al., 2011; Poffenbarger et al., 2011; Hopkinson et al., 2012). Globally, the organic-rich soils of many coastal wetlands contain exceptionally large C stocks, which can be two to three times higher than those in most terrestrial ecosystems (Chmura et al., 2003; Donato et al., 2011; Livesley and Andrusiak, 2012). Thus the soil C stocks in the coastal soils have been received much interest because the minor change of C pool will have a remarkable impact on the global C cycle (Chambers et al., 2013). Due to low elevation and proximity to the ocean, shallow groundwater may be present in many coastal wetlands under different geologic settings (Hoover et al., 2016). Therefore, the surface soils in coastal wetlands may experience large fluctuations between fresh-water and seawater, as well as between groundwater and surface water, which have the potential to significantly alter the C mineralization rate, microbial activity and nutrient dynamics (Cui et al., 2009; Fan et al., 2012; Han et al., 2014). Except of tidal wetlands, the most area of coastal wetlands are lie beyond the reach of the tides, where the hydrologic regimes are dominated by the interaction of precipitation, saline water tables, and marine sediments (Zhang et al., 2011; Han et al., 2015). The hydraulic connection between soil water and groundwater directly influences the water and salt conditions in the soil (Xie and Yang, 2013). When the water table and capillary fringe are close to the soil surface, then only small amounts of applied water are necessary to saturate the soil profile completely (Sophocleous, 2002). Because water and water-soluble salts from the groundwater are transported upward to the root zone through capillary rise and evaporation (Zhang et al., 2011; Han et al., 2015), soil moisture in coastal wetlands is relatively high even when there is no precipitation. In addition, saturated soils including flooded or ponded soils are often observed following rainfall events (Han et al., 2015). Therefore, the soils in coastal wetlands exposed to shallow groundwater are sensitive to precipitation events and might easily induce changes between aerobic and anaerobic status, which can regulate soil respiration. Thus, accurately quantifying response of soil respiration to precipitation events is essential to understand C balance dynamics in these belowground dominated ecosystems (Rey et al., 2017).

Unfortunately, relatively few long-term (multi-year) studies of soil respiration covering periods of interannual variability in seasonal weather are available from coastal wetlands. Therefore, it is unclear how the soil respiration responses to precipitation events and associated changes in moisture conditions in these regions. The development of automated soil respiration measurements with high temporal resolution under natural conditions provides an excellent opportunity to examine and evaluate soil respiration response to precipitation evens. We expected that as precipitation occurred in coastal wetlands, the soils might become quickly saturated for several days due to shallow water tables, which leaded to the development of anoxic conditions. We further hypothesized that such anoxic conditions might decrease soil respiration by limiting oxygen availability, and hence the increasing in soil moisture due to increasing precipitation could protect soil C by decreasing soil respiration. Based on continuous automated soil respiration data collected in a coastal wetland in the Yellow River Delta over 4 years (2012–2015), our objectives are (1) to characterize seasonal and interannual variations of soil respiration of the ecosystem, (2) to quantify the main environmental drivers behind the seasonal variations of soil respiration, (3) to identify the response patterns and magnitudes of rain-induced soil respiration, and (4) to gain new insights into the underlying mechanisms responsible for the changes in soil respiration following precipitation events.

2. Materials and methods

2.1. Site description

The Yellow River Delta, one of the most active regions of land-ocean interaction in the world, is located in the southern bank of the Bohai Sea and the western Laizhou Bay. The Yellow River has changed its course more than ten times since 1855, and created more than 2500 km^2 of new wetlands. Due to the low elevation (generally below 10 m) and being near the sea, the hydrological characteristics in the Yellow River Delta are affected by the interactions between freshwater and seawater and between groundwater and surface water (Cui et al., 2009). The groundwater table in this region is shallow with an average depth of 1.1 m (Fan et al., 2012), with a high level of ground-water mineralization averaging 30.1 $g\,L^{-1}$ (Yang et al., 2009), which are mainly influenced by the tidal process and the Yellow River runoff (Luan and Deng, 2013).

It has a warm-temperate and continental monsoon climate with distinctive seasons and rainy summer. The annual average temperature is 12.9 °C, with minimum and maximum mean daily temperatures of −2.8 °C in January and 26.7 °C in July, respectively. The average annual precipitation is 560 mm, and nearly 70% of the annual precipitation is concentrated in the period of July to September. Thus, surface flooding is often observed in this region, especially following heavy rainfall events. During dry season (April–June), driven by strong evaporation, water and soluble salt in the shallow water table are transported upward to the root zone, therefore the surface soil moisture and salinity are relatively high. Generally, the soil type of coastal wetlands in the Yellow River Delta gradually varies from fluvo-aquic to saline soil, and the soil texture is mainly sandy clay loam (Nie et al., 2009).

The study sites are located at the Research Station of Coastal Wetland in the Yellow River Delta (37° 45′ 50″N, 118° 59′ 24″E), Chinese Academy of Sciences, in Kenli County, Shandong Province, China. In our research sites, the vegetation is relatively homogeneous and strongly dominated by common reed (*Phragmites australis*), with other associated species including *Suaeda salsa*, *Tamarix chinensis*, *Imperata cylindrical,* and *Tripolium vulgare*. The maximum canopy height at the peak of the growing season (early July to mid-August) can reach up to 1.7 m, and the closure index was between 0.3 and 0.8 (Han et al., 2015). The growing season of the coastal wetland ecosystem spans from

