


Extreme rainfall and snowfall alter responses of soil respiration to nitrogen fertilization: a 3-year field experiment

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Abstract

Extreme precipitation is predicted to be more frequent and intense accompanying global warming and may have profound impacts on soil respiration (R_s) and its components, that is, autotrophic (R_a) and heterotrophic (R_h) respiration. However, how natural extreme rainfall or snowfall events affect these fluxes are still lacking, especially under nitrogen (N) fertilization. In this study, extreme rainfall and snowfall events occurred during a 3-year field experiment, allowing us to examine their effects on the response of R_s , R_h , and R_a to N supply. In normal rainfall years of 2011/2012 and 2012/2013, N fertilization significantly stimulated R_s by 23.9% and 10.9%, respectively. This stimulation was mainly due to the increase of R_a because of N-induced increase in plant biomass. In the record wet year of 2013/2014, however, R_s was independent on N supply because of the inhibition effect of the extreme rainfall event. Compared with those in other years, R_h and R_a were reduced by 36.8% and 59.1%, respectively, which were likely related to the anoxic stress on soil microbes and decreased photosynthates supply. Although N supply did not affect annual R_h , the response ratio (RR) of R_h flux to N fertilization decreased firstly during growing season, increased in nongrowing season and peaked during spring thaw in each year. Nongrowing season R_s and R_h contributed 5.5–16.4% to their annual fluxes and were higher in 2012/2013 than other years due to the extreme snowfall inducing higher soil moisture during spring thaw. The RR of nongrowing season R_s and R_h decreased in years with extreme snowfall or rainfall compared to those in normal years. Overall, our results highlight the significant effects of extreme precipitation on responses of R_s and its components to N fertilization, which should be incorporated into models to improve the prediction of carbon-climate feedbacks.

Keywords: autotrophic respiration, extreme precipitation, heterotrophic respiration, nitrogen fertilization, nongrowing season, soil respiration, soil waterlogging, spring thaw

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Introduction

It is expected that extreme precipitation events will increase in both frequency and magnitude accompanied by climate warming (Fischer & Knutti, 2015; Donat *et al.*, 2016). The intensified global hydrological cycle can have profound consequences on the terrestrial carbon (C) cycle and its feedbacks to climate change (Knapp *et al.*, 2008; Frank *et al.*, 2015). Soil respiration

(R_s) is the largest C flux from terrestrial ecosystems to the atmosphere in the global C cycle with a range of 68–98 Pg C yr⁻¹ and exceeds carbon dioxide (CO₂) emissions from fossil fuel burning by an order of magnitude (Raich & Schlesinger, 1992; Raich *et al.*, 2002; Bond-Lamberty & Thomson, 2010).

Increasing nitrogen (N) input to ecosystems is another global change factor. Although a large number of studies have been conducted, the effects of N enrichment on R_s still remain controversial, with increases, decreases, and no changes being reported (Janssens *et al.*, 2010; Zhou *et al.*, 2014; Zhong *et al.*, 2016). Inconsistence of these results is partly because R_s is a multi-source flux, mainly including the heterotrophic (R_h)

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and autotrophic respiration (R_a). R_h originates from the decomposition of soil organic matter (SOM) and plant residues and is driven by the microbial activities and the quantity and quality of organic C substrates (Luo & Zhou, 2006; Trumbore, 2006). R_a integrates the respiration of roots and rhizosphere microbes and is closely related with belowground allocation of recently assimilated photosynthates (Högberg *et al.*, 2001; Wan & Luo, 2003; Tang *et al.*, 2005). N addition may increase soil microbial biomass and activity (Allison *et al.*, 2010) or decrease enzyme activity and SOM decomposability (Treseder, 2008), resulting in corresponding changes of R_h . Likewise, N application may stimulate R_a due to increased plant growth (Cleveland & Townsend, 2006) or suppress it by reducing belowground C allocation (Kuzuyakov *et al.*, 2002; Wang *et al.*, 2017). On the other hand, R_s is regulated by numerous environmental factors, mainly including soil temperature and moisture, which can interact with N supply in affecting R_s . Xu & Wan (2008) showed that the stimulation effect of N fertilization on R_s was greater in a year with more precipitation, while Yan *et al.* (2010) reported that N addition increased R_s in a wet year, but decreased it in a dry year. Different sensitivities of R_h and R_a to changing soil moisture complicate the effects of N fertilization on R_s . It has been suggested that R_h responded more rapidly to the variation in soil moisture than R_a because larger amount of moisture are needed to trigger the activities of plant roots than the shallowly located soil microbial communities (Parton *et al.*, 2012). However, in a grassland ecosystem, R_a declined more greatly with decreasing soil moisture content than R_h (Gomez-Casanovas *et al.*, 2012). Based on the collected global dataset, Chen *et al.* (2014) showed that R_a was related more closely with precipitation than R_h .

A number of manipulation experiments have examined the effects of increased precipitation on R_s . Recently, Liu *et al.* (2016) synthesized these results and found that increased precipitation stimulated R_s , R_h , and R_a . However, cautions should be taken when predicting the trends of R_s under future precipitation scenario. To date, the number of precipitation manipulation studies separating R_s components is very limited (Liu *et al.*, 2016). Moreover, these studies simulated increased rainfall amount through water addition, which may not necessarily reflect the real conditions of natural extreme rainfall events that may exceed the past and current variation range (Beier *et al.*, 2012; Kayler *et al.*, 2015). It is very likely that the extreme rainfall events could lead to soil water saturation or even being flooded (Knapp *et al.*, 2008). As a result, the limited oxygen (O_2) condition is expected to suppress the activities of soil microbes and plant roots and then lower R_h

and R_a (Rich & Watt, 2013; Philben *et al.*, 2015). Despite the critical influences of extreme rainfall events on R_s , its magnitude and direction is unclear under real-world condition. To the best of our knowledge, no studies have investigated the effects of N fertilization on R_s and its components under extreme precipitation conditions.

In the majority of previous studies, R_s is only measured during the warm or growing season assuming that soil microbial activity is extremely low at low temperature (Fahnestock *et al.*, 1999; Hirano, 2005). However, it has been demonstrated that soil microbes can remain active in cold environments, even at -39 °C (Panikov *et al.*, 2006). The contribution of cold-season R_s to annual budget has been reported to be higher than 10% in Arctic tundra (Fahnestock *et al.*, 1999), temperate mountain forest (Mo *et al.*, 2005), and Tibetan alpine grassland (Wang *et al.*, 2014). Particularly, peak CO_2 fluxes can be observed during the spring thaw period, which are probably sourced from the physical release of CO_2 trapped below the frozen horizons (Elberling & Brandt, 2003) or microbial decomposition as a result of increased temperature, moisture, or substrates (Hirano, 2005; Monson *et al.*, 2006; Wang *et al.*, 2013). Grogan & Jonasson (2006) proposed that the seasonal maximum snow depth was a primary determinant of wintertime CO_2 releases in a Swedish subarctic region. More snowfall can induce higher CO_2 fluxes as a result of higher soil temperature under the deeper snow cover (Björkman *et al.*, 2010) or higher moisture content after snow melting (Wu *et al.*, 2010). However, Schindlbacher *et al.* (2014) reported that snowfall played a rather marginal role on soil CO_2 emissions from a mid-elevation temperate forest. It is predicted that although future climate warming will cause a decrease in mean snowfall, the frequency of snowfall extremes will be higher in many Northern Hemisphere regions (O'Gorman, 2014). Therefore, the impacts of snowfall on R_s and its response to N input need to be better understood to improve the predictions of R_s under future climate change.

This study investigated the response of R_s and its components to N fertilization under extreme rainfall and snowfall events. We measured R_s and separated R_h and R_a with the root exclusion method in a temperate cropland during both growing and nongrowing seasons for three years. Our objectives were to (i) examine the effects of N fertilization on R_s and its components, (ii) evaluate the impacts of extreme rainfall on the responses of R_s and its components to N fertilization, and (iii) quantify the magnitude of nongrowing season respiration and its responses to N fertilization under extreme precipitation conditions.

Materials and methods

Site description

The experiment was carried out in a rainfed maize-cultivated cropland at the Hailun National Agro-ecological Experimental Station, Heilongjiang Province, China (47°26'N, 126°38'E). The study region has a temperate continental monsoon climate. From 1953 to 2013, the mean annual air temperature was 1.9 °C (Fig. 1) with the monthly average ranging from -21.6 °C in January to 21.6 °C in July. Mean annual precipitation is 556 mm, with 87% falling during the crop growing season from May to October. The long-term climate data were sourced from the National Meteorological Information Center of China (<http://cdc.nmic.cn/home.do>).

