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Tidal effects on ecosystem CO_2 exchange in a *Phragmites* salt marsh of an intertidal shoal



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ABSTRACT

Understanding the mechanisms and controlling factors of ecosystem CO2 exchange in tidal wetlands is of great benefit for research concerning the global carbon cycle and climate change. In spite of this, the multiple controls of ecosystem-atmosphere CO₂ exchange in coastal wetlands subject to subdaily tidal flooding have yet to be adequately addressed. In this study, we investigated the tidal influence on ecosystem CO_2 exchange in a Phragmites salt marsh of an intertidal shoal in the Changjiang estuary, based on eddy covariance (EC) measurements. The results revealed that the study area acted as a strong sink for atmospheric CO₂ (net ecosystem exchange, NEE = -901 g C m⁻²) in 2018. Photosynthetically active radiation (PAR), air temperature (T_a), and vapor pressure deficit (VPD) were major drivers of NEE on both diel and multi-day scales. The tides, along with the bio-meteorological variables, strongly affect ecosystem photosynthesis (gross primary production, GPP) and ecosystem respiration (R_{eco}) in the tidal wetland, especially on the multi-day scale. Regardless of which flux partitioning method was utilized, tidal inundation generally imposed inhibitory effects on GPP, which were directly attributed to tidal water level (TWL) and salinity. The daytime data-based estimates of R_{eco} was also suppressed on average under the tidal inundation condition when T_a was higher relative to the non-inundation condition, reflecting the influence of TWL on R_{eco} and the reduced sensitivity of R_{eco} to T_a . We observed that NEE responded positively or negatively to tidal flooding, depending on the magnitude of tidal suppression on GPP and R_{eco} . When T_a was roughly between 28 and 32°C and PAR was > 1200 μ mol m⁻² s⁻¹, GPP was suppressed by tides more than R_{eco} during the early and rapid vegetative stage, while during the peak vegetative stage, the opposite was true. This study not only shows the unique impact of tidal salt marsh wetlands on carbon uptake, but it also represents an example of a coastal wetland in which tidal inundation promotes the net uptake of CO₂.

1. Introduction

Coastal wetlands are among the most biologically productive natural ecosystems (Kirwan and Megonigal 2013), and they have been increasingly recognized as playing an important role worldwide in mitigating climate change, due to their significant carbon sink capacity. Despite being much smaller in size, coastal wetlands sequester and store far more carbon per unit area from the atmosphere into soil (as cocalled coastal blue carbon) than the terrestrial carbon pool (McLeod et al., 2011). The mechanisms and controlling factors of the carbon sink from coastal wetlands remain largely unknown, however, and research on the land-ocean interface affected by tidal activities has only just begun (Tang et al., 2018). The global network measurements of net ecosystem CO_2 exchange (NEE) using the eddy covariance (EC) method are mostly located in terrestrial ecosystems (Baldocchi et al., 2018), without considering the subdaily flooding of tides. Therefore, elucidating the tidal effects of coastal wetlands on NEE is required in order to improve our knowledge of the mechanism driving carbon sequestration processes and the quantification of coastal blue carbon.

Relative to upland ecosystems, the CO_2 exchanges between coastal wetlands and the atmosphere are not only controlled by bio-meteorological variables, such as solar radiation, air temperature (T_a), humidity, precipitation and soil water content (SWC), but they are also regulated by unique features of coastal wetlands such as tides (Huang et al., 2019; Knox et al., 2015, 2018; Forbrich and Giblin, 2015). Because of this, the multiple controls of meteorological

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Fig. 1. Locations of the EC flux tower (red dot) in the Jiuduansha Nature Reserve, the tide gauge (purple triangle), and the buoy stations (orange triangle) in the Changjiang estuary of China. A Landsat 7 ETM + image (RGB = bands 6, 5, and 2, respectively) acquired on June 8, 2018 provides the background. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

variables on the CO_2 exchange process in coastal wetlands are quite different from those of upland ecosystems. For instance, precipitation tends to play a small role, since the soil moisture is regularly flooded by the tides and thus not primarily controlled by precipitation. Tidal flooding also leads to wet and/or saturated soil, which provides an adequate water supply to plants but it may limit the oxygen availability needed for microbial and root activities in the soil (Jimenez et al., 2012). Moreover, the different temporal cycles of tides from meteorological variables, such as photosynthetically active radiation (PAR), may increase the nonlinearity of the multiple controls on CO_2 fluxes (Han et al., 2015; Guo et al., 2009).

Tides can exert effects on the net uptake of CO₂, which results from the competing processes of ecosystem photosynthesis and respiration, in several different ways. For instance, tidal inundation can cause soil hypoxia or anoxia that, on the one hand, decreases plant metabolism and diminishes stomatal opening (Banach et al., 2009: Schedlbauer et al., 2010), while on the other hand, limits microbial activity and decomposition rates of soil organic matter (Chivers et al., 2009; Jimenez et al., 2012). The saline water brought in by the tides may also significantly influence plant photosynthesis and other functions, since plants obtain fresh water by filtering salt ions out of their tissues (Pagter et al., 2009). More specifically, saline stress, on the one hand, suppressed the activity of carboxylation enzymes in the chloroplasts of salt marsh vegetation, while on the other hand, affected ion homeostasis and osmotic pressure, leading to a reduction in photosynthetic activity and GPP (Li et al., 2018). Moreover, tidal water coverage can affect ecosystem respiration (R_{eco}) directly through preventing gas diffusion and the flux of trapped CO2 from the soil (Guo et al., 2009; Han et al., 2015), and indirectly by modulating micro-meteorological conditions such as T_a (Knox et al., 2018).