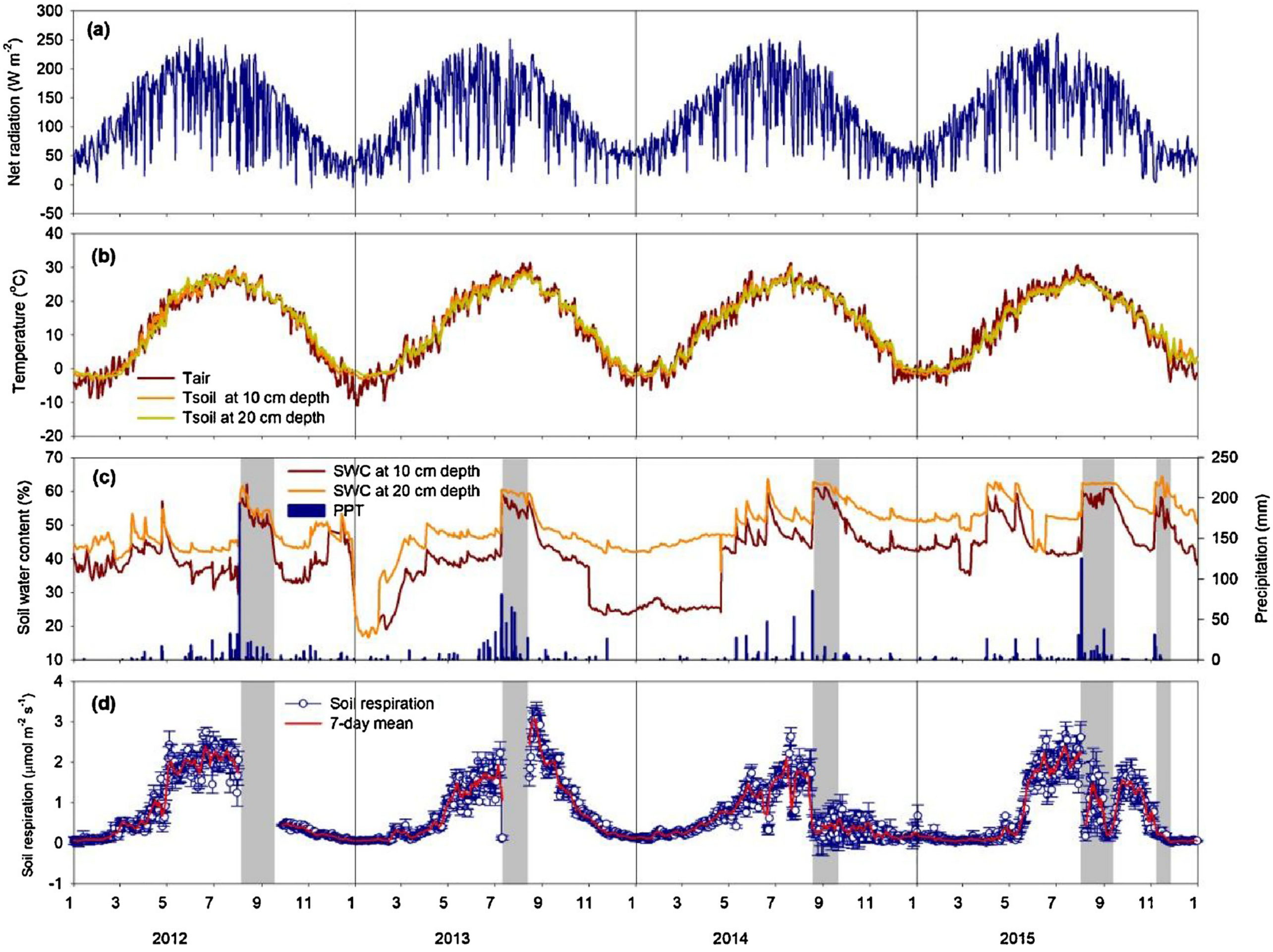

Fig. 1. Seasonal and annual variation of (a) net radiation; (b) air temperature, soil temperature at 10 cm and 20 cm depth; (c) daily precipitation and volume soil water content at 10 cm and 20 cm depth; and (d) daily soil respiration and its 7-day mean over a four-year period (2012–2015). Shading periods represent the surface flooding season. Vertical bars represent the standard error of four soil chambers.

mid-April to mid-November.

2.2. Soil respiration measurements

Soil respiration was measured continuously for 4 years (February 2012–December 2015) using a LI-8100 automated soil respiration measurement system and LI-8150 multiplexer with four 8100-104 long-term chambers (Li-Cor Inc, Lincoln, NE, USA). More details about soil respiration measurements presented elsewhere (Han et al., 2014). Four soil collars (11.4 cm in height and 21.3 cm in diameter) were randomly distributed in the study site and inserted 2 cm into the soil one week before the first measurement. The soil collars were left in place throughout the entire study period. Individual chambers were continuously measured at least once every 2 h. Each measurement took 120 s and the linear increase of CO_2 concentration in the chamber was used to estimate soil respiration. During the entire study period, all living plants inside the collars were carefully clipped from the soil surface to exclude aboveground plant respiration. During the rainfall-driven episodic flooding, soil respiration could not be measured, which lasted 1–2 months every year (Han et al., 2015).

2.3. Meteorological measurements

A variety of meteorological parameters including net radiation (Rn), air temperature, wind speed and direction, atmospheric pressure, and precipitation, were measured simultaneously with an array of sensors as described elsewhere (Han et al., 2015). Soil temperature was measured at five depths (5 cm, 10 cm, 20 cm, 30 cm and 50 cm) with thermistors (109SS, Campbell Scientific Inc., USA). Soil water content (SWC) was measured by time domain reflectometry probes (EnviroSMART SDI − 12, Sentek Pty Ltd., USA) at seven depths (10 cm, 20 cm, 30 cm, 40 cm, 60 cm, 80 cm and 100 cm). A previous study in this region showed that soil respiration was more significantly related to soil temperature and soil water content of the top layer than at the deeper depths (from 20 cm to 80 cm) (Han et al., 2014). Thus, soil temperature at 10 cm depth and SWC at 10 cm depth were chosen to investigate the influence of temperature or moisture on soil respiration. All meteorological data were measured every 15 s and then averaged half−-hourly. Long-term climate data (1961–2015) were received from local meteorological stations in the Yellow River Delta.

2.4. Data processing and analysis

Since the measuring system worked well during four-year measurement period except surface flooding, short gaps (4–6 h) in data of soil respiration were filled by linear interpolation. Hourly mean of soil respiration were computed as the mean of the four chambers, and daily means (g CO_2 m^{-2} d^{-1}) were computed as the average of the hourly means (μmol CO_2 m^{-2} s^{-1}). Daily mean values were used to examine the seasonal responses of soil respiration to soil temperature and moisture.

Regression analysis was used to evaluate the effects of soil temperature and moisture on the seasonal variation in soil respiration during the growing and nongrowing seasons for the years 2012–2015, respectively. The relationship between daily soil respiration and soil temperature was fitted using the simple empirical exponential model: $SR = ae^{bT}$, where SR is soil respiration (g CO_2 m^{-2} d^{-1}), T is soil temperature (°C), a and b are model parameters. Temperature sensitivity of soil respiration (Q_{10}) can be estimated as $Q_{10} = e^{10b}$. Linear and nonlinear regression analyses were used to determine the effect of soil moisture on the seasonal variation in soil respiration.

In order to determine changes in soil respiration in response to precipitation, we selected 12 sampling periods during the growing season for the years 2012–2015. Linear and nonlinear regression analyses were used to assess the correlation between daily soil respiration and soil moisture following precipitation. In addition, a linear regression was used to evaluate the effect of the changes in soil moisture on the changes in daily soil respiration driven by precipitation for the four years. A two-tailed two-sample t-test was used to test the significant differences in SWC between measurements before and after precipitation events. In all tests, a significance level of $P = 0.05$ was used. We also compared the relationships between soil respiration and soil temperature at 10 cm depth before and after precipitation for the years 2012–2015. All statistical analyses were performed using SPSS 11.5 (SPSS for Windows, Chicago, IL, USA).

3. Results

3.1. Meteorological conditions

The site is characterized by two distinct contrasting seasons within a year (Fig.1, Table 1). The non-growing season (from mid-November to mid-April of the following year) is characterized by low air and soil temperatures, low soil moisture, and almost no rainfall. The growing season (from mid-April to mid-November) is characterized by higher air temperatures and greater precipitation compared to the non-growing season. Seasonal patterns of daily averaged Rn and air and soil temperature were similar (Fig. 1a and b). Average daily Rn followed a similar trend with means 114.8, 113.1, 115.9, and 120.8 W m^{-2} in the years of 2012, 2013, 2014, and 2015, respectively. Minimum daily average Rn of -5.6 W m^{-2} was observed in November 2012, while maximum daily average value was 261.2 W m^{-2} in July 2015 (Fig. 1a). The air temperature in each year showed single peak variation, with daily average air temperature ranged from -10.9 °C in January 2013 to 31.5 °C in July 2013 (Fig. 1b). Annual mean soil temperature ranged from 12.6 °C in 2013 to 13.5 °C in 2014, with a 4-year mean of 13.0 °C and a CV of only 3.2% (Table 1).

The seasonal variations in precipitation and soil moisture (soil volumetric water content, SWC) reflected typical wetland hydrologic conditions, with a series of short flooding periods followed by longer intervals of higher SWC during the growing season, and lower SWC during the non-growing season (Fig. 2c).Over the 4-year period, precipitation was the environmental factor that differed markedly in the study years due to the changes in both the amount and pattern of rain (Fig. 2c). Daily precipitation on the coastal wetland in the Yellow River Delta was highly variable, ranged from 0.1 mm to 193.6 mm. Many daily precipitation events were small (< 1 mm), but about 25% exceeded 5.0 mm.

