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Different Response Patterns of Soil Respiration to a Nitrogen Addition Gradient in Four Types of Land-Use on an Alluvial Island in China

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ABSTRACT

It has been well documented that nitrogen (N) additions significantly affect soil respiration (R_s) and its components [that is, autotrophic (R_a) and heterotrophic respiration (R_h)] in terrestrial ecosystems. These N-induced effects largely result from changes in plant growth, soil properties (for example, pH), and/ or microbial community. However, how R_s and its components respond to N addition gradients from low to high fertilizer application rates and what the differences are in diverse land-use types remain unclear. In our study, a field experiment was conducted to examine response patterns of R_s to a N addition gradient at four levels (0, 15, 30, and 45 g N m^{-2} y^{-1}) in four types of land-use (paddy rice–wheat and maize–wheat croplands, an abandoned field grassland, and a *Metasequoia* plantation) from December 2012 to September 2014 in eastern China. Our results showed that N addition significantly stimulated R_s in all four land-use types and R_h in croplands (paddy rice–wheat and maize–wheat). R_s increased linearly with N addition rates in croplands and the plantation, whereas in grassland, it exhibited a parabolic response to N addition rates with the highest values at the moderate N level in spite of the homogeneous matrix for all four land-use types. This suggested higher response thresholds of R_s to the N addition gradient in croplands and the plantation. During the wheat-growing season in the two croplands, R_h also displayed linear increases with rising N addition rates. Interestingly, N addition significantly decreased the apparent temperature sensitivity of R_s and increased basal R_s. The different response patterns of R_s to the N addition gradient in diverse land-use

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types with a similar soil matrix indicate that vegetation type is very important in regulating terrestrial C cycle feedback to climate change under N deposition.

Key words: carbon cycle; climate change; heterotrophic respiration; land-use types; nitrogen addition; soil respiration.

INTRODUCTION

Atmospheric nitrogen (N) deposition, largely originating from fertilizer application and fossil fuels combustion (McPhee and others 2015; Morillas and others 2015), has increased by three- to fivefold in the past century and is likely to continue to increase in the near future (Basto and others 2015; Galloway and others 2008). Increased N deposition, together with excess application of fertilizers in farmlands, has induced N enrichment in the biosphere, which may substantially influence ecosystem structure and function, especially the carbon (C) and N cycles (Chen and others 2016; Janssens and others 2010; Lu and others 2011a, 2011b). The C and N cycles are highly coupled in terrestrial ecosystems (Thornton and others 2007). Specifically, N deposition-induced effects on the ecosystem C cycle will affect the build-up of atmospheric CO_2 concentrations and then impact global climate change (Gruber and Galloway 2008). One of the most important C processes affected by N deposition is CO_2 release from the soil (that is, soil respiration, R_s).

R_s refers to carbon dioxide (CO_2) efflux from the soil surface, including heterotrophic respiration (R_h) during the decomposition of litter and soil organic matter (SOM) and autotrophic respiration (R_a) from live roots and their symbionts (Wang and Yang 2007). As the largest CO_2 efflux from terrestrial ecosystems to the atmosphere (Luo and Zhou 2006; Wang and others 2014), R_s is an important regulator of climate change, as well as a determinant of net ecosystem C balance (Hopkins and others 2013). It is well known that a complex array of biotic and abiotic factors affects R_s, such as temperature, precipitation, soil moisture, oxygen, and substrate supply (Reynolds and others 2015). Global change (for example, elevated CO_2, warming, N deposition) may also substantially mediate R_s and its components (Carol Adair and others 2011; Lu and others 2011b, 2013).

Currently, a number of manipulative experiments have been carried out to examine the effects of N addition on R_s and its components in terrestrial ecosystems. However, the results are controversial, showing positive (Tu and others 2013), negative (Mo and others 2008), and nonsignificant changes (Allison and others 2008) in R_s in response to N addition. In grassland and farmland, significant positive effects of N addition on R_s were more common than decreasing and nonsignificant changes (Graham and others 2014; Jia and others 2012; Zhang and others 2014aa), whereas most studies found that R_s had negative responses to N addition in forests (Janssens and others 2010; Ramirez and others 2010; Zhou and others 2014). On one hand, increased N availability under N addition can enhance plant growth and litter input to the soil, and thus R_h (Craine and others 2001). Simultaneously, N-induced stimulation of root biomass and rhizosphere exudation also increase R_a (Deng and others 2010). On the other hand, possible soil acidification caused by N addition may inhibit microbial activity, reduce microbial biomass, and thus decrease R_s (Phillips and Fahey 2007). The responses of R_s to N addition thus depend on the combined effects of the two opposing mechanisms, which may be related to climate, ecosystem type, and duration of the experiment.

Previous studies have found that fertilization regimes (for example, N application rate) significantly affected plant performance and soil microbial activities and thus R_s and its components (Hossain and others 1995; Iyyemperumal and Shi 2007). Along N addition gradients from low to high N application rates, the responses of R_s showed diverse patterns among ecosystems or individual studies, including increasing, decreasing, and nonlinear trends (Supplementary Figure S1; Zhong and others 2016; Zhou and others 2014). For example, Lee and Jose (2003) found that R_s decreased linearly with N application rate in plantations, whereas the opposite pattern was observed in Tu and others' (2009) study in a bamboo (*Pleioblastus amarus*) forest. In addition, Song and Zhang (2009) demonstrated a nonlinear response of R_s to a N addition gradient with positive effects at low N levels and negative ones at high N levels in a cropland. It should be noted that these studies were located in different regions of the world with heterogeneous backgrounds. The different responses of R_s to N addition gradients in diverse ecosystems or land-use types may largely be related to site-specific differences (for example, climatic condition, soil properties, Zhou and others 2014). However, how R_s responds intrinsically to a N addition gradient in different ecosystems or land-use types in the same soil matrix remains unknown, which limits our ability to explore the responses of the ecosystem C cycle to N fertilization or deposition (Gruber and Galloway 2008).