In recent years, research based on EC measurements of the

environmental controls on CO_2 fluxes under tidal influence in coastal wetland ecosystems has attracted increasing attention (Barr et al., 2010; Forbrich and Giblin, 2015; Guo et al., 2009; Knox et al., 2018; Lee et al., 2015). These studies are of great value in understanding the coastal wetland-atmosphere CO_2 exchange processes, and have demonstrated that the tides exert non-negligible effects on the CO_2 uptake of coastal ecosystems. Further research is required, however, to elucidate the controls on CO_2 fluxes over a variety of time scales, and to improve the current understanding of the monitoring and predicting of atmospheric carbon fluxes in tidal ecosystems. The currently used approaches for gap-filling and partitioning of EC measurements have not explicitly incorporated the effects of tides (Reichstein et al., 2005; Lasslop et al., 2010). Tidal systems require finer understanding of the mechanisms and controlling factors, over a variety of time scales, to do proper gap-filling and partitioning.

Studies of the tidal effects on CO₂ fluxes under diverse climatic and hydrological conditions are still limited. At present, there have been no reports concerning the measurement of the continuous CO2 fluxes over a recently formed intertidal shoal that is strongly affected by the complex interaction between river discharge and ocean tide. This knowledge gap impedes realistic parameterizations of CO2 flux exchange between tidal ecosystems and the atmosphere, making it difficult to predict the net blue carbon uptake in coastal wetlands based on environmental conditions, and to assess the role of coastal wetlands in climate mitigation (Tang et al., 2018). To our knowledge, Earth System Models (ESMs) have not explicitly considered the effects of tides on CO₂ fluxes, and they have rarely incorporated parameterizations of tidal processes for coastal ecosystems (Hurrell et al., 2013). Consequently, current models are unable to reliably and consistently reproduce the blue carbon exchange processes, thus making the accurate quantification of blue carbon challenging.



Fig. 2. Variations of (a) daily average net ecosystem CO2 exchange (NEE) (black line) and photosynthetically active radiation (PAR) (red line); (b) halfhourly tidal water level (TWL) of the Zhongjun tidal station (light gray shading), daily average salinity of buoy station 2 (purple line) and salinity of buoy station 1 (purple dotted line); (c) daily total precipitation (blue bars) and daily average soil water content (SWC) at a depth of 0.5 m (gray line); (d) daily average vapor pressure deficit (VPD) (dark cyan line) and air temperature (T_a) (orange line); (e) daily average evapotranspiration (ET) (turquoise line) and soil temperature at a depth of 5 cm (T_{s1}) (yellow line) at the study site in Jiuduansha during 2018. The gray dotted line represents the TWL at a height of 4 m, and the black dotted line is the position on 7 July 2018 (DOY 189). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In this study, we investigated the tidal effects on the CO_2 fluxes measured using the EC technique during the year 2018 in the natural salt marsh of an intertidal shoal in a mesotidal estuary. During spring tides, tidal flooding occurred over the flux footprint area in both the daytime and nighttime, while during neap tides, no inundation occurred, providing us with the opportunity to examine the tidal influences on R_{eco} as well as photosynthesis. We also investigated the influence of salinity on ecosystem photosynthesis. Our specific objectives were to: (1) identify the relative importance of the environmental drivers on NEE at hourly, diel, and multi-day timescales, (2) examine the responses of ecosystem photosynthesis and respiration to tidal inundation, and (3) investigate the tidal influence on net CO_2 uptake under both offshore and onshore wind direction conditions in the natural *Phragmites* salt marsh of an intertidal shoal in the mesotidal Changjiang estuary.

2. Materials and methods

2.1. Study site

Our study site was located within the Jiuduansha Shoal of the Changjiang River estuary in China (Fig. 1). Jiuduansha is a collection of 4 young islands—Shangsha, Zhongsha, Xiasha, and Jiangya'nansha—growing from the constant deposition of sediments carried by the Changjiang River, which were emerged in the 1950s and have been developing as stable islands over the past half-century. Vegetation began to colonize the islands in about 1990, and has been continuously increasing. The area covered by vegetation was only 0.45 km² in 1990, and it had rapidly expanded to 79.35 km² by 2013 (Li et al., 2016). The plant communities on Jiuduansha are rather simple, with the marshes being dominated by *Phragmites australis, Scirpus mariqueter*, and *Spartina alterniflora*. Of these, *P. australis* and *S. mariqueter* are native species, while *S. alterniflora* was transplanted to the island in 1997 under the

Greening Engineering project (Chen, 2003).