Soil at the study site is characterized by a clay loam texture with 8% sand, 72% silt, and 20% clay, and classified as black soil or Typic Hapludoll based on genetic classification and the USDA soil taxonomy, respectively. The soil (0–20 cm) prior to the experiment had a pH of 5.9, bulk density of 1.0 g cm⁻³, and contained 27.5 g kg⁻¹ organic C, 2.2 g kg⁻¹ total N, 6.7 mg N kg⁻¹ ammonium (NH₄⁺), 30.7 mg N kg⁻¹ nitrate (NO₃⁻), and 33.7 mg kg⁻¹ dissolved organic C (DOC). Soil texture was determined by a laser particle size analyzer (LS13320, Beckman Coulter, Brea, CA, USA). Soil pH was measured in a 1 : 2.5 soil–water ratio. Bulk density was determined with the intact core method. The soil organic C and total N contents were analyzed using the wet oxidation redox titration and micro-Kjeldahl method, respectively, and the mineral N and DOC concentrations were measured as described below.

Experiment design

The field experiment was conducted throughout three consecutive growing and nongrowing seasons, that is, from May 13, 2011 to May 10, 2012; from May 17, 2012 to May 14, 2013; and from May 19, 2013 to April 24, 2014. Two treatments were included in this study: a N-fertilized treatment (NF) and the control without N application (CK). In May 2011, six plots of

12 × 4.2 m² were established with three replicates for each treatment. In the other two years, four replicates were arranged to reduce the spatial variation and the plots were set in 4 × 4.2 m². N fertilizer was applied as urea at the rate of 150, 200, and 150 kg N ha⁻¹ in 2011/2012, 2012/2013, and 2013/2014, respectively. Urea application was split between preplant and sidedress with a ratio of 1 : 1. The preplant fertilization occurred on May 13, 2011; May 16, 2012; and May 19, 2013. Sidedress urea was applied at the maize V6–V8 growth stage on June 15, 2011; June 27, 2012; and June 28, 2013.

As a local practice, field is split into ridges and furrows at a distance of 70 cm. After the preplant fertilizer banded in the ridges, maize seeds were immediately sown in a plant spacing of 25 cm. The pre-emergent herbicide was used for weed control, and visible weeds were removed by hand throughout the experiment. Mature maize was harvested on September 27, 2011; October 2, 2012; and October 5, 2013. All the crop residues were removed from the plots followed by manual tillage. Samples of maize grain and straw were oven-dried at 60 °C until constant weight to obtain the grain yield and above-ground biomass.

Soil respiration measurement

Soil CO₂ fluxes were measured over a 3-year period with the static closed chamber method. A root exclusion method was used to partition *R_s* into *R_h* and *R_a*. In each plot, a cylindrical polyvinyl chloride (PVC) tube was inserted 5 cm into soil at the center of one ridge, including one maize plant. A PVC base frame (70 cm width, 30 cm length, and 20 cm height) was pushed into soil at a depth of 10 cm, making the tube located at its center. The PVC tube and base frame were fixed before sowing and permanently during each year's measurement period. When taking gas samples, a PVC pipe was embedded to the tube. A stainless steel chamber (70 cm width, 25 cm length, and 20 cm height) insulated with white foam was fitted to the base frame. The chamber was custom-made, consisting of two separate parts that were connected by two hinges and sealed with rubber strips. In the middle of the chamber top, an opening was made to fit the pipe with sealing trips to

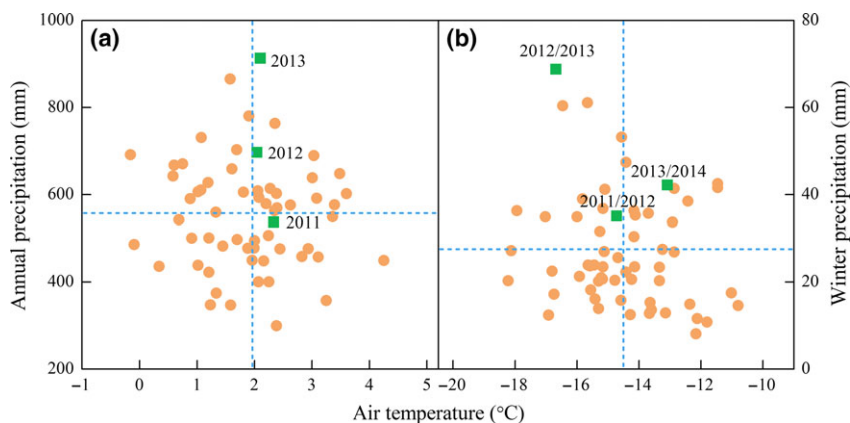


Fig. 1 Scatter plots of total precipitation and mean air temperature for the whole year (a) and winter period (November to March) (b) of the study region from 1953 to 2013. Solid squares indicate the measurement years. Dashed lines represent the 60-year averages. [Colour figure can be viewed at wileyonlinelibrary.com]

ensure airtightness. An area of $1.4 \times 2.1 \text{ m}^2$ in each plot was left unplanted. The base frame was inserted 20 cm into soil at the center of this area. A PVC chamber was used for gas sampling. See Ding *et al.* (2007) for further detailed information of the devices.

Gas samples were taken twice per week during the growing season and spring thaw period, weekly after harvest until soil freezing, and biweekly during the frozen period, resulting in 69, 65, and 71 times in 2011/2012, 2012/2013, and 2013/2014, respectively. Gas samples were collected between 09:00 and 12:00 h to minimize diurnal variation in the flux pattern. Each time, four-chamber headspace air samples were drawn using a plastic syringe at 0, 10, 20, and 30 min after chamber closure and injected into pre-evacuated 20 mL glass vials. Meanwhile, the chamber air temperature was recorded. Gas CO_2 concentration was analyzed on a gas chromatograph equipped with a flame ionization detector (Agilent 7890, Santa Clara, CA, USA). The chamber CO_2 concentration generally increased linearly during the closure time. Thus, the CO_2 flux rate was calculated from the slope of the linear regression between time and CO_2 concentration. Data were discarded if the R^2 of the linear fitting was below 0.85. The cumulative emission was calculated by linear interpolation between measurement days.

The R_a is calculated as the difference between R_s and R_h measured in the planted and unplanted area, respectively, after seedling emergence until maize roots were removed from soil. It should be noted that the root exclusion method has some known drawbacks. Carbon input from the root exudates and turnover may have priming effect on the decomposition of bulk SOM and affect the heterotrophic soil microorganisms (Kuzyakov & Gavrichkova, 2010). However, Kuzyakov & Cheng (2004) reported that the rhizosphere priming effect on R_h was very minor in a maize-planted soil. In this study, to avoid long-term bias caused by the lack of organic matter input from plant, a new area in the same field was used to establish the experimental plots in each year. Another possible bias is that root exclusion may change soil temperature and moisture conditions (Subke *et al.*, 2006). Our previous experiments in the same study region showed that there were no significant differences of soil temperature and moisture between the planted and unplanted plots during the maize growing season (Ni *et al.*, 2012). Suleau *et al.* (2011) pointed out that compared with forest and grassland ecosystems, the root exclusion method was more effective and introduced less biases in cropland. A trenching experiment evaluating the effect of root exclusion on soil microbial biomass and community structure will help to assess the uncertainty in examining the response of R_s and its components to N fertilization using this method. Indeed, Gavrichkova & Kuzyakov (2008) reported that responses of maize root respiration to N fertilization evaluated by ^{14}C labeling and comparison of planted and unplanted soils were similar.

Auxiliary measurement

Precipitation, air temperature, photosynthetically active radiation (PAR), and the depth of snow cover and soil frost were obtained from a meteorological station. PAR data were lack in

August 2013 due to instrument failure after the extreme rainfall event. During the nonfrozen period, soil moisture content was determined in each plot with a TDR probe simultaneously with gas measurement and expressed as water-filled pore space (WFPS). Soil temperature was measured with a digital thermometer or geothermometer (in winter) at 5 cm depth. After fertilization until soil freezing, soil mineral N concentrations were measured weekly in each year, soil DOC concentrations were measured biweekly in 2012/2013 and weekly in 2013/2014. In addition, soil mineral N and DOC were detected at the end of each year's experiment and weekly after soil thaw in 2014. Field-moist soil samples were extracted with 2 M KCl solution (shaken for 1 h and filtered through Whatman #42 filter paper), and the NH_4^+ and NO_3^- concentrations were analyzed on a continuous-flow autoanalyzer (San++, Breda, the Netherlands). Soil DOC was extracted with deionized water (shaken for 1 h, centrifuged for 10 min at 10000 rpm, and filtered through 0.45 μm polyethersulfone membrane) and measured on a TOC analyzer (vario TOC Cube, Elementar, Hanau, Germany).

