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# Carbon Flux Dynamics and Response to Extreme High Temperature in Rice Ecosystems Across the Lower Reaches of the Yangtze River, China

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## Abstract

Under global climate warming, the impact of extreme high temperatures on carbon exchange in paddy rice ecosystems remains unclear, yet they exert a profound influence on the carbon cycle in agricultural ecosystems. The characteristics of carbon dioxide ($CO_2$) fluxes and their response to temperature were explored at two sites (Jurong and Jiangdu) across the lower reaches of the Yangtze River in China using open-path eddy covariance observations in 2021–2024. During the rice-growing season, considerable inter-annual spatial variability in high temperature was observed, with a higher frequency and larger intensity in Jurong relative to Jiangdu and more severe heat stress in 2022 relative to 2023. The jointing–booting stage was identified as the hotspot exposed to the highest frequency and longest duration of high temperature across multiple years. There was obvious variation in net ecosystem $CO_2$ exchange (NEE) throughout the rice-growing season, with the cumulative values being $-462.2 \pm 55.2$ gC·m$^{-2}$ in 2021–2023 at Jurong and $-362.4 \pm 43.0$ gC·m$^{-2}$ in 2022–2024 at Jiangdu. The period from jointing to flowering was identified as the most sensitive time slice for NEE variation, with a daily average value of $-6.3 \pm 0.2$ gC·m$^{-2}$·d$^{-1}$ in jointing–booting and $-5.2 \pm 2.2$ gC·m$^{-2}$·d$^{-1}$ in booting–flowering at Jurong, as well as $-4.0 \pm 0.7$ gC·m$^{-2}$·d$^{-1}$ in jointing–booting and $-5.7 \pm 1.1$ gC·m$^{-2}$·d$^{-1}$ in booting–flowering at Jiangdu. The respective correlation coefficients were $-0.59$ and $-0.37$ between periodical NEE and mean air temperature at Jurong and Jiangdu, meaning that NEE showed a decreasing trend as temperature increased, owing to the simultaneous but heterogeneous changes in gross ecosystem $CO_2$ exchange and ecosystem respiration. When the temperature was lower than 38 °C, the corresponding correlation coefficient reached $-0.85$ at Jurong and $-0.52$ at Jiangdu, suggesting that extreme high temperature prevented a decline in NEE. The response of NEE to temperature highlighted that NEE ceased to decrease when temperature surpassed 38 °C, implying that a critical threshold existed for limiting the carbon sink under extreme high temperature. These findings could provide insight for understanding carbon cycling in agricultural systems under an extreme climate.

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**Keywords:** net ecosystem $CO_2$ exchange; high temperature; eddy covariance; rice ecosystem

## 1. Introduction

Carbon dioxide ($CO_2$) cycling between vegetation and the atmosphere is one of the key processes affecting atmospheric $CO_2$ concentrations and contributes to our understanding of the carbon cycle in regional and global terrestrial ecosystems [1,2]. Remarkably, agricultural ecosystems, as an important part of terrestrial ecosystems, display great potential to sequester carbon emissions [3,4]. Currently, $CO_2$ fluxes in ecosystems are measured in two main ways: transparent static chamber (STC) and eddy covariance (EC) methods. The EC method has been recognized as the standard technique to monitor carbon exchange between cropland surfaces and the atmosphere [5,6] because it requires no additional empirical constants to directly measure fluxes [7,8]. Using EC observations, long-term measurements of exchanges of carbon, water, and energy between the biosphere and atmosphere have been available [9–11], which have critical contributions in the assessment of global biosphere–atmosphere interactions [12]. China, with multiple agriculture ecosystems, has developed the progress and prospects of the Chinese terrestrial ecosystem flux observation and research network (ChinaFLUX) in the past few decades to measure the carbon and water flux exchanges at dozens of sites. These observations have been open accessed in recent years, helping researchers explore the carbon dynamics of different crops and further assess carbon budget [13–15]. There is an extensive range of variance in $CO_2$ fluxes for different croplands [16–19], referring to periodical variations in $CO_2$ exchange as well as their associations with influencing environments [20,21]. Climate change, particularly high temperature, has a significant impact on ecosystem carbon uptake capacity [22].

Rice, as a typical wetland ecosystem different from dryland crops, supplies food production as well as carbon absorption and emissions. General warming has mainly influenced the growth, yield and grain quality for rice [23–25], whereas the influences are inconsistent for specific types and regions [26–28]. The Yangtze River region, as a typical hotspot for rice cultivation, has experienced a significant increase in the intensity, duration and exposure of high temperature [29]. Explorations on the mechanisms and synthesis suppression of extreme high temperature on rice growing such as photosynthesis have gained prominence [30,31]. Exposed to extreme high temperature, flowering, pollination and fertilization are expected to be impaired, leading to an increased proportion of empty or sterile grains. Concurrently, extreme high temperature during the grain filling stage can shorten the growing duration, thereby causing substantial yield losses [32,33]. From the perspective of $CO_2$ cycling in rice ecosystems, there is a complex balance between photosynthetic uptake and respiratory emissions from both plants and soil organisms, which is influenced by varying climatic and biological conditions [34,35]. It has been pointed out that net ecosystem $CO_2$ exchange is significantly correlated with air temperature, suggesting that warming can enhance both daytime uptake and nighttime emissions, whilst the net seasonal carbon sequestration remains variable. Elevated temperature during the growing season can enhance both gross ecosystem $CO_2$ exchange and respiration increase, with the former potentially outpacing the latter and leading to a negative net $CO_2$ exchange [36].

