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Asymmetric response of ecosystem carbon components and soil water consumption to nitrogen fertilization in farmland



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ABSTRACT

Farmlands receive large amounts of nitrogen (N) through fertilization, which can affect ecosystem carbon (C) and water fluxes. However, the responses of ecosystem C components to N fertilization and their relationships with soil water consumption under N fertilization remain unclear. In the present study, we investigated the ecosystem C components and evapotranspiration under three N fertilizer rates application (0, 180 and 360 kg N ha⁻¹ year⁻¹ , referred to as N0, N180 and N360, respectively) of two wheat varieties in three continuous growing seasons. We found that N fertilization increased all ecosystem C components as well as evapotranspiration. Excessive N application rates (N360) did not increase the net ecosystem C exchange (NEE) compared with that in the N180 treatment, which was mainly due to the larger increase in aboveground plant respiration (Rab) in the N360 treatment than the N180 treatment. The effects of N fertilization on NEE were larger than the effects on evapotranspiration, which led to an increase in water use efficiency (WUE). In addition, N fertilization increased soil respiration (Rs) by promoting both heterotrophic respiration (Rh) and root respiration (Ra), but a threshold effect of the N application rate on the Rs components was observed. Furthermore, the ecosystem C components showed different sensitivities to N fertilization, with Rab showing the highest sensitivity. Moreover, the changes in the C components were affected by the growing season and varieties, and mainly driven by biomass rather than by soil temperature or evapotranspiration. Our results demonstrate that N fertilization promoted ecosystem C fluxes, but that excessive N did not enhance the C fixation rate of the agroecosystem. These findings can inform global C-cycling models aimed at predicting C balances under N fertilization.

1. Introduction

As the most active part of the global carbon (C) cycle, farmland ecosystems are important components of terrestrial ecosystems and play critical roles in global C cycling processes (Anthoni et al., 2004; Wang et al., 2015). Agricultural land accounts for 37 % of the world's ice-free land area (FAO, 2014); thus, small changes in the ecosystem C balance in farmland cause farmland to act as a C sink or source that generates significant effects for land-atmosphere CO₂ fluxes (Ceschia et al., 2010; Revill et al., 2019). In addition, large amounts of N fertilizer (>100 kg N ha⁻¹) are applied to agroecosystems every year (Fierer et al., 2011), which affects plant growth and the soil microbial community and eventually impacts C cycling in the ecosystem (Li et al., 2017). Thus, understanding ecosystem C components under N fertilization is important for predicting C cycling in agroecosystems.

Previous studies reported that net ecosystem C exchange (NEE) in

croplands was not lower than that in natural ecosystems (Law et al., 2002; Hollinger et al., 2004; Li et al., 2006), and wheat croplands have been reported to be C sinks (Wang et al., 2013, 2015) or even C sources (Anthoni et al., 2004; Béziat et al., 2009). This function is affected by many factors (e.g., fertilization, climate, crop rotation, tillage and irrigation) (Béziat et al., 2009; Davis et al., 2010; Dufranne et al., 2011; Wang et al., 2015; Moinet et al., 2017). NEE is determined by gross ecosystem productivity (GEP, mainly driven by photosynthesis) and ecosystem respiration (ER), the latter of which is composed of plant respiration (Rp) (from aboveground parts (Rab) and roots (Ra)) and heterotrophic respiration (Rh). Thus, NEE = GEP – ER = GEP – Rp – Rh = GEP – Rab – Ra – Rh.

In general, N is often the limiting element for plant growth in farmland ecosystems; thus, N application is expected to increase the leaf area index (LAI) and enhance the GEP (Sampson et al., 2006; Moinet et al., 2017). However, increases in GEP under N fertilization do not

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Received 9 April 2020; Received in revised form 30 August 2020; Accepted 4 September 2020 Available online 19 September 2020 0167-8809/© 2020 Elsevier B.V. All rights reserved. necessarily lead to increases in C fixation, which is also determined by ER (Verburg et al., 2004). In certain situations, a high N fertilization rate may have little effect on assimilation but cause a significant increase in respiration (Aeschlimann et al., 2005). Threshold effects on ecosystem C fluxes under N addition have been observed in grasslands (Tian et al., 2016), but whether they exist in agroecosystems remains unclear. In addition, due to the different driving sources of each C component, understanding the response of different C components to N fertilization could help us understand the mechanisms of N effects on ecosystem C balance. However, studies distinguishing ecosystem aboveground and belowground C component responses to N fertilization are still lacking.