Data analysis and statistics

Before statistical analysis, data normality was tested using the Kolmogorov–Smirnov test, and square root or natural-log transformation was used as necessary. Paired *t*-test was performed to evaluate the effects of N fertilization on respiration and plant biomass. The interannual differences were analyzed with one-way analysis of variance (ANOVA) with the least significant difference test for multiple comparisons at $P < 0.05$. Repeated-measures ANOVA was used to examine the effects of sampling time and treatment on the fluxes of R_s , R_h , and R_a , and soil NH_4^+ , NO_3^- , and DOC concentrations. Pearson analysis was conducted to probe the correlations between CO_2 flux and environmental factors. The temperature sensitivity of R_s , R_h , and R_a was assessed by exponential function and the Q_{10} value (the change in CO_2 flux with a 10 °C increase in soil temperature at 5 cm). A forward stepwise multiple regression analysis was used to explore the key factors among PAR, soil temperature, moisture, NH_4^+ , and NO_3^- that controlled R_s , R_h , or R_a . Linear or exponential regression models were developed to evaluate the relationships between R_s , R_h , or R_a with soil or plant parameters. A response ratio (RR) of R_s , R_h , or R_a to N fertilization was calculated as the ln-ratio of the value in NF to CK. The temporal pattern of RR of R_h flux was described by a cubic regression model in each year. All statistical analyses were conducted with SPSS 18.0 (SPSS Inc., Chicago, IL, USA) or ORIGIN PRO 8.5 (OriginLab, Northampton, MA, USA).

Results

Meteorological conditions

The annual mean air temperature in each year did not deviate from the long-term average (Fig. 1a). Daily air temperature ranged from -31.7 °C on January 8, 2013

to 28.3 °C on June 19, 2011 during the 3-year experimental period (Fig. 2a). Photosynthetically active radiation (PAR) showed large variation from day to day and followed the seasonal pattern of air temperature except in summer 2013. Annual precipitation was similar in 2011/2012, but higher in 2012/2013 and 2013/2014 than the long-term average (Table S1). A record-breaking extreme rainfall event occurred on July 30, 2013 with a daily rainfall of 178 mm (Liu *et al.*, 2014), leading this year to be the wettest in the study region since record began in 1953 (Fig. 1a). An extreme snowfall event of 17 mm was recorded on November 12, 2012. Total snowfall and the maximum snow depth were higher in 2012/2013 than 2011/2012 and 2013/2014 (Table S1). Winter (November to March) precipitation in 2012/2013 was the highest on record (Fig. 1b). The highest

water-filled pore space (WFPS) was detected after field was waterlogged in early August 2013 (Fig. 2b). After soil thaw, WFPS increased in each year, especially in 2012/2013 with a value of up to 88%.

Soil mineral N and DOC

Soil mineral N concentrations increased after fertilization at first and then gradually declined in the NF treatment but always maintained at lower levels in CK (Fig. S1). A significant increase in soil NH_4^+ concentration was found after the extreme rainfall in August 2013, but the NO_3^- was largely suppressed. Soil DOC varied less than mineral N and tended to increase after soil waterlogging and thawing in 2013/2014. N fertilization did not affect soil NH_4^+ concentration in the

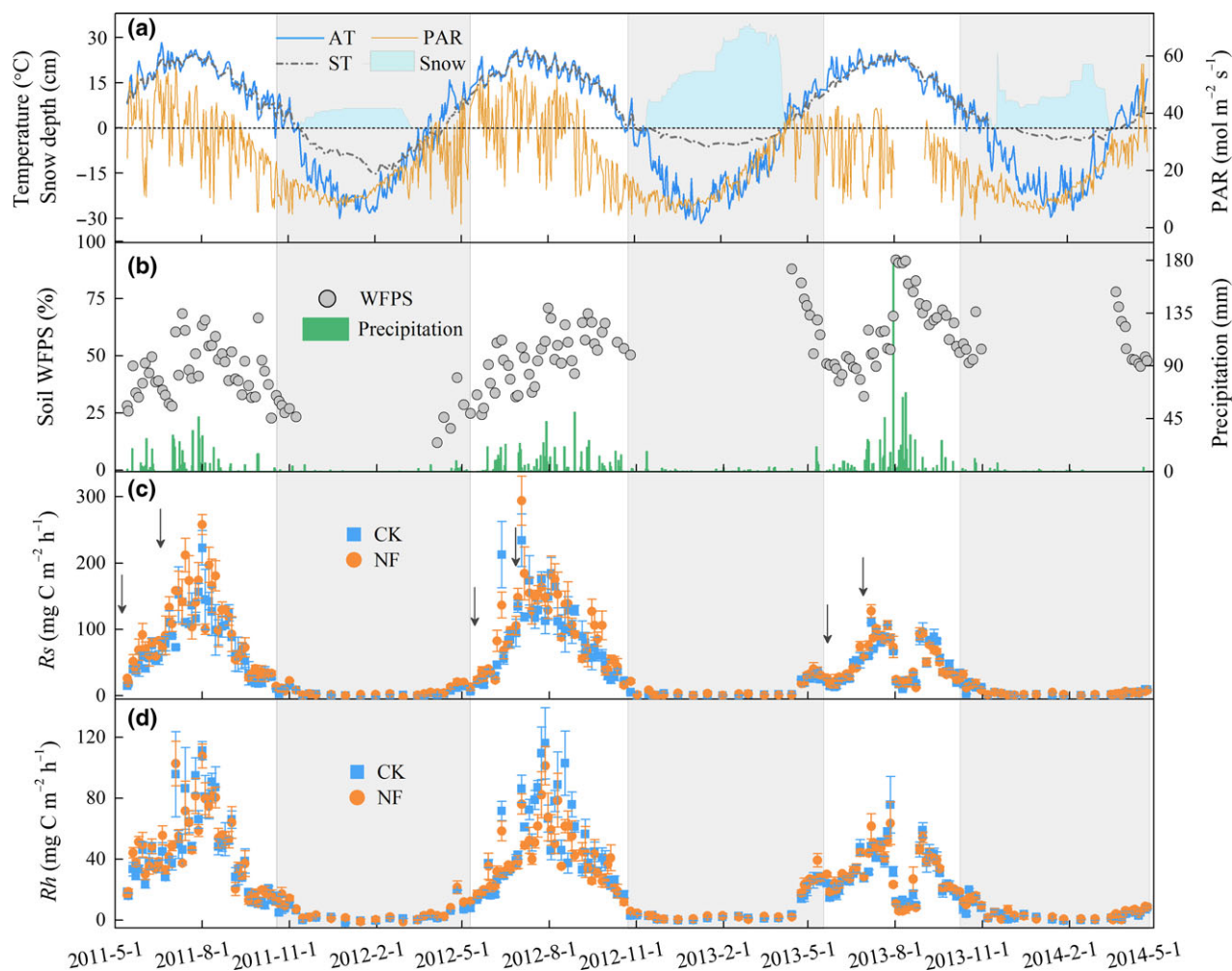


Fig. 2 Air (AT) and soil temperature (ST), photosynthetically active radiation (PAR), snow depth (a), precipitation, soil water-filled pore space (WFPS; b), soil respiration (R_s ; c), and heterotrophic respiration (R_h ; d) from soils without (CK) and with (NF) nitrogen fertilization from May 2011 to April 2014. Vertical bars are the standard errors of the means. Arrows denote the fertilization time. Shading parts represent the nongrowing season. [Colour figure can be viewed at wileyonlinelibrary.com]

first year, but significantly increased it in 2012/2013 ($P < 0.01$) and 2013/2014 ($P < 0.05$). The NF treatment exhibited higher NO_3^- level compared to CK in all three years ($P < 0.01$). The mean soil DOC concentration was increased by N fertilization in 2012/2013 ($P < 0.01$), but not in 2013/2014.