Extreme high temperature can damage rice production by reducing photosynthetic capacity and accelerating senescence, while its effect on $CO_2$ cycling is relatively limited. Moreover, significant research gaps persistently concern the impacts of intensifying extreme high-temperature events. The potential responses of the $CO_2$ cycle in rice ecosystems to extreme high temperature are poorly understood and require deeper exploration to our knowledge. Whether there is a specific threshold or breakpoint for the temperature that governs $CO_2$ cycling in exhibiting abrupt changes or decoupling is rarely mentioned. Therefore, it is further needed to explicitly investigate the carbon budget and how extreme high temperature affects carbon fluxes. With the novel intention to characterize carbon fluxes and their response to extreme high temperature reliably, this study focused on the rice cropping ecosystem with the use of multi-year EC measurements at two sites across the lower reaches of the Yangtze River in China. The temporal dynamics of carbon fluxes in multiple years are analyzed at the scales of growing season, phenology and day. In particular, the response of carbon fluxes to air temperature is proposed to explore the sensitivity of carbon fluxes to extreme high temperature. Addressing these gaps is vital for tracing the carbon source/sink in rice ecosystems and understanding its feedback to climate change, which can improve adaptive management strategies to stabilize sustainability in rice production.

## 2. Materials and Methods

### *2.1. Site Description*

The field experiments were conducted at two sites, i.e., Jurong and Jiangdu, in Jiangsu province, across the lower reaches of the Yangtze River region (Figure 1). The detailed descriptions are as follows: (a) Jurong site (31.841° N, 119.217° E) is the ecological experiment station of Nanjing University. The cultivation was wheat–rice rotation system before 2017; after that, it changed to a rice system with a growing duration from mid-June to November. (b) Jiangdu site (32.417° N, 119.717° E) is the green agriculture research and demonstration base of Nanjing University of Information Science and Technology in Yangzhou City. The cultivation was rice–wheat rotation from 2022, with the growing duration from mid-June to October for rice.

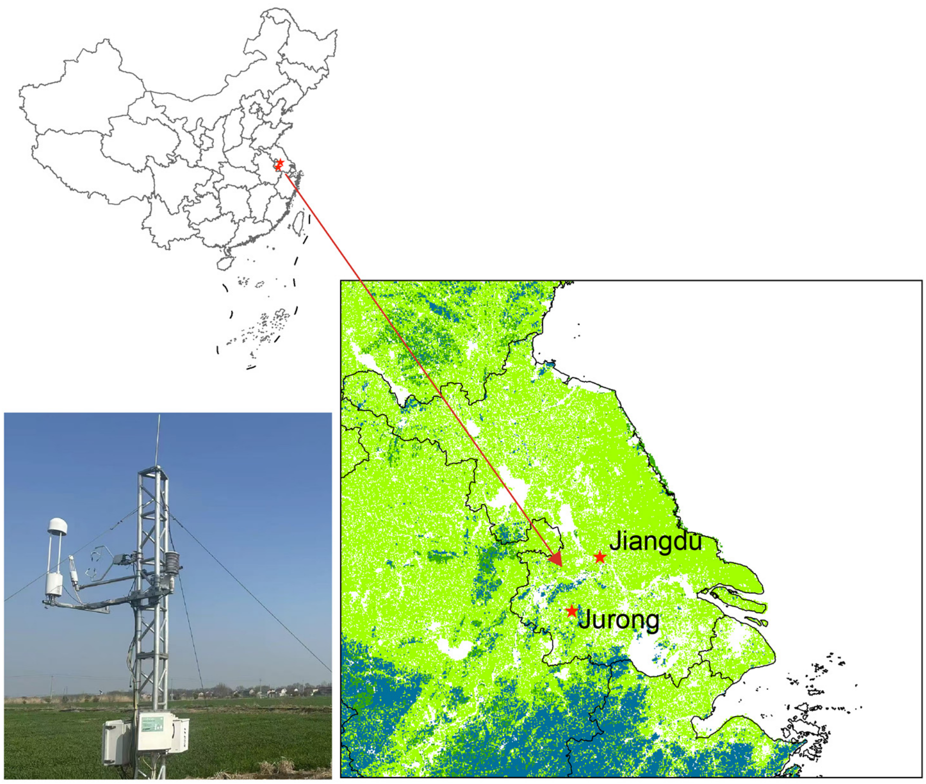


**Figure 1.** The eddy covariance system in the study locations.

### *2.2. Flux and Meteorology Measurements*

At the sites, the fluxes in gas, energy, and momentum were measured in an EC system, including an open-path $CO_2/H_2O$ analyzer (LI-7500A, LI-COR, Lincoln, NE, USA) and a 3D ultrasonic anemometer (CSAT3, Campbell Scientific, Logan, UT, USA), to measure $CO_2$ and $H_2O$ fluxes at a sampling frequency of 10 Hz, which was installed at 3–4 m height above the ground. Simultaneously, meteorological variables were measured automatically. The raw $CO_2$ and $H_2O$ flux data were filtered and corrected through the technical standard processes, including coordinate rotation, sonic temperature correction, frequency correction, Webb–Pearman–Leuning correction, outlier filtering, and nighttime $CO_2$ flux correction [37,38]. After raw data were controlled by using open-source software EddyPro (version 7.0.9), half-hourly net ecosystem $CO_2$ exchange (NEE), sensible heat and latent heat flux were obtained.