Jiuduansha experiences a subtropical monsoon climate, with an annual mean temperature of 16°C. The warmest average temperature occurs in July (27.3°C) while the coolest occurs in January (4.2°C). The annual precipitation of the shoal is approximately 1145 mm. The Jiuduansha wetland was approved by the Shanghai Municipal People's Government as a national nature reserve in 2003, due to its limited human disturbance. The reserve includes the 4 intertidal wetland shoals as well as the submerged land surrounding them above -6 m (Fig. 1). To date, Jiuduansha is uninhabited and is representative of the natural coastal ecosystems in eastern China. Jiuduansha is an excellent model ecosystem for addressing many ecological issues, such as carbon cycling and global change (Chen, 2003).

The EC measurements were conducted in 2018 on a P. australis monoculture (31.2131°N, 121.9069°E) covering 10.51 km² of Shangsha, and 19.05 km² of the entire Jiuduansha Shoal (Fig. 1). In 2018, the flux footprint area reached a maximum length of roughly 600 m (Chen et al., 2020), and the elevation ranged from 4.0-4.2 m based on the Wusong datum level. After 20-30 years of vegetation development, the wetland is relatively stable and well-established. The soil is mainly composed of silt and sandy silt, and the lodging and decay of aboveground litter form most of the organic carbon in the topsoil. The P. australis exerts a positive "priming effect" on the mineralization of original soil organic carbon, which helps to improve the content and stability of soil organic carbon (Yan et al., 2020). The growing season of the P. australis ecosystem usually extends from April to October, with budding around mid-April, heading in mid-August, blooming in mid-September, and withering beginning in early October. Based on this, we divided the entire growing season into three stages: (1) the early and rapid vegetative stage from April-May (referred to as "early vegetative"), (2) the peak vegetative stage from June-July ("peak vegetative"), and (3) the flowering and ripening stage from August-October ("flowering and ripening"). The vegetation grew to a height of



Fig. 3. Occurrence of tidal inundation during the periods (a) January 1-December 31 and (b) June 1-August 31, 2018.

approximately 2.5 m during the peak growing season at the study site. The simplicity and high spatial homogeneity of the ecosystem structure made it ideal for EC measurements.

The tides exhibited strong semidiurnal, fortnightly, and seasonal variations, as indicated by the tidal water level (TWL) variations based on the Wusong datum level measured by the nearest Zhongjun tidal gauge station (Fig. 2b). More specifically, the mean and maximum tidal ranges were approximately 2.8 and 4.4 m, respectively. The mean sea level (MSL), mean high water (MHW), and mean higher high water (MHHW) were 2.5, 3.2, and 3.5 m, respectively, while the lower high water and higher high water respectively reached 4.7 and 5.9 m. It is estimated that the flux footprint area was partly or entirely waterlogged when the TWL was higher than the lowest elevation of the area (4 m). In the study area, tidal inundation can occur during either the day or night, and also during both day and night (Figs. 3 and 4). In summer, the higher high water mainly occurred during the night, whereas the higher low water occurred during the day, although the occurrence

time varied, leading to the fact that tidal inundation occurred during either the night or during both day and night (Fig. 4).

2.2. Eddy covariance and environmental measurements

We used the eddy correlation technique (Baldocchi, 2003) to continuously measure the CO_2 , water vapor (H₂O), and heat fluxes between the salt marsh ecosystem and the atmosphere during the 2018 study year. The EC system, mounted on a tower at a height of 10 m, consisted of an open-path infrared CO_2/H_2O gas analyzer (LI-7500A, LI-COR Inc., Lincoln, NE, USA) and a 3-axis ultrasonic anemometer (GILL-WM, Gill Instruments Ltd., UK). The former measured the molar densities of CO_2 and H₂O, while the latter produced the sonic temperature, speed of sound and wind speed and direction. The measurements were made at 10 Hz, storing and averaging the data at half-hour intervals.

The Biomet system (7900–101, LI-COR Inc., Lincoln, NE, USA) was used to monitor the biological and meteorological parameters for the



Fig. 4. Daily gross primary production (GPP, black lines) and respiration (R_{eco} , red lines) and the occurrence of tidal inundation in the study area during 2018. Vertical shaded areas indicate the periods when tidal flooding occurred only during the day (lavender), only at night (green), and during both day and night (gray). Unit: µmol m⁻² s⁻¹. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

EC measurements. A four-component radiometer (CNR4, Kipp and Zonen, Delft, Netherlands) was utilized to measure incoming (downwelling) and reflected (upwelling) radiation in two spectral bands, and thus the net radiation (R_n) above the canopy (3 m). A quantum sensor (LI-190SZ, LI-COR, Inc., USA) was empolyed for PAR measurement. Those data were collected at a height of 6 m on the tower. T_a and RH were measured with a temperature and humidity probe (HMP155, Vaisala, Helsinki, Finland). Soil temperature and water content data were obtained from three soil temperature sensors (7900–180, LI-COR Inc., Lincoln, NE, USA) and soil moisture sensors (Stevens Hydra Probe II, Stevens Water Monitoring Systems, Inc., Oregon, USA) at depths of 0.05, 0.10, and 0.20 m. Precipitation was measured with a tipping bucket rain gage (TR-525 M, Texas Electronic, Dallas, TX, USA). The data were averaged over half-hour intervals, and logged using a data logger (7900–120 Sutron, LI-COR Inc., Lincoln, NE, USA).