Soil respiration and its components

The flux rates of R_s and R_h during the growing season exhibited similar temporal dynamics in 2011/2012 and 2012/2013 for both control and N fertilization treatments (Fig. 2c, d). In these two years, R_s and R_h increased with soil temperature, reached a maximum of above 200 and 100 $\text{mg C m}^{-2} \text{h}^{-1}$, respectively, in July or early August, and then gradually declined until maize harvest. In general, CO_2 fluxes increased after rainfall. However, the extreme rainfall event occurring on July 30, 2013 led to sharp declines of R_s and R_h to below 36 and 27 $\text{mg C m}^{-2} \text{h}^{-1}$, respectively, until August 27, 2013. The flux of R_a showed similar seasonal pattern to R_s and R_h and was generally higher in NF than CK (Fig. S2). However, after the extreme rainfall event in August 2013, R_a reduced to $<15 \text{ mg C m}^{-2} \text{h}^{-1}$ in both treatments. During the nongrowing season, R_s and R_h decreased to no more than 15 $\text{mg C m}^{-2} \text{h}^{-1}$ after soil freezing in each year, but increased with increasing soil temperature and moisture after surface soil thaw in spring, particularly in April 2013. Repeated-measures ANOVA analysis showed significant ($P < 0.001$) effects of sampling time on the fluxes of R_s , R_h , and R_a , but the N treatment effect was not significant (Table S2). No distinct temporal variation was detected for the response ratio (RR) of R_a flux (Fig. 3). However, the RR of R_h flux showed consistent variation pattern among the 3 years, that is, gradually decreased to below zero at 40–60th day after experiment onset, then got positive during the nongrowing season and peaked during the spring thaw period, which could be well depicted by a cubic function in each year.

Annual R_s ranged from 186 to 407 g C m^{-2} across the 3 years for the two treatments (Fig. 4a). R_s in 2013/2014 was significantly lower than 2011/2012 and 2012/2013, with a reduction by 45.2% and 51.0% on average for CK and NF, respectively. N fertilization significantly ($P < 0.05$) increased R_s by 23.9% and 10.9% in 2011/2012 and 2012/2013, respectively. However, in 2013/2014, N fertilization did not affect R_s . There was no significant difference in R_h between CK and NF in each year, averaging at 166 and 164 g C m^{-2} across the 3 years, respectively (Fig. 4b). Compared with the first two years, R_h in 2013/2014 was reduced by 39.1% and 34.6% for CK and NF, respectively. R_a was more greatly decreased in 2013/2014 than R_h , with a reduction of

53.3% and 64.9% for CK and NF, respectively (Fig. 4c). R_a in the NF treatment was significantly higher than CK in 2011/2012 and 2012/2013, but not in 2013/2014. The average contribution of annual R_h to R_s in the CK treatment was 59.0% (Fig. 4d) and significantly decreased to 53.0% by N fertilization. However, the ratio of R_h/R_s in 2013/2014 was similar between CK and NF and was higher than the other two years.

Nongrowing season cumulative R_s and R_h were higher in 2012/2013 in comparison with the other two years with an average increase of 28.7% and 26.0%, respectively (Fig. 5). Nongrowing season R_s and R_h were significantly ($P < 0.05$) enhanced by N fertilization in all three years. Particularly, in 2011/2012, R_s and R_h were 57.2% and 40.2% greater in NF than CK, respectively, and the RR of R_s and R_h were significantly ($P < 0.01$) higher than those in 2012/2013 and 2013/2014. The contribution of nongrowing season R_s and R_h to the annual budget ranged at 5.5–13.8% and 8.2–16.4%, respectively, across the 3 years.

Abiotic and biotic factors controlling soil respiration and its components

Correlations between soil temperature and R_s , R_h , or R_a fluxes were significant in all 3 years except R_a for CK in 2013/2014 (Tables S3–S5). Generally, the Q_{10} value of R_s was higher in CK than NF as a result of decreased Q_{10} for R_h by N fertilization (Table S6). The Q_{10} values were lower in 2013/2014 than the other years, especially for R_a . Both R_s and R_h had higher Q_{10} values during the nongrowing season of 2012/2013 and 2013/2014 than the corresponding values in growing season of these two years and nongrowing season of 2011/2012.

There were significant correlations between total precipitation over 3 days prior to CO_2 measurement and R_s or R_h in 2011/2012 and 2012/2013 ($P < 0.01$), but not in 2013/2014. Correlation of R_a with precipitation was weaker, only significant in 2011/2012. Soil WFPS and R_s , R_h , or R_a significantly correlated in 2011/2012, but not in the other years. For the growing season, linear models could describe the effects of soil moisture on R_s , R_h , and R_a in 2011/2012 and R_h in 2012/2013 (Fig. 6), while in 2013/2014, Gaussian models fitted well, with an optimal WFPS of 60%, 57%, and 60% for R_s , R_h , and R_a , respectively.

R_a was more correlated with PAR, especially with PAR_3 (average over 3 days prior to CO_2 measurement) than R_s and R_h , except in 2013/2014. This was corroborated by the stepwise regression analysis which showed that soil temperature and moisture were the key factors driving R_h , while R_a was primarily regulated by PAR_3 instead of PAR (Table 1).

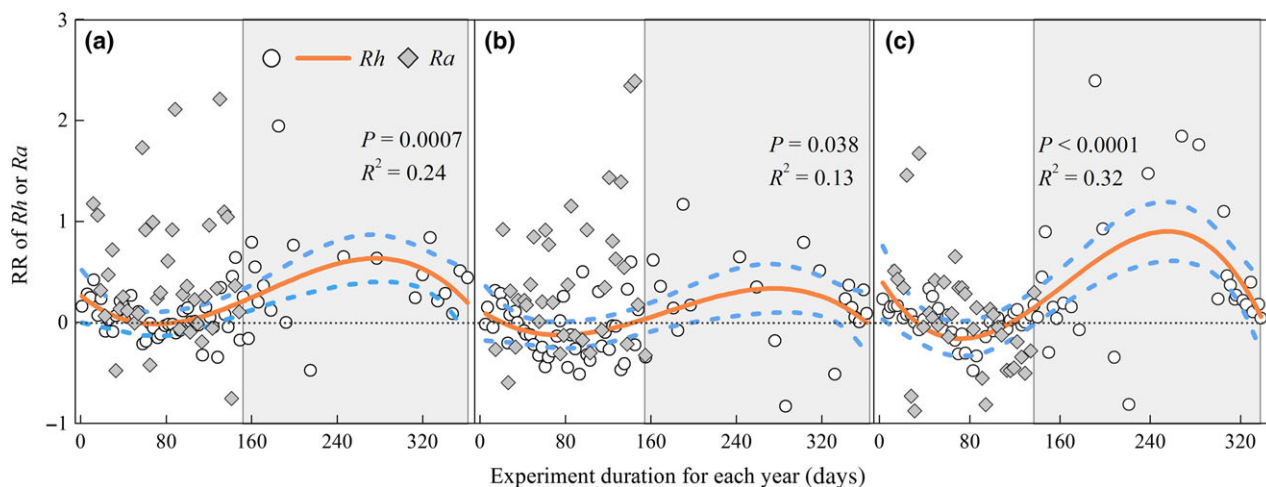


Fig. 3 Temporal variation of the response ratio (RR) of the flux of autotrophic (R_a) or heterotrophic (R_h) respiration to nitrogen fertilization in 2011/2012 (a), 2012/2013 (b), and 2013/2014 (c). Relationship between RR of R_h and experimental day was fitted with a cubic model in each year. Dashed lines indicate the bounds of the 95% confidence intervals. [Colour figure can be viewed at wileyonlinelibrary.com]