The meteorological measurements referring to air temperature, relative humidity, net radiation, photosynthetically active radiation, wind speed, rainfall, soil temperature and volumetric soil water content were recorded using a data logger and then averaged to half-hourly data. As an important factor, vapor pressure deficit was further calculated by the difference between saturation vapor pressure and actual vapor pressure.

### 2.3. Data Analysis

As NEE and meteorological measurements were quality checked, the following steps were needed:

(a) Determination and filtering of periods with low-friction velocity (u*) filtering, meaning that measurements during the nighttime with u* smaller than the estimated u* threshold (which was specifically estimated during rice-growing season at the two sites in this study) were flagged as invalid [39].

(b) Gap filling of missing and invalid measurements by using the method of marginal distribution sampling [40].

(c) Flux partitioning, i.e., partitioning of NEE into gross ecosystem $CO_2$ exchange (GEE) and ecosystem respiration (Re), with the algorithm as below.

$$\mathrm{NEE} = \mathrm{Re} - \mathrm{GEE} \tag{1}$$

where Re is combined by Re during the nighttime and Re during the daytime, which is estimated by using a temporally varying relationship between respiration and temperature.

$$\mathrm{Re(T)} = \mathrm{Re_{ref}} \exp\left[\mathrm{E_0}\left(\frac{1}{\mathrm{T_{ref}} - \mathrm{T_0}} - \frac{1}{\mathrm{T} - \mathrm{T_0}}\right)\right] \tag{2}$$

where Re(T) is the ecosystem respiration at air temperature T. $T_0$ and $T_{ref}$ are constants of −46.02 °C and 10 °C. $Re_{ref}$ is respiration at the reference temperature, and $E_0$ is the temperature sensitivity, which are estimated by using the date of NEE and temperature during the nighttime when the temperature response function of NEE is accepted as the representative of Re. Under the assumption that this relationship during the nighttime is also applicable for daytime, Equations (1) and (2) can be used to calculate Re and GEE during the daytime [15]. The REddyProc package (version 1.3.4) was utilized to fill the missing data and flux partitioning [20,39].

Water use efficiency (WUE), as the indicator of energy for crop growing, was obtained as below:

$$\mathrm{WUE} = \frac{\mathrm{GEE}}{\mathrm{ET}} \tag{3}$$

where ET is the evapotranspiration, which is calculated as the latent heat flux divided by parameter λ corresponding to the function of temperature.

The temporal dynamics of fluxes and environmental factors were assessed and compared at the scales of rice-growing seasonal, phenological and daily duration, by integrating the half-hourly period into corresponding time period. Here, the time slice of fluxes and environmental factors was 2021–2023 at Jurong and 2022–2024 at Jiangdu, respectively. The dates of different phenological stages for rice at Jurong were sowing on 20 June, jointing on 31 July, booting on 22 August, flowering on 1 September, grain filling on 15 September, and maturing at mid-November. At Jiangdu, the dates for rice were sowing on 20 June, jointing on 17 July, booting on 14 August, flowering on 23 August, grain filling on 4 September, and maturing at late October. The negative value of NEE signified uptake, and negative cumulative NEE was, thus, carbon sink during the analytic duration.

In general, heat events were defined as the maximum air temperature being greater than 35 °C [29,41,42]. Therefore, the intensity, frequency and duration of heat events were extracted during the rice-growing season in multiple years. The $CO_2$ flux variation and response to temperature, especially for extreme high temperature, were further explored considering the temporal trend, correlation and sensitive analysis, based on the data control of available and proper environmental factors, such as vapor pressure deficit, photosynthetically active radiation, soil temperature and volumetric soil water content. Moreover, segmented regression with significance test was used to quantify and compare the trend of flux as well as the responses to changes in temperature. Additionally, comparisons of GEE, Re, WUE, ET were comparatively implemented to explore the potential impacts on the dynamic change in NEE. Of course, it was assumed that the potential relationship between NEE and high temperature would be utilized to estimate the likely change in NEE across Jiangsu province.

## 3. Results

### *3.1. The Characteristics of High Temperature During Rice Growth*

During the rice-growing season, there was an overall consistent trend of maximum air temperature, characterized by inverted 'U' style from planting to maturing (Figure 2). At Jurong, 19, 56 and 25 d endured heat in 2021, 2022 and 2023, with the maximum temperature being 41.31 °C (14 August 2022). Comparatively, there were 21, 4 and 27 heat days in 2022, 2023 and 2024, with the maximum temperature being 38.78 °C (4 August 2024) at Jiangdu. From the perspective of hours exposed to high temperature in growing stages (Figure 3), a higher value was recorded in jointing–booting when there were 22 d in 2022 (with average 9.0 heat hours and even more than 9.5 heat hours in 13 continuous days) and 14 d in 2023 at Jurong. At Jiangdu, jointing–booting was also exposed to higher frequency in heat, characterized by 20 d (with average daily 3.5 heat hours and even more than 6.0 heat hours in 13 continuous days) in 2024 and 15 d in 2022. However, in the stages of booting–flowering, flowering–grain filling and grain filling–maturing, no more than 4 heat days were observed, although occasional days experienced more than 6 heat hours.