The TWLs during 2018 were recorded at one-hour intervals by the nearest tide gauge station, Zhongjun (Fig. 1). The water salinity and temperature were measured by the nearby buoy stations at 10-min intervals. In order to allow comparison with the EC measurements, the TWL and water salinity and temperature data were interpolated to half-hour intervals.

2.3. Eddy covariance data quality control and gap-filling

We used Eddypro 7.0.4 software for the post-processing of CO2 flux measurements at half-hour intervals. The "w-boost bug" correction was applied to fix a bug that leads to the underestimation of vertical wind speed for the Gill Windmaster anemometer produced between 2006 and 2015 (Nakai and Shimoyama, 2012). The double-rotation method was used for anemometer tilt correction (Wilczak et al., 2001). We selected the block-averaging method (Gash and Culf, 1996) to remove turbulent fluctuations, and covariance maximization for time lag compensation. A Webb-Pearman-Leuning (WPL) correction (Webb et al., 1980) was implemented to compensate for air density fluctuations due to, for instance, temperature and pressure fluctuations. Spectral corrections, namely the corrections of low-pass and high-pass filtering effects, were applied in order to correct flux estimates for low and high frequency losses due to instrument set-up, intrinsic sampling limits, and certain data processing choices. We also applied statistical analyses for quality filtering, which included spike count and removal, amplitude resolution, drop-outs, absolute limits, and skewness and kurtosis tests.

In addition to the corrections, the steady state and developed turbulence tests (Foken et al., 2004) were applied in order to quality check the remaining dataset, and the poor-quality fluxes were deleted. Moreover, the CO₂ fluxes measured under the following conditions were removed: (a) nocturnal low atmospheric turbulence conditions with $u_* \leq 0.39 \text{ m s}^{-1}$, in which the u_* threshold was determined using the moving point method (Papale et al., 2006); (b) atmospheric stability parameter (Z/L) > 1 or < -1 and the Monin-Obukhov length (L) > 5000 or < -2000. As a result of the quality control, roughly 36% of the measurements were excluded for the study period. Subsequently, the data gaps due to unfavorable micro-meteorological conditions or instrument failure were filled based on the standardized methods of Falge et al. (2001) and Reichstein et al. (2005), implemented using the REddyProc R software package offered by the Max Planck Institute for Biogeochemistry (MPI-B) (Wutzler et al., 2018).

2.4. Eddy covariance CO_2 flux partitioning

We used two different algorithms to disaggregate the measured NEE into the main components, GPP and $R_{\rm eco}$ (NEE = $R_{\rm eco}$ – GPP). One of the methods was the nighttime data-based algorithm according to Reichstein et al. (2005), referred to as "NB." The NB approach used an Arrhenius-type model (Eq. [S1]) to describe the temperature dependency of $R_{\rm eco}$ (Lloyd and Taylor, 1994). For the NB flux partitioning, the nighttime $R_{\rm eco}$ was estimated using the measured nighttime NEE

data (defined here as global solar radiation [Rg] < 10 W m⁻² and cross-checked against sunrise and sunset time), since it was assumed that daytime $R_{\rm eco}$ could be extrapolated with $T_{\rm a}$ from the nighttime measurement of NEE (i.e., $R_{\rm eco}$).

The second algorithm was the daytime data-based (DB) estimate including the temperature sensitivity of respiration (Gilmanov et al., 2003) and the VPD limitation of GPP (Körner, 1995), referred to as "DB VPD" (Lasslop et al., 2010). The DB VPD approach was based on the Michaelis-Menton model (Eq. [S2]) that was used to describe the relationships between daytime NEE (or GPP) and PAR among the most biologically productive natural ecosystems (Falge et al., 2001). It should be noted that in this study a positive NEE represented a net flux of CO_2 to the atmosphere. These procedures were also implemented based on the REddyProc R software package offered by the MPI-B (Wutzler et al., 2018).

2.5. Information theory analysis of eco-atmosphere interaction

The interactions between the NEE and the environmental variables, i.e., PAR, T_a, VPD, evapotranspiration (ET), wind direction (WD), wind speed (WS), soil temperature at the depth of 5 cm (T_{s1}) , soil water content at the depth of 5 cm (SWC1), TWL, and salinity, were characterized using information theory analysis. The mutual information $(I_{X,Y})$ represents the average tendency for the paired states of two variables (X, Y) to coexist, and is able to detect both the linear and nonlinear interactions between them. The relative mutual information (IR_{X,Y}), a relative form of $I_{X,Y}$, is a normalized measure of the statistical dependence of Y on X, the degree of which indicates the interaction between X and Y. We used the IR_{X,Y} to present our results following Knox et al. (2018) and Sturtevant et al. (2016), since it is the most intuitive. Furthermore, the power of $IR_{X,Y}$ was enhanced for the identification of the asynchrony of complex eco-atmosphere interactions by adding temporal directionality to it (Schreiber, 2000). If the maximum IR_{X X} was found at the zero time lag ($\tau = 0$), the interaction was characterized as "synchronous." Otherwise, it was identified as "asynchronous," i.e., variations in Y either lagged (maximum $IR_{X,Y}$ at $\tau > 0$) or led (maximum $IR_{X,Y}$ at $\tau < 0$) variations in X (Knox et al., 2018; Sturtevant et al., 2016).