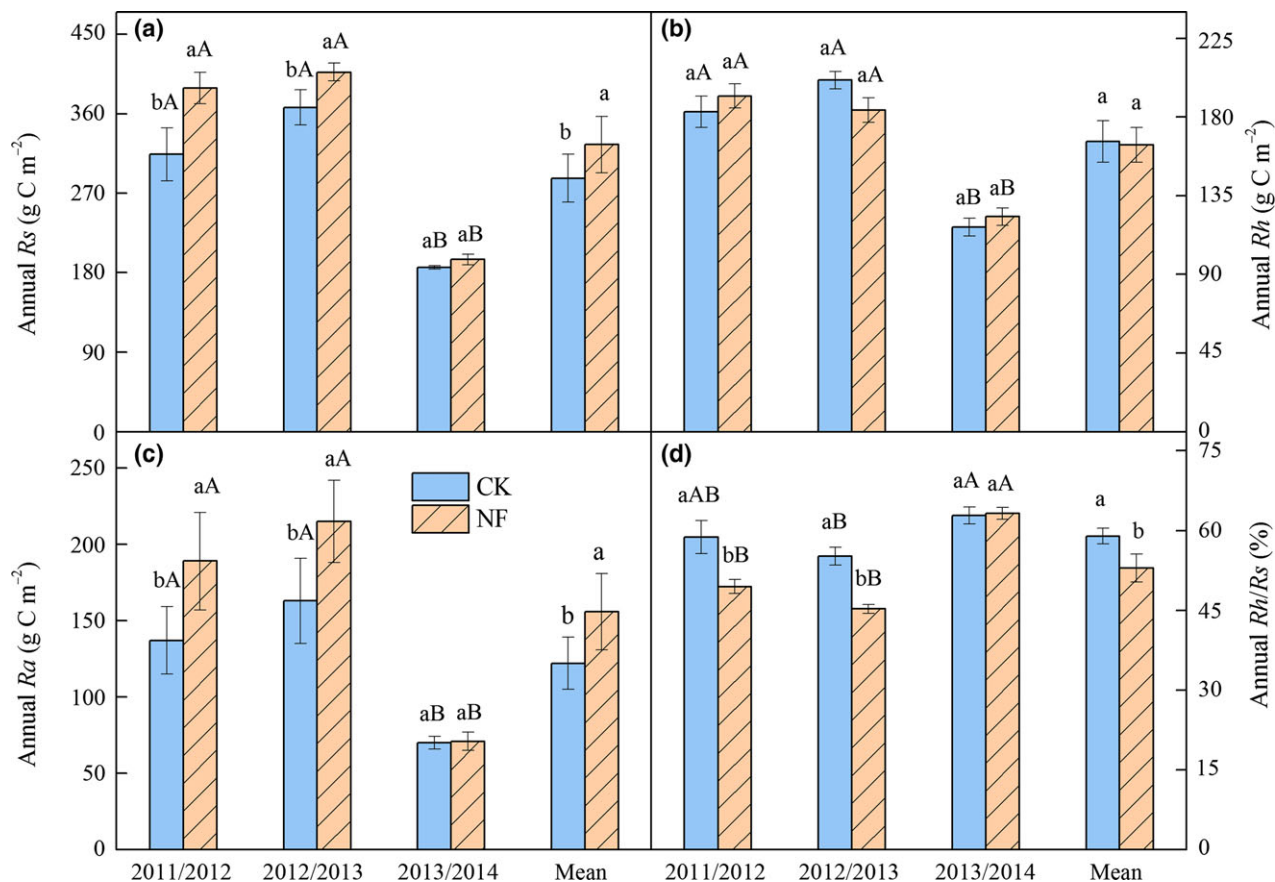


Fig. 4 Annual soil respiration (R_s ; a), heterotrophic respiration (R_h ; b), autotrophic respiration (R_a ; c), and the contribution of annual R_h to R_s (d) for the experimental year of 2011/2012, 2012/2013, and 2013/2014 and across the three years. Values are means \pm SE. Significant differences between treatments and years at $P < 0.05$ are indicated by different lowercase and capital letters, respectively. [Colour figure can be viewed at wileyonlinelibrary.com]

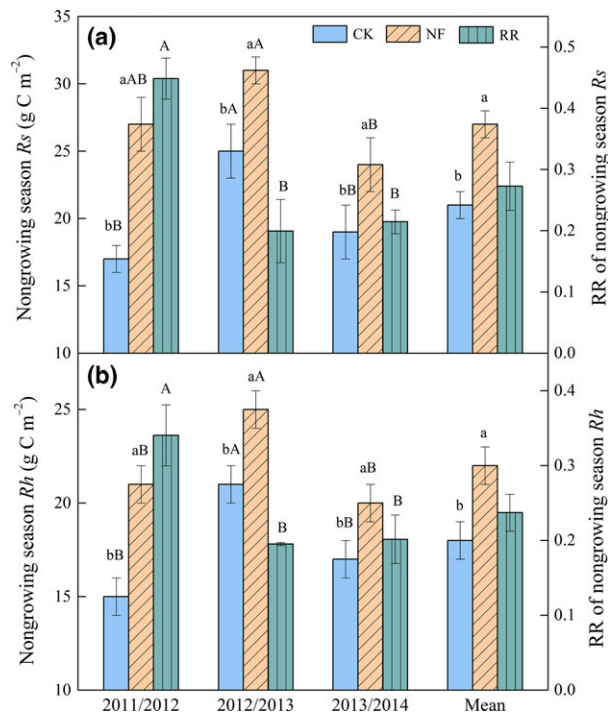


Fig. 5 Nongrowing season soil respiration (R_s ; a), heterotrophic respiration (R_h ; b), and their response ratio (RR) to nitrogen fertilization for the experimental year of 2011/2012, 2012/2013, and 2013/2014 and across the three years. Values are means \pm SE. Significant differences between treatments and years at $P < 0.05$ are indicated by different lowercase and capital letters, respectively. [Colour figure can be viewed at wileyonlinelibrary.com]

In general, R_s , R_h , and R_a were more closely correlated with soil NO_3^- than NH_4^+ . Soil DOC exhibited significant ($P < 0.05$) correlations with R_s , R_h , and R_a with the combined data in 2012/2013 and 2013/2014. Consistently, annual R_s , R_h , or R_a increased linearly with the annual mean concentration of soil NO_3^- or DOC, but not with NH_4^+ (Fig. 7). The aboveground biomass was significantly related with R_a ($P < 0.05$), but not with R_s and R_h .

Discussion

Effects of extreme rainfall on soil respiration and its components

A synthesis of precipitation manipulation studies suggested that soil respiration (R_s) would increase under future scenarios with increased precipitation (Liu *et al.*, 2016). However, we found that annual R_s under control (CK) and N fertilization (NF) treatments in the wettest year of 2013/2014 was 45.2% and 51.0%, respectively, lower than the average in the other two years (Fig. 4a). To examine the effects of rainfall on R_s in the same

region, we collected the published R_s measured in cultivated black soils during the maize growing season in normal rainfall years (Li *et al.*, 2009, 2013; Liang *et al.*, 2012; Ni *et al.*, 2012). After combining these data with our results measured in 2011/2012 and 2012/2013, we found that R_s from both unfertilized and N-fertilized soils increased linearly with total rainfall (Fig. 8a), which was in line with Liu *et al.* (2016). In contrast, R_s measured in 2013/2014 for both CK and NF treatments were greatly lower than the values calculated based on the linear functions obtained from the normal rainfall years. The decreased R_s largely resulted from the inhibition effects of extreme rainfall on each respiration component. Annual R_h in 2013/2014 was 39.1% and 34.6% lower than the averages in the other two years for CK and NF, respectively (Fig. 4b). R_a was more strongly suppressed, with a reduction of 53.3% and 64.9% for CK and NF, respectively (Fig. 4c).

In 2011/2012 and 2012/2013, R_h was generally promoted by rainfall and increased with increasing soil moisture. Similar phenomenon has been widely reported in previous studies (e.g., Lee *et al.*, 2004; Matteucci *et al.*, 2015). Increased R_h after rainfall is mainly due to the enhanced microbial decomposition as a result of improved diffusion and availability of labile organic substrates, and increased microbial biomass and activity (Lee *et al.*, 2004; Borcken & Matzner, 2009; Moyano *et al.*, 2013). In 2013/2014, however, R_h was not correlated with rainfall and decreased if soil moisture exceeded the threshold of 57% WFPS. Specifically, the extreme rainfall event occurred on July 30, 2013 led soil to near saturation and reduced R_h to 6.0–27 $mg\ C\ m^{-2}\ h^{-1}$ for one month. These values were similar to the R_h fluxes (13.5–27.2 $mg\ C\ m^{-2}\ h^{-1}$) from rice paddies in the Sanjiang Plain of northeast China (Ouyang *et al.*, 2015). Suppression of flooding on R_s has also been observed in peatland (Mcnicol & Silver, 2014) and floodplain (Batson *et al.*, 2015). The O_2 diffusion rate can be decreased by 10 000-fold in wet soil (De-Campos *et al.*, 2012), which is the main cause for decreased R_h (Philben *et al.*, 2015). Under anoxic condition, the activities of extracellular oxidative enzymes could be restrained, which has been referred as an 'enzymatic latch' mechanism for C store in peatlands (Freeman *et al.*, 2001). In a laboratory experiment, we found that soil microbial biomass measured as total phospholipid fatty acids (PLFAs) content in this soil exhibited a quadratic relationship with WFPS (Fig. S3a). The PLFAs content decreased with increasing soil moisture at $> 59\%$ WFPS. Therefore, R_h was largely reduced after soil was waterlogged by the extreme rainfall, although soil DOC concentration tended to increase (Fig. S1c) due to physical disaggregation and organo-mineral complexes destabilization (Mcnicol & Silver, 2014).