As the major component of ER, soil respiration (Rs) is also affected by N fertilization, and increases, decreases and no changes in Rs under N fertilization have been observed (Tu et al., 2013; Comeau et al., 2016; Chen et al., 2018). The variation in responses is mainly due to the inconsistent responses of Rh and Ra to N enrichment (Olsson et al., 2005; Zhong et al., 2016a; Zhou et al., 2016; Chen et al., 2018; Fang et al., 2018; Yue et al., 2019). Previous studies on ER have mainly focused on Rs components under N fertilization (Moinet et al., 2017). However, studies that concentrate on all ER components (Rh, Rab and Ra) under N fertilization are rare, and the relative importance of ER components to C balance remains unclear. Therefore, there exists great uncertainties and challenges in predicting C cycling. The determination of ER components is of great importance for understanding the driving mechanisms of C cycling under N fertilization.

Evapotranspiration is an important index for evaluating ecosystem water fluxes. N fertilization may affect evapotranspiration by altering transpiration and/or soil evaporation caused by plant growth under N fertilization (Niu et al., 2009). Hence, ecosystem evapotranspiration varies under N fertilization depending on the balance between increased transpiration and reduced soil evaporation. However, soil water availability is closely related to the C cycle (Huxman et al., 2004; Aguilos et al., 2018; Zhang et al., 2018). Moreover, both an increase in NEE and a decrease in evapotranspiration can lead to an increase in water use efficiency (WUE). Increasing WUE and carbon use efficiency (CUE) are the main goals in dryland farmland ecosystems, but it is unclear whether the response of C is consistent with that of water under N fertilization. A previous study reported that N addition would alter C fluxes, which were also greatly affected by precipitation (Tian et al., 2016). Thus, quantitative research on the C components across different growing seasons combine with the ecosystem water cycle is very important for understanding C cycling under N fertilization.

In this study, to evaluate the effects of N application on C components (GEP, NEE, ER, Rab, Rs, Rh and Ra) and water processes (evapotranspiration and WUE) in a farmland ecosystem across different growing seasons, we conducted a three-year field experiment employing long-term N fertilization with two varieties of winter wheat (*Triticum aestivum* L.) that have different drought resistances. Specifically, our objectives were to determine 1) the changes in ecosystem C components and evapotranspiration under N fertilization; 2) the patterns and sensitivities of ecosystem C components to N fertilization and the key C components that cause ER changes; and 3) the relative importance of biomass, soil temperature and evapotranspiration for ecosystem C components under N application.

2. Materials and methods

2.1. Site description

The experiment was conducted at a field site located in Yangling, Shaanxi province (34.3 °N, 108.07 °E). The mean annual temperature and precipitation at the site are 13 °C and 632 mm, respectively. The monthly air temperature and precipitation during the experiment are shown in Fig. S1. The soil type in this area is a Lou soil (Eum-Orthic Anthrosol), which is developed from loess parent materials and classified as a Udic Haplustalf in the United States Department of Agriculture (USDA) system and as a Calcic Cambisol according to the Food and Agriculture Organization of the United Nations (FAO) soil classification. The physico-chemical properties of the upper soil layer (0-20 cm) are presented in Table 1 (Zhong et al., 2016b).