The procedure to characterize the interactions between NEE and environmental variables was as follows: (a) We decomposed the measured data into the hourly (scales 1–2; 1–2 h), diel (scales 3–6; 4 h–1.3 days), and multi-day (scales 7–10; 2.7–21.3 days) time scales using the maximal overlap discrete wavelet transform (MODWT); (b) ProcessNetwork software version 1.5 (Ruddell et al., 2008) was applied to calculate the relative mutual information (IR) between the GPP, R_{eco} and environmental variables. The maximum evaluated lags were respectively set to 0.5, 1, and 10 days at the hourly, diel, and multi-day time scales, and the statistical significance at the 95% level was estimated using a Monte Carlo approach (Sturtevant et al., 2016).

2.6. Tidal effects on ecosystem photosynthesis and respiration

The tidal effects on NEE were investigated by comparing the GPP and R_{eco} during the flooded and non-flooded periods, respectively. The days during which the maximum daytime and nighttime TWL reached 400 cm were respectively identified as flooded periods, otherwise they were treated as non-flooded periods, due to the unequal high tides in the daytime and nighttime. The lengths of day and night were determined by the times of sunrise and sunset.

In order to investigate the tidal influence on photosynthesis, the following analyses were conducted. We examined and compared the responses of (a) the partitioned daytime GPP to PAR and T_{a} ; (b) the daytime NEE to PAR, on the basis of the Michaelis-Menton model (Falge et al., 2001), at different phenological growth stages; (c) the daytime NEE to PAR at different phenological growth stages for three tidal water salinity groups: salinity group (1), ≥ 10 ppt; salinity group

(2), ≥ 5 and <10 ppt; and salinity group (3), <5 ppt; and (d) the daytime NEE to PAR under offshore (180–360°) and onshore (0–180°) wind conditions during the peak vegetative stage.

To study the tidal effects on R_{eco} , we examined at the response of nighttime NEE to T_{a} , since photosynthesis rarely occurs at night. The parameters (*rb*, E_0) of Eq. (S1) fitted to the nighttime half-hourly NEE and T_a values were derived using nonlinear least squares regression during flooded and non-flooded periods for each plant phenophase. These estimated parameters were identified as valid if the temperature range was > 5°C and more than 6 points were available for each period (Reichstein et al., 2005). Subsequently, we compared the effective parameters (*rb*, E_0) between flooded and non-flooded conditions. The mean, minimum (min), and maximum (max) of T_a were also calculated for each period in order to investigate the confounding effects of T_a and tidal inundation on R_{eco} . Moreover, we compared the mean diurnal patterns of the DB VPD and NB R_{eco} under tidal and non-tidal inundation conditions at different phenological stages.

3. Results

3.1. Environmental conditions and net ecosystem CO₂ exchange

The seasonal cycle of meteorological variables at our study site was governed by its eastern subtropical monsoon climate (Fig. 2). Incoming radiation, VPD, T_{a} , and T_{s1} reached their maximum values in July-August, and dropped to their minima during December–February. Precipitation mainly occurred from May–September, exhibiting the greatest intensity during the summer. SWC displayed a different seasonal pattern than precipitation, with low values in summer and high values in winter (Fig. 2c). The warm weather with sufficient sunlight and rainfall that began in late April favored the growth of plants. Fig. 2b also shows that the salinity levels measured by buoy stations 1 and 2 exhibited a significant spring-neap tidal cycle, although the values in the first half of the year were generally much higher than those during the second half of the year.

The salt marsh wetland mainly functioned as a net carbon sink from late April to October in 2018, with the daily mean NEE varying from a net carbon gain of $-18.6 \ \mu mol \ CO_2 \ m^{-2} \ s^{-1}$ in mid-July to a loss of 4.7 $\mu mol \ CO_2 \ m^{-2} \ s^{-1}$ in mid-March.

3.2. Interactions between CO_2 fluxes and environmental variables

As shown in Fig. 5, the maximum IR_{PAR, NEE}, found at the zero time lag, had the highest values (0.06, 0.30, and 0.19) at the hourly, diel, and multi-day time scales, respectively, whereas the respective values between GPP and PAR were 0.29, 0.38, and 0.25, demonstrating that NEE and GPP shared the largest amount of mutual information with PAR, and their interaction processes were nearly synchronous at the three time scales. Apart from PAR, the diel time scale also revealed significant, nearly synchronous, interactions of NEE and GPP with T_a , while they both exhibited negative lags of 6.5 h with the T_{s1} . VPD appeared to play a more important role at the multi-day scale compared with the diel scale, since VPD shared the second-largest mutual information with NEE and GPP at the multi-day scale. There were synchronous, significant, and relatively strong interactions between NEE, GPP, and ET at the diel and multi-day scales, implying the strong coupling of water and carbon fluxes in the wetland ecosystem.