To probe the response patterns of R_s to a N addition gradient in different types of land-use with a similar soil matrix, a field experiment was carried out on Chongming Island in Shanghai, China, where the natural N deposition rate is 25.6 kg N ha^{-1} y^{-1} (Lü and Tian 2007). The N addition gradient included four levels (0, 15, 30, and 45 g N m^{-2} y^{-1}), which were applied to the four land-use types (a paddy rice (*Oryza sativa* L.)–wheat (*Triticum aestivum* L.) cropland, a maize (*Zea mays* L.)–wheat cropland, an abandoned field grassland, and a *Metasequoia* plantation) from December 2012 to September 2014 in eastern China. The R_s in different land-use types was measured on diel, seasonal, and annual scales under the same background conditions. In this study, our objectives are (1) to examine the response of R_s to four N addition rates, (2) to investigate the effects of land-use type on the response patterns of R_s to the N addition gradient, and (3) to explore the responses of R_s to soil temperature under N addition.

METHODS

Site Description

The experiment was conducted on Chongming Island (121°09′–121°54′E, 31°27′–31°51′N) in Shanghai, China. This is an alluvial island formed by deposited sand and other sediments in the Yangtze River delta. The study site has a flat terrain and low spatial heterogeneity, which eliminates the confounding effects of soil properties and geological processes on R_s. According to the meteorological record from 1956–2000, the mean annual temperature was 15.2°C, with the monthly air temperature ranging from 2.8°C in January to 27.5°C in July. The mean annual precipitation was 1025 mm, with the majority occurring from April to September. The soil is sandy loam characterized by low organic matter content and water-holding capacity, and preservation of fertility (Yang and others 2012).

Experimental Design

The N addition experiment was conducted in four land-use types: a paddy rice–wheat cropland, a maize–wheat cropland, an abandoned field grassland, and a *Metasequoia* plantation. Each land-use type set one study site, which was surrounded by buffer strips wider than 3 m. The N addition treatments contained four N levels with an annual added rate of 0 (control), 15 (N1), 30 (N2), and 45 (N3) g N m^{-2} y^{-1}, respectively, which were evenly applied four times per year (March, May, July, and September in 2012 and 2013) using solid granules of urea ($CO(NH_2)_2$). Each treatment had four replicates. There were a total of 16 plots at each site. The plots were randomly assigned to the four treatments (that is, a completely randomized design).

In the paddy rice–wheat rotation cropland, sixteen 5 × 5 m^2 plots were randomly assigned to the four N treatment levels. Buffer strips surrounding each plot were wider than 2 m. At the beginning of the experiment, plots were separated from each other by plastic shelves inserted into soil to avoid water circulating in the rice growing season. Conventional tillage management practices such as rotation, plowing, sowing, irrigation, and harvesting were conducted on October 16 and 22, 2013 and May 6, 2014 under both control and N addition treatments. Straw and wheat stems were not incinerated in the field. In the maize–wheat rotation cropland, experimental operations were the same as in the paddy rice–wheat cropland. In the abandoned field grassland, sixteen 3 × 3 m^2 plots were randomly assigned to the four N treatment levels. The buffer strips surrounding each plot were wider than 3 m. In the *Metasequoia* plantation, sixteen 15 × 15 m^2 plots were randomly assigned to the four N treatment levels. The buffer strips surrounding each plot were wider than 5 m.

Measurement Protocols

To measure R_s, a PVC collar (20 cm in inner diameter and 11 cm in height) was inserted 5–6 cm into the soil permanently at the center of each plot. Each PVC collar had 24 8-mm holes distributed evenly in its pipe wall below ground level to allow the roots in and surrounding the collar to grow normally. To eliminate aboveground plant respiration from the measurements, living plants inside the soil collars were clipped at the soil surface at least 24 h before measurements were taken. The clipped plant materials were left in the collars. The rate of R_s was measured monthly from January 2013 to September 2014 in the days when rain was absent, using a LI-8100 portable monitoring system (LI-COR, Lincoln, NE, USA) with the R_s measurement chamber being firmly placed on each collar. Measurements were carried out between 9:00 and

16:00. Each of the measurements usually took 2 min and the data were recorded per second by the data logger and then transmitted to a notebook computer. Standard procedures were applied to compute the R_s rate (Zhou and others 2006).

To detect the responses of R_h to different N addition levels in the croplands, PVC shelves (0.6 cm in thickness, 50 × 50 cm^2) were inserted 50 cm into the soil in the four directions to prevent new roots from growing inside the collar and then a PVC collar was inserted into the soil in the middle of the trenching area. The measurement procedure for R_h was the same as that for R_s. R_h was measured only in the wheat-growing season for the two croplands, which were referred to as 'paddy rice–wheat (wheat) cropland' or 'maize–wheat (wheat) cropland' hereafter.

Soil temperature at a depth of 5 cm was monitored adjacent to each PVC collar using a measuring probe connected to the LI-8100 at the same time as we measured the R_s rate. In addition, soil temperature and moisture were measured with a Oneset HOBO system (S-SMD-M005, Onset Computer Corporation, Bourne, MA, USA) with the data loggers buried at 5 cm depth to record temperature and moisture every 30 min. The air temperature and precipitation data were obtained from China's meteorological data network (http://202.96.202.174/Index.aspx).