2.2. Experimental design

The N fertilization experiment began in October 2004, and it utilized a randomized block design, with three treatments of N fertilization at 0, 180 and 360 kg N ha⁻¹ year⁻¹ (termed N0, N180 and N360, respectively). Two hard winter wheat varieties were used: Changhan No. 58 (CH), which is drought-tolerant, and Zhengmai No. 9023 (ZM), which is water sensitive and poorly drought-tolerant (Zhong and Shangguan, 2014). Three replicates of each treatment were established, yielding a total of 18 plots. Each plot had an area of 6 m² (2×3 m), and the guard rows set between the two plots had an area of 1 m² (2 \times 0.5 m). Each plot consisted of 20 rows (15 cm spacing) of wheat, which was sown at a density of 90 seeds per row, and the guard rows were planted with CH. N was applied as urea, and P was applied as superphosphate (33 kg P ha^{-1}), with all fertilizers broadcast simultaneously onto the soil surface and then incorporated into the whole soil layer (0-20 cm depth) with a rake before sowing at one time. During the study, no irrigation or other tillage was performed, and weeds were removed regularly.

In each of the plots, two 200-mm inner-diameter polyvinyl chloride (PVC) collars with heights of 110 mm and 800 mm were inserted into the soil. The shallow collars were used for measurements of Rs, and were inserted approximately 5 cm into the soil. The deep collars were used for the measurement of Rh and had several small holes from the top that extended down the tube, and fine mesh (100 μ m) was placed on the surface to allow the exchange of soil water with the adjacent soil and prevent root growth (Zhong et al., 2016b; Tiruvaimozhi and Sankaran, 2019). The soil collars remained in place throughout the growing season, and the plants growing inside the collar were completely removed. In addition, a metal base ($50 \times 50 \times 10$ cm, length \times width \times height) was inserted into the soil for the measurement of NEE and ER. The measurements lasted three growing seasons, from 2015 to 2017; the measurement extended from November to April of the following year during each growing season.

2.3. Measurements of CO₂ exchange components

Rs and Rh were monitored continuously by an LI-8100 automated soil CO_2 flux measurement system and an LI-8150 multiplexer with 8100-104 long-term chambers (Li-Cor Inc., Lincoln, NE, USA) during the 2015–2017 growing seasons. The respiration was measured once every 0.5 h for a total of 48 times during the measuring day. Ra was calculated from Rs and Rh.

The NEE and ER of the wheat was measured using an LI-8100 attached to a 125-L (50 \times 50 \times 50 cm, length \times width \times height) or 250-L (50 \times 50 \times 100 cm) transparent Perspex chamber because plant height could reach 60–70 cm in the late growth stage. The ecosystem C

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Properties of the 0-20 cm soil layer before fertilization.

Property	Value
Taxonomy	Udic Haplustalf
Texture	
2000–50 μm (g kg ⁻¹)	64
50–2 μm (g kg ⁻¹)	694
$<\!2\mu{ m m}~({ m g~kg^{-1}})$	242
Bulk density (g cm^{-3})	1.23
Water-holding capacity (%)	23.6
Soil organic C (g kg ⁻¹)	8.79
Total N (g kg ⁻¹)	0.96
Available N (mg kg ⁻¹)	25.1
Available P (mg kg $^{-1}$)	7.9

exchange was measured five times during the growth stage and at least six times from 00:00–24:00 each time. When the NEE was measured, the chamber was placed on the metal base, and four or eight small fans in the chamber were used to mix the air. The NEE was measured for 90 s after the chamber was placed on the metal base. After the NEE measurement, the chamber was vented, repositioned and covered by a thick opaque tarpaulin layer to measure the ER rate (including plant and microbial respiration) (Williams et al., 2014; Yan et al., 2017). GEP was calculated as the sum of NEE and ER.

2.4. Measurements of soil water content and temperature and yield

The volumetric soil water content was measured every 10 cm from 0 to 100 cm of soil and every 20 cm from 100 to 300 cm by using a neutron moisture meter (CNC100, Nuclear Technology Ltd., Beijing, China) following a previous study (Zhong and Shangguan, 2014). The 3-m-long neutron gauge access tube was buried vertically in the center of each plot at the beginning of the study. To determine the evapotranspiration, the soil water content was measured after the wheat was planted and harvested. The yield (dry weight) was determined in late May or early June by weighing the grain from the harvesting of six rows per plot. The soil temperature at a depth of 10 cm was measured by inserting a thermocouple probe into the soil and recording with the LI-8100 system.