It is clear from Fig. 5 that NEE and GPP have very similar interaction patterns with the environmental variables. The main drivers of the R_{eco} variations differed from those of GPP and NEE, however. T_a and VPD appeared to exert dominant effects on R_{eco} , with $IR_{Ta, Reco} = 0.31$ and $IR_{VPD, Reco} = 0.11$, at the diel and multi-day scales, respectively. R_{eco} shared the second-largest amount of mutual information with PAR at the diel scale, and with T_a at the multi-day scale. This indicates that the NEE variations were controlled less by the drivers of R_{eco} relative to GPP, and PAR exerted dominant controls on the NEE of the *P. australis*

ecosystem at the diel and multi-day time scales. The interaction strengths between NEE, GPP, and R_{eco} and the environmental variables were generally low at the hourly scale, since EC measurement uncertainty is expected to be large at this relatively short time scale (Hollinger and Richardson, 2005).

NEE had significant interactions with TWL and salinity at both diel and multi-day scales, and multi-day variation in NEE was more strongly linked to TWL and salinity, although the interactions were asynchronous (Fig. 5 (c, f, i)). This corresponds to the semi-diurnal and springneap tidal cycles at the study site, suggesting that tidal activities exert strong effects on the net exchange of CO_2 fluxes, which will be discussed later.

3.3. Tidal effects on ecosystem photosynthesis and respiration

It appeared that NEE had varied responses to tidal flooding. For instance, we observed a suppressed NEE under tidal inundation when $T_{\rm a}$ was roughly between 28 and 32°C and PAR was > 1200 µmol m⁻² s⁻¹ during the early vegetative stage, but an enhanced NEE in the same range as that of PAR and $T_{\rm a}$ during the peak vegetative stage (Fig. 6 (a, b, d, e)). The tidal effects on NEE resulted from the differing amounts of tidal influence on GPP and $R_{\rm eco}$.

Both Figs. 4 and 7 show that the rate of photosynthesis reached its maximum during the peak vegetative stage, followed by the early vegetative stage. The contours of daytime GPP estimated based on both the DB VPD and NB algorithms (Figs. 7 and S1) illustrate that photosynthesis in the salt marsh plants generally increased with PAR for a given T_a , whereas it increased with T_a until the peak T_a (24–32°C) under non-tidal inundation conditions. The tidal flooding notably changed the responses of plant photosynthesis to PAR and T_a , regardless of which flux partition method was used. The hotspots of daytime GPP decreased or disappeared under inundation conditions, and pronounced suppression of plant photosynthesis occurred at T_a ranging from 28 to 30°C and PAR roughly > 1200 µmol m⁻² s⁻¹ during both the early and peak vegetative stages (Figs. 7 (a, b, d, e) and S1).

The relationships between daytime NEE and PAR were well-described by Eq. (S2), as indicated by the values of R^2 ranging from 0.49–0.85 in Table 1. The relatively low values of R^2 under high tides suggest that, overall, tidal waterlogging decreased the goodness of fit between daytime NEE and PAR. However, comparison of the estimated parameters A_{max} and α under the two conditions revealed that, during different phenological stages, tidal flooding on average exerted distinct effects on photosynthesis. More specifically, tidal flooding enhanced the plant photosynthetic capacity A_{max} , but decreased initial light use efficiency α during the entire vegetative growth stage, whereas during the flowering and ripening period, the opposite was true.

The parameters for Eq. (S2) derived from the three salinity groups indicate that the plant photosynthetic capacity A_{max} generally increased with decreasing salinity range (Table 2). More specifically, A_{max} increased from 18.4 at salinity (1) (\geq 10 ppt) to 38.9 and 54.2 at salinity (2) (\geq 5 and < 10 ppt) and (3) (<10 ppt), respectively, in the early vegetative stage, whereas in the peak vegetative stage, the value increased from 59.1 at salinity (1) to 74.7 and 63.5 at salinity (2) and (3), respectively. We also found that when the salinity was < 5 ppt, A_{max} increased by approximately 18.6% compared with its value when the salinity was > 5 ppt during the flowering and ripening stage, although the salinity dropped below 10 ppt during this stage, due to the increased runoff of the Changjiang River.