Statistical Analysis

The effects of the N addition treatments (0, 15, 30, and 45 g N m^{-2} y^{-1}) on R_s and R_h were tested by one-way analysis of variance with N addition levels as a fixed factor. The sensitivity of R_s to soil temperature was estimated by fitting an exponential equation with the R_s rate against temperature from each treatment:

$$R_s = R_0 Q_{10}^{\frac{T}{10}}, \quad (1)$$

where R_s is soil respiration rate (μmol m^{-2} s^{-1}), T is soil temperature (°C) at 5 cm depth, and R_0 is the R_s rate when the temperature is 0°C (that is, the basal respiration rate). Q_{10} represents the temperature sensitivity of R_s, which describes the change in respiration rate over a 10°C increase in soil temperature. The differences in the parameters (that is, R_0 and Q_{10}) among N addition levels were assessed by the t test according to the method presented by Toutenburg (2002) and Zhou and others (2006). Briefly, the t value was calculated for the difference between any two treatments of the four via equation (2).

$$t = \frac{\overline{x_2} - \overline{x_1}}{\sqrt{\frac{\sum S_{ij}^2}{4}}} \quad (i, j = 1, 2). \quad (2)$$

The annual R_s for each treatment was estimated by summing the products of the mean daily R_s and the number of days between samples. Total R_s and R_h during the wheat-growing season in croplands were also estimated from the accumulated R_s and R_h within this period (Figure 6e, f). All analyses described above were performed in SPSS 17 (International Business Machines Corporation) and SigmaPlot 10.0 (SYSTAT Software) for Windows. The significance level (α) was 0.05.

RESULTS

Microclimate

During the study period, the seasonal dynamics of air and soil temperature were similar (Figure 1a, b), with less fluctuation for soil temperature. The maximum monthly air and soil temperature occurred in July 2013 with values of 31.20 and 26.91°C, respectively, whereas the minimums occurred in January 2013 with values of 3.71 and 3.32°C, respectively.

Unlike soil temperature, soil moisture at the depth of 5 cm fluctuated greatly over the period with a range from 16.5 to 80.3%. The higher values appeared in February–April 2013 and February–April 2014 and June 2014, when precipitation was usually high (Figure 1b).

Effects of N Addition on Diel and Seasonal Variability in R_s and Its Components

The diel dynamics of R_s at four N levels followed a unimodal curve in the paddy rice–wheat (wheat) cropland, the abandoned field grassland, and the *Metasequoia* plantation, with high values during the daytime and low values at night (Figure 2). The R_s rate was 4.18–11.95 and 4.05–10.35 μmol m^{-2} s^{-1} in the paddy rice–wheat (wheat) cropland and the abandoned-field grassland, respectively (Figure 2a, b). In both of the two land-use types, the peak R_s appeared at 12:00 under the control and N1 (15 g N m^{-2} y^{-1}) treatments and at 14:00 under the N2 (30 g N m^{-2} y^{-1}) and N3 (45 g N m^{-2} y^{-1}) treatments, respectively. R_s in the *Metasequoia* plantation ranged from 1.22 to 4.28 μmol m^{-2} s^{-1}, with the diel variability being much smaller than that in the paddy rice–wheat cropland and grassland. The peak R_s appeared at 14:00 in the plan-

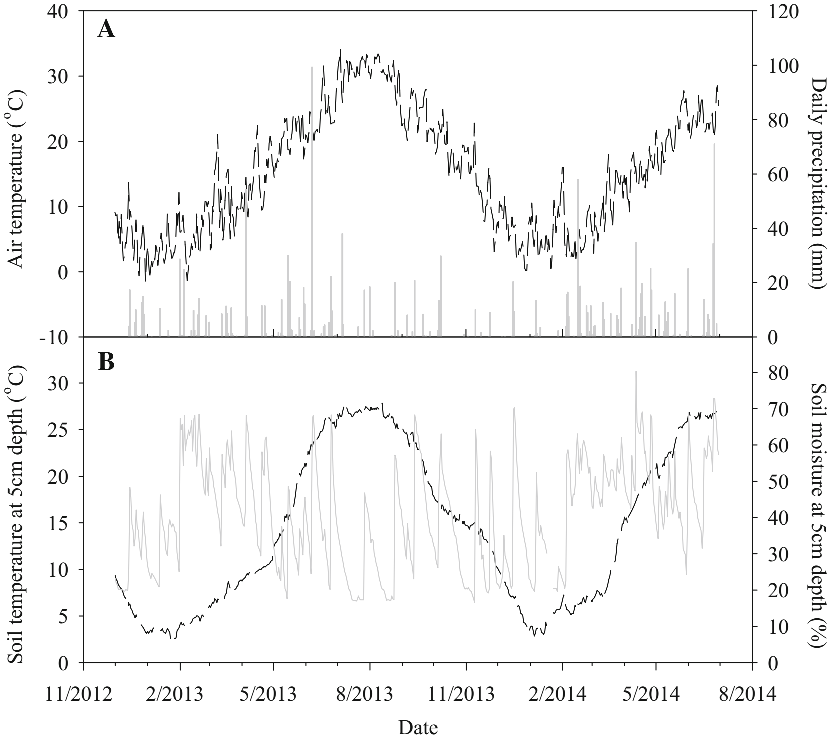

Figure 1. Air temperature and daily precipitation at the experimental site (**A**) and the seasonal variability of soil temperature and moisture at 5 cm depth (**B**) from January 2012 to July 2014.

tation for the four treatments (Figure 2c). On average, R_s rates under all four N treatments were higher than those in the control. The N3 treatment in the paddy rice–wheat cropland and N2 in grassland significantly increased R_s, with the highest average rate being 8.84 and 7.53 μmol m^{-2} s^{-1}, respectively ($P < 0.05$). The other N treatments did not significantly affect R_s either in the paddy rice–wheat cropland or grassland (Figure 2d, e). In the plantation, N addition had a significant effect on R_s under the N2 and N3 treatments, with the average rates being higher than 2.52 μmol m^{-2} s^{-1} ($P < 0.05$, Figure 2f).

The seasonal dynamics of R_s followed the seasonality of soil temperature, with high rates in summer and low rates in winter. The seasonal variability substantially differed among the four land-use types, with the plantation having the lowest range of variation. The point-in-time maximum and minimum R_s under the four N treatments were 7.73–11.43 and 2.22–5.37 μmol m^{-2} s^{-1} in the paddy rice–wheat cropland, respectively (Figure 3a), whereas these values were 8.55–12.18 and 0.57–3.93 μmol m^{-2} s^{-1} in the maize–wheat cropland (Figure 3b), 9.27–12.58 and 0.83–4.17 μmol m^{-2} s^{-1} in the abandoned field grassland (Figure 3c), and 5.17–7.15 and 1.43–4.13 μmol m^{-2} s^{-1} in the *Metasequoia* plantation (Figure 3d), respectively. The average R_s across the study period increased along the N gradient in croplands and the plantation, but in the abandoned field grassland, the largest R_s was seen under the N2 treatment (Figure 3e–h).