2.5. Calculations and statistical analyses

In this study area, no irrigation was used, measured surface runoff was typically negligible, and deep-water percolation did not occur. Thus, evapotranspiration was calculated as evapotranspiration = ΔS + P, where ΔS is the change of soil water storage and P is precipitation. WUE was calculated as WUE = Y/ET, where Y is grain yield (kg/ha).

The daily Rs and Rh rates were averaged from the 48 measurements in a day. The daily C exchange rate was calculated as $Dc = \sum_{i=1}^{n} (R_i + R_{i+1}) \times (T_{i+1} - T_i)$, where n is the measurement time in a day and $(R_{i+1} - T_i)$.

 $\sum_{i=1}^{\infty} \sum_{2\times 24}^{\infty}$, where n is the measurement time in a day and $(R_{i+1}-R_i)/2$ and $T_{i+1}-T_i$ represent the C exchange rate (µmol m⁻² s⁻¹) and the time (s) between two successive measurements, respectively. The average C exchange was calculated as Ac $=\sum_{l=1}^{\infty} (Dc_l + Dc_{l+1}) \times (T_{l+1} - T_i)/T_t$, where x is the measurement time during the growing season, $(Dc_l + Dc_{l+1})/2$ and $(T_{l+1} - T_i)$ represent the daily C exchange rate (µmol m⁻² s⁻¹) and the time (s) between two successive measurements, respectively, and T_t is the total time (s) during the experiment during the growing season. In this study, Rab = ER – Rs, Ra = Rs - Rh, and CUE = $\frac{\text{NEE}}{\text{GEP}}$. The response ratios of the components of ecosystem CO₂ exchange = $100 \times \frac{N \text{treatment} - N0}{N0}$.

One-way ANOVAs were used to determine the differences in C components and water processes among the N fertilization rate treatments at the 95 % confidence level, and post hoc comparisons (Tukey's HSD test) were used to correct for multiple comparisons. Three-way ANOVAs were used to determine the effect of growing season, variety, and N treatment on the C components and water processes, and one-way repeated measures ANOVAs were conducted to assess the effects of the N treatment on each ecosystem C component. Moreover, stepwise multiple regression analysis was used to determine the contributions of biomass, evapotranspiration and soil temperature to the ecosystem C components.

3. Results

3.1. Ecosystem C components and evapotranspiration under N fertilization

The average C fluxes showed similar trends under N fertilization

across all growing seasons (Fig. 1). GEP, NEE and ER showed lower rates in N0 than in the N180 and N360 treatments (Table S1), except for the NEE of CH in 2016. Overall, the GEP, NEE and ER rates were lower in 2016, whereas a higher CUE was observed in 2016. In addition, the NEE rate did not differ significantly between the N180 and N360 treatments for either variety. Three-way ANOVA showed that variety, N application rate and growing season had significant effects on GEP, NEE, ER and CUE, except that variety had no effect on ER (Table 2).

The N180 treatment resulted in the highest Rs rate in both varieties (Fig. 2, Table S1), and N fertilization increased the Rs and Ra, whereas Rh showed no significant difference between N360 and N0 (Table S1). In addition, the average Rs and Rh rates were higher in the 2017 than in the 2015 and 2016 growing seasons. Moreover, across all data, the ratio of Rh to Rs was 60 % in this study, and N fertilization decreased it from 64.5 % to -59.3% and 55.1 % in the N0, N180 and N360 treatments (Fig. S2). Variety, N application rate, growing season, and their interactions had significant effects on Rs and its components (Table 3).

Precipitation varied across the three growing seasons; thus, different evapotranspiration rates were observed (Fig. 3), and N fertilization increased evapotranspiration except in 2016. However, variety showed no effect on evapotranspiration (Table 3). In addition, WUE increased and exhibited a threshold and saturation with N fertilization rates in all three seasons.

3.2. Sensitivity of ecosystem C components to N fertilization

With N application, the response ratios for the three C flux parameters, NEE, GEP and ER, all exhibited an increase in all growing seasons (Fig. 4). A lower increase in the ecosystem C fluxes of both varieties under N fertilization was observed in 2016 than in 2015 and 2017 (Fig. S3). In addition, the increase in ER was slightly larger than that in GEP and NEE under the N360 treatment.

