Tidal effects on ecosystem CO₂ exchange at multiple timescales in a salt marsh in the Yellow River Delta

Siyu Wei, Guangxuan Han, Xin Jia, Weimin Song, Xiaojing Chu, Wenjun He, Shandong, 264003, China
Yanchi Research Station, School of Soil and Water Conservation, Beijing Forestry University, Beijing, 100083, China
Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun, 130102, China
Key Laboratory of Coastal Zone Environmental Processes and Ecological Remediation, Yantai Institute of Coastal Zone Research, Chinese Academy of Sciences, Yantai, Shandong, 264003, China
University of Chinese Academy of Sciences, Beijing, 100049, China
School of Ecological and Environmental Sciences, East China Normal University, Shanghai, 200241, China

A B S T R A C T

The tide plays a crucial role in maintaining the carbon sink strength in salt marsh ecosystems. Furthermore, the effects of tides on ecosystem carbon exchange could vary with different timescales. Using the eddy covariance technique combined with wavelet analysis, we analyzed the time-frequency characteristics of net ecosystem CO₂ exchange (NEE) to address the tidal effects on NEE at multiple timescales. The wavelet analysis showed that NEE displayed a tidal-driven pattern with distinct characteristics at the multiday scale (i.e., 8–16 days) and the seasonal scale (i.e., 64–128 days). Moreover, a more significant controlling effect of light rather than air temperature on NEE was found at the diel scale. Tides also affected the variation of the diurnal pattern of NEE. Tidal flooding inhibited nighttime CO₂ emissions (NEE_{nighttime}) as well as decreased temperature sensitivity (Q_{10}) of NEE_{nighttime} from 1.37 to 1.16. In contrast, the response of daytime NEE (NEE_{daytime}) to tidal activities was more complicated, as the NEE_{daytime} reacted differently with different months during the growing season. Overall, our findings can contribute to a better understanding of tidal effects on ecosystem carbon exchange in salt marshes.

1. Introduction

Salt marshes are an important component in the blue carbon sink system and play a vital role in the global carbon balance (McLeod et al., 2011; Macreadie et al., 2019; Meng et al., 2019). Moreover, the carbon cycle in salt marshes is also a crucial part of the global carbon cycle. Due to the unique geographical location, the carbon cycle in salt marshes includes several carbon exchange processes between various kinds of carbon pools. These carbon pools mainly include five kinds: the plant carbon pool, the water carbon pool, the microbial carbon pool, the soil carbon pool, and the greenhouse gas pool (Chen et al., 2018). Besides, these carbon exchange processes are influenced by a unique environmental factor—the tide.

Currently, there is a growing body of literature that recognizes the tide as a major factor for ecosystem CO₂ exchange in salt marshes. Tides can directly or indirectly affect ecosystem CO₂ exchange in several pathways (Knox et al., 2018). For example, results from several studies suggest that tides can directly influence not only the emission (respiration) but also the uptake (photosynthesis) of CO₂ over the ecosystem scale (Kathilankal et al., 2008; Moffett et al., 2010). A study conducted in a saline coastal marsh reported that ecosystem CO₂ exchange is completely suppressed under prolonged tidal inundation (Moffett et al., 2010). Moreover, it is known that tides can lead to changes in the hydrological condition and soil properties of salt marshes due to the tide-induced dry-wet alternation (Chmura et al., 2011; Han, 2017). Soil alternate drying-wetting is an important determinant of soil redox condition, which will further influence microbial activity and decomposition rates of soil organic matter (Chivers et al., 2009). Also, several studies have considered the effects of tide-affected changes in soil salinity due to its significant impact on ecosystem CO₂ fluxes in salt marshes (Abdul-Aziz et al., 2018; Doroski et al., 2019; Helton et al., 2019). Thus, the tide is undoubtedly a major environmental factor that drives the variation of ecosystem CO₂ exchange in salt marshes. Although previous studies have found that tides have a vital

---

* Corresponding author.
E-mail address: gxhan@yic.ac.cn (G. Han).

https://doi.org/10.1016/j.ecss.2020.106727
Received 25 November 2019; Received in revised form 18 February 2020; Accepted 18 March 2020
Available online 24 March 2020
0272-7714/© 2020 Elsevier Ltd. All rights reserved.
significantly influence net ecosystem CO\textsubscript{2} exchange (NEE) of salt marshes at the multiday scale (Guo et al., 2009; Knox et al., 2018). This tidally driven pattern of NEE at the multiday scale was affected by a collective effect with other environmental factors, such as light, temperature, water table level, and vapor pressure deficit (Knox et al., 2018). In particular, the response of the photosynthesis to light and the ecosystem respiration to temperature are also changed with the spring-neap tide cycle (Guo et al., 2009). At a shorter timescale, tides can also affect the diurnal pattern of NEE through the direct effect of tidal inundation (Kathilankal et al., 2008; Moffett et al., 2010). For instance, several studies have found the negative correlation between tidal inundation and ecosystem CO\textsubscript{2} emissions (Guo et al., 2009; Barr et al., 2013), while the response of ecosystem CO\textsubscript{2} uptake to tidal effects is more variable (Kathilankal et al., 2008; Guo et al., 2009). Overall, these results provide valuable insights into the regulation of ecosystem carbon exchange by tides at multiple timescales.

Previously, it is difficult for researchers to study ecosystem carbon exchange and its influencing factors at multiple timescales (Baldocchi et al., 2001). Fortunately, recent work has established that wavelet analysis offers the ability to study ecosystem carbon exchange at multiple timescales (Hong and Kim, 2011; Koebisch et al., 2015; Montagnani et al., 2018). For example, using wavelet analysis, researchers investigated how the timescale affects the relative importance of environmental variables in explaining NEE (Montagnani et al., 2018). In another study, researchers used wavelet analysis to investigate the Asian monsoon system and to determine its impact on NEE (Hong and Kim, 2011). Wavelet analysis has several advantages over traditional analysis methods including the following aspects: (1) it can investigate the time-frequency characteristics of a variable at multiple timescales (Grinsted et al., 2004); (2) it can identify the correlation between two time series after eliminating the influence of a third dependence (Ng and Chan, 2012); (3) it is capable of showing the combined effect of multiple independent variables on a dependent variable (Ng and Chan, 2012).