The annual precipitation amount was 614.8, 634.1, 425.3, and 519.3 mm in 2012, 2013, 2014, and 2015, respectively, with a mean precipitation of 548.4 mm and a CV of 17.5% (Table 1). Continuous measurements of SWC showed that generally soils were wetter during the growing season (45.0%) compared to the non-growing season (35.8%). Intensive rainfall occurred during the summer monsoon period (from July to September) and concomitantly SWC reached values constantly above 45% (Fig. 3c). Additionally rain events occurred in July and August led to surface flooding in the wetland, and the flooding duration lasted varied one to two months in each study year (Fig. 2c). There were significant differences in SWC across years, which was expected because the difference in the amount and pattern of rain across years.

3.2. Seasonal and interannual variations of soil respiration

The seasonal pattern of soil respiration was broadly similar for each of the 4 years, with the relatively low value occurring during the non-growing season and the high value recorded during the growing season (Table 1). Soil respiration was consistently lowest in the cold months of the year, and increased rapidly in April and reached a maximum between July and September, with additional, a gradual decline as the wetland senescence during late season (Fig. 1d). Overall, during the growing season, the mean soil respiration was 4.60 g CO_2 m^{-2} d^{-1}, which was 4.13 g CO_2 m^{-2} d^{-1} higher than during the non-growing season (Table 1).

Over the 4-year period, soil respiration greatly varied and ranged from 0.01 μmol CO_2 m^{-2} s^{-1} in February 2015 to 3.21 μmol CO_2 m^{-2} s^{-1} in August 2013 (Fig. 1d). The daily average soil respiration was 3.18, 3.22, 2.32, and 2.75 g CO_2 m^{-2} d^{-1}, in 2012, 2013, 2014 and 2015, respectively, with a mean soil respiration of 2.87 g CO_2 m^{-2} d^{-1} and a CV of 14.7% (Table 1). On the annual scale, cumulative soil respiration was 317, 321, 231, and 274 g C m^{-2} yr^{-1} for 2012, 2013, 2014, and 2015, respectively, with an average of 286 g C m^{-2} yr^{-1}.

3.3. Effects of soil temperature and moisture on the seasonal variation in soil respiration

Soil respiration increased exponentially with soil temperature ($P < 0.01$) during all years, growing seasons, and non-growing seasons (Fig. 2). During the four-year study period, soil temperature accounted for 69%, 87%, 58%, and 70% of the variations in soil respiration in 2012, 2013, 2014, and 2015, respectively. Moreover, changes in soil temperature explained more of the variations in soil respiration during the non-growing season (51%–76%) than during the growing season (27%–50%). The mean annual Q_{10} values were 2.7, 3.0, 2.1, and 3.6 in 2012, 2013, 2014, and 2015, respectively, with a mean Q_{10} of 2.9. Although not significantly, the Q_{10} values were greater for the non-growing season (4.5, 4.0, 2.5, and 2.5 in 2012, 2013, 2014, and 2015,

Table 1
Environmental variables and soil respiration during the non-growing season (from mid-November to mid-April) and the growing season (from mid-April to mid-November) over a 4-year period (2012–2015).

Year	Non-growing season				Growing season				Annual			
	Ts(°C)	SWC(%)	PPT(mm)	Rs(g CO_2 m^{-2} d^{-1})	Ts(°C)	SWC(%)	PPT(mm)	Rs(g CO_2 m^{-2} d^{-1})	Ts(°C)	SWC(%)	PPT(mm)	Rs(g CO_2 m^{-2} d^{-1})
2012	1.4	40.6	49.4	0.24	20.8	40.6	565.4	5.31	12.7	40.6	614.8	3.18
2013	1.6	26.7	55.9	0.16	20.4	42.5	578.2	5.30	12.6	35.9	634.1	3.22
2014	3.5	31.1	28.2	0.46	20.6	47.9	397.1	3.30	13.5	40.9	425.3	2.32
2015	3.5	45.0	57.0	1.00	20.3	49.0	462.3	4.48	13.3	47.3	519.3	2.75
Mean	2.5	35.8	47.6	0.47	20.5	45.0	500.7	4.60	13.0	41.2	548.4	2.87

Note: Ts, soil temperature; SWC, soil water content; PPT, precipitation; Rs, soil respiration.

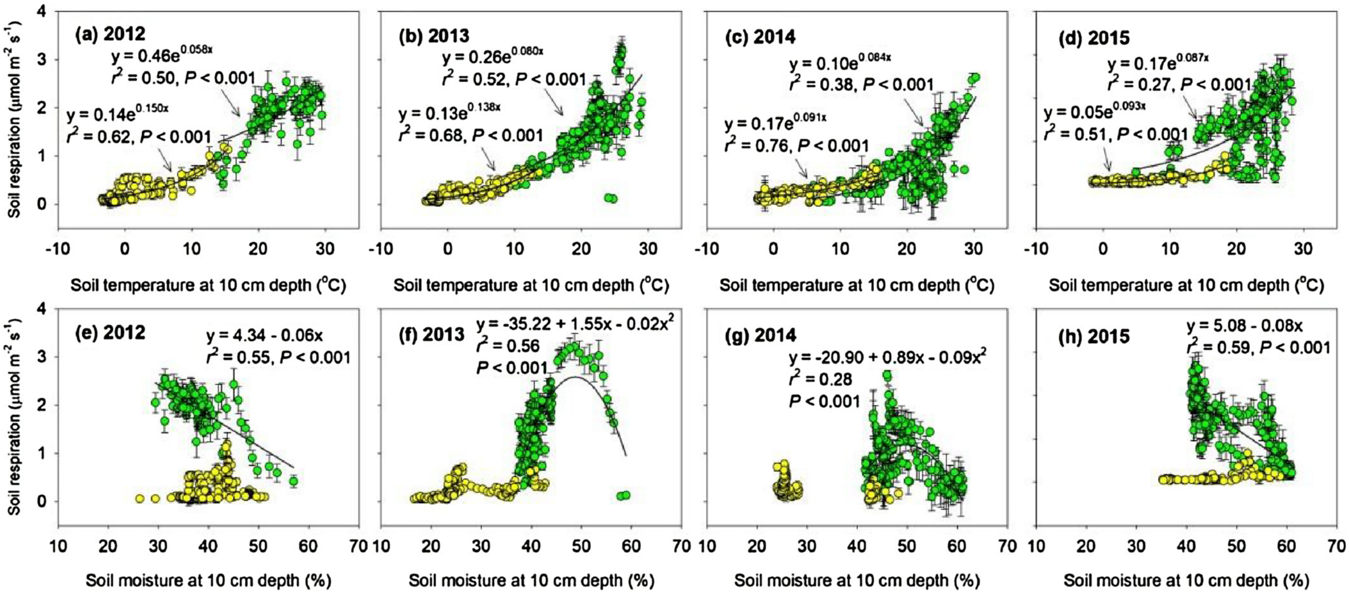

Fig. 2. The relationship between soil respiration and soil temperature (a–d) and soil volumetric moisture content (e–h) at 10 cm depth during the growing (green circle) and nongrowing (yellow circle) seasons for the years 2012–2015. Error bars for soil respiration are representing the standard error of four soil chambers (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

respectively) than for the growing season (1.8, 2.2, 2.3, and 2.4, respectively).