Rab was the main source of ER, which contributed over 50 % to the ER (Fig. 5a, b and c). N fertilization significantly increased the contribution of Rab to ER but decreased the contribution of Rh to ER; both varieties showed similar results (Fig. S4). In addition, N fertilization significantly increased Rab and Ra (Fig. 5d, e and f), except Ra under N360 in 2015. Rh did not differ significantly among the N fertilization treatments except in 2017 (Fig. S5).

3.3. Biotic and abiotic factors affecting ecosystem C components

Across all experimental plots, ecosystem C fluxes (NEE, GEP and ER) and soil C effluxes (Rs, Rh and Ra) increased linearly with increasing yield (Fig. 6), although only ER, Rs and Rh increased with increasing soil temperature. Interestingly, the GEP, ER, Rs and Rh showed parabolic relationships with evapotranspiration, whereas NEE and Ra increased with evapotranspiration. In addition, different relationships between the ecosystem C component and yield and the soil temperature and evapotranspiration were observed at the three N fertilization rates (Fig. S6 and S7).

Further stepwise multiple regression indicated that these N-induced changes in ecosystem C fluxes and soil C effluxes were mainly driven by the changes in biomass, which could explain approximately 70 %, 68 % and 57 % of the variation in NEE, GEP and ER and 24 %, 11 % and 33 % of the variation in Rs, Rh and Ra (Table 4), respectively. In addition, soil temperature also had significant effects on NEE, GEP, ER, Rs and Rh, while evapotranspiration significantly affected only NEE, Rs and Rh.

4. Discussion

4.1. Differential responses of C components and evapotranspiration to N fertilization

N availability is often the most limiting resource in agroecosystems; thus, N application often promotes plant growth by improving



Fig. 1. Average of seasonal gross ecosystem productivity (GEP), net ecosystem exchange (NEE) and ecosystem respiration (ER) rate and carbon use efficiency (CUE) of CH and ZM varieties under N fertilization in growing seasons of 2015, 2016 and 2017. The N0, N180 and N360 treatments represent the N application rates of 0, 180 and 360 kg ha⁻¹, respectively. Bars indicate means \pm SE with three replications. Different letters indicate the significant difference among treatments at P < 0.05.

Table 2

Three-way ANOVA (growing season, variety, and nitrogen (N) application rate) results for gross primary production (GEP), net ecosystem exchange (NEE), ecosystem respiration (ER) and carbon use efficiency (CUE). Bold values indicate a significant effect (P < 0.05).

Source	df	GEP	GEP		NEE		ER		CUE	
		F	Sig.	F	Sig.	F	Sig.	F	Sig.	
Variety	1	11.64	0.002	19.91	<0.001	0.22	0.645	6.36	0.016	
Year	2	368.39	< 0.001	4.18	0.023	798.38	< 0.001	177.15	< 0.001	
Ν	2	549.20	< 0.001	139.07	< 0.001	582.85	< 0.001	9.44	0.001	
Variety \times Year	2	1.57	0.222	2.43	0.102	5.98	0.006	3.50	0.041	
Variety \times N	2	3.12	0.056	5.92	0.006	9.84	< 0.001	8.99	0.001	
$N \times Year$	4	64.50	< 0.001	12.62	< 0.001	88.68	< 0.001	4.00	0.009	
$Variety \times N \times Year$	4	2.75	0.043	1.18	0.338	4.81	0.003	1.28	0.296	

photosynthetic capacity and allowing the accumulation of more C assimilation products over time (Makino, 2011; Hawkesford, 2014). In this study, the average GEP rate showed a significant increase under N fertilization (Fig. 1 and Table S1), consistent with the results of previous studies, due to the increase in the photosynthetic rate and LAI (Bakht et al., 2009; Gao et al., 2009). In addition, an increase in the ER rate was

also observed under N application, which was mainly due to the large increase in wheat yield under the N treatment (Fig. S9). Interestingly, although the N360 treatment had a higher GEP rate than the N180 treatment in several growing seasons, the NEE of both varieties showed no difference between the N180 and N360 treatments, indicating that the excessive N application rate did not promote NEE beyond that in the



Fig. 2. Average of seasonal soil respiration (Rs), root respiration (Ra) and heterotrophic respiration (Rh) of CH and ZM under N fertilization. Different letters indicate the significant difference among treatments at P < 0.05.