The seasonal dynamics of R_h in croplands also followed the changes in soil temperature, with the lowest value in January 2014 and the highest in May 2014. R_h during the wheat-growing season increased with the increasing N rate in the two croplands (Figure 4). The peak R_h was 5.61–6.83 and 5.61–6.46 μmol m^{-2} s^{-1} along the N addition gradient from the control to N3 in the paddy rice–wheat and maize–wheat croplands, respectively (Figure 4).

N-induced Effects on the Apparent Temperature Sensitivity of R_s (Q_{10})

In our study, there were no significant relationships between R_s and soil moisture under the different treatments (Supplementary Figure S2), but the significant relationships between R_s and soil temperature were found. Our regression analysis showed that R_s increased exponentially with soil temperature in all four land-use types, with explained variances (r^2) of more than 78, 74, 81, and 66% for R_s in the paddy rice–wheat cropland, the maize–wheat cropland, the grassland, and the plantation, respectively, for the four N treatments (Figure 5). For all the land-use types, the R_0 (R_s at 0°C) under N addition was significantly higher than

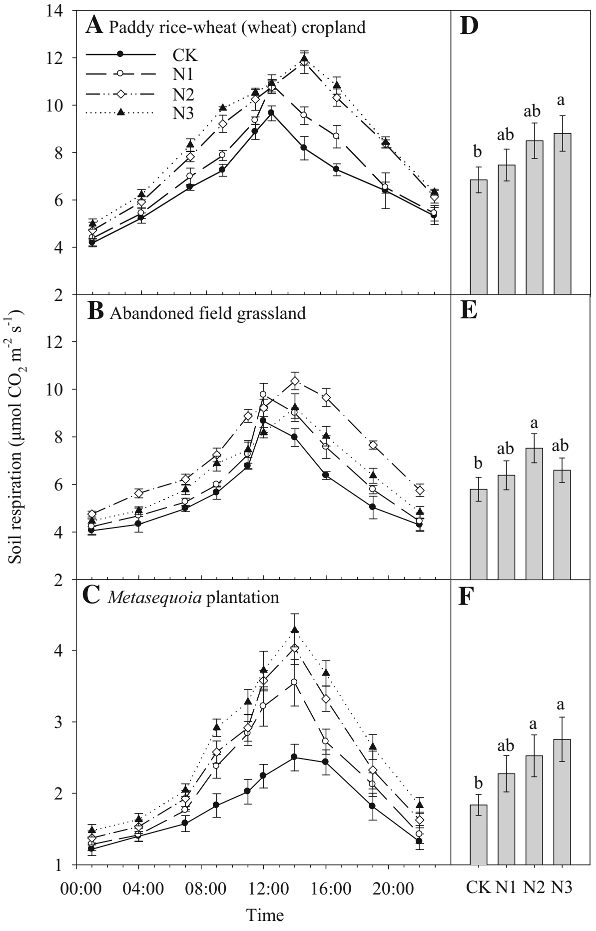

Figure 2. Diel variability of soil respiration (**A–C**) and mean values of soil respiration (**D–F**) in three different land-uses: a paddy rice–wheat (wheat) cropland (**A**, **D**), an abandoned field grassland (**B**, **E**), and *Metasequoia* plantation (**C**, **F**). CK, control; N1, N2, and N3: nitrogen (N) levels at 15, 30, and 45 g N m^{-2} y^{-1}. *Vertical bars* represent the standard error of the mean. *Different lowercase letters* above the *bars* show significant differences among the four N treatments. Here the ‘(wheat)’ in ‘paddy rice–wheat (wheat) cropland’ means that the diel R_s was measured in wheat-growing season for paddy rice–wheat cropland

that in the control ($P < 0.05$). Along the N addition gradient, R_0 increased in all the land-use types except for the abandoned field grassland, in which the largest R_0 was seen under the N2 treatment (Table 1). N addition decreased the Q_{10} of R_s in the four land-use types. Significant effects of N addition on Q_{10} were found for all three N addition treatments in the paddy rice–wheat cropland and abandoned field grassland, whereas significant effects only occurred under the N2 and N3 treatments in the maize–wheat cropland and the N3 treatment in the *Metasequoia* plantation. In addition, the response of Q_{10} to the N addition gradient was opposite to that of R_0 in the maize–wheat cropland and the *Metasequoia* plantation. In the paddy rice–wheat cropland and the abandoned field grassland, Q_{10} exhibited a minimum value under the N2 treatment, but there was no significant difference between the N2 and N3 treatments ($P > 0.05$, Table 1).

Responses of Annual R_s to the N Addition Gradient

The annual R_s in the two croplands was significantly stimulated by N addition as well as the total R_s during the wheat-growing season ($P < 0.05$). The magnitude of the response increased with the N addition rate (Figure 6a, b, e, f). For total R_h during wheat-growing season, a significant increase was only found under the N2 and N3 treatments (Figure 6e, f). N addition also significantly enhanced the annual R_s in the abandoned field grassland ($P < 0.05$), with the maximal stimulation being seen under the N2 treatment (Figure 6c). In the *Metasequoia* plantation, the response of annual R_s increased with the N addition rate, although there was no significant difference between the control and N1 treatments (Figure 6d).