On the other hand, the response of soil respiration to soil moisture was complex at seasonal timescale (Fig. 2). During the growing season, the seasonal variation of soil respiration was significantly related to soil moisture (Fig. 2a–d). In contrast, however, soil respiration was not affected by soil moisture during the non-growing season (Fig. 2e–h). During the growing season in 2012 and 2015, soil respiration was significantly negatively related to soil moisture (Fig. 2a and d; $r^2 = 0.55$, 0.59, respectively). This demonstrated that the increase of soil moisture following rainfall events restrained daily soil CO_2 efflux. Moreover, soil respiration had a parabolic relation with soil moisture during the growing season in 2013 and 2014 (Fig. 2b and c; $r^2 = 0.56$, 0.28, respectively). This indicated that soil respiration was restrained under both wet and dry conditions at seasonal timescale. The results also showed that higher temperature during the growing season was not necessarily resulted in higher soil respiration.

3.4. Effect of soil moisture following precipitation events on the rate of soil respiration

The effect of precipitation events on soil respiration over the 4-year period was analyzed by considering only precipitation events that induced relatively highly changes in SWC (Fig. 3). As expected, precipitation events resulted in significant differences in soil moisture and soil respiration (Fig. 3). Before precipitation, soil moisture contents were all relatively high ($>$ 30%). Precipitation events resulted in significant increases in the water contents, even the rapid saturation (to approximately $0.55\,m^3\,m^{-3}$). In the following days after the precipitation events, the water contents steadily declined and reached initial levels within several days. Meanwhile, increased soil moisture induced by precipitation largely reduced soil respiration (Fig. 3). Soon after the precipitation events, soil respiration decreased rapidly with increasing initial soil moisture conditions, but gradually increased in the following days as the soil became dry. For instance, before precipitation events from 6 to 9 June in 2014, soil respiration rate was relatively high ($1.46\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$ on 6 June). The precipitation events (6.3 mm and 9.6 mm on 8 and 9 June, respectively) resulted in rapid decreases in soil respiration. The bottom value was $0.87\,\mu mol\,CO_2\,m^{-2}\,s^{-1}$ on 9 June, which subsequently decreased by 40% compared with the initial value. As the soil dried, soil respiration then gradually increased, which lasted a few days until 15 June (Fig. 3h).

After each precipitation event during the four years, soil respiration was significantly negatively correlated with soil moisture under different soil moisture conditions (Fig. 4). The values of soil respiration followed linear or quadratic regression relationships with soil moisture, and soil moisture explained 61–93% of the variability in daily soil respiration (Fig. 4). This demonstrated that the increase of soil moisture following precipitation events reduced daily soil respiration. This is further supported by the observation that there was a significant positive correlation between changes in soil respiration (ΔSR) and changes in SWC (ΔSWC) following precipitation events ($r^2 = 0.80$, $P < 0.01$) (Fig. 5).

3.5. Effect of soil moisture following precipitation events on the temperature response of soil respiration

Based on measurements taken prior to precipitation events, soil respiration increased exponentially with soil temperature (Fig. 6). Overall, soil temperature explained 62%–94% of the variability of soil respiration. That is, over the measurement periods before precipitation events, soil temperature exerted principle control on the variability of soil respiration, and the sensitivity of soil respiration to soil temperature (Q_{10}) ranged from 1.8 to 3.2. After precipitation events, soil moisture increased significantly ($P < 0.05$) as compared to data collected before precipitation events (Fig. 6). Consequently, increasing soil moisture following precipitation events changed the relationships between soil respiration and soil temperature. On the one hand, soil respiration was not correlated with soil temperature when soil moisture was relative high after precipitation events (Fig. 6a, b, d, and e). However, compared to soil temperature, the significant and negatively relationships between soil respiration and soil moisture were observed (Fig. 4). This demonstrated that higher temperature after precipitation events was not necessarily resulted in higher soil respiration, and in this case soil moisture was a better predictor of soil respiration. In addition, although soil respiration sometimes also responded strongly to soil temperature after precipitation events (Fig. 6c and f), the increase of soil moisture changed the exponential regression curve and the temperature sensitivity of soil respiration. For instance, Q_{10} was 2.2 and

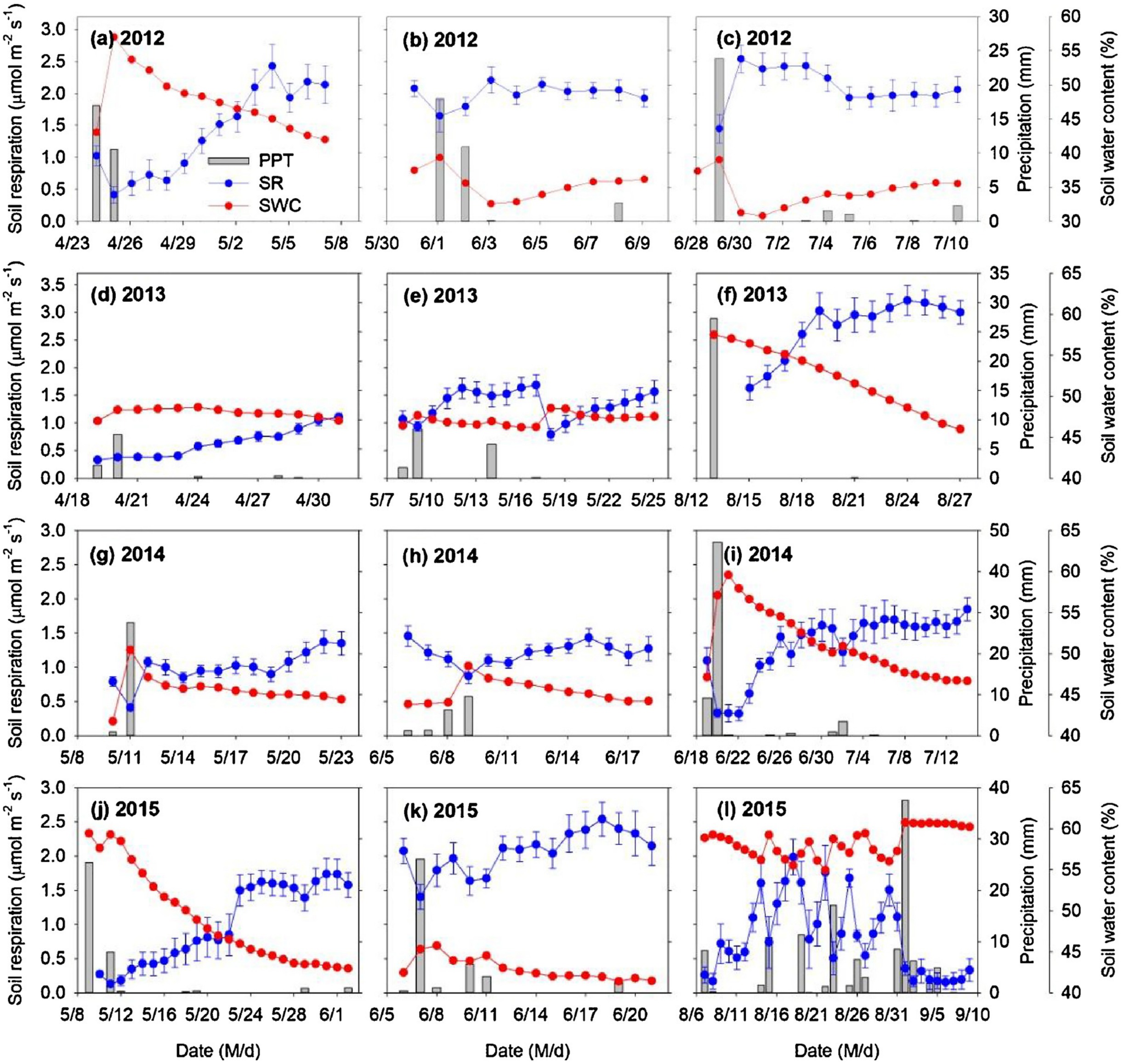

Fig. 3. The sum of precipitation (PPT), daily soil respiration (SR) and soil water content (SWC) during the 12 sampling periods for the years 2012–2015. Error bars for soil respiration are representing the standard error of four soil chambers.