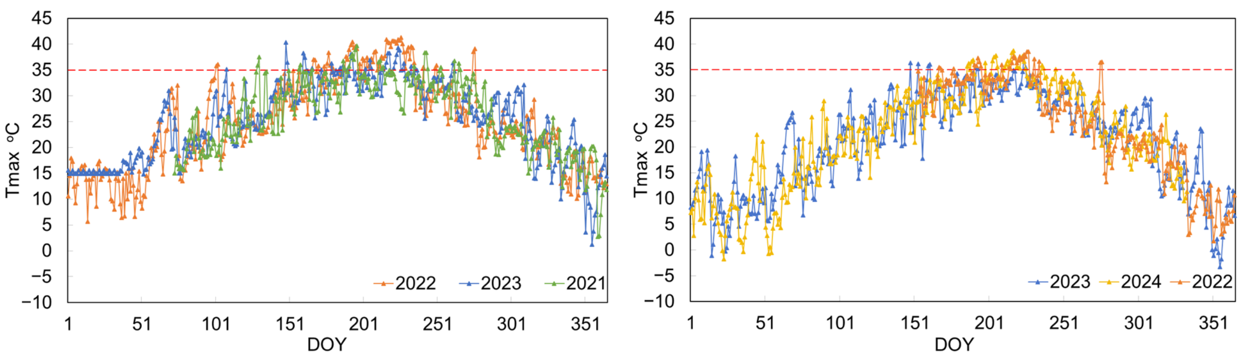


**Figure 2.** Daily change in maximum air temperature at Jurong (**left**) and Jiangdu (**right**) (the red dashed line represents the position of 35 °C for heat event, and the abbreviations of Tmax and DOY are maximum air temperature and Julian day of year, respectively).

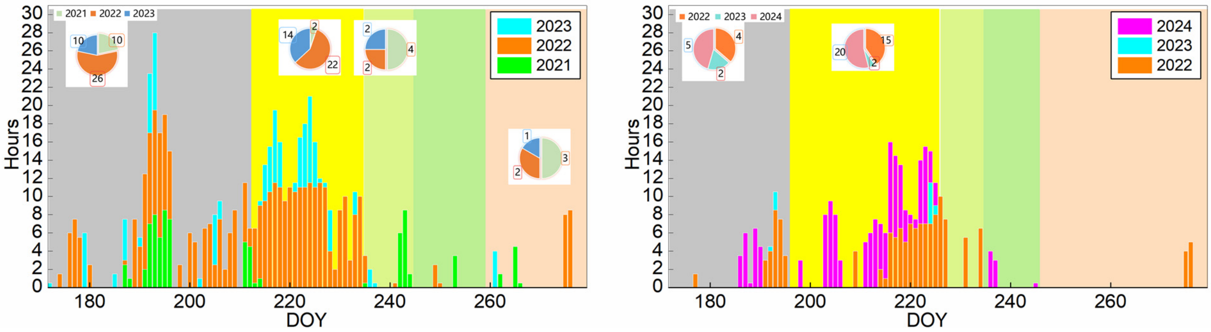


**Figure 3.** Daily change in the number of hours exposed to high temperature at Jurong (**left**) and Jiangdu (**right**) (the bar in the figure represents the number of days exposed to heat in a specific year, and the background color represents the different stages during rice-growing season).

### *3.2. Dynamic Variations in NEE*

Clear temporal variation (decrease–increase) in NEE was observed within the period of rice development at two sites (Figure 4). The cumulative NEE during the whole growth period was $-462.2 \pm 55.2$ gC·m$^{-2}$ at Jurong and $-362.4 \pm 43.0$ gC·m$^{-2}$ at Jiangdu (Figure 5). Comparisons among different stages demonstrated that lower cumulative NEE was detected in jointing–booting and grain filling–maturing, with a magnitude of $-143.6 \pm 4.2$ gC·m$^{-2}$ and $-105.7 \pm 19.0$ gC·m$^{-2}$ at Jurong, $-128.6 \pm 22.4$ gC·m$^{-2}$ and $-127.7 \pm 32.9$ gC·m$^{-2}$ at Jiangdu. In view of daily average NEE, lower values were distilled in jointing–booting, booting–flowering, and flowering–grain filling, with respective magnitudes being $-6.3 \pm 0.2$ gC·m$^{-2}$·d$^{-1}$, $-5.2 \pm 2.2$ gC·m$^{-2}$·d$^{-1}$, and $-4.3 \pm 1.9$ gC·m$^{-2}$·d$^{-1}$ at Jurong. Similarly, respective daily average NEE at Jiangdu was $-4.0 \pm 0.7$ gC·m$^{-2}$·d$^{-1}$, $-5.7 \pm 1.1$ gC·m$^{-2}$·d$^{-1}$, and $-4.1 \pm 2.8$ gC·m$^{-2}$·d$^{-1}$ in the three stages. Therefore, the period of jointing–flowering was accepted as the most sensitive stages to NEE uptake.