To date, global climate change, especially sea-level rise, has a serious threat to carbon sink strength of salt marshes. Sea-level rise impacts directly upon the frequency and range of tidal activities, which will further affect the carbon cycle in salt marshes (Najar et al., 2010; Lewis et al., 2014; Jones et al., 2018). Therefore, there is an urgent need to address how the tide-induced variation of the carbon exchange process in salt marshes may respond to global climate change. To evaluate how tidal effects could influence NEE at multiple timescales, we conducted the study in a salt marsh in the Yellow River Delta based on the eddy covariance technique combined with wavelet analysis to answer the following questions: (1) At which timescale does the tide influence the variation of NEE? And (2) Does the tide alter the response of NEE to light and air temperature?

2. Materials and methods

2.1. Study site

The study site is located at the intertidal zone observation site of the Research Station of Coastal Wetland in the Yellow River Delta, Chinese Academy of Sciences (37°36′56"N, 118°57′51"E). The Yellow River Delta is one of the most active regions of land-ocean interaction. The region is characterized as a warm-tropical and continental monsoon climate with distinctive seasons and rainy summer. The mean annual temperature is 12.9 °C, and the mean annual precipitation is 560 mm, and nearly 72% of the annual precipitation is concentrated from July to September (Han et al., 2015). The soil type of coastal wetlands in the Yellow River Delta varies from fluvo-aquic to saline soil, and the soil texture is mainly sandy clay loam (Nie et al., 2009). The dominant plant species in our study site is *Suaeda salsa*, with a maximum height of 20–30 cm during the growing season. *Suaeda salsa* is an annual herbaceous plant, with the germination stage in April, flowering in July, and fade in late November (He et al., 2017).

The hydrological condition of the study site is mainly controlled by tidal activities. Since the study site is located in the middle-high tidal flat, the soil and plant will be periodically submerged in tidal water or exposed to the atmosphere. Tidal flooding occurs mostly during the growing season, while tidal flooding usually occurs twice a month during the non-growing season (Fig. 1C). Moreover, tidal activities are also affected by meteorological factors such as wind speed and wind direction.

2.2. Flux and micrometeorological measurements

Net ecosystem CO\textsubscript{2} exchange (\textmu mol m\textsuperscript{-2} s\textsuperscript{-1}) was continuously measured using the eddy covariance (EC) system. The eddy covariance technique is a quasi-continuous, non-destructive, and micrometeorological approach to carbon and water fluxes measurements over the ecosystem scale (Baldocchi, 2003). The EC system includes an integrated three-dimensional ultrasonic anemometer and open-path infrared CO\textsubscript{2}/H\textsubscript{2}O analyzer (IRGASON, Campbell Scientific Inc., USA), which was mounted on a scaffold tower at the height of 2.5 m. The raw data were recorded at 10 Hz by a data logger (CR6, Campbell Scientific Inc., USA) at 30 min intervals. Continuous micrometeorological measurements included standard meteorological, and soil parameters were measured simultaneously around the eddy covariance system. The micrometeorological system mainly included air temperature and relative air humidity (HMP155A, Vaisala, Helsinki, Finland), photosynthetic photon flux density (Li-190R, Li-COR Inc., USA), net radiation (CNR4, Kipp & Zonen USA Inc., Bohemia, NY, USA), wind speed, and wind direction (034B, Campbell Scientific Inc., USA), precipitation (TE525 tipping bucket gauge, Texas Electronics, Texas, USA), soil temperature (109S, Campbell Scientific Inc., USA), and soil salinity (ECH2O-5 TE, Decagon Devices, USA). The hydrological condition was monitored by continuous measurements of surface water level (SR50A-L, Campbell Scientific Inc., USA). Meteorological and hydrological data were monitored every 15 s and then averaged half-hourly by a data logger (CR1000, Campbell Scientific Inc., USA).

2.3. Flux data processing and quality control

Due to the interference of weather conditions, instrument failures, and power outages, erroneous data could be generated during long-term field measurements. Therefore, raw flux data needs to be further processed. Data processing was performed by calculation programs built into CR6 data logger with standard methods, which mainly included despiking, time delay removal, coordinate rotation, and Webb-Pearman-Leuning (WPL) correction (Webb et al., 1980). Subsequently, quality control was applied to the half-hour flux data following steps according to Han et al. (2015). After post-processing and quality control, 44% of daytime data were gap-filled to obtain continuous data set, compared to nearly 76% during nighttime. In addition, the negative and positive values of NEE represent the absorption and emission of CO\textsubscript{2}, respectively.

2.4. Flux gap filling

In order to obtain a continues data set for data analysis, the gaps were filled with the following steps. Small gaps (less than 2 h) were filled by linear interpolation. For large gaps (more than 2 h), the gaps were filled based on empirical models separately for daytime and nighttime data.

When PAR was > 5 W m\textsuperscript{-2}, daytime NEE data were filled with the Michaelis-Menten model (Falge et al., 2001):
Estuarine, Coastal and Shelf Science 238 (2020) 106727

\[ NEE = - \frac{A_{\text{max}} \alpha \text{PAR}}{A_{\text{max}} + \alpha \text{PAR}} + R_{\text{eco}} \]  
(1)

where the coefficient \( \alpha \) is the apparent quantum yield (\( \mu \text{mol CO}_2 \mu \text{mol}^{-1} \) photon), \( A_{\text{max}} \) is the light-saturated net CO\(_2\) exchange (\( \mu \text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1} \)), \( R_{\text{eco}} \) is the daytime ecosystem respiration (\( \mu \text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1} \)), and \( \text{PAR} \) is the photosynthetically active radiation (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)). Particularly, photosynthetic photon flux density (PPFD) was used instead of PAR for calculation in our study (Ratcliffe et al., 2019).