4.2, based on measurements taken before (22 October–5 November in 2015) and after (7 November to 21 November in 2015) precipitation events, respectively.

4. Discussion

4.1. Seasonal controls on soil respiration

Soil respiration varied temporally, with higher rate during the growing season (4.60 g CO_2 m^{-2} d^{-1}), which was approximately 10 times higher than that measured during the non-growing season (0.47 g CO_2 m^{-2} d^{-1}). The same seasonal variation was observed in a reclaimed coastal wetland in the Yangtze Estuary (Zhong et al., 2016) and in a coastal saline wetland in southeast China (Xu et al., 2014). Over the four years, the mean annual soil respiration (286 g C m^{-2} yr^{-1}, ranged from 231 to 321 g C m^{-2} yr^{-1}) was comparable to a boreal peatland (220–320 g C m^{-2} yr^{-1}) in Southern Finland (Alm et al., 1999). In addition, the average soil respiration in this study was higher than that at a subarctic peatland (80–180 g C m^{-2} yr^{-1}) in eastern Canada (Moore, 1986) and lower than that reported in the global soil respiration database for wetlands (344 ± 278 g C m^{-2} yr^{-1}) (Bond-Lamberty and Thomson, 2010), a coastal plain forested wetland (960–1103 g C m^{-2} yr^{-1}) in the southeastern USA (Miao et al., 2013), and a short-hydroperiod floodplain wetland (1091 ± 54 g C m^{-2} yr^{-1}) in the Piedmont of Virginia, USA (Batson et al., 2015).

Seasonal variation in soil respiration appears to be controlled primarily by soil temperature and water availability (Figs. 2 and 3). Both laboratory and field experiments have demonstrated that soil temperature and moisture are important environmental factors driving the temporal variations of soil respiration in wetlands (e.g. (Miao et al., 2013; Xu et al., 2014; Yoon et al., 2014). In the coastal wetland, soil temperature explained 58–87% of the variability in soil respiration in the four investigated years, which has been found in a wide range of wetland ecosystem types, such as a subtropical floodplain wetland (Chen et al., 2013), a coastal saline wetland (Xu et al., 2014), a wetland in a montane permafrost region (Liu et al., 2015), and a lower coastal plain forested wetland (Miao et al., 2013). Most often, in wetlands the response of soil respiration to temperature is similar to upland ecosystems (Xu et al., 2014; Yoon et al., 2014; Liu et al., 2015). For example, a strong exponential increase in soil respiration with soil temperature existed in both aerobic and anaerobic conditions in wetland

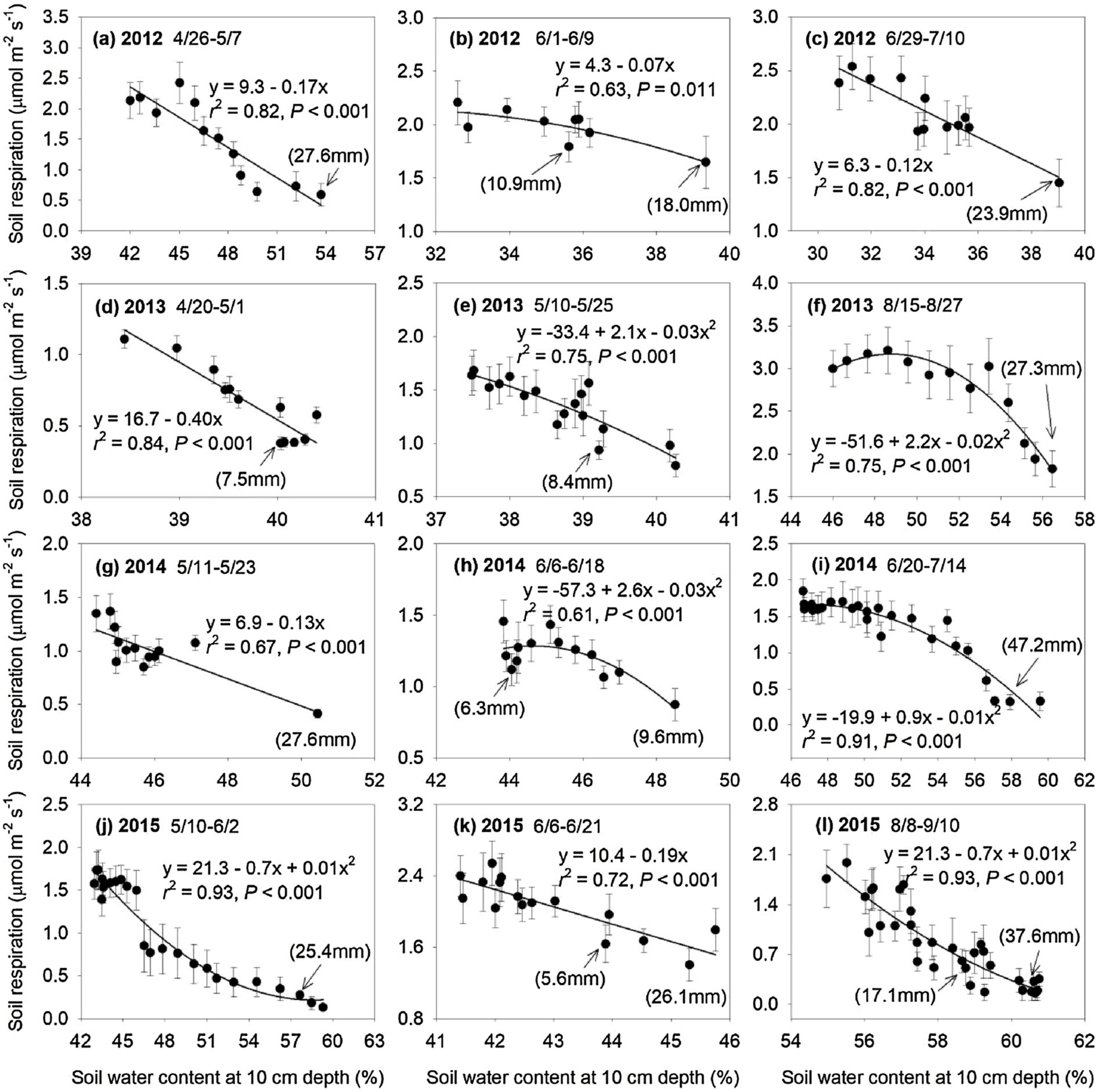

Fig. 4. Relationship between daily soil respiration and soil water content (10 cm) during the 12 sampling periods for the years 2012–2015. Error bars for soil respiration are representing the standard error of four soil chambers. The number in brackets is the amount of precipitation.

soils of different vegetation (Inglett et al., 2012). Moreover, we found that soil temperature explained more of the variability in soil respiration during the non-growing season (51%–76%) than during the growing season (27%–50%), which was consistent with that in semiarid grasslands (Bowling et al., 2011). The mean annual Q_{10} of 2.9 (3.0, 3.0, 2.1, and 3.6 for 2012, 2013, 2014 and 2015, respectively) was higher than the global median of 2.4 (Raich and Schlesinger, 1992) and the mean value of 2.7 in a global temperate dataset (Chen and Tian, 2005), but within the range of 1.6–4.6 for a river-floodplain mosaic (Doering et al., 2011). The clear differences in the Q_{10} values among the four years might be attributable to varied environmental conditions, such as hydrologic regime, activity of microorganisms, even root biomass and substrate quality (e.g. (Inglett et al., 2012; Han et al., 2014; Yoon et al., 2014; Liu et al., 2015). For example, soil respiration is strongly related to recent plant photosynthesis on different time scales (Kuzyakov and Gavrichkova, 2010; Han et al., 2014), and the newly produced photoassimilates could even account for 65%–70% of total soil respiration (Högberg et al., 2001; Søe et al., 2004). The presence of direct photosynthetic contribution to soil respiration distorts the temperature sensitivity (Gu et al., 2008). Specifically, photosynthetic contribution reduces the apparent temperature sensitivity of soil respiration such that it appears to be larger than it actually is in winter and smaller in summer (Gu et al., 2008).