Discussion

Positive Effects of N Addition on R_s in the Four Land-Use Types

Diverse effects of N addition on R_s have been observed in different ecosystems, commonly being positive in farmlands and grasslands and negative in forests (Zhou and others 2014). Our results showed that N addition significantly increased R_s and the R_0 (that is, R_s when soil temperature is 0°C) in all four land-use types (that is, paddy rice–wheat and maize–wheat croplands, the abandoned-field grassland, and the *Metasequoia* plantation). The positive responses of R_s to N addition might be ascribed to several factors. First, additional N input increased the content of inorganic N in the mineral soil layer (Lu and others 2011bb), inducing greater N uptake and assimilation by plants as well as leaf photosynthesis and biomass (Chapin and others 2011aa; Lu and others 2011aa). In our study, N addition stimulated aboveground biomass in croplands and grassland, having a similar response trend to R_s (Supplementary Figure S3). Moreover, root biomass may also increase with N addition, which has been supported by several meta-analyses

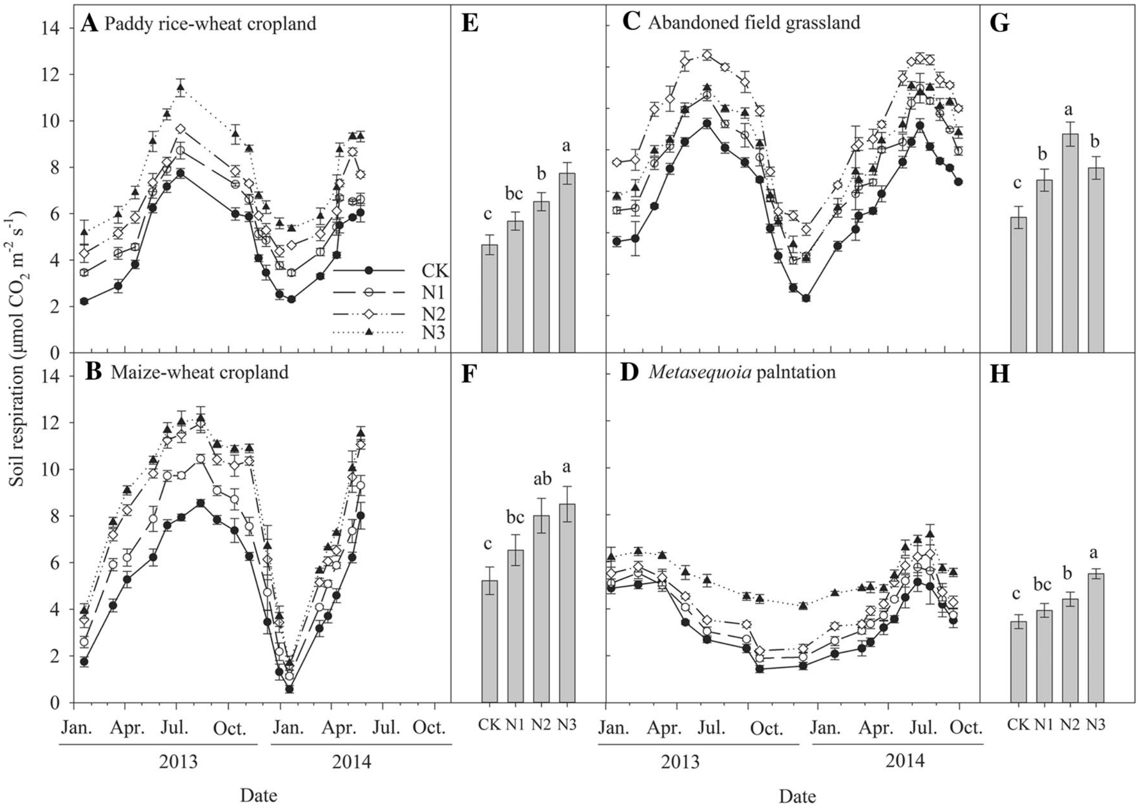

Figure 3. Seasonal variability of soil respiration (**A**–**D**) and their mean values (**E**–**H**) in four land-use types: a paddy rice–wheat cropland (**A**, **E**), a maize–wheat cropland (**B**, **F**), an abandoned field grassland (**C**, **G**), and a *Metasequoia* plantation (**D**, **H**). CK, control; N1, N2, and N3: nitrogen (N) levels at 15, 30, and 45 g N m^{-2} y^{-1}. *Vertical bars* represent the standard error. *Different lowercase letters* above the *bars* show significant differences among the four N treatments.

(Liu and Greaver 2010; Lu and others 2011b; Xia and Wan 2008). Second, root metabolic rate may increase under N addition due to its close relationship with root N concentration, resulting in high specific root respiration, including both growth and maintenance respiration (Burton and others 1998). The N-induced stimulation of specific root respiration and root biomass could positively contribute to an increase in R_a (Cleveland and Townsend 2006; Zhang and others 2014a, 2014b). Third, increased aboveground and belowground biomass under N addition may increase organic C input to the soil through litter and root deposits (Xu and Wan 2008). N addition also improved litter quality (low C:N ratio; Song and others 2011). As a consequence, the elevated substrate supply and the improved litter quality probably stimulated R_h and then R_s, which was consistent with our results in paddy rice–wheat and maize–wheat croplands during the wheat-growing season (Figure 6e, f).

The positive effects in the croplands and grassland were comparable to those observed in many analogous ecosystems (Craine and others 2001; Xu and Wan 2008; Zhou and others 2014), whereas the enhanced effects in the plantation were opposite to those in most previous studies in forests (Janssens and others 2010; Mo and others 2008). The contrasting responses of R_s to N addition between our *Metasequoia* plantation and other forests may largely result from the difference in N-induced changes in soil pH (Liang and others 2013). In our study, soil pH did not vary during the experimental period (Supplementary Table S1). However, the negative effects of N addition on R_s largely resulted from the decreased pH in most relatively long-term N addition experiments, which might inhibit root biomass and microbial activity as well as extracellular enzyme activity (Lu and others 2011bb; Russell and others 2006; Tian and Niu 2015) and thus decreased R_s in those forests.