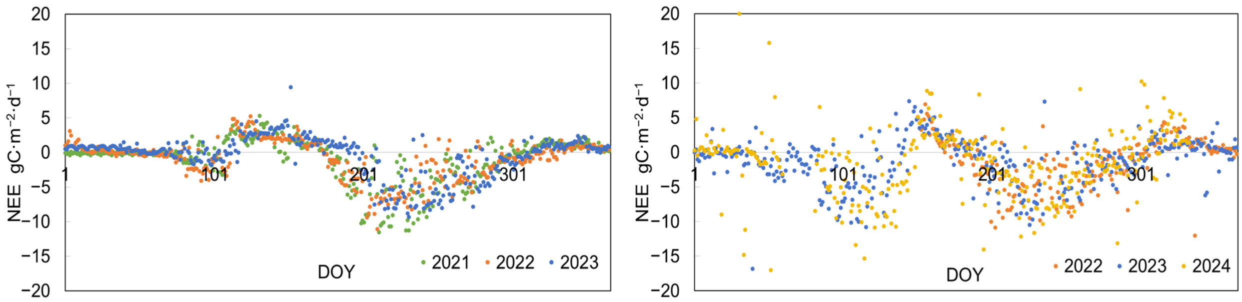


**Figure 4.** Daily change in NEE at Jurong (**left**) and Jiangdu (**right**).

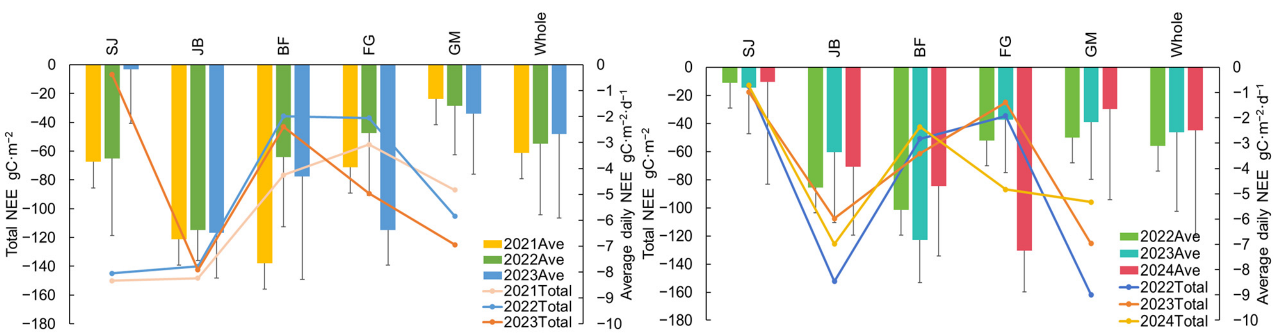


**Figure 5.** The statistic of phenological NEE during rice season at Jurong (**left**) and Jiangdu (**right**) (the abbreviations of SJ, JB, BF, FG, GM and Whole represent sowing–jointing, jointing–booting, booting–flowering, flowering–grain filling, grain filling–maturing and the whole stages, respectively).

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Considering the diurnal variation in NEE, the average NEE in heat days was generally higher during the nighttime than the non-heat days and the period prior to heat days (Figure 6). Moreover, average NEE varied to a larger extent on heat days during the daytime, and the lowest NEE occurred during 11:00 a.m.–1:00 p.m.

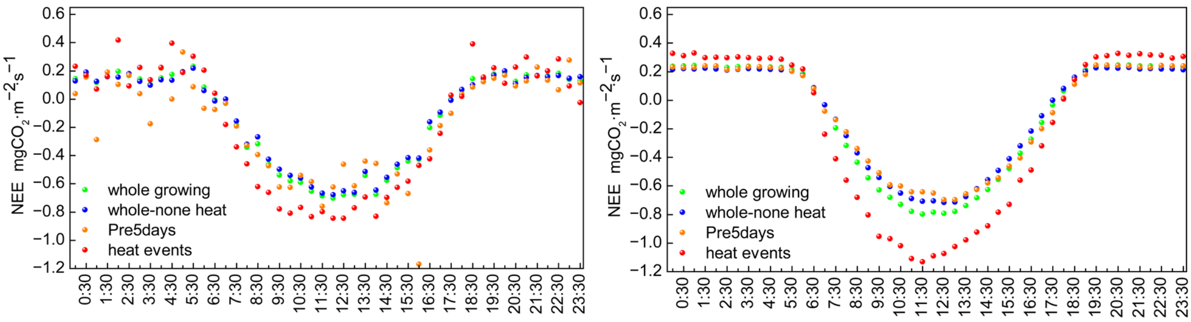


**Figure 6.** Diurnal variation in NEE under different scenarios at Jurong (**left**) and Jiangdu (**right**).

### *3.3. The Response of Carbon Flux to High Temperature*

Seen from the response of NEE to air temperature during the daytime (Figure 7), it was demonstrated that NEE remained relatively stable within a small extent of fluctuation when the temperature was lower than 26 °C, and it significantly decreased from 26 °C to 38 °C (with respective tendency of −0.062 $mgCO_2 \cdot m^{-2} \cdot s^{-1}$ per 1 °C increment at Jurong and −0.045 $mgCO_2 \cdot m^{-2} \cdot s^{-1}$ per 1 °C increment at Jiangdu). However, NEE ceased to decrease when the temperature was higher than 38 °C (with 384 observations at Jurong and 29 observations at Jiangdu), implying a plateau in carbon sequestration efficiency existed under the extreme high-temperature condition. Meanwhile, the response of GEE and Re to air temperature during the daytime indicated continuously increasing Re as the temperature increased (Figure 8), while GEE tended to increase when the temperature was lower than 38 °C; above that, this became a decrease.