Table 3

Three-way ANOVA (growing season, variety, and nitrogen (N) application rate) results for soil respiration (Rs), heterotrophic respiration (Rh), root respiration (Ra) and evapotranspiration. Bold values indicate a significant effect (P < 0.05).

Source	df	Rs		Rh		Ra		Evapotranspiration	
		F	Sig.	F	Sig.	F	Sig.	F	Sig.
Variety	1	60.58	< 0.001	18.34	<0.001	16.37	<0.001	2.37	0.132
Year	2	443.97	< 0.001	328.27	< 0.001	35.23	< 0.001	177.74	< 0.001
Ν	2	235.82	< 0.001	110.39	< 0.001	65.85	< 0.001	10.44	< 0.001
Variety \times Year	2	43.99	< 0.001	30.91	< 0.001	20.92	< 0.001	0.27	0.769
Variety \times N	2	25.55	< 0.001	2.37	0.108	12.89	< 0.001	0.16	0.857
$N \times Year$	4	44.72	< 0.001	38.82	< 0.001	6.14	0.001	5.66	0.001
$Variety \times N \times Year$	4	6.03	0.001	17.26	<0.001	2.44	0.065	1.14	0.352

N180 treatment. This lack of difference was due mainly to the higher ER rate in the N360 than the N180 treatment (Figs. 1 and S3), which counteracted the increase in GEP under N360; moreover, in some cases, high N application has a greater effect on respiration than on photosynthesis (Aeschlimann et al., 2005). With increasing N fertilization rates, the C components exchange and CUE exhibited a threshold response, suggesting that excessive N input did not always increased the C sink capacity of the agroecosystem but might cause increases N₂O emissions and N leaching (Mapanda et al., 2012). This finding is consistent with previous studies (Tian et al., 2016; Kim et al., 2017), which also reported a N saturation threshold on C fluxes in grassland (105 kg N ha-1 year⁻¹) and rice (145 kg N ha-1 year⁻¹).

Rs is the second largest C flux of terrestrial ecosystems (Xu and Shang, 2016; Chen et al., 2018). Thus, small changes in Rs are expected to have large effects on the global C cycle. Although numerous experiments on the effect of N enrichment on Rs have been conducted, the effect of N input on Rs is still debated, mainly due to the different

responses of its components (Zhong et al., 2016a; Chen et al., 2018). In this study, N application increased both Rh (14.5 %) and Ra (56.4 %), eventually resulting in increases in the Rs rate (28.9 %), which is consistent with previous studies (Morell et al., 2010; Shao et al., 2014; Chen et al., 2018). This finding might be related to the increased C mineralization rates and plant fine root biomass after N application in this experimental area (Shao et al., 2014; Zhong et al., 2015). In addition, the N360 treatment yielded a lower Rs than the N180 treatment, indicating that an increase in the N application rate does not always promote soil CO₂ efflux and may suggest that N fertilization has a saturation threshold effect on Rs. However, due to the limited N treatments in this study (only three N rates), we could not obtain an accurate threshold of N rates on Rs, which needs to be further investigated. Previous studies reported that excessive N enrichment could change the microbial community and function (Zhong et al., 2015), inhibit the activity of soil enzymes, such as oxidative and peroxidase enzymes (Cusack et al., 2010), reduce belowground C allocation, eventually cause



Fig. 3. Seasonal evapotranspiration and water use efficiency (WUE) under N fertilization in the growing seasons from 2015 to 2017. Different letters indicate the significant difference among treatments at P < 0.05.



Fig. 4. Response ratios of GEP, NEE and ER to N fertilization. Asterisks indicate significant differences with N0 treatment (P < 0.05).