Table 3 lists the derived parameters (*rb*, *E*₀) of Eq. (S1) fitted to nighttime half-hourly NEE, namely R_{eco} , and T_a during flooded and non-flooded periods. The parameters were expected to be estimated from reasonable regressions of R_{eco} and T_a , since the temperature range was > 5°C and more than 6 points were available for each period (Reichstein et al., 2005). The data fit the Arrhenius-type model well (*p* < 0.005) during both the peak vegetative and flowering and ripening stages. In those stages, the values of E_0 were consistently higher, while



Fig. 5. Relative mutual information ($IR_{X, NEE}$, $IR_{X, GPP}$, and $IR_{X, Reco}$) between (a, b, c) NEE; (d, e, f) GPP; and (g, h, i) R_{eco} and the potential drivers at (a, d, g) hourly; (b, e, h) diel; and (c, f, i) multi-day time scales for the Jiuduansha wetland. The subscript X represents each variable on the y-axis. The length of each black bar represents the IR without any time lag, whereas the colored extension indicates the maximum IR, with the color showing whether the process involves a lead or lag. Red (blue) indicates that variability in NEE, GPP, and R_{eco} lagged (led) the variability in the environmental variables. The vertical gray lines indicate the 95% significance threshold. The GPP and R_{eco} values were the DB VPD estimates. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the *rb* values were lower under tidal inundation conditions compared with the values when tidal flooding did not occur in the nighttime hours. In the daytime, R_{eco} generally increased during flooded periods in the early vegetative and the flowering and ripening stages, while decreasing in the peak vegetative stage, relative to the values during non-tidal inundation periods (Table 3).

3.4. Tidal effects on CO₂ fluxes associated with wind direction

As shown in Fig. 8, during the peak vegetative stage, the salt marsh ecosystem acted as a much stronger carbon sink, with negative peak NEE values of -39.2 and $-32.5 \ \mu\text{mol}\ \text{m}^{-2}\ \text{s}^{-1}$ under offshore (180–360°) and onshore (0–180°) wind conditions, respectively, and values of -22.4 and $-23.3\ \mu\text{mol}\ \text{m}^{-2}\ \text{s}^{-1}$ for flooded and non-flooded periods, respectively. Correspondingly, both the DB VPD and NB day-time GPP and the ratio of GPP to R_{eco} (not shown) were higher when offshore winds prevailed (Figs. 8 and S2), although to differing extents. It appears that the offshore winds favored CO₂ uptake of the coastal wetland during the day.

fluxes under offshore and onshore wind conditions. When the wind was blowing offshore, tidal flooding had pronounced effects on the amplitudes of the diel patterns of NEE and GPP, whereas under onshore wind conditions, the tidal effects were rather small. More specifically, when offshore winds prevailed, tidal inundation enhanced the daytime net CO_2 uptake rate by 5.0 µmol m⁻² s⁻¹ on average, as the GPP values and the ratio of GPP to Reco were respectively increased by 3.9 µmol $m^{-2} s^{-1}$ and 2.9 for the DB VPD estimates, and 4.6 μ mol $m^{-2} s^{-1}$ and 2.4 for the NB estimates. Tidal inundation resulted in a reduction of the DB VPD Reco value under both wind conditions, whereas for the NB estimates, tidal inundation only led to a decrease in R_{eco} under the offshore wind condition. Waterlogging consistently led to a greater increase in photosynthetic capacity A_{max} under offshore winds during the peak vegetative period (Table 4). The aforementioned wind effects were mainly attributed to spatial heterogeneity and varying meteorological conditions, which will be discussed later.

The tides appeared to exert differing amounts of influence on CO2



Fig. 6. Contours of the observed NEE in response to PAR and T_a in the daytime with and without tidal inundation during (a, d) early vegetative, (b, e) peak vegetative, and (c, f) flowering and ripening stages at the study site.

4. Discussion

4.1. Carbon uptake among marsh ecosystems

The annual NEE during 2018 in our study area was $-901 \text{ g C m}^{-2} \text{ y}^{-1}$, which was generally higher than the values of the previously studied tidal marsh ecosystems (Table 5). The marsh ecosystem with the closest NEE value is the Dongtan wetland ($-737 \text{ g C m}^{-2} \text{ y}^{-1}$), with *P. australis* and *S. alterniflora* dominating the plant community in the same delta (Yan et al., 2010). This indicates that the tidal salt marshes in the Changjiang Delta exhibited superior performance in net CO₂ uptake among marsh ecosystems.

The area covered by *P. australis* was approximately 19.05 km^2 (the values were from the unpublished report of the Shanghai Municipality) in Jiuduansha during 2018. Therefore, it is estimated that the native plant *P. australis* in Jiuduansha had the potential to sequester 17,160 Mg C in 2018, which was relatively high compared to the sequestration potentials in the other parts of the Changjiang Delta (Guo et al., 2009; Yan et al., 2010).

From the annual carbon budgets (Table 5), we can see that most tidal marsh ecosystems functioned as carbon sinks, although they exhibited large variabilities in their net CO_2 uptakes. Salt marshes appeared to be large carbon sinks among the tidal marsh ecosystems, with NEE values ranging from -256 to -901 g C m⁻² y⁻¹ and the highest NEEs in the *P. australis* ecosystems. This indicates that the CO_2 uptake capacity is not only related to plant species, but it is also highly associated with climatic and ecohydrological conditions.