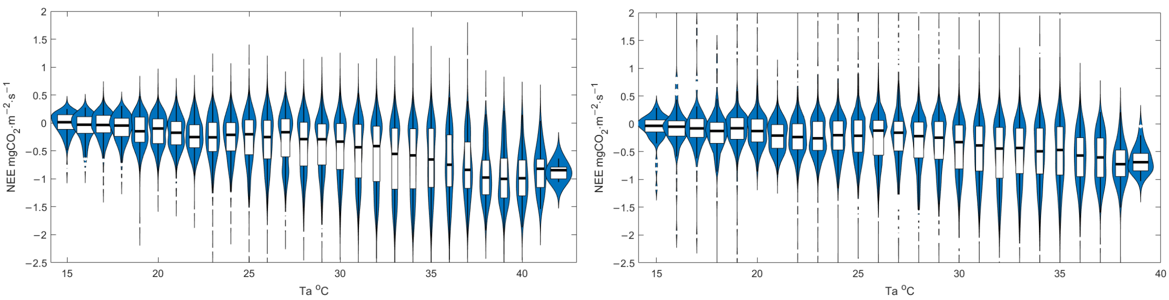


**Figure 7.** The response of NEE to air temperature during the daytime at Jurong (**left**) and Jiangdu (**right**) (the black line in the box represents the median value, and the abbreviation of Ta is air temperature).

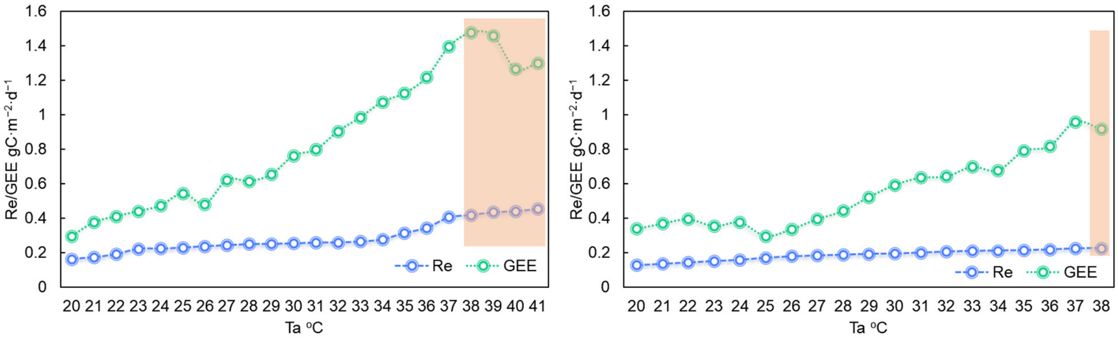


**Figure 8.** The response of GEE and Re to air temperature during the daytime at Jurong (**left**) and Jiangdu (**right**) (the orange shadow represents the part with temperature being above 38 °C).

Regarding the change in ET, there was an upward trend, characterized by a smaller tendency (0.13 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$ per 1 °C increment) when the temperature was lower than 26 °C, followed by a higher tendency (0.55 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$ per 1 °C increment) from 26 °C to 38 °C but a nonsignificant tendency (0.23 mmol $H_2O \cdot m^{-2} \cdot s^{-1}$ per 1 °C increment) when the temperature was higher than 38 °C (Figure 7). For WUE (Figure 9), it significantly decreased when the temperature exceeded 38 °C. Therefore, a transition from decrease to increase in NEE occurred at a breakpoint of 38 °C, due to the faster decreasing trend for GEE than the increasing trend for ET. Moreover, given that temperature was higher than 38 °C, the tendency of NEE was estimated at 0.064 $mgCO_2 \cdot m^{-2} \cdot s^{-1}$ per 1 °C increment at Jurong, while the trend value could not be estimated at Jiangdu owing to fewer observations. Extending this tendency to the domain of Jiangsu province (Figure 10), the loss of NEE was estimated by the decrement from south to north. Furthermore, the largest loss was illustrated in 2022, followed by 2024, while a very small magnitude was shown in 2021 and 2023.