Fig. 5. Percentages of aboveground parts of plants (Rab), Ra and Rh to ER under N fertilization (a-c) and response ratios of Rh, Ra and Rab to N fertilization (d-f). Different letters indicate the significant difference among treatments at P = 0.05 and asterisks indicate significant differences with N0 treatment (P < 0.05).



Fig. 6. Relationships between ecosystem carbon components with soil temperature, yield and evapotranspiration across all experimental plots in three growing seasons. Dots represent the season means of each plot.

Table 4

Stepwise multiple regression analysis for the impacts of yield, soil temperature and evapotranspiration on ecosystem carbon components.

Carbon fluxes	Independent variables	Parameter estimate	Partial r ²	P-value
	Yield	0.007	0.699	< 0.001
GEP	Soil temperature	0.539	0.063	< 0.001
	Evapotranspiration	-0.005	0.024	0.012
	Yield	0.002	0.681	< 0.001
NEE	Soil temperature	-0.002	0.042	0.005
	Evapotranspiration			
	Yield	0.004	0.569	< 0.001
ER	Soil temperature	0.502	0.143	< 0.001
	Evapotranspiration			
	Yield	0.001	0.244	< 0.001
Rs	Soil temperature	0.15	0.093	0.001
	Evapotranspiration	-0.001	0.053	0.024
	Yield	0.001	0.108	< 0.001
Rh	Soil temperature	0.119	0.112	< 0.001
	Evapotranspiration	-0.001	0.083	0.01
	Yield	0.001	0.329	< 0.001
Ra	Soil temperature			
	Evapotranspiration			

GEP, gross ecosystem productivity; NEE, net ecosystem exchange; ER, ecosystem respiration; Rs, soil respiration; Ra, root respiration; Rh, heterotrophic respiration.

reductions in Rh (Maaroufi et al., 2015) or Ra (Högberg et al., 2010; Hasselquist et al., 2012). These findings are consistent with our results that Rh and Ra in N360 were lower than those in the N180 treatment. However, in this study, we did not observe a significant inhibition of Rh in the N360 treatment (Figs. 2, 4 and S5) compared with that in the N0 treatment due to the N limitations in farmland. All these results indicate that different ecosystem C balance components have different sensitivities to different N fertilization rates (Fig. 7).

In this study, N fertilization had a slight effect on CUE but significantly increased the WUE (Figs. 1 and 3). A higher CUE was observed in the growing season of 2016, which had low evapotranspiration, consistent with a previous study (Zhang et al., 2009), thus indicating that respiration is more sensitive than assimilation under low precipitation conditions. In addition, a parabolic relationship between CUE and WUE was observed across all plots (Fig. S8). This relationship indicates that when WUE was low, CUE initially increased with increasing WUE but then decreased. Furthermore, N fertilization altered the relationship between CUE and WUE in this study. Moreover, we found that N fertilization slightly increased evapotranspiration but significantly increased NEE (Fig. 7), indicating that the increase in NEE, not evapotranspiration, was the main cause of the increasing WUE under N fertilization and the different responses of C and water to N fertilization.

The three-way ANOVA (Table 2 and 3) identified differences in the C components among the growing seasons and between the varieties. The variations in temperature and precipitation in the study area might be the main reasons for the C exchange observed during the study. In addition, genotypic variation could affect gas exchange parameters, as reported previously in wheat (Xue et al., 2002) due to the plant's inherent characteristics. The C exchange fluxes were higher in 2017 than in the other years, mainly due to the high temperature (Fig. S1).