The current results also indicated that seasonal variation of soil respiration during the growing season was strongly related to soil moisture conditions (Fig. 3a–d). Soil respiration under different soil moisture conditions has been widely studied in a variety of ecosystems (Fissore et al., 2009; Drake et al., 2014; Hu et al., 2016). Soil moisture influences soil respiration directly through physiological processes of roots and microorganisms, and indirectly via diffusion of substrates and O_2 (Luo and Zhou, 2006). Even at optimal soil temperatures, soil respiration was inhibited at high or low extremes of soil moisture across a wide range of terrestrial ecosystems (e.g. (Almagro et al., 2009; Bowling et al., 2011; Drake et al., 2014). In 2012 and 2015, soil respiration was negatively related to soil moisture (Fig. 2a and d), however, in 2013 and 2014 it was parabolic related with soil moisture (Fig. 2b and c). In contrast, during the non-growing season soil respiration was not affected by soil moisture (Fig. 2e–h). The response

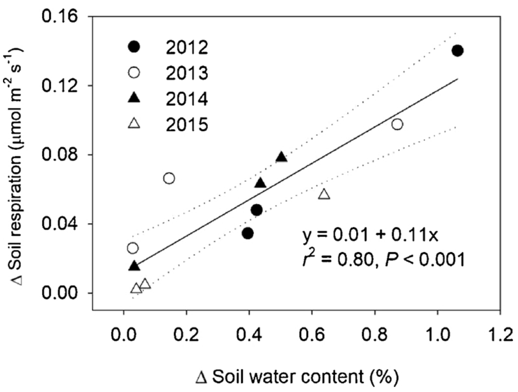

Fig. 5. Relationship between changes in soil respiration and changes in soil water content (10 cm) driven by precipitation for 2012 (black circle), 2013 (white circle), 2014 (black triangle) and 2015 (white triangle). Changes are calculated as the difference between consecutive sampling dates. Black line indicates linear regression. Dotted lines indicate 95% confidence intervals of the regression.

patterns of soil respiration to soil moisture were complex (e.g., linear or nonlinear and positive or negative), depending on factors such as the wet–dry regime, water potential, O_2 and nutrient availability, and duration of the drought period (Reichstein et al., 2002; Luo and Zhou, 2006; Yoon et al., 2014). During dry seasons or drought events, low soil moisture can directly inhibit soil microbial activity and root respiration (Yoon et al., 2014; Hu et al., 2016), thus increasing soil moisture during the transition from dry to wet soil conditions was accompanied by increasing soil respiration (Liu et al., 2014). Previous studies also found that at low SWC the aerobic soil respiration increased with increasing soil moisture in many wetlands, such as a salinity-affected ephemeral wetland (Drake et al., 2014), a lower coastal plain forested wetland (Miao et al., 2013), and high and low tidal flats (Hu et al., 2016).

Furthermore, soil respiration is strongly suppressed by high soil moisture when high soil moisture reduces air-filled soil porosity, decreases oxygen and substrate availabilities, and impedes the diffusion of CO_2 in soils (Luo and Zhou, 2006; Fissore et al., 2009). This observation showed that soil water content was negatively correlated with soil respiration at high water content (Fig. 3). The link between decreased soil respiration and increased soil moisture in wetlands has been demonstrated in other studies (Drake et al., 2014; Yoon et al., 2014; Batson et al., 2015). Generally, there is optimum soil water content for soil respiration, which is usually somewhere near field capacity (Luo and Zhou, 2006; Almagro et al., 2009). In this site, soil field capacity of 10 cm is about 48.3% by volume, and the parabolic relation between soil respiration and soil moisture in 2013 and 2014 suggests the potential soil moisture between 40 and 55% for an optimal flux contribution (Fig. 2b and c). At below-optimal water contents, moisture levels were within the range required for optimal microbial and root activities (Zhang et al., 2015), thus soil respiration usually increases with soil moisture until reaching a turning point of maximum respiration (Almagro et al., 2009; Wu and Lee, 2011). When beyond the optimum, soil moisture is in a super-saturated state, and soil respiration decreases with increasing soil moisture because soil micropore spaces are mostly water-filled, thus facilitating the diffusion of soluble substrates (Qi and Xu, 2001; Luo and Zhou, 2006; Wu and Lee, 2011).

4.2. Likely mechanisms of rain-induced decreases in soil respiration

In our study, even small rainfall events (6.3, 7.5 and 8.4 mm) could decrease daily soil respiration rapidly with increasing initial soil moisture conditions (Fig.3d, e, and h). In addition, after precipitation events all daily soil respiration data were significant and negatively correlated with soil moisture (Fig. 4). Moreover, we have identified that there was a significant positive correlation between changes in soil respiration and changes in SWC following precipitation events (Fig. 5). This observation is in accordance with results from previous studies showing that soil respiration was depressed when precipitation events occurred during wet soil conditions (McIntyre et al., 2009; Wang et al., 2012; Liu et al., 2014). On the other hand, our results showed that as soil water moisture levels decreased, soil respiration gradually increased, which lasted a few days (Fig. 3). Several studies have shown that the drying of previously wet soil can trigger increases in soil respiration for several days and accelerate soil C loss in wetlands (Miao et al., 2013; Batson et al., 2015). This finding is also supported by other precipitation manipulation experiments that precipitation reduction or drought increased CO_2 fluxes to the atmosphere via the decreased soil moisture in the wetter soils (Cleveland et al., 2010; Zhang et al., 2015). These results suggest that precipitation events might act as a critical factor regulating soil respiration in coastal wetlands.

There are several potential mechanisms that could have contributed to the suppression of soil respiration following increasing soil moisture induced by precipitation events. Firstly, when under humid soil conditions, rainfall-induced high soil moisture could limit the diffusion of O_2 when the soil macropore spaces are mostly water-filled. Thus, lower O_2 availability and inhibition of aerobic respiration lead to lower CO_2 emissions by limiting microbial activities (Jimenez et al., 2012; McNicol and Silver, 2014). Soil moisture levels in the coastal wetland were generally high (> 30%) because of shallow groundwater (Fig. 7a, Han et al., 2015). Thus, following precipitation events, the soils had high moisture content or were saturated for short periods (a few days), which led to the development of anoxic conditions and dampened decomposition and respiration (Fig. 7b, Batson et al., 2015; Vidon et al., 2016). Secondly, hypoxia or anoxia conditions resulting from high soil moisture contents lead to a switch of aerobic metabolism of plants into less efficient anaerobic fermentation (Bailey-Serres and Voesenek, 2008), which can have a negative impact on plant photosynthesis (Sairam et al., 2008). Therefore, changes in photosynthesis could affect soil respiration via alterations in belowground substrate availability (Sampson et al., 2007; Bartholomeus et al., 2011; Han et al., 2014). Thirdly, soil respired-CO_2 dissolves in the infiltrating water (Fa et al., 2015). Fourthly, the diffusion rate of CO_2 in the wetter soil is slow (Rochette et al., 1991), thus reducing rates of CO_2 emission through the surface soil. Moreover, rainfall could result in absorption of atmospheric CO_2 by soil, possibly owing to mass flow of CO_2 induced by a gradient of gas pressure between atmosphere and soil (Fa et al., 2015). Therefore, rainfall-induced high soil moisture in wetlands generally is expected to decrease soil respiration. As soil water moisture levels decrease, soils become more aerated and oxidizing aerobic respiration increases (Batson et al., 2015), stimulating soil respiration via increased soil O_2 availability (Zhang et al., 2015).