When \( \text{PAR} \) was < 5 W m\(^{-2}\), the missing nighttime NEE (i.e., nighttime ecosystem respiration, \( R_{\text{eco, nighttime}} \)) was filled using the exponential relationship between \( R_{\text{eco, nighttime}} \) and air temperature (\( T_a \)) (Lloyd and Taylor, 1994):

\[ R_{\text{eco, nighttime}} = R_0 \exp(bT_a) \]  
(2)

where \( R_{\text{eco, nighttime}} \) is nighttime ecosystem respiration, \( T_a \) is air temperature (°C), \( R_0 \) and \( b \) are two empirical coefficients, where \( R_0 \) represents the rate of ecosystem respiration at 0 °C and \( b \) represents the temperature response coefficient. Moreover, \( Q_{10} \) can be estimated as:

\[ Q_{10} = \exp(10b) \]  
(3)

2.5. Wavelet analysis

Previous studies have demonstrated that wavelet analysis is suitable for ecological time series analysis (Grinsted et al., 2004; Cazelles et al., 2008; Ng and Chan, 2012). Here, we only briefly introduce the related concepts involved in our study. Detailed descriptions of wavelet analysis have already been well documented in Torrence and Compo (1998), Grinsted et al. (2004), and Cazelles et al. (2008).

The continuous wavelet transform (CWT) of a time series \( \{x_n, n = 1, \ldots, N\} \) with a constant time interval \( \delta t \) is defined as the convolution of \( x_n \) with a scaled and translated mother wavelet, \( \psi_s(t) \):
where $*$ denotes the complex conjugate, $s$ is the wavelet scale at which the transform is applied (Grinsted et al., 2004). In addition, we used the Morlet wavelet (with $\omega_0 = 6$) as the mother wavelet in our study as it provides a good balance between the localization of time and frequency domain. The Morlet wavelet is a complex function with both a real and an imaginary part, therefore allowing for separate investigations of phases and amplitudes (Grinsted et al., 2004). The wavelet power spectrum ($S_n$) of $x_n$ is defined as:

$$S_n(s) = |W_n^s(s)|^2$$

(5)

In the study, we also used wavelet coherence (WTC) to investigate the local correlation between two time series (environmental factors and NEE) in the time-frequency domain (Stoy et al., 2005; Vargas et al., 2010). The wavelet coherence of two time series $X$ and $Y$ is defined as (Grinsted et al., 2004):

$$R_n^2(s) = \frac{|S_x(s)(s)^{-1/2}R_x(s, Y)(s)|^2}{S_x(s)(s)^{-1/2}S_y(s)(s)^{-1/2}}$$

(6)

where $S$ is a smoothing operator, $s$ is the set of scales used as in Eq. (4), and $W$ is the wavelet coherence operator.

Partial wavelet coherence (PWC) is a technique that facilitates the identification of the resulting WTC between two time series $y$ and $x_1$ after eliminating the influence of their common dependent time series $x_2$ (Ng and Chan, 2012). The PWC square is defined as:

$$RP^2(y, x_1, x_2) = \frac{|R(y, x_1) - R(y, x_2)R(y, x_1) *|^2}{|1 - R(y, x_2)|^2|1 - R(y, x_1)|^2}$$

(7)

where $R$ is the WTC operator.

Multiple wavelet coherence (MWC) works like multiple correlation that is capable of seeking the resulting coherence of multiple independents on a dependent (Ng and Chan, 2012). The MWC is defined as:

$$RM^2(y, x_1, x_2) = R(y, x_1) + R(y, x_2) - 2Re[R(y, x_1)R(y, x_2) * R(y, x_1)]$$

(8)

where $R$ is the WTC operator. MWC gives the resulting wavelet coherence squared that computes the proportion of wavelet power of the dependent time series $y$ that is explainable by the two independents $x_1$ and $x_2$ at a given time and frequencies (Ng and Chan, 2012).

### 2.6. Data analysis

We applied wavelet analysis with non-gap-filled data (zeros were padded in gaps) because gap-filling could produce spurious peaks and artificial co-spectral correlation in wavelet analysis (Mitra et al., 2019). All time series were normalized to have zero means before wavelet analysis. The statistical significance (at 5% level) of wavelet spectra was tested using Monte Carlo methods against red noise (Grinsted et al., 2004). Also, we only focused on the results of wavelet analysis outside the “cone-of-influence” (COI), in which the wavelet transform suffers from edge effects due to incomplete time-locality across frequencies (Vargas et al., 2010). All wavelet analyses were calculated in Matlab 2019a software by codes distributed by Grinsted et al. (2004) and Ng and Chan (2012).

Gap-filled data were used to investigate the temporal variation in NEE and other environmental factors. Besides, the CO$_2$ flux were calculated after grouped into the tide-affected condition (during and after tidal flooding within two days) and non-tide-affected condition (before tidal flooding) in order to investigate the effect of tides on NEE. All statistical analyses were performed using SPSS 13.0 (SPSS for Windows, Chicago, IL, USA), and all graphs were made by OriginLab Inc., Northampton, Massachusetts, USA.

### 3. Results

#### 3.1. Environmental factors and NEE variation in the time-frequency domain

Seasonal patterns of daily averaged $T_a$ and PPFD were similar. The minimum daily average $T_a$ of $-7.57\, ^\circ C$ was observed in late December of 2018, while the maximum daily average value of $31.56\, ^\circ C$ occurred in early August of 2018 (Fig. 1A). Daily mean PPFD ranged from 27.81 $\mu$mol m$^{-2}$ s$^{-1}$ in December 2018 to 659.34 $\mu$mol m$^{-2}$ s$^{-1}$ in July 2018 (Fig. 1B). Furthermore, the wavelet analysis of $T_a$ and PPFD showed a significant pattern at the diel scale (Fig. 2A and B).

Tidal activities reflected the typical hydrological condition of the study area (Fig. 1C). Notably, due to the influence of the Super Typhoon Lekima, the maximum daily tide height (2.60 m) occurred on August 11 of 2019. In the wavelet analysis, the significant oscillated characteristics of tidal activities at the diel scale was indicated by a few hotspots. Besides, wavelet spectral peaks of TH (tide height) were also observed at the midday scale (i.e., 8–16 days), the monthly scale (i.e., 32–64 days), and the seasonal scale (i.e., around 128 days) (Fig. 2C).