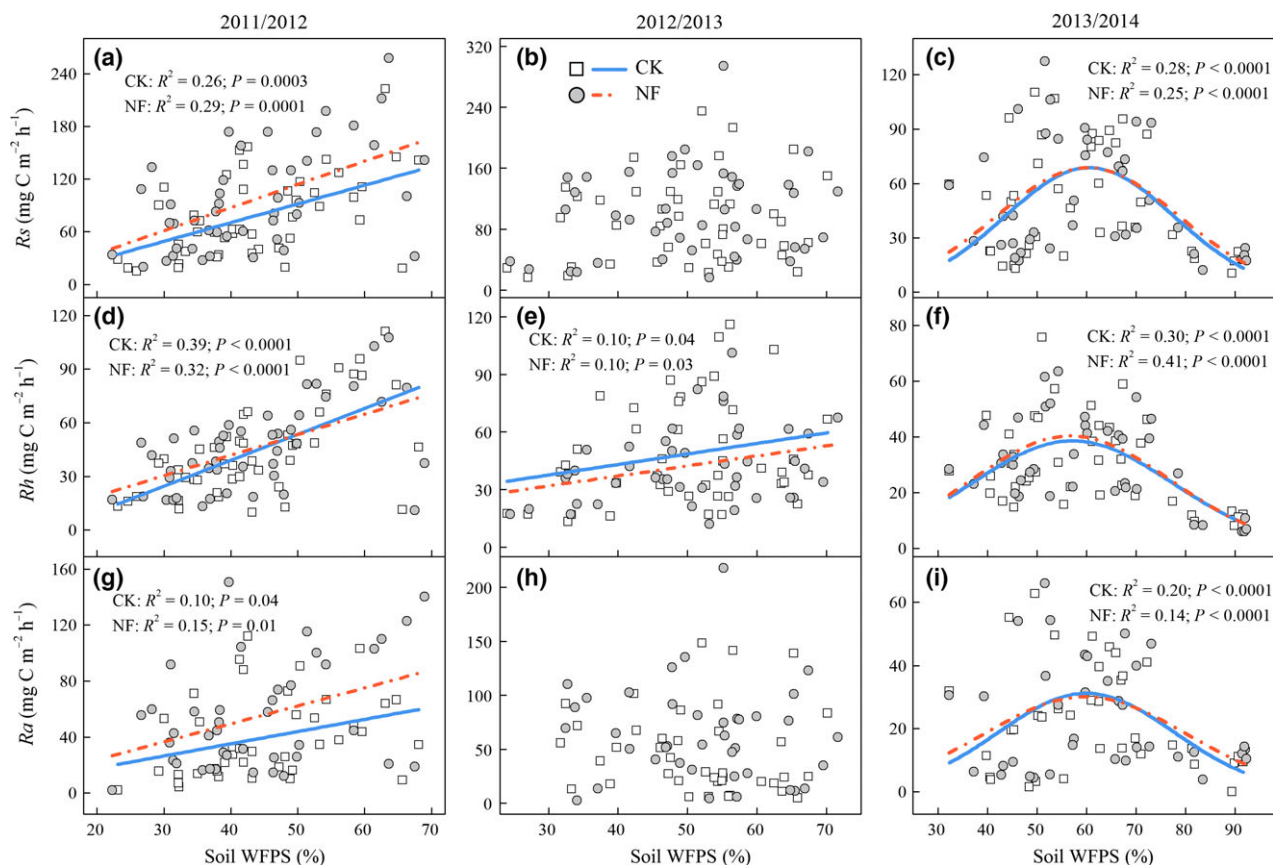


Fig. 6 Relationships between soil water-filled pore space (WFPS) and soil respiration (R_s), heterotrophic (R_h) or autotrophic (R_a) respiration during the growing season of 2011/2012 (a, d, and g), 2012/2013 (b, e, and h), and 2013/2014 (c, f, and i). [Colour figure can be viewed at wileyonlinelibrary.com]

Compared to R_h , correlations between R_a and rainfall or soil WFPS were less significant (Table S5). The stepwise regression analysis showed that soil temperature and moisture were the main factors controlling R_h , while PAR_3 was the only parameter entering the final function for R_a (Table 1). Furthermore, annual R_a but not R_h increased linearly with the aboveground biomass (Fig. 7d). These results suggested that in comparison with R_h , R_a was less sensitive to the variation in soil moisture (Zimmermann *et al.*, 2010; Casals *et al.*, 2011) but more dependent on plant photosynthate supply (Högberg *et al.*, 2001; Gomez-Casanovas *et al.*, 2012). The entrance of PAR_3 rather than PAR in the regression model indicated a time lag between plant photosynthesis and R_a (Kuz'yakov & Gavrichkova, 2010).

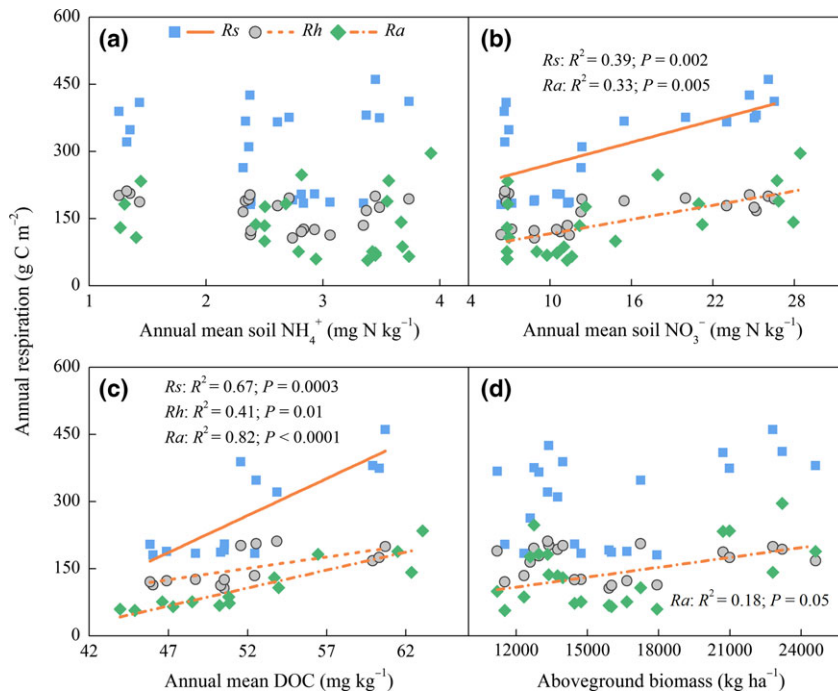
In the extreme rainfall year of 2013/2014, negative effect of increasing soil moisture on R_a occurred at >60% WFPS (Fig. 6i). During the soil waterlogging period, R_a was reduced to <15 mg C m⁻² h⁻¹ in both CK and NF treatments. Decreased R_a under high soil moisture was mainly due to the restrained activities of roots and rhizosphere microbes by the hypoxia

stress (Kreuzwieser & Gessler, 2010; Nottingham *et al.*, 2010). Soil waterlogging can rapidly induce stomatal closure to maintain turgor under low leaf water potential and suppress leaf CO₂ assimilation and photosynthetic activity, leading to lower belowground allocation of photosynthates, and thus the decrease in root growth, biomass, and exudates (Ashraf & Habibur-Rehman, 1999; Milroy & Bange, 2013; Rich & Watt, 2013). After the extreme rainfall, 14 rainfall events occurred in August 2013. During this period, the PAR data were not available (Fig. 2a), but it could be deduced that PAR should be lower than the corresponding period in normal rainfall years as indicated by the negative relationship between rainfall and PAR ($P < 0.0001$; data not shown). Accordingly, respiration of active roots and rhizospheric microbes would be largely reduced as a result of limited substrates supply (Kuz'yakov & Cheng, 2004; Gomez-Casanovas *et al.*, 2012).

Based on the decrease in R_s after flooding observed under natural conditions, we suggest that a short-term manipulation experiment, with intensive measurement of R_h and R_a fluxes, should be conducted under water

Table 1 Stepwise regression analysis of soil respiration (R_s), heterotrophic (R_h), and autotrophic (R_a) respiration with photosynthetically active radiation (PAR), mean PAR over 3 days prior to gas measurement (PAR_3), soil temperature (ST), water-filled pore space (WFPS), ammonium (NH_4^+), and nitrate (NO_3^-) concentrations across the three years

		Equation	n	F	R^2	P
CK	R_s	$Y = 2.79 PAR_3$	53	203	0.80	<0.0001
		$Y = 3.29 PAR_3 - 1.85 NO_3^-$	53	111	0.81	<0.0001
		$Y = 1.95 PAR_3 - 2.06 NO_3^- + 2.13 ST$	53	82	0.83	<0.0001
	R_h	$Y = 2.10 ST$	53	281	0.84	<0.0001
		$Y = 1.44 ST + 0.31 WFPS$	53	162	0.86	<0.0001
		$Y = 1.63 ST + 0.36 WFPS - 0.78 NO_3^-$	53	118	0.88	<0.0001
	R_a	$Y = 1.34 PAR_3$	53	98	0.65	<0.0001
		$Y = 1.68 PAR_3 - 1.30 NO_3^-$	53	55	0.68	<0.0001
		$Y = 0.86 PAR_3 - 1.70 NO_3^- + 0.95 PAR$	53	42	0.72	<0.0001
NF	R_s	$Y = 4.36 ST$	53	227	0.81	<0.0001
		$Y = 3.29 ST + 8.38 NH_4^+$	53	123	0.83	<0.0001
	R_h	$Y = 2.02 ST$	53	447	0.90	<0.0001
		$Y = 1.37 ST + 0.30 WFPS$	53	288	0.92	<0.0001
	R_a	$Y = 1.69 PAR_3$	53	112	0.68	<0.0001
	All	R_s	$Y = 4.21 ST$	106	423	0.80
$Y = 2.26 ST + 1.40 PAR_3$			106	231	0.82	<0.0001
R_h		$Y = 2.06 ST$	106	688	0.87	<0.0001
		$Y = 1.40 ST + 0.31 WFPS$	106	417	0.89	<0.0001
R_a		$Y = 1.52 PAR_3$	106	206	0.66	<0.0001