4.2. Rab is the most sensitive ecosystem C component and alters ER

N fertilization affected the C balance of the ecosystem by changing each component. However, the sensitivity of these C processes to N fertilization remains unclear, as does the main process that responds to the variation in ER. In this study, Rab showed the highest sensitivity to N fertilization, followed by Ra, which is consistent with previous studies and was due to the increase in plant biomass under N enrichment (Aeschlimann et al., 2005; Zhong et al., 2016b; Moinet et al., 2017). However, lower response ratios to N fertilization were observed in 2016, which may be due to the low evapotranspiration (Fig. 3), as soil water availability was the main limitation on plant growth in 2016. In addition, Ra showed a higher sensitivity in N180 than in N360, which might due to the decreased root biomass in this experimental area (Shao et al., 2014) because the plants did not need to develop many roots to absorb the nutrients under the N360 treatment. Moreover, a lower sensitivity of Rab was observed in N180 than N360, which may be related to the higher plant N content under the N360 treatment (Table S2) (Yan et al., 2015) because plant respiration increases linearly with plant N content (Ryan, 1995; Maier, 2001; Vose and Ryan, 2002).

Among the ER components, different sensitivities of C exchange components to N fertilization were observed (Fig. 5), consistent with



Fig. 7. A diagram showing the mechanisms and magnitudes of N fertilization effects on ecosystem carbon components. We combined the data of both varieties. + indicate positive effect of N fertilization, and black and red numbers represent N180 and N360 treatment, respectively.

previous studies (Aeschlimann et al., 2005; Bubier et al., 2007; Moinet et al., 2016, 2017). In this study, Rab made a large contribution to ER, i. e., more than 50 %, indicating that plant respiration is a critical component of C exchange in the biosphere (Atkin et al., 2010; Smith and Dukes, 2013). In addition, Rab showed a greater response to N application than the other ER components, mainly due to the significant increases in temperature, LAI, photosynthesis and biomass (Fig. S9) (Zhong et al., 2016b). With the application of N fertilizer, the contribution of Rab to ER increased (Figs. 5 and S4) mainly due to the increasing aboveground biomass and respiration capacity (Mahecha et al., 2010; Atkin et al., 2015), whereas the Rh contribution to ER decreased due to the smaller increase compared with that of Rab under N application. These results indicate that changes in the sensitivity of ER components caused by N fertilization may alter the C balance, which should be considered when modeling C-climate feedbacks.

4.3. Key factors affecting C components under N fertilization

Across all plots, the stepwise multiple regression analysis showed that although soil temperature and evapotranspiration contributed to the change of C components under N fertilization, the C fluxes were mainly driven by changes in biomass, which is consistent with previous studies (Table 4) (Yan et al., 2011; Tian et al., 2016). In this study, N fertilization significantly increased the yield (Fig. S9) and the C components increased linearly with yield (Fig. 6), suggesting that plant growth strongly affected the C processes under N application. The positive effects of soil temperature on ER, Rs and Rh suggest that an increase of soil temperature could promote C emissions from this farmland. However, the ecosystem C components first increased with increasing evapotranspiration and then decreased with a decline in evapotranspiration, indicating that excessive soil water consumption did not always increase the ecosystem C fluxes (Fig. 6). These results suggest that changes of soil temperature and evapotranspiration caused by plant growth under N fertilization could facilitate increases in C fluxes, which is consistent with previous studies (Niu et al., 2008; Tian et al., 2016). These results highlight the importance of soil temperature and soil moisture caused by N fertilization to the ecosystem C balance in farmland.

5. Conclusion

This study contributed new insights into C cycling under N

fertilization by integrating measurements of ecosystem C components in wheat farmland over a three-year period. Our study demonstrated that N fertilization increased the rates of all ecosystem C components but that excessive N application rates had no significant effect on NEE due to the N-driven increase in Rab. In addition, Rs increased by promoting both Rh and Ra under N fertilization, and threshold effects of the N rate (180 kg N ha⁻¹ year⁻¹) on Rs and its components was observed in this study. Furthermore, the ecosystem C components showed different sensitivities to N fertilization, and were also influenced by precipitation. Among the components, Rab showed the highest sensitivity to N fertilization and contributed greatly to the ecosystem C balance in the farmland ecosystem. In view of the sustainable intensification of agroecosystems, studies on the impact of N fertilization on C components have implications for achieving high yields with low N inputs.

Declaration of Competing Interest

We declared that we have no conflicts of interest to this work. We declare that we do not have any commercial or associative interest that represents a conflict of interest in connection with the work submit.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2020.107166.

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