The variation of NEE followed a significant seasonal pattern (Fig. 1D). Daily mean values for NEE throughout the study ranged from $-3.68\, \mu$mol m$^{-2}$ s$^{-1}$ in mid-June of 2018 to 0.17 $\mu$mol m$^{-2}$ s$^{-1}$ in early December of 2018. Moreover, due to continuous high tides, there were some negative values deviated from the daily average level during the period from June 14th to June 21st and July 16th to July 18th of 2018. As expected, NEE showed a significant pattern at the diel scale (Fig. 2D). However, this pattern gradually disappeared during the non-growing season. We also found significant areas at the midday (i.e., 8–16 days) and monthly scale (i.e., 32–64 days).

#### 3.2. Regulation of NEE by $T_a$ and PPFD at multiple timescales

The significant correlation between $T_a$ and NEE was located at the diel scale, whereas the significant anti-phase relationship between PPFD and NEE was also observed at the diel scale (Fig. 3A and B). At the midday scale, $T_a$ and PPFD were correlated with NEE, as shown by a few discontinuous bands or hotspots. Since the similar performance of $T_a$ and PPFD on NEE in WTC analysis, we further used PWC to disentangle the confounding effects of $T_a$ and PPFD on NEE. After eliminated the effect of PPFD, almost all the significant areas between $T_a$ and NEE in WTC (Fig. 3A) disappeared at the diel scale (Fig. 4A). In contrast, the significant areas in WTC (Fig. 3B) remained in PWC (Fig. 4B), indicating that PPFD rather than $T_a$ dominated the effect on NEE at the diel scale.

#### 3.3. Regulation of NEE by tides at multiple timescales

In WTC analysis, it is apparent that TH was significantly correlated to NEE at the midday scale (i.e., 8–16 days) represented by a few non-continuous areas (Fig. 3C). Meanwhile, TH regulated the variation of NEE at the seasonal scale (i.e., 64–128 days) throughout the study period (Fig. 3C). In PWC analysis, significant areas at the diel scale in WTC (NEE-TH) (Fig. 3C) almost disappeared after eliminated the effect of PPFD (Fig. 4C). Further analysis showed that the significant regions at the seasonal scale (i.e., 64–128 days) between TH & NEE in WTC analysis (Fig. 2C) narrowed after eliminated the effect of $T_a$ (Fig. 4D).

For the MWC analysis, as a result of the combined effects on NEE, the significant areas of MWC (Fig. S1) were more significant than any single factor in WTC analysis. Thus, tidal activities collectively with PPFD and $T_a$ explained most of the variability of NEE at multiple timescales during the study period.
Fig. 2. Continuous wavelet transform (CWT) for (A) air temperature ($T_a$); (B) photosynthetic photon flux density (PPFD); (C) tide height (TH); (D) net ecosystem CO$_2$ exchange (NEE). Black contour lines represent the 0.05 significance level, and the thin line indicates the cone-of-influence that delimits the region not influenced by edge effects.

Fig. 3. Wavelet coherence (WTC) between NEE and (A) air temperature ($T_a$), (B) photosynthetic photon flux density (PPFD), (C) tide height (TH). The phase difference is shown by arrows. Arrows pointing up indicate environmental factors lagging NEE by 90° or leading NEE by 270°, while arrows pointing down indicate environmental factors leading NEE by 90° or lagging NEE by 270°. Arrows pointing right (left) indicate environmental factors and NEE vary in-phase (anti-phase). Black contour lines represent the 0.05 significance level, and the thin line indicates the cone-of-influence that delimits the region not influenced by edge effects.
3.4. The response of NEE to light and air temperature with tidal effects

Fig. 5 shows the effects of tides on the diurnal pattern of NEE averaged over different months during the growing season for 2018 and 2019. What stands out in Fig. 5 was the reduction of nighttime NEE (NEE_{nighttime}) for all months due to the tidal effects. For instance, in July, the average NEE_{nighttime} influenced by the tide (0.25 \mu mol m^{-2} s^{-1}) was reduced by 55% compared to that of non-tide-affected condition (0.55 \mu mol m^{-2} s^{-1}), although its air temperature was higher than that of tide-affected condition (Fig. S2). Moreover, we found that NEE_{nighttime} exhibited exponential dependence on T_a (Table 2, \R^2 = 0.151 and 0.025 of the non-tide-affected condition and tide-affected condition, respectively). In addition, the temperature sensitivity coefficient Q_{10} decreased from 1.37 of non-tide-affected to 1.16 of tide-affected, indicating that tidal flooding weakened the response of NEE_{nighttime} to T_a.

Compared with the nighttime NEE, the response of daytime NEE (NEE_{daytime}) to tidal effects was more complicated. The peak values of NEE_{daytime} were higher under the impact of tides than the non-tide-affected condition in the first three months (May, June, and July). In contrast, the maximum daytime CO_2 uptake was greater of the tide-affected condition than non-tide-affected in August and September, with peak values reaching −2.07 and −1.84 \mu mol m^{-2} s^{-1} of tide-affected condition, as compared to −1.75 and −1.70 \mu mol m^{-2} s^{-1} of non-tide-affected condition. Furthermore, the effects of tides on the response of NEE_{daytime} to PPFD is shown in Fig. 6. A significant correlation was found between NEE_{daytime} and PPFD for both tide-affected (\R^2 = 0.56) and non-tide-affected (\R^2 = 0.50) using equation (1). Interestingly, we found that daytime CO_2 uptake increased dramatically as the PPFD increased during two special periods (June 14th to June 21st, 2018, and July 16th to July 18th, 2018) in the study (Fig. 6). The differences of the coefficients (A_{max}, \alpha, and R_{eco, day}) in equation (1) between two conditions are listed in Table 1. Both the A_{max} and \alpha of tide-affected condition (4.76 ± 0.20 \mu mol m^{-2} s^{-1} and 0.0034 ± 0.0002 \mu mol \mu mol^{-1}, respectively) were lower than that of non-tide-affected condition (4.45 ± 0.19 \mu mol m^{-2} s^{-1} and 0.0031 ± 0.0002 \mu mol \mu mol^{-1}, respectively). Meanwhile, the R_{eco, day} was also reduced due to tidal effects (decreased from 0.21 ± 0.04 \mu mol m^{-2} s^{-1} to 0.17 ± 0.04 \mu mol m^{-2} s^{-1}).