Different Response Patterns of R_s to the N Addition Gradient in Four Land-Use Types

Previous studies found that the response patterns of R_s to a N addition gradient from low to high N application rates were different in diverse envi-

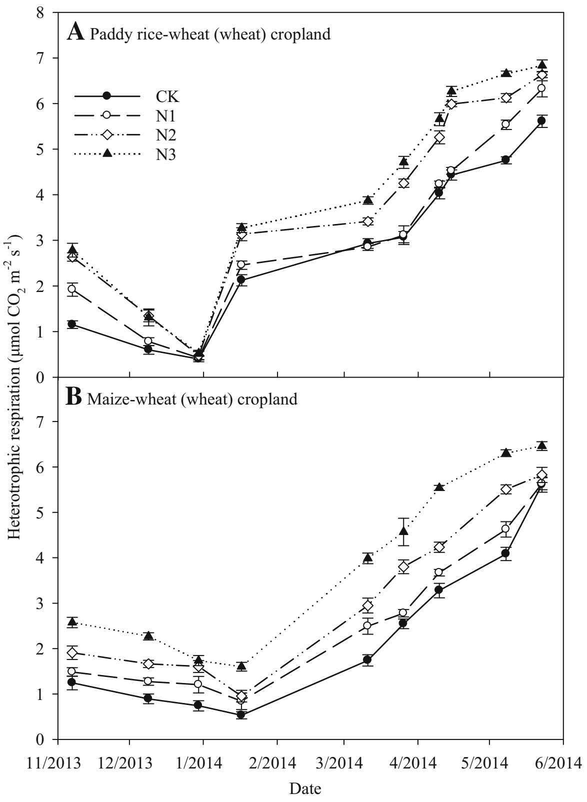

Figure 4. Seasonal variability of heterotrophic respiration in a paddy rice–wheat (wheat) cropland (**A**) and a maize–wheat (wheat) cropland (**B**). CK, control; N1, N2, and N3: nitrogen (N) levels at 15, 30, and 45 g N m^{-2} y^{-1}. *Vertical bars* represent the standard error of the mean. The 'wheat' in *parentheses* means that heterotrophic respiration was measured only in the wheat-growing season for the two croplands.

ronmental and soil conditions (Supplementary Figure S1, Zhong and others 2016; Zhou and others 2014), which may confound the effects of vegetation type. In our study with a relatively homogeneous soil matrix, the effects of N addition on R_s increased linearly from low to high N application rates in three land-use types, but they showed parabolic-like trends in the grassland, with an initial increase and then decrease after the maximum (Figures 3e–h, 6a–d). The different response trends occurred because the distinctive vegetation in four land-use types usually leads to a varying quality and quantity of C input and nutrient availability in the soil as well as microbial communities and enzyme activity (Liu and Greaver 2010; Liu and others 2006; Yang and Zhu 2015). Given the plant-specific characteristics, it has been suggested that the optimum N rate for plant growth and microorganism activity varied across land-use types, which was in line with our results (Allison and others 2009; Bai and others 2010). The optimum N rate that plants and microorganisms preferred in the abandoned field grassland might be close to the N2 level, whereas in the croplands and the plantation, the threshold for N requirements might be beyond the N3 level (Figures 2, 3, 6).

In croplands, agricultural exports of food or feed may make the ecosystem need more N to ensure a balanced nutrient cycle (Brentrup and others 2004) and thus the N threshold would be larger. In plantations, trees generally have a higher N uptake efficiency to sustain the rapid and massive growth, which would lead to a higher N requirement than that for herbaceous plants (Bredemeier and others 2015). In our croplands and plantation, N addition rates did not reach the threshold for its organisms, as gradually increasing N input enabled microorganisms to immobilize and plants to absorb more N (Tu and others 2009) and thus R_s increased with the N addition gradient. These positive linear responses were consistent with those in a winter wheat field (Shao and others 2014) and a *Pleioblastus amarus* plantation in China (Tu and others 2010). However, the N demand rate in the grassland was smaller than that in the croplands and the plantation, as the field was not being harvested and little biomass was produced. Applying N at the N3 level exceeded the optimal N dose for organisms in grasslands and the effects of N addition decreased (Harapiak and others 1992). Thus in our grassland, R_s on diel, seasonal, and annual scales reached their maximal values under a moderate N level (N2) rather than at the highest level (N3, Figures 2e, 3g, 6c). This result was supported by Li and others' (2015) study in a temperate grassland in China, which also showed that the responses of R_s to increasing N rates followed a parabolic trend along the N addition gradient, as did soil microbial biomass C. Aside from the two response patterns mentioned above, R_s also displayed a linearly decreasing response trend to increasing N rates in a natural tropical forest (Mo and others 2008), largely resulting from the excessive N addition rate, which surpassed the threshold for plants and microorganisms in this ecosystem.

The diminishing positive effects or gradually increasing negative effects with increasing N rates can be largely ascribed to soil pH and abiotic interactions. As mentioned earlier, soil acidification might considerably inhibit fine root growth and microbial activity, which were closely related to decreases in R_s and its components under N addition. Although soil pH was not altered by N addition at modest rates (Hogberg and others 2007), it