4.2. Ecosystem CO_2 exchange dynamics and the drivers

Across all of the time scales, PAR, VPD and temperature were the key drivers for the NEE variabilities in the coastal salt marsh (Fig. 5). More specifically, PAR played a dominant role in controlling NEE at the hourly, diel, and multi-day scales, indicated by the strongest interactions between PAR and NEE at the scales. Moreover, T_a was the second largest controlling factor of NEE at the diel scale, while VPD at the multi-day scale. Tides, however, co-control CO2 flux exchange with the meteorological variables, forming a complex NEE pattern, as demonstrated by the significant interactions between NEE and TWL at various time scales (Fig. 5). It should be noted that, although VPD and R_{eco} shared the largest amount of IR at the multi-day scale, they were not mechanistically related, since their relationship was mainly attributed to the fact that the R_{eco} was estimated using the DB VPD approach that included the VPD limitation of GPP, which can be confirmed by the less amount of mutual information between the NB Reco and VPD at both the diel and multi-day scales (figure not shown here). Moreover, the relationship can be partly explained by the strong interaction between VPD and T_a , which was a main driver of R_{eco} .

The interactions of NEE with TWL and salinity were the strongest at the multi-day time scale (Fig. 5), implying that the net CO_2 uptake was driven more by spring-neap (fortnightly) tidal cycles than semi-diurnal tidal cycles. Consistently, Fig. 2 (a, b) also indicated that NEE fluctuated with the spring-neap tidal cycle during the vegetative growth stage, with generally greater net CO_2 uptake during the spring tides than the neap tides. This is reasonable since the tidal dynamics followed the lunar cycle, and the diurnal tidal effects were greatly obscured by the diel solar cycle. We also found that the NEE interacted considerably



Fig. 7. Contours of the DB VPD GPP estimates in response to PAR and T_a in the daytime with and without tidal inundation during (a, d) early vegetative, (b, e) peak vegetative, and (c, f) flowering and ripening stages at the study site.

more with tidal water salinity than TWL at the multi-day scale, indicating that tidal water salinity had a greater influence than TWL, and was a major contributor to the direct tidal effects on the ecosystem CO_2 exchange. This was further confirmed by the fact that high salinity reduced plant photosynthetic capacity during inundation regardless of seasonality (Table 2).

We observed that tidal flooding led to an increase in plant photosynthetic capacity in flooded periods relative to non-flooded periods during both the early and peak vegetative growth phases (Table 1). This indicates that tidal flooding favored the net uptake of CO_2 during the vegetative growth stage in the study area, which is in contrast to the suppression of daytime NEE induced by tides reported in some previous studies (Forbrich and Giblin, 2015; Kathilankal et al., 2008; Moffett et al., 2010). This difference may be due to the facts that (1) Eq. (S2) did not incorporate the effects of T_a and VPD, and (2) our study area tended to be inundated by short-duration tides with low water depth during the day (Fig. 3), which exerted a different effect on CO_2 fluxes.

Apart from the environmental variables discussed above, wind direction was also an important factor that strongly interacted with NEE at the multi-day scale (Fig. 5). The effects of wind direction on NEE (Fig. 8) can be largely explained by the spatial heterogeneity in addition to different meteorological conditions. As illustrated in Fig. S3, during the peak vegetative stage, the flux footprint of the EC measurements under offshore winds was more spatially homogeneous than the footprint under onshore winds, indicating either denser vegetation or more tidal creeks. As a result, the daytime GPP and NEE values were, on average, greater when offshore winds prevailed (Fig. 8).

4.3. Mechanism and implications

The net uptake of CO_2 in a coastal salt marsh can be directly and indirectly affected by tides via the competing processes of ecosystem photosynthesis and respiration. Regardless of which flux partition

Table 1

Comparison of parameters A_{max} and α for Eq. (S2) and R^2 fitted to half-hourly daytime data of NEE and PAR with and without tidal inundation during the early vegetative, peak vegetative, and flowering and ripening stages at the study site.

Period	Tidal inundation	A _{max}	α	R _{eco}	\mathbb{R}^2	Average PAR (μ mol m ⁻² s ⁻¹)	Average T_a (°C)	Average VPD (kPa)
Early vegetative	No	27.7	0.074	4.87	0.49*	536.2	18.7	0.5
	Yes	34.2	0.063	5.05	0.50*	667.1	20.5	0.5
Peak vegetative	No	61.6	0.058	4.24	0.85*	640.4	26.4	0.9
	Yes	71.7	0.051	3.55	0.69*	824.4	28.2	1.2
Flowering and ripening	No	47.3	0.015	2.31	0.63*	636.0	26.4	1.2
	Yes	21.0	0.027	3.15	0.49*	684.6	25.7	1.1

Note: *, p < 0.005.

Table 2

Comparison of parameters A_{max} , α , and R_{eco} for Eq. (S2) and R^2 fitted to half-hourly daytime data of NEE and PAR for three tidal water salinity groups, salinity (1) ≥ 10 ppt, salinity (2) ≥ 5 and < 10 ppt, and salinity (3) < 5 ppt, during tidal inundation periods for the early vegetative, peak vegetative, and flowering and ripening stages at the study site.

Period	Salinity (ppt)	A _{max}	α	R _{eco}	\mathbb{R}^2	Average PAR (μ mol m ⁻² s ⁻¹)	