4. Discussion

4.1. The effects of PPFD and T_a on NEE at the diel scale

The results of this study indicated that significant diurnal variation of NEE was mainly driven by light rather than T_a. Both PPFD and T_a were significantly related to the NEE variation at the diel scale (Fig. 3A and B). However, since there was no delay (as shown by phase arrows pointing left in Fig. 3B) between NEE & PPFD, NEE was more tightly related to PPFD rather than T_a. More importantly, PWC analysis disentangled the confounding effects of PPFD and other factors (T_a and TH) on NEE and further proved that PPFD dominated the effect on NEE at the diel scale (Fig. 4B and C).

Ecosystem CO_2 exchange includes two processes: photosynthesis and respiration (Zhao et al., 2019). It is generally accepted that photosynthesis is mainly driven by light, while respiration is a function of temperature (Jia et al., 2014). Previous studies have proved that photosynthesis, rather than respiration, control the diurnal variation pattern of NEE (Hong and Kim, 2011; Ouyang et al., 2014). Thus, light dominates photosynthesis and further controls the diurnal variation of NEE. Moreover, since researchers have found that photosynthesis or photosynthetically active radiation (PAR) can regulate soil respiration at the diel scale (Vargas et al., 2011; Jia et al., 2018a; Mitra et al., 2019), this result further emphasizes the essential role of light in driving NEE.

Our finding is in agreement with the previous studies (Ouyang et al., 2014; Jia et al., 2018b; Wang et al., 2019b). For instance, an eddy covariance-based study conducted in an oak-dominated forest with
7-year measurements indicated that NEE oscillated in-phase with PAR at the diurnal scale (Ouyang et al., 2014). Another study conducted in temperate semiarid shrubland based on 5-year eddy covariance measurements revealed that PAR, rather than $T_a$, dominates the diurnal variation of NEE as indicated by a shorter lag time (Jia et al., 2018b).

4.2. The effect of tides on NEE at multiple timescales

For the multiple timescales, our study found that tidal activities affected the variation of NEE at the multiday scale (i.e., 8–16 days) and the seasonal scale (i.e., 64–128 days) as showed by the wavelet analysis. Additionally, the PWC analysis further confirmed that tidal activities, rather than PAR or $T_a$, control the diurnal variation of NEE as indicated by a shorter lag time (Jia et al., 2018b).

4.2. The effect of tides on NEE at multiple timescales

For the multiple timescales, our study found that tidal activities affected the variation of NEE at the multiday scale (i.e., 8–16 days) and the seasonal scale (i.e., 64–128 days) as showed by the wavelet analysis. Additionally, the PWC analysis further confirmed that tidal activities, rather than PAR or $T_a$, control the diurnal variation of NEE as indicated by a shorter lag time (Jia et al., 2018b). The influence of tides at the multiday scale could be primarily caused by the spring-neap tide cycle. The spring-neap tide cycle could strongly modulate the water table level, temperature, and humidity. Therefore, the spring-neap tide cycle has a critical influence on NEE at the multiday scale (Guo et al., 2009; Schafer et al., 2014; Knox et al., 2018). In line with our study, in an estuarine wetland, the NEE measurements over one year from two eddy-flux towers demonstrated that the dynamics of CO$_2$ flux exhibited a tidal-driven pattern with obvious characteristics at time scales between 10 and 20 days (Guo et al., 2009). Likewise, researchers found that NEE exhibiting a tidal-driven pattern in a brackish marsh at the multiday scale (Knox et al., 2018).

At the diel scale, our results indicate that the response of daytime CO$_2$ uptake to tidal effects varied with different months during the growing season (Fig. 5). In accordance with the present results, previous studies have demonstrated that the effects of tides on photosynthesis was complicated in salt marshes (Guo et al., 2009; Knox et al., 2018). It

---

**Fig. 5.** The diurnal pattern for NEE during the growing season of our study period. Data is presented as mean ± SE. The blue lines indicate a tide-affected condition, and the gray lines indicate the non-tide-affected condition. The comparison of PPFD and $T_a$ between the two conditions are presented in Fig. S2. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
effects of tides on daytime CO\textsubscript{2} uptake may be the dominating factor in two aspects. First, the tidal water restricted CO\textsubscript{2} emissions from the soil and plant to the atmosphere. Second, part of the CO\textsubscript{2} could dissolve in the tidal water. Also, standing water and water in pores reduces the availability of O\textsubscript{2} in the soil, which means an inhibition effect of heterotrophic respiration (Jimenez et al., 2012; Han et al., 2015; Wang et al., 2019a). Furthermore, we also found that tidal flooding reduced the temperature sensitivity of the nighttime ecosystem respiration (Table 2). The significant relationship between NEE\textsubscript{daytime} and \( T_s \) with the reduced \( Q_{10} \) indicates that the tidal effects on NEE\textsubscript{daytime} are a “weakening” rather than “offset” of the temperature effects. A similar finding has been reported in a brackish marsh that the temperature sensitivity (expressed in soil temperature sensitivity, \( Q_{S10} \)) before the tidal flooding was higher than that of the after ebbing (Yang et al., 2018). The decreased \( Q_{10} \) value of NEE\textsubscript{daytime} could be mainly explained by higher soil moisture due to the tidal flooding. The high soil moisture could reduce soil respiration and subsequently affect the \( Q_{10} \) value of ecosystem respiration (Han et al., 2013).