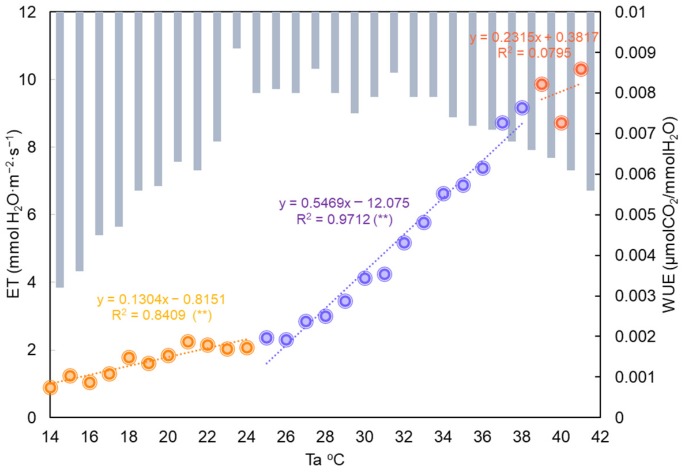


**Figure 9.** The response of ET and WUE to air temperature during the daytime at Jurong (the bar and scatter represent WUE and ET, respectively, and the colored dotted line is the linear trend of ET with symbol of ** signifying the trend being at the significant level of 0.01 during the data slice).

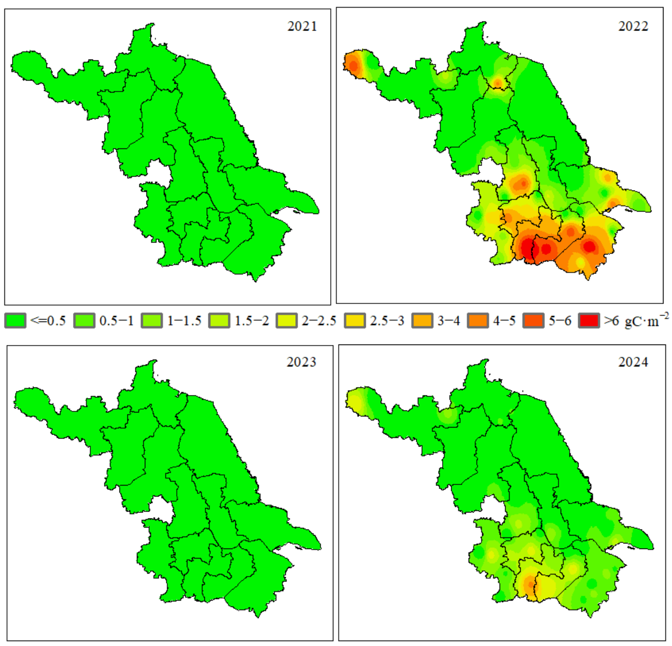


**Figure 10.** The loss of NEE induced by extreme high temperature during 2021–2024 across Jiangsu province.

## 4. Discussion

### *4.1. Carbon Flux Dynamics During Rice-Growing Season*

During the rice-growing season, it was previously reported that NEE in the reproductive stages was significantly higher than that in the early growth stage and maturing stage [3], with lowest negative NEE declared during the heading−flowering stage [6,43]. Specifically, the value of NEE was −0.6 mg $CO_2 \cdot m^{-2} \cdot s^{-1}$ in the early growth stage, −1.8 mg $CO_2 \cdot m^{-2} \cdot s^{-1}$ in the middle growth stage, and from −0.2 to 0.3 mg $CO_2 \cdot m^{-2} \cdot s^{-1}$ in the late growth stage [44]. In comparison with these, this study conducted detailed explorations among finer stages and extracted clearly lower NEE in the reproductive stages, including jointing−booting, booting−flowering, and flowering−grain filling. This might be attributed to the fact that the photosynthetic fixation of $CO_2$ by plants was minor in the early stage but with a higher $CO_2$ fixation rate in the middle growth stages [45].

The diurnal pattern of NEE was characterized as negative during the daytime and positive during the nighttime, and the minimum value appeared around noon. This was in line with the reported synchronous diurnal pattern [44,46], although the magnitudes were different among locations due to the interaction between the atmosphere and physiological response [43,47]. Integrating the daily value to the whole growing season, NEE was negative, acting as the sink of $CO_2$. It was previously validated that rice is an atmospheric sink for $CO_2$, owing to the higher photosynthetic capacity of rice fields to maintain carbon and inhibit respiration [48]. Of course, the recorded experiments inevitably acknowledged the large differences in NEE across studies [49,50], due to inconsistent climate and planting conditions.

### *4.2. The Potential Mechanism of Temperature Impact on Carbon Flux Dynamics*

Air temperature is generally accepted as the predominant contributor regulating NEE dynamics in farmland ecosystems [51–54]. One study briefly stated that high temperature significantly reduced $CO_2$ uptake in tropical regions [55], but diverse effects were seen in temperate and cold regions, where NEE decreased proportionally with air temperature up to 34 °C [6]. As temperature was elevated, the increasing rate of GEE outpaced that of Re during the rice-growing season [36], leading to a negative value in NEE. Demonstration of this link was achieved by quantifying the relationship between NEE and temperature at two sites. The respective correlation coefficients were −0.59 and −0.37 between periodical NEE and mean air temperature at Jurong and Jiangdu and were −0.62 and −0.43 between periodical NEE and maximum air temperature at Jurong and Jiangdu. Moreover, the mean air temperature was 26.7 °C in 2022 and 26.0 °C in 2023 at Jurong and was 26.8 °C in 2022 and 26.0 °C in 2023 at Jiangdu, which corresponded to lower NEE in 2022 relative to 2023.