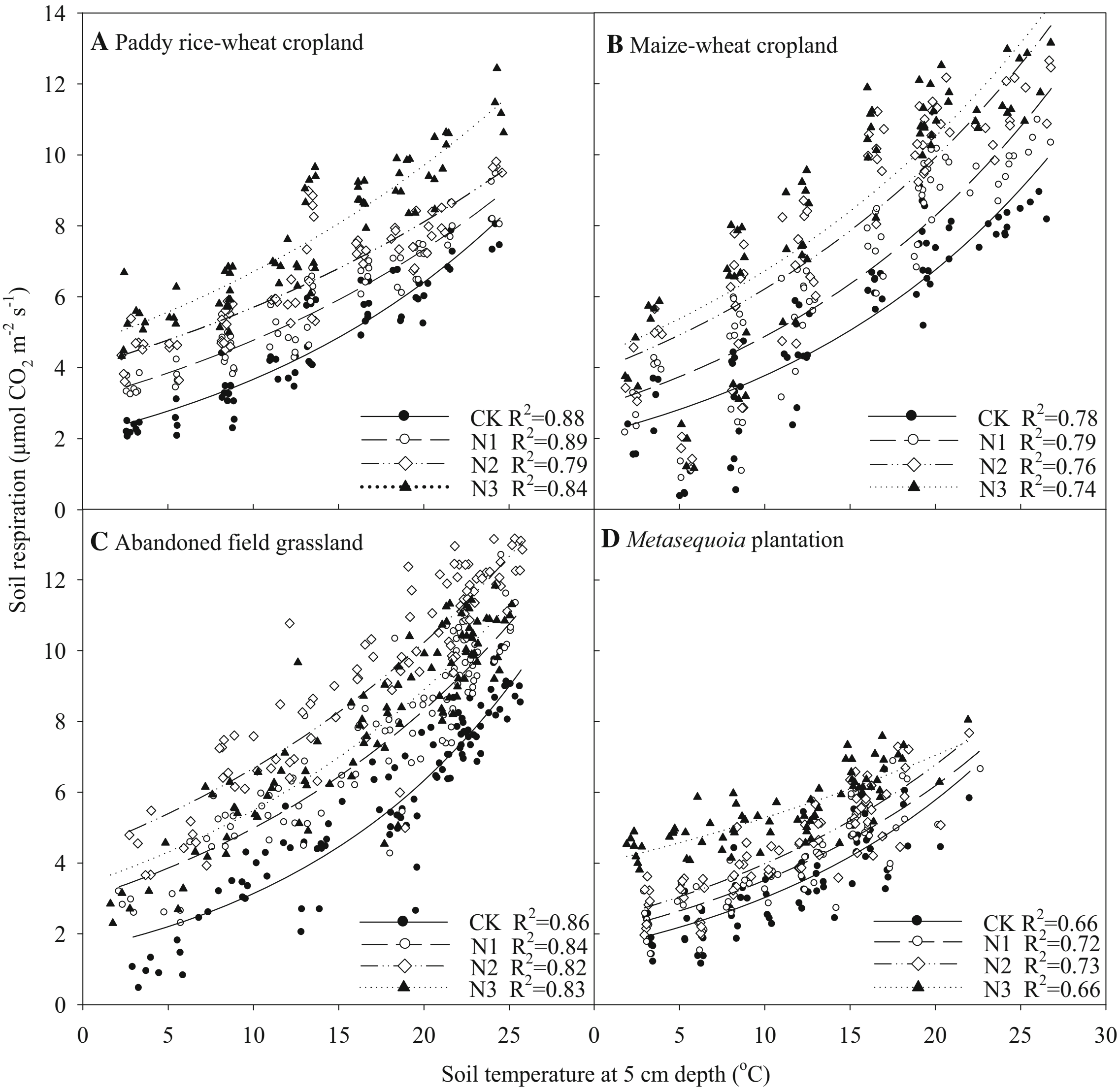

Figure 5. Exponential relationships between soil respiration and soil temperature at 5 cm depth in a paddy rice–wheat cropland (**A**), a maize–wheat cropland (**B**), an abandoned field grassland (**C**), and a *Metasequoia* plantation (**D**). CK, control; N1, N2, and N3: nitrogen (N) levels at 15, 30, and 45 g N m^{-2} y^{-1}. The *P* values of all curves fitted in the four subfigures were less than 0.01.

declined with an increasing N rate when the N dose was superfluous (that is, beyond the threshold for the organisms, Biederbeckl and others 1996). In addition, the abiotic reaction might partially account for the negative effects of N addition on CO_2 emissions other than changes in soil pH (Chapin and others 2011bb; Du and others 2014). N addition complicated the molecular architecture through the polymerization of simple C compounds and inorganic N and retarded the mineralization of soil organic carbon (SOC, Ouyang and others 2008). This resulted in more SOC being sequestrated and thus less CO_2 being released (Jagadamma and others 2007), which could offset the positive effects of N addition on R_s to a certain extent.

Responses of Apparent Q_{10} to N Addition

Soil temperature typically exhibits diel and seasonal variations, which mainly account for the temporal variations of R_s, especially in temperate zones (Zhou and others 2015). Our results followed this trend for R_s in all land-use types, as did R_h in croplands (Figures 2, 3, and 4). The relationship between R_s and soil temperature was often represented by an exponential equation ($R_s = R_0 Q_{10}^{\frac{T}{10}}$) to show its temperature sensitivity (Q_{10}) in most

Table 1. The Parameters (Mean ± SE) of the Exponential Equation Quantifying the Relationship Between Soil Respiration and Soil Temperature

Land-use types	Parameters	CK	N1	N2	N3
Paddy rice–wheat cropland	R_0	2.10 ± 0.10d	3.11 ± 0.10c	4.01 ± 0.16b	4.63 ± 0.16a
	Q_{10}	1.75 ± 0.05a	1.53 ± 0.03b	1.42 ± 0.03d	1.45 ± 0.03cd
Maize–wheat cropland	R_0	2.11 ± 0.18c	2.87 ± 0.21b	3.89 ± 0.27a	4.30 ± 0.29a
	Q_{10}	1.79 ± 0.08a	1.70 ± 0.06ab	1.60 ± 0.06b	1.56 ± 0.05b
Abandoned field grassland	R_0	1.55 ± 0.12c	2.99 ± 0.17b	4.36 ± 0.21a	3.38 ± 0.18b
	Q_{10}	2.02 ± 0.07a	1.67 ± 0.05b	1.53 ± 0.04c	1.62 ± 0.04bc
Metasequoia plantation	R_0	1.58 ± 0.14c	2.00 ± 0.13b	2.34 ± 0.14b	3.96 ± 0.13a
	Q_{10}	1.91 ± 0.12a	1.76 ± 0.08a	1.70 ± 0.07a	1.33 ± 0.03b

R_0, rate of soil respiration when the temperature is 0°C; Q_{10}, the temperature sensitivity of soil respiration, described by the change in respiration rate over a 10°C increase in soil temperature; CK, control; N1, N2, and N3: nitrogen (N) levels at 15, 30, and 45 g N m^{-2} y^{-1}.
Different lowercase letters next to the standard errors indicate a significant difference among the four nitrogen treatments ($P < 0.05$).