### 4.3. Limitations

Although this study has promoted the understanding of the tidal effect on ecosystem carbon exchange in salt marshes, there are still some limitations that highlight ways in which our further study could be improved. First, the time series length of our data was not long enough to reveal the effects of multiple environmental factors due to their

---

**Table 1**

Comparison of coefficients \( A_{\text{max}} \), \( \alpha \), and \( R_{\text{eco, day}} \) estimated using equation (1) between the non-tide-affected condition and the tide-affected condition.

| Condition                | \( A_{\text{max}} \) (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)) | \( \alpha \) (\( \mu \text{mol} \text{ mol}^{-1} \)) | \( R_{\text{eco, day}} \) (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)) | \( R^2 \) | \( n \) |
|--------------------------|-------------------------------------------------|-------------------------------------|-------------------------------------------------|------|------|
| Non-tide-affected        | 4.76 ± 0.20                                     | 0.0034 ± 0.0002                     | 0.21 ± 0.04                                     | 0.50 | 5075 |
| Tide-affected            | 4.45 ± 0.19                                     | 0.0031 ± 0.0002                     | 0.17 ± 0.04                                     | 0.56 | 3550 |

Parameter \( A_{\text{max}} \) is the ecosystem light-saturated net CO\textsubscript{2} exchange, \( \alpha \) is the ecosystem apparent quantum yield, \( R_{\text{eco, day}} \) is ecosystem respiration in the daytime estimated from the NEE-PPFD response curve, \( R^2 \) is the coefficient of determination, and \( n \) is the number of observations. The values of coefficients represent the mean ± SE.

---

**Table 2**

Comparison of coefficients \( R_0 \), \( b \), and \( Q_{10} \) of equation (3) between the non-tide-affected condition and the tide-affected condition.

| Condition         | \( R_0 \) | \( b \) | \( Q_{10} \) | \( R^2 \) | \( n \) |
|-------------------|----------|-------|-------------|------|------|
| Non-tide-affected | 0.206    | 0.031 | 1.37        | 0.151| 2236 |
| Tide-affected     | 0.156    | 0.015 | 1.16        | 0.025| 1482 |

Parameter \( R_0 \) and \( b \) are two empirical coefficients, \( Q_{10} \) is the temperature sensitivity coefficient, \( R^2 \) is the coefficient of determination, and \( n \) is the number of observations.

---

**Fig. 6.** Comparison of the light-response curves for daytime NEE (NEE\textsubscript{daytime}) between the non-tide-affected condition (gray closed circles) and the tide-affected condition (blue open circles). The blue closed circles represent data of the period from June 14th to June 21st and July 16th to July 18th of 2018. The curves were fitted using equation (1), and regression coefficients are presented in Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
relative importance varied with both time and frequency domain (Stoy et al., 2005; Jia et al., 2018b). For example, the temperature may drive the dynamics of NEE at the multiday scale and the seasonal scale, while NEE exhibiting a distinct diel pattern under the control of light. Moreover, tidal flooding inhibited NEEdiurnal and further decreased the Q10 of nighttime ecosystem respiration. However, the response of NEEdiurnal to tidal effects was more complicated during the growing season. The critical role of tides for NEE in our study emphasizes several implications: (1) the effect of tides needs to be considered at different timescales when illustrating the mechanism of the tidal effects on NEE, and (2) modeling efforts should take into account the relationship between the tide and ecosystem carbon exchange in salt marshes across multiple timescales.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

CRediT authorship contribution statement

Siyu Wei: Conceptualization, Formal analysis, Investigation, Data curation, Visualization, Writing - original draft. Guangxuan Han: Supervision, Conceptualization, Writing - review & editing, Project administration. Xin Jia: Data curation, Visualization. Weimin Song: Investigation, Resources. Xiaojing Chou: Formal analysis, Data curation, Writing - original draft. Wenjun He: Investigation, Visualization. Jianyang Xia: Writing - review & editing, Project administration. Haitao Wu: Writing - review & editing, Project administration.

Acknowledgments

This research was funded by the Strategic Priority Research Program of the Chinese Academy of Sciences, China (XDA23052020) and the National Natural Science Foundation of China (41671089). We are grateful for the support from the Yellow River Delta Ecological Research Station of Coastal Wetland, CAS, and also thank two anonymous reviewers for their expert advice and fruitful comments.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2020.106727.

References

Abdul-Aziz, O.I., Ishaq, K.S., Tang, J.W., Moseman-Valierra, S., Kroeger, K.D., Gommez, M.E., Mora, J., Morkeski, K., 2018. Environmental controls, emergent scaling, and predictions of greenhouse gas (GHG) fluxes in coastal salt marshes. J. Geophys. Res.-Biogeo. 123, 2234-2256.

Baldochci, D., Falge, E., Wilson, K., 2001. A spectral analysis of biosphere-atmosphere trace gas flux densities and meteorological variables across hour to multi-year time scales. Agric. For. Meteorol. 105, 1-27.

Baldocchi, D.D., 2003. Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: present, past and future. Global Change Biol. 9, 47-99.

Barr, A.D., Angel, V., Fuentes, J.D., Fuller, D.O., Kwon, H., 2013. Modeling light use efficiency in a subtropical mangrove forest equipped with CO2 eddy covariance. Biogeosciences 10, 2145-2158.

Bo, N.S., Qu, J.F., Zhao, H., Yan, Q.W., Zhao, B., Fan, J.L., Fang, C.M., Li, G., 2015. Effects of semi-lunar tidal cycling on soil CO2 and CH4 emissions: a case study in the Yangtze River estuary, China. Wet. Ecol. Manag. 23, 727-736.

Baznel, B., Chavarje, M., Beretxe, D., Menard, F., Vik, J.O., Jenouvrier, S., Senneth, N., 2006. Hydrodynamics of tidal wetlands. J. Geophys. Res.-Biogeo. 111, C11012.

Chen, Q.F., Guo, B.B., Zhao, C.S., Xing, B.X., 2018. Characteristics of CH4 and CO2 emissions and influence of water and salinity in the Yellow River delta wetland, China. Environ. Pollut. 239, 289-299.

Chivers, M.R., Turetsky, M.R., Waddington, J.M., Harden, J.W., McGuire, A.D., 2009. Effects of experimental water table and temperature manipulations on ecosystem CO2 fluxes in an Alaskan rich fen. Ecosystems 12, 1329-1342.