It was highlighted that NEE decreased when the temperature increased before 38 °C, after which NEE ceased to decrease and even increased, suggesting a reduction in the net carbon sink. Interestingly, the novel threshold of 38 °C was larger than the general threshold of 35 °C defined in heat events [41,42], which was attributed to the fact that temperatures lower than 38 °C are still within the tolerance for rice through its intrinsic adjustment mechanism [49]. Similar relationship analysis for NEE–temperature observations under temperatures lower than 38 °C illustrated that the correlation coefficients reached −0.85 at Jurong and −0.52 at Jiangdu, indicating that extreme high temperature can diminish the decrement in NEE. The critical mechanism underlying the reduced negative NEE at temperatures above 38 °C might be the asymmetrical response of ecosystem processes, whereby GEE was strongly inhibited in comparison with Re stimulation. Threatened by high temperature, partial stomata could close to minimize water loss via transpiration and affect the key photosynthetic apparatus (e.g., damage to Photosystem II and thermal instability in Rubisco), leading to a decline in $CO_2$ assimilation [56,57]. Above 38 °C, GEE collapsed relative to the delayed rise in ET, revealing divergent responses that caused a disproportionate decline in WUE, which is a critical nonlinearity missed from mechanistic models. This change resulted from stomatal closure at a high temperature, which suppressed transpiration, whereas evaporation continued to increase. ET, thus, remained high or even increased, as stomatal closure failed to reduce transpiration enough to counteract the increase in evaporation [58]. The decrease in WUE implied that the amount of carbon fixation per unit of water consumed by rice decreased when temperature was over 38 °C, weakening the net carbon uptake capacity [59].

### *4.3. Uncertainties and Perspectives*

Since the main intention of this study was to explore the effect of extreme high temperature on the NEE for rice, temperature was taken as the main driver of NEE. However, NEE is generally influenced by complex environmental conditions, such as water vapor deficit, solar radiation, soil temperature, etc. [15,53]. Typically, solar radiation is crucial for the crop photosynthesis process and, thus, influences NEE during the daytime [60,61]. Photosynthetically active radiation (PAR), as it increased, often induced a positive contribution to NEE to some extent, out of which its contribution would be low or even negative, suggesting the existence of a light saturation point [11]. The water vapor deficit (VPD), known to modulate stomatal conductance, drove the evapotranspiration and carbon fluxes, especially through direct dependency on temperature under warming [62]. Deeper analysis at Jurong and Jiangdu also indicated that there were breakpoints in VPD and PAR governing the change in NEE from decrease to increase. Alternatively, the multiple regression method was used to quantify the impacts of temperature, PAR and VPD on NEE at Jurong. It was found that their contributions were inevitable. In addition, the contribution of temperature was negative (with the coefficient being −0.018) when the temperature was less than 38 °C, while it changed to positive (with the coefficient being 0.072) and outpaced the contributions of VPD and PAR when the temperature was over 38 °C. This also confirmed the reliability of the threshold of 38 °C highlighted in this study.

It is worth noting that the single impact of environmental factors is likely to be strongly dependent on species [63]. Moreover, evidence pointed out the relevance of VPD–temperature interactions at the critical time of a rapid VPD increase [64], implying interaction between multiple factors. Additionally, biotic factors, represented by LAI and NDVI, showed large influences on carbon fluxes, which could reflect the growth conditions and the effective areas of crop photosynthesis [33]. Therefore, interactions among environmental and biotic factors might lead to uncertainty in the identification of controlling factors [17], which regulate NEE during rice growth. However, the availability of water was generally not identified as the main constraint or a high contributor affecting the carbon fluxes for rice, different from water-limited ecosystems like wheat and maize [65,66]. Therefore, further explorations are needed to improve knowledge of the mechanism of single and interconnected factors on carbon fluxes.

Owing to the limitation that the data used in this study were from two sites and less extreme heat observation was at Jiangdu, the results might be observational rather than statistically derived. In addition, as the crop cultivation was different at Jurong and Jiangdu, management differences (i.e., residue inputs, soil carbon, flooding regime and timing) might affect carbon fluxes [34,35,67]. A comprehensive understanding of the carbon cycle should, therefore, necessitate analysis that encompasses the entire rice ecosystems and crop cultivation chain across broader spatial and temporal scales.

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## 5. Conclusions

Carbon fluxes and meteorological observations measured using the eddy covariance system were used to analyze the dynamic characteristics of NEE and the response to extreme high temperature during the rice-growing season at two sites, Jurong and Jiangdu. Obviously, the respective cumulative NEEs of rice were $-462.2 \pm 55.2$ gC·m$^{-2}$ in 2021–2023 at Jurong and $-362.4 \pm 43.0$ gC·m$^{-2}$ in 2022–2024 at Jiangdu, acting as a net sink for $CO_2$. The jointing−booting, booting−flowering, and flowering−grain filling stages contributed most to NEE accumulation, compared to the early and late phenology. The significant correlation between NEE and temperature pointed to temperature as an important factor regulating NEE dynamics. An innovative point of 38 °C was proposed as a critical threshold limiting the $CO_2$ sink for rice ecosystems. The response of carbon dynamics to temperature for rice cultivation was recorded across the lower reaches of the Yangtze River, the potential application of which deserves future research for other extreme high-temperature-sensitive hotspots. Based on the results, actionable policy measures related to extreme high temperature should be implemented for rice cultivation, according to local contexts and resource availability.

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