**Fig. 7** Relationships between the annual soil respiration (R_s), heterotrophic (R_h) or autotrophic (R_a) respiration, and annual mean soil ammonium (NH_4^+ ; a), nitrate (NO_3^- ; b), and dissolved organic carbon (DOC; c) concentrations and total aboveground biomass (d). [Colour figure can be viewed at wileyonlinelibrary.com]

flooding conditions. Dynamics of soil O₂ concentration, microbial biomass, enzyme activities, DOC fraction, and plant root biomass are needed to be investigated to get deep insights into mechanisms of R_s inhibition by extreme rainfall events.

Effects of extreme snowfall on nongrowing season soil respiration

Most studies on winter C fluxes were conducted in the Arctic, boreal, and alpine systems (e.g., Björkman *et al.*,

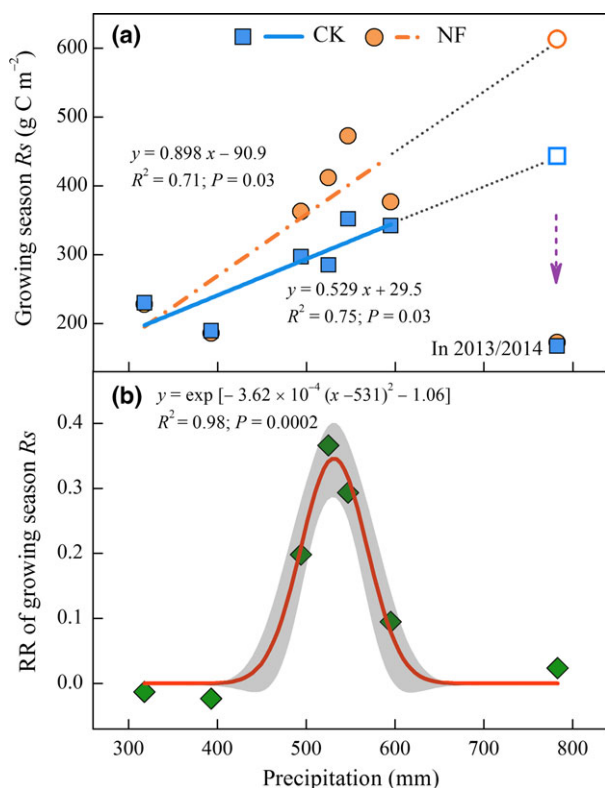


Fig. 8 Relationships between precipitation and soil respiration (R_s) from the N-unfertilized (CK) and N-fertilized (NF) black soils (a) or the response ratio (RR) of R_s to N fertilization (b) during the maize growing season. The shading part represents the 95% confidence intervals. Data were sourced from this study and previous studies conducted in the same region as ours (Li *et al.*, 2009, 2013; Liang *et al.*, 2012; Ni *et al.*, 2012). In the upper panel, data in the year of 2013/2014 with the extreme rainfall events in this study were not included in the regression analysis, and the open square and dots represent data calculated based on the linear function and precipitation during the growing season in 2013/2014. [Colour figure can be viewed at wileyonlinelibrary.com]

2010; Haei *et al.*, 2011; Wang *et al.*, 2014). Our study in the temperate cropland further highlights the significance of cold-season C cycles. R_s and R_h during the nongrowing season were 15–31 g C m^{-2} and contributed 5.5–16.4% to their annual budget. These values fell within the range of previous records as summarized by Liptzin *et al.* (2009).

Compared with the other two years, nongrowing season R_s and R_h in 2012/2013 were increased by 28.7% and 26.0%, respectively (Fig. 5). This increment was mainly due to the distinctly higher fluxes during spring thaw (Fig. 2). During the nongrowing season, both R_s and R_h stemmed from heterotrophic process as no plant roots existed. Elberling & Brandt (2003) indicated that increased CO_2 fluxes after soil freeze–thaw cycles were mainly derived from the physical release of trapped CO_2

in deep layer below the frozen soil. However, we speculated that microbial processes in the thawed soil might be the main source because high CO_2 fluxes appeared when soil had thawed only in the surface (0–30 cm) layer (Monson *et al.*, 2006; Wang *et al.*, 2013). Soil microbial biomass and activity can be promoted after soil thaw due to the increases in soil temperature, moisture, or labile substrates (Liptzin *et al.*, 2009; Haei *et al.*, 2011). Among these factors, substrate supply has been proposed as the limiting factor for microbial respiration in cold season (Brooks *et al.*, 2004; Hirano, 2005). In a laboratory experiment, we found that soil DOC concentration increased, but its specific ultra violet absorption (SUVA, indicator for DOC aromaticity) decreased after a freeze–thaw cycle in test soil at 20–100% WFPS (Z.M. Chen, Y.H. Xu, W.X. Ding, unpublished data). However, in the field, significant spring thaw CO_2 fluxes were only observed in 2013. During the surface soil thawing period, R_s and R_h increased more closely with soil moisture than temperature (Fig. S4). WFPS after soil thaw was higher in 2013 than the other two years, while soil temperature was similar among the 3 years (Table S1). Unlike the cases during the growing season, soil microbes were unresponsive to high moisture condition after exposure to freeze–thaw (Fig. S3). Accordingly, we speculated that higher soil moisture content was likely the main contributor for higher R_s and R_h during the spring thaw period in 2013. More frequent snowfall and especially the extreme snowfall event in winter of 2012/2013 resulted in more total snowfall and deeper snow cover than 2011/2012 and 2013/2014 (Table S1). More melting water induced higher soil moisture content (Maurer & Bowling, 2014) and thus higher CO_2 fluxes in spring 2013. In accordance with our findings, Nobrega & Grogan (2007) observed higher R_s during the spring thaw period in the snow fence treatment with deeper snow cover. Björkman *et al.* (2010) also reported an exponential relationship between snow depth and winter soil CO_2 fluxes in Arctic ecosystems.

The occurrence of extreme snowfall event is predicted to intensify in the Northern Hemisphere under warming climate (O’Gorman, 2014). Moreover, higher Q_{10} values of R_s and R_h during the nongrowing season (Table S6) indicated greater sensitivity of respiration to climate warming at lower temperature, especially under wetter condition (Davidson & Janssens, 2006; Wang *et al.*, 2014). Thus, it is crucial to pay more attention on cold-season respiration and its responses to climate warming.

Effects of N fertilization and its responses to extreme precipitation

N fertilization increased R_s by 23.9% and 10.9% in the normal rainfall years of 2011/2012 and 2012/2013,

respectively. Similarly, with a meta-analysis, Zhou *et al.* (2014) found that N addition enhanced R_s by 12.4% for the cropland ecosystems. Stimulated R_s by N fertilization in the normal years was mainly due to the positive response of R_a , which was increased by 38.0% and 31.9% in 2011/2012 and 2012/2013, respectively. On the other hand, no significant difference in R_h was observed between CK and NF in each year. Likewise, Hasselquist *et al.* (2012) reported that N addition increased R_s as a result of elevated R_a in a boreal forest. We found that R_a increased linearly with increase in the aboveground biomass (Fig. 7d), which was higher in NF than CK in 2011/2012 and 2012/2013 (Table S7). Consistently, Yan *et al.* (2010) showed that N addition increased R_a as a result of increased plant productivity in a temperate steppe. Zhang *et al.* (2014) proposed that N addition improved root growth and N accumulation in root tissues and thus facilitated root respiration, which was speculatively also the case in the normal rainfall years of our studies.