Chmura, G.L., Kellman, I., Guntensger, G.R., 2011. The greenhouse gas flux and potential global warming feedbacks of a northern macrotidal and microtidal salt marsh. Environ. Res. Lett. 6 (4), 044016.

Doroski, A.A., Helton, A.M., Vadas, T.M., 2019. Greenhouse gas fluxes from coastal wetlands at the intersection of urban pollution and saltwater intrusion: a core sample experiment. Soil Biol. Biochem. 138, 258-277.

Falge, E., Baldocchi, D., Olson, R., Anthophi, P., Aubinet, M., Berghofer, B., Burba, G., Ceulemans, R., Clement, R., Dolman, H., Granier, A., Grös, P., Grünwald, T., Hollinger, D., Jensen, N.O., Katul, G., Keronen, P., Kowalchik, A., Li, C.T., Lamp, B.E., Meyers, T., Moncrieff, H., Munger, J.W., Pilegaard, K., Rannik, U., Rebmann, C., Suyker, A., Tenhunen, J., Tu, K., Verma, S., Veta, S., Vadas, T., Han, G.X., 2017. Effects of drying and wetting cycles induced by tides on net ecosystem exchange of a supratidal wetland in the Yellow River Delta. J. Geophys. Res.-Biogeo. 120, 1506-1520.

Han, G.X., Yang, L.Q., Yu, J.B., Wang, G.M., Mao, P.I., Gao, J.Y., 2013. Environmental controls on net ecosystem CO2 exchange over a reed (Phragmites australis) wetland in the Yellow River Delta, China. Ecosystems. 30, 401-413.

Han, W.J., He, W.J., Han, G.X., Xu, X.N., Zhang, X.T., Wang, A.D., Che, C.G., Sun, B.Y., Zhang, X.S., 2015. Controls for multi-scale temporal variation in ecosystem methane exchange during the growing season of a temperate semiarid shrubland. Agric. For. Meteorol. 259, 250-259.

Koebsch, F., Jurasinski, G., Koch, M., Hofmann, J., Glatzel, S., 2015. Controls for multi-scale temporal variation in ecosystem methane exchange during the growing season of a permanently inundated fen. Agric. For. Meteorol. 204, 90-105.

Lewis, D.B., Brown, J.A., Jenouvrier, S., 2004. Application of the cross wavelet transform and wavelet coherence to geophysical time series. Nonlinear Process Geophys. 11, 561-566.

Guo, H.Q., Noormets, A., Zhao, Z., Chen, J.Q., Sun, G., Gu, Y.J., Li, B., Chen, J.K., 2009. Tidal effects on net ecosystem carbon exchange of an estuarine wetland. Agric. For. Meteorol. 149, 1820-1828.

Gal, M.S., 2017. Conducting water and wetting cycles on carbon exchange in a salt marsh: progress and prospects. Acta Ecol. Sin. 37, 8170-8178 (in Chinese).

Han, G.X., Wang, X.J., Xing, Q.H., Li, J.J., Yu, J.B., Luo, Y.Q., Wang, G.M., Mao, P.I., 2018. Effects of tidal flooding on the net ecosystem CO2 exchange of a supratidal wetland in the Yellow River Delta. J. Geophys. Res.-Biogeo. 123, 1916-1928.

Han, G.X., Yang, L.Q., Yu, J.B., Wang, G.M., Mao, P.I., Gao, J.Y., 2013. Environmental controls on net ecosystem CO2 exchange over a reed (Phragmites australis) wetland in the Yellow River Delta, China. Ecosystems. 30, 401-413.

He, W.J., Han, G.X., Xu, X.N., Zhang, X.T., Wang, A.D., Che, C.G., Sun, B.Y., Zhang, X.S., 2017. Effects of drying and wetting cycles induced by tides on net ecosystem exchange of CO2 over a salt marsh in the Yellow River Delta, China. J. Appl. Ecol. 29, 269-277 (in Chinese).

Han, H., Wu, G., Huang, Y., Xing, Q., Dang, J., Yuan, J., Luo, Z., Gao, Y., 2018. Effects of semi-lunar tidal cycling on ecosystem carbon and water exchanges: a wavelet analysis and its ecosystem modeling implications. Global Change Biol. 17, 1900-1916.

Jia, X., Zha, T.S., Wang, S., Bourque, C.P.A., Wang, B., Qin, S.G., Zhang, Y.Q., 2018a. Canopy photosynthesis modulates soil respiration in a temperate semi-arid shrubland at multiple timescales. Plant Soil 432, 437-450.

Jia, X., Zha, T.S., Gong, J.N., Zhang, Y.Q., Xu, B., Qin, S.G., Peltola, H., 2018b. Multiscale dynamics and environmental controls on net ecosystem CO2 exchange over a temperate semi-arid shrubland. Agric. For. Meteorol. 259, 250-259.

Koebusch, F., Jurasinski, G., Koch, M., Hofmann, J., Glatzel, S., 2015. Controls for multi-scale temporal variation in ecosystem methane exchange during the growing season of a permanently inundated fen. Agric. For. Meteorol. 204, 90-105.

Lewis, D.B., Brown, J.A., Jenouvrier, S., 2004. Effects of flooding and warming on soil organic matter mineralization in the Avicennia germinans mangrove forests and Juncus effusus salt marshes. Estuar. Coast. Shelf Sci. 139, 11-19.
Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Funct. Ecol. 8, 315–323.

Macreadie, P.I., Anton, A., Raven, J.A., Beaumont, N., Connolly, R.M., Friess, D.A., Fong, L.W., Kennedy, J.H., Kuwahara, T., Lavery, P.S., Lovelock, C.E., Smale, D.A., Apostolaki, E.T., Atwood, T.B., Baldock, J., Bianchi, T.S., Chamura, G.L., Eyre, B.D., Fourqurean, J.W., Hall-Spencer, J.M., Huxham, M., Hendriks, I.E., Krause-Jensen, D., Laffoley, D., Luizetti, T., Marba, N., Masque, P., McClatchey, K.J., Megenical, J.P., Murdiyarso, D., Russell, B.D., Santos, R., Serrano, O., Silliman, B.R., Watanabe, K., Duarte, C.M., 2019. The future of blue carbon science. Nat. Commun. 10.