In contrast, other studies suggested that the wetting of previously dry soils after a precipitation event can trigger abrupt increases in soil respiration for several days in a variety of ecosystems, especially in arid, semi-arid and Mediterranean ecosystems (Almagro et al., 2009; Rey et al., 2017). These occurrences, often called the "Birch effect", can have a marked influence on the ecosystem C balance (Wu and Lee, 2011; Waring and Powers, 2016). The enhanced soil CO_2 efflux following rainfall could be explained by enhancement of microbial biomass and activity after rewetting (Wu and Brookes, 2005; Kim et al., 2012), increase in available substrates derived from dead microbial biomass killed by drought (Van Gestel et al., 1993), root respiration following enhanced photosynthesis in response to water availability (Borken and Matzner, 2009), and degassing of CO_2 stored in soil pores during the previous dry period (Huxman et al., 2004).

These contradictory results of the effect of rainfall on soil respiration might be explained by differences in initial soil moisture content (Shi et al., 2011; Wu and Lee, 2011; Yoon et al., 2014). Namely, when initial soil moisture is lower, soil respiration increases with an increase in soil moisture due to rainfall (Almagro et al., 2009; Shi et al., 2011; Waring and Powers, 2016). In arid and semi-arid regions, soil moisture

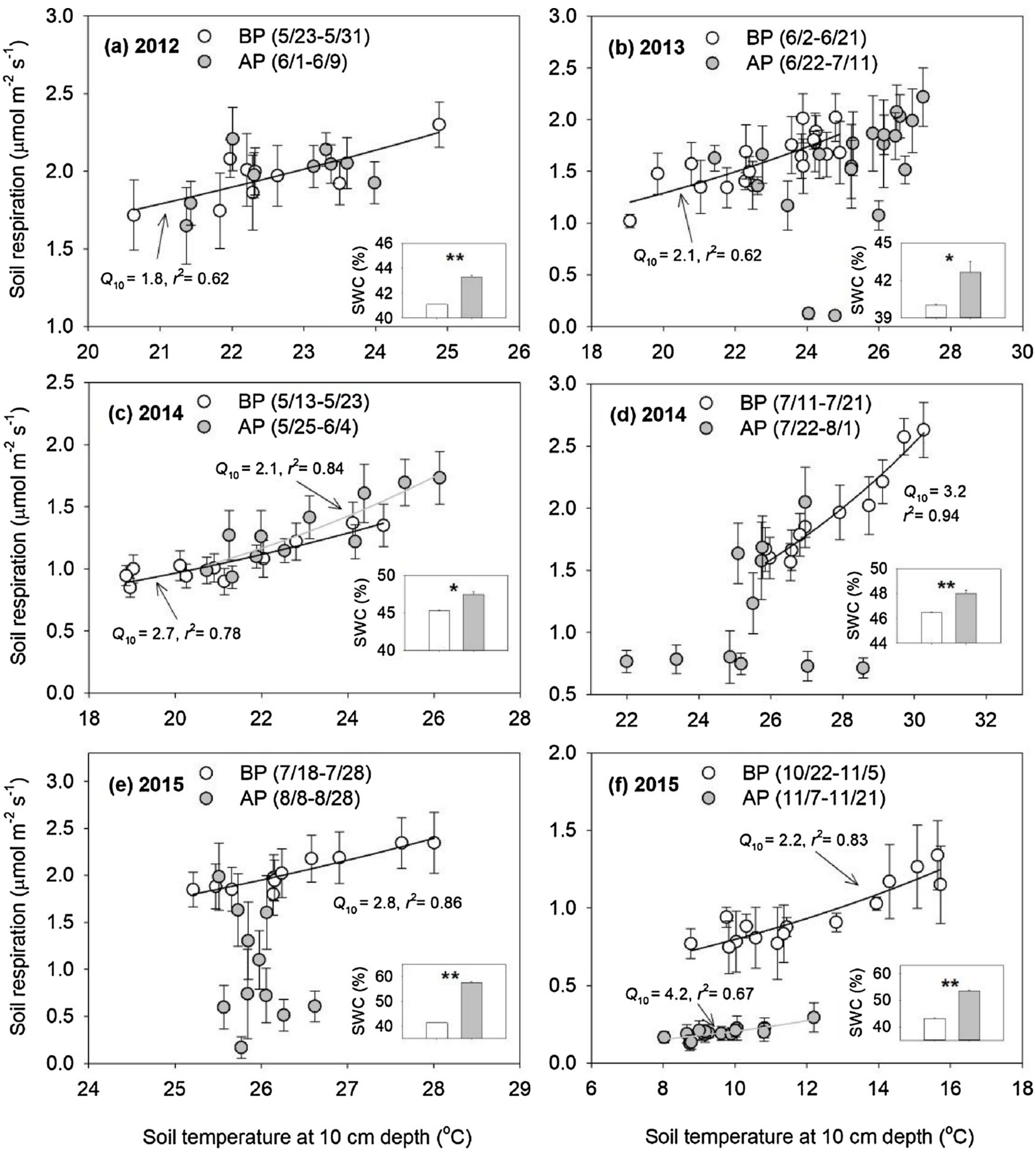

Fig. 6. Comparison of relationships between soil respiration and soil temperature at 10 cm depth before precipitation (BP) and after precipitation (AP) for the years 2012–2015. The equation $y = ae^{bx}$ was used to descript the relations between soil temperature and soil respiration. $Q_{10} = \exp(10b)$. Black and grey lines are the regressive curve of BP and AP. Error bars represent the standard error of four chambers. The insert shows the mean soil water content (SWC) before (white column) and after (grey column) precipitation events. Asterisks indicate significant differences ($^{*}p < 0.05$, $^{**}p < 0.01$) between measurements before and after precipitation events for soil water content.

from rainfall generally increases the rates of production and decomposition of soil organic matter in dry soils (Shi et al., 2011; Rey et al., 2017). If initial soil moisture content was higher, further increases in soil moisture might suppress soil respiration during or after rewetting (Miao et al., 2013; Liu et al., 2014; Yoon et al., 2014). For example, soil respiration were suppressed following precipitation events because the initial high-moisture conditions in wetlands (Jimenez et al., 2012; Batson et al., 2015) or tropical rain forests (Cleveland et al., 2010). Previous studies showed that soil respiration usually increases with soil moisture until reaching a turning point (a threshold value) of maximum respiration, and decreases with increasing soil moisture beyond that point (Almagro et al., 2009; Shi et al., 2011; Wu and Lee, 2011; Jiang et al., 2013). For instance, approximately 60% of the water-holding capacity was the threshold at which soil respiration begins to decline with increased soil water content (Shi et al., 2011). In a coniferous forest, the turning point of maximum is at 20.6% by volume in soil moisture content (Qi and Xu, 2001). Contradictory to some previous studies, by following the natural rain events, our results did not show a distinct threshold of soil moisture above which soil respiration is suppressed (Fig. 4). Further studies are needed to clarify the uncertainties about the response of soil respiration to changes in rainfall and soil moisture (Sitch et al., 2008).