In the record wet year of 2013/2014, R_s was almost equal between CK and NF (Fig. 4). Based on the synthetic data, we found that the effect of N fertilization on R_s could be well fitted to precipitation by a Gaussian function with an optimal precipitation of 531 mm during the maize growing season in the study region (Fig. 8b). These previous studies did not partition respiration component. In the present study, we found that the neutral effect of N fertilization on R_s under excessively wet condition was mainly due to the inhibition of R_a . After soil was waterlogged by the extreme rainfall, R_a was decreased to no more than 15 mg C m⁻² h⁻¹ in both CK and NF treatments lasting for about one month. Limited photosynthate supply as a result of inhibited plant photosynthesis was suggested as the main cause for decreased R_a as discussed above. Ashraf & Habib-ur-Rehman (1999) reported that the decreases of chlorophylls content and substomatal CO₂ concentration in maize leaves induced by waterlogging were greater under higher rate of N fertilization. They pointed out that increased N supply could have injurious effects on the growth of maize experiencing soil waterlogging. In the current study, we found that, in contrast to the other years, the plant biomass in CK was higher, albeit not significantly, than in NF in 2013/2014 (Table S7). As a consequence, the positive effects of N fertilization on R_a and accordingly R_s disappeared in the extreme rainfall year.

No significant effect of N fertilization on annual R_h was found in each year, regardless of the occurrence of extreme precipitation event. Interestingly, the temporal variation of the RR of R_h flux was consistent among the 3 years (Fig. 3). Initial positive effect of N fertilization on R_h was probably because of the stimulated

decomposition of labile SOM compounds. It has been suggested that N addition could enhance the activities of hydrolytic enzymes that primarily decompose the labile organic matter (Knorr *et al.*, 2005) and the competitive ability of r-strategist microbes that are more N-demanding (mainly bacteria) under sufficient C supply (Ågren *et al.*, 2001). As the labile substrates were gradually consumed, the RR of R_h became lower and turned to below zero. At this time, a higher proportion of heterotrophic CO₂ fluxes were likely sourced from the fungal decay of more recalcitrant organic matter (Knorr *et al.*, 2005; Berg, 2014), which could be inhibited by N addition (Treseder, 2008; Xu *et al.*, 2016). During the nongrowing season, R_h in NF tended to be higher again than in CK. Nutrients availabilities are suggested to be low and play a key role for microbes maintaining metabolically activity in frozen soils (Lukas *et al.*, 2013). N addition could alleviate nutrient limitation and thus promote microbial respiration. Our laboratory experiment showed that the concentration and decomposability of soil DOC as well as microbial biomass were increased after thaw in test soil (Z.M. Chen, Y.H. Xu, W.X. Ding, unpublished data) as supported by Haei *et al.* (2011). Consequently, peak value of the RR of R_h was found during the spring thaw period in each year.

The RR of nongrowing season cumulative R_s and R_h was greater in the normal year of 2011/2012 than the year of 2012/2013 and 2013/2014 with extreme rainfall or snowfall events (Fig. 5). The impact of soil moisture on CO₂ fluxes during the spring thaw period was the main reason causing the interannual variations of nongrowing season R_s and R_h as discussed above. The RR of R_s and R_h decreased with increasing soil WFPS during the spring thaw period across the 3 years (Fig. S5). Higher soil moisture condition is beneficial for microbial nutrient acquisition and thus alleviates the restriction of nutrients on microbial activities in cold environment (Lukas *et al.*, 2013). Compared with the spring thaw period in 2011/2012, soil moisture was higher in 2012/2013 and 2013/2014 (Fig. 2b) due to more snow melting water and the legacy effect of the extreme rainfall in summer 2013 (Chen *et al.*, 2016), respectively. Accordingly, R_s and R_h were less responsive to N fertilization during the nongrowing season of 2012/2013 and 2013/2014 than 2011/2012.

In summary, our 3-year field experiment showed that R_s was stimulated by N fertilization in normal rainfall years as a result of the increase in R_a , while R_h was unresponsive to N fertilization. However, in the record wet year, there was no significant effect of N fertilization on R_s due to the inhibited effects of an extreme summer rainfall event on R_h and particularly R_a . Reduced R_h and R_a were mainly attributable to the

anoxic stress on soil microorganisms and decreased plant photosynthesis, respectively. Nongrowing season R_s and R_h played an important role in their annual budgets and were increased by the extreme snowfall event due to high soil moisture content during spring thaw. The positive effect of N fertilization on nongrowing season R_s and R_h was weaker in the years with extreme snowfall or rainfall than normal year. These findings have important implications on soil C flux and its feedback to climate change because extreme rainfall and snowfall will be more frequent and intense with warming climate in the Northern Hemisphere, especially in mid-high latitudes (Fischer *et al.*, 2013; O’Gorman, 2014). Reduced R_s and its response to N supply by extreme rainfall may generate a negative feedback to climate change. However, considering higher temperature sensitivity of R_s at lower temperature (Carey *et al.*, 2016), increased nongrowing season R_s under extreme snowfall regimes would have a large potential for causing positive climate change feedback. Therefore, the effects of extreme precipitation on soil C cycling and its response to N fertilization should be incorporated into earth system models to improve the prediction of C-climate feedbacks. However, cautions should be taken when extrapolating our results to other regions. Cross-site and cross-biome studies are necessary to confirm our findings at a large scale. Manipulation studies, combining a wide gradient of precipitation and N addition rate and focusing on soil microbial processes and plant physiology, are needed for better quantitative and mechanistic understanding on the responses of soil C flux to N enrichment under extreme precipitation events.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Weather parameters over a 3-year period from May 2011 to April 2014.

Table S2 Results of the repeated-measures ANOVA analysis of the effects of sampling time, treatment and their interaction on the fluxes of soil respiration (*R_s*), heterotrophic (*R_h*) and autotrophic respiration (*R_a*) in 2011/2012, 2012/2013 and 2013/2014.

Table S3 Correlations between soil respiration and total precipitation over 3 days prior to gas measurement (*P_r*), photosynthetically active radiation (PAR), average PAR (PAR₃) over 3 days prior to gas measurement, soil temperature (ST), water-filled pore space (WFPS), ammonium (NH₄⁺), nitrate (NO₃⁻) or dissolved organic carbon (DOC) concentrations.

Table S4 Correlations between heterotrophic respiration and total precipitation over 3 days prior to gas measurement (*P_r*), photosynthetically active radiation (PAR), average PAR over 3 days prior to gas measurement (PAR₃), soil temperature (ST), water-filled pore space (WFPS), ammonium (NH₄⁺), nitrate (NO₃⁻) or dissolved organic carbon (DOC) concentrations.

Table S5 Correlations between autotrophic respiration and total precipitation over 3 days prior to gas measurement (*P_r*), photosynthetically active radiation (PAR), average PAR over 3 days prior to gas measurement (PAR₃), soil temperature (ST), water-filled pore space (WFPS), ammonium (NH₄⁺), nitrate (NO₃⁻) or dissolved organic carbon (DOC) concentrations.

Table S6 Temperature sensitivity (*Q₁₀* value) of soil respiration (*R_s*), heterotrophic (*R_h*) and autotrophic (*R_a*) respiration during the growing and nongrowing seasons and the whole year in 2011/2012, 2012/2013, 2013/2014 and across the three years.

Table S7 Soil organic carbon (SOC), total nitrogen (TN), ammonium (NH₄⁺), nitrate (NO₃⁻) and dissolved organic carbon (DOC) concentrations at the end of experiment and plant biomass in the experimental year of 2011/2012, 2012/2013 and 2013/2014.

Fig. S1 Soil ammonium (NH₄⁺; a), nitrate (NO₃⁻; b) and dissolved organic carbon (DOC; c) concentrations in the treatment without (CK) and with (NF) nitrogen fertilization over a 3-year measurement period from May 2011 to April 2014. Soil DOC concentrations were not determined in 2011/2012. Vertical bars are the standard errors of the means. Arrows denote the fertilization time. Shading parts represent the nongrowing season period.

Fig. S2 Autotrophic respiration (*R_a*) from soils without (CK) and with (NF) nitrogen fertilization in each measurement year from 2011 to 2013. Vertical bars are the standard errors. Arrows denote the fertilization time.

Fig. S3 Relationship between total phospholipid fatty acids (PLFAs) in test soil and water-filled pore space (WFPS) in laboratory incubation experiments. Data in the right panel were measured after a freeze-thaw cycle (soils were frozen at -25 °C for 7 days and then thawed at 8 °C). Vertical bars are the standard errors (*n* = 4).

Fig. S4 Relationships between soil respiration (*R_s*; a, b) or heterotrophic respiration (*R_h*; c, d) and soil water-filled pore space (WFPS) or temperature during the surface (0–30 cm) soil thawing period over the three measurement years. Dashed lines indicate the bounds of the 95% confidence intervals.

Fig. S5 Relationships between soil water-filled pore space (WFPS) and the response ratio of soil respiration (*R_s*) or heterotrophic respiration (*R_h*) to nitrogen fertilization during the spring thaw period over the three measurement years.