McLeod, E., Chamura, G.L., Bouillon, S., Salm, R., Bjork, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., Silliman, B.R., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. Front. Ecol. Environ. 9, 552–560.

Meng, W.Q., Peng, R.A., Hu, B.B., He, M.X., Li, H.Y., 2019. The spatial distribution of blue carbon in the coastal wetlands of China. Estuar. Coast Shelf Sci. 222, 13–20.

Mitra, B., Miao, G., Minick, K., McNulty, S.G., Sun, G., Gavazzi, M., King, J.S., Noormets, A., 2019. Disentangling the effects of temperature, moisture, and substrate availability on soil CO2 efflux. J. Geophys. Res.-Biogeosci. 124, 2060–2075.

Moffett, K.B., Wolf, A., Berry, J.A., Gerecki, S.M., 2010. Salt marsh-atmosphere exchange of energy, water vapor, and carbon dioxide: effects of tidal flooding and biophysical controls. Water Resour. Res. 46, W10525.

Montagnani, L., Zanotelli, D., Tagliavini, M., Tomelleri, E., 2018. Timescale effects on the environmental control of carbon and water fluxes of an apple orchard. Ecol. Evol. 8, 416–434.

Najjar, R.G., Pyke, C.R., Adams, M.B., Breitburg, D., Hershner, C., Kemp, M., Howarth, R., Mulholland, M.R., Paulison, M., Secor, D., Sellner, K., Wardrop, D., Wood, R., 2010. Potential climate-change impacts on the Chesapeake Bay. Estuar. Coast Shelf Sci. 86, 1–20.

Ng, E.K.W., Chan, J.C.L., 2012. Geophysical applications of partial wavelet coherence and multiple wavelet coherence. J. Atmos. Ocean. Technol. 29, 1845–1853.

Nie, M., Zhang, X.D., Wang, J.Q., Jiang, L.F., Yang, J., Quan, Z.X., Cui, X.H., Fang, C.M., Li, B., 2009. Rhizosphere effects on soil bacterial abundance and diversity in the Yellow River Deltaic ecosystem as influenced by petroleum contamination and soil salinization. Soil Biol. Biochem. 41, 2535–2542.

Ouyang, Z., Chen, J., Becker, R., Chu, H., Xie, J., Shao, C., John, R., 2014. Disentangling the confounding effects of PAR and air temperature on net ecosystem exchange at multiple time scales. Ecol. Complex. 19, 46–58.

Quan, Q., Tian, D.S., Luo, Y.Q., Zhang, F.Y., Crowthers, T.W., Zhu, K., Chen, H.Y.H., Zhou, Q.P., Niu, S.L., 2019. Water scaling of ecosystem carbon cycle feedback to climate warming. Sci. Adv. 5, eaav1131.

Ratcliffe, J.L., Campbell, D.I., Clarkson, B.R., Wall, A.M., Schipper, L.A., 2019. Water table fluctuations control CO2 exchange in wet and dry bogs through different mechanisms. Sci. Total Environ. 655, 1037–1046.

Schafer, K.V.R., Duman, T., Tomasicchio, K., Tripathee, R., Sturtevant, C., 2019. Carbon dioxide fluxes of temperate urban wetlands with different restoration history. Agric. For. Meteorol. 275, 223–232.

Schafer, K.V.R., Tripathee, R., Artigas, F., Morin, T.H., Bohrer, G., 2014. Carbon dioxide fluxes of an urban tidal marsh in the Hudson-Raritan estuary. J. Geophys. Res.-Biogeosci. 119, 2065–2081.

Stoy, P.C., Katal, G.G., Siquetra, M.B.S., Jiang, Y.-V., McCarthy, H.R., Kim, H.-S., Oishi, A.C., Oren, R., 2005. Variability in net ecosystem exchange from hourly to inter-annual time scales at adjacent pine and hardwood forests: a wavelet analysis. Tree Physiol. 25, 887–902.

Torrence, C., Compo, G.P., 1998. A practical guide to wavelet analysis. Bull. Am. Meteorol. Soc. 79, 61–78.

Vargas, R., Baldocchi, D.D., Bahn, M., Hannon, P.J., Hosman, K.P., Kulmala, L., Pumpansen, J., Yang, B., 2011. On the multi-temporal correlation between photosynthesis and soil CO2 efflux: reconciling lags and observations. New Phytol. 191, 1006–1017.

Vargas, R., Betto, M., Baldocchi, D.D., Allen, M.F., 2010. Multiscale analysis of temporal variability of soil CO2 production as influenced by weather and vegetation. Global Change Biol. 16, 1589–1605.

Wang, F.M., Kroeger, K.D., Gonneea, M.E., Pohlman, J.W., Tang, J.W., 2019a. Water salinity and inundation control soil carbon decomposition during salt marsh restoration: an incubation experiment. Ecol. Evol. 9, 1911–1921.

Wang, Y., Zhou, L., Jia, Q.T., Ping, X.Y., 2019b. Direct and indirect effects of environmental factors on daily CO2 exchange in a rainfed maize cropland—a SEM analysis with 10 year observations. Field Crop. Res. 242.

Webb, E.K., Pearman, G.L., Leuning, R., 1980. Correction of flux measurements for density effects due to heat and water vapour transfer. Q. J. R. Meteorol. Soc. 106, 85–105.

Yang, P., Lai, D.Y.F., Huang, J.F., Zhang, L.H., Tong, C., 2018. Temporal variations and temperature sensitivity of ecosystem respiration in three brackish marsh communities in the Min River Estuary, southeast China. Geoderma 327, 138–150.

Zhao, J., Malone, S.L., Oberbauer, S.F., Olivas, P.C., Schindlbauer, J.L., Staudhammer, C.L., Starr, G., 2019. Intensified inundation shifts a freshwater wetland from a CO2 source to a sink. Global Change Biol. 25, 3319–3333.