4.3. Implications for soil carbon balance in coastal wetlands under climate change

Our study indicates that precipitation events can decrease soil respiration by increasing soil moisture and inducing anoxic conditions in coastal wetlands. In addition, in coastal wetlands CH_4 emissions are very low even under anoxic conditions because the presence of abundant sulfate and high salinity inhibit CH_4 production (Choi and Wang, 2004; Olsson et al., 2015). Therefore, we can conclude that the increase

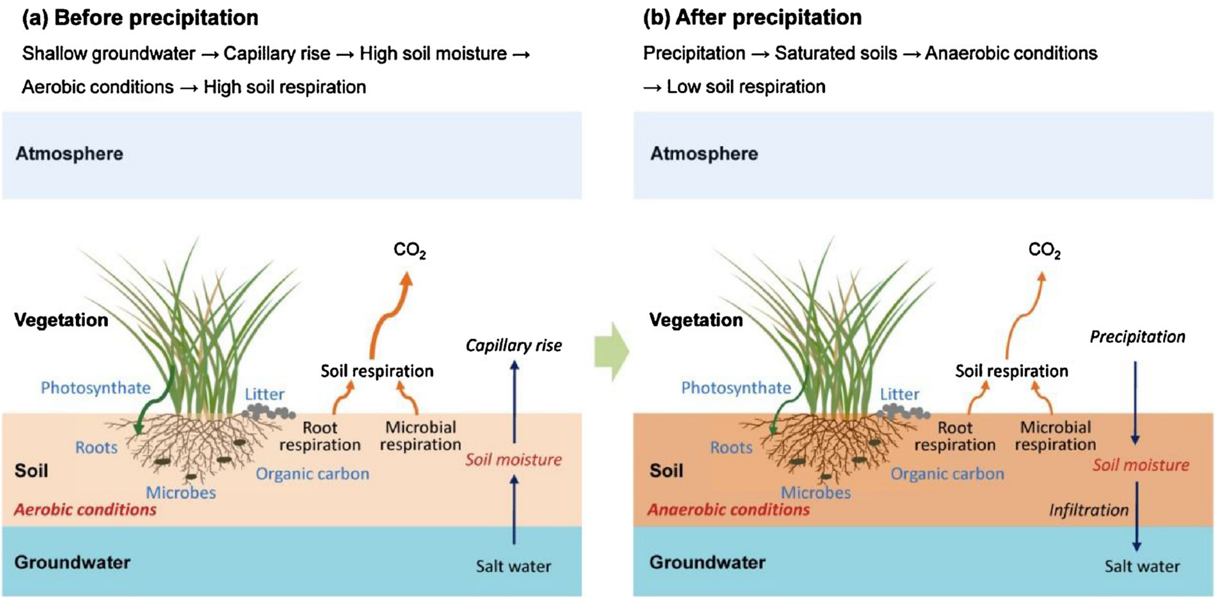

Fig. 7. Schematic illustration of the effect of precipitation events on soil respiration in a coastal wetland. (a) Given exposed to shallow water tables, water from groundwater is transported upward to the root zone through capillary rise, thus soil moisture in the coastal wetland is relatively high even when there is no precipitation. (b) After precipitation events, the soils had high moisture content or were saturated for short periods (a few days), which limiting soil oxygen availability. Therefore the shift from aerobic to anaerobic conditions results in the decrease in soil respiration.

in soil moisture due to precipitation can protect soil C by decreasing soil respiration. Traditional model concepts of soil respiration are developed primarily from knowledge gained in mesic ecosystems, therefore they fail to capture precipitation event dynamics (Carbone et al., 2011). Considering that quantity and seasonality of precipitation are expected to become increasingly variable in future (IPCC, 2013), the effect of rainfall-induced moisture changes on soil respiration is one of the key sources of the uncertainty in the modeled ecosystem C cycle (Carbone et al., 2011; Yan et al., 2014; Rey et al., 2017). These findings have important implications for predicting soil CO_2 responses to changes in rainfall regime under climate change (Waring and Powers, 2016; Rey et al., 2017).

Moreover, average annual precipitation in this site has decreased by 241.8 mm over the 55-year interval (1961–2015), with a decreasing rate of 4.5 mm yr^{-1} (Fig. 8a). Importantly, the average number of annual rainy days has significantly decreased by 6.9 days each decade over the past 55 years (Fig. 8b). Therefore, the decreases in amount and frequency of precipitation can trigger aerobic respiration in wetlands when oxygen availabilities increase correspondingly (Miao et al., 2013), which will accelerate soil C loss from coastal wetlands. Meanwhile, average annual air temperature in this site has increased by 1.7 °C over the past 55 years (1961–2015), equivalent to an increase rate of 0.31 °C $decade^{-1}$ (Fig. 8c). Using the eddy covariance technique, we have found the coastal wetland was a C sink (Han et al., 2015). Integrating effects of both temperature and moisture, we speculate that the continuation of decreasing precipitation and increasing temperature trends may increase soil C losses from the coastal wetland due to the increase in soil respiration. On the other hand, the higher temperatures and decreased precipitation can intensify soil moisture evaporation and increased soil salinity, which will influence soil respiration. However, contradictory results have been reported on the effect of salinity on soil respiration, which may be due to differences in soil properties, especially the levels of salinity, soil pH and salt iron composition (Muhammad et al., 2008). For example, decreasing respiration with elevated salinity was found in many studies (Reviewed by Rath and Rousk, 2015; Hu et al., 2016). A contrasting view is that salinity will stimulate CO_2 release by stimulating inefficient conversion of substrate carbon to energy (Saviozzi et al., 2011). This makes predictions of the soil C balance under a drier climate and soil salinity rather difficult.

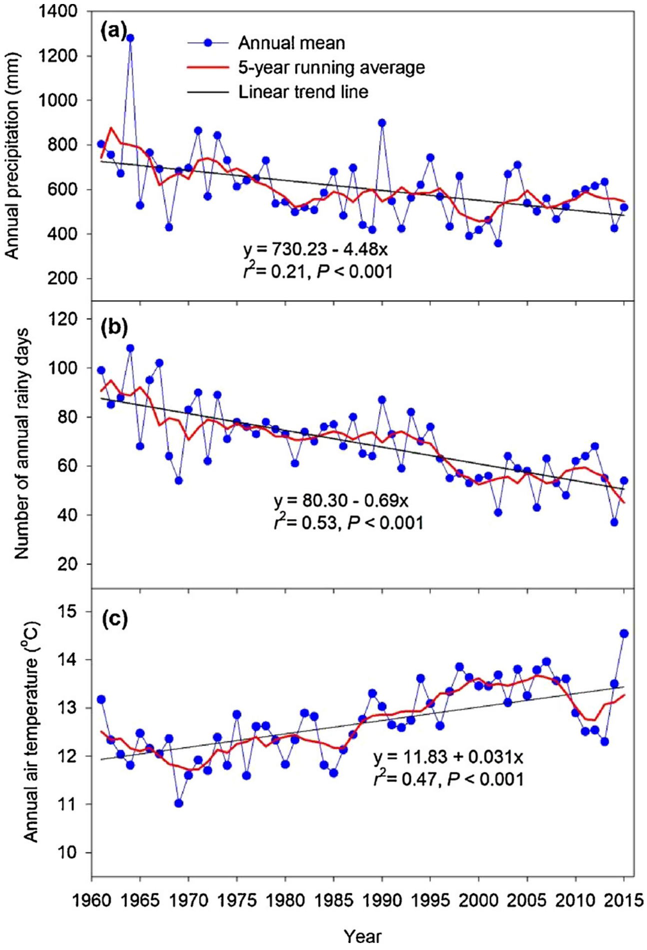

Fig. 8. The inter-annual variability of (a) annual average air temperature, (b) average annual precipitation and (c) number of annual rainy days in the Yellow River Delta from 1961 to 2015.

Therefore, long-term observations are essential to capture the large temporal variability and better quantification of wetland C fluxes (Miao et al., 2013).

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