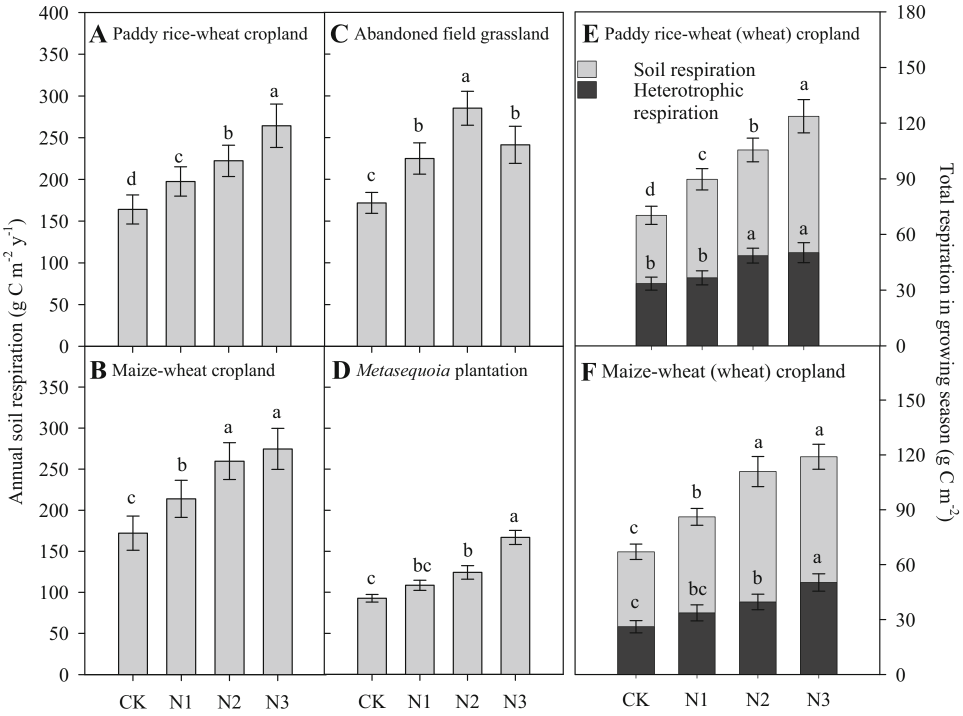

Figure 6. Annual soil respiration in a paddy rice–wheat cropland (**A**), a maize–wheat cropland (**B**), an abandoned field grassland (**C**), and a *Metasequoia* plantation (**D**). Total soil respiration and heterotrophic respiration during the wheat-growing season of the paddy rice–wheat (wheat) cropland (**E**) and the maize–wheat (wheat) cropland (**F**). CK, control; N1, N2, and N3: nitrogen (N) levels at 15, 30, and 45 g N m^{-2} y^{-1}. *Vertical bars* represent the standard error of the mean. *Different lowercase letters* above the *bars* show significant differences among these four N treatments. The 'wheat' in *parentheses* means that respiration was measured only in the wheat-growing season for the two croplands.

ecosystems (Boone and others 1998; Deng and others 2010; Schlesinger and Anderws 2000; Figure 5). Although Q_{10} has been affected by global climate change (for example, warming, Luo and others 2001) and some modern models have adopted a variable Q_{10}, other land surface models still used a constant Q_{10} (often equal to 2, Kicklighter and others 1994; Makita and others 2012) to simulate the effects of environmental changes with large uncertainty despite the different values of Q_{10} seen across ecosystems (Burke and others 2003; Peng and others 2009; Tang and Riley 2014). Our study found that the Q_{10} of R_s was reduced by N addition in the four land-use types, whereas R_0 was stimulated (Table 1; Karhu and others 2014; Luo and others 2001; Zhou and others 2006). The increases in R_0 may partly result from elevated substrate supply under N addition, which was supported by the close correlation between R_0 and photosynthesis (Sampson and others 2007). These results indicate that the increases in R_s with rising temperature (that is, the slope in Figure 5) were slower under the N addition treatments than those in the control, which was similar to that of other studies (Mo and others 2008; Sun and others 2014).

The decreased Q_{10} under N addition may also be attributed to the changes in the soil environment with additional N input (Sun and others 2014). Specifically, the reduction in Q_{10} might be more closely related to the responses of R_h to N addition (Li and others 2015; Thurgood and others 2014). The decomposition of SOM is modified by the physicochemical properties of the soil (Doetterl and others 2015). The environmental constraints on decomposition were responsible for the decrease in the apparent Q_{10} under N addition. The soil metabolism was regulated as a result of additional N input (Lu and others 2011aa). SOM could be adsorbed onto mineral surfaces through electrostatic or covalent bonds, resulting in chemical protection, which may obscure the intrinsic temperature sensitivity for decomposition (Davidson and Janssens 2006; Doetterl and others 2015). Through organic–inorganic interactions, thus, the apparent Q_{10} for R_h decreased under N addition.

CONCLUSIONS

Our study demonstrated that N addition stimulated R_s and R_h. More importantly, our research revealed different response patterns of R_s along the N addition gradient in four different land-use types with a relatively homogeneous background. In particular, in the croplands and the plantation, the increase in R_s exhibited a linear trend with increasing N addition rates. However, in the grassland, R_s showed a parabolic-like trend with the highest values under a moderate N level. R_s showed distinct seasonal patterns, with higher values observed in warmer seasons and lower ones in colder seasons in the four land-use types, which was primarily driven by fluctuations in soil temperature. Our results also showed that the Q_{10} values for R_s were reduced by N addition in the four land-use types. It is yet to be examined whether this finding can be generalized across environmental zones, especially in the long-term. Chronic N addition experiments in combination with modeling may work efficiently in the future to examine the underlying mechanisms controlling CO_2 efflux from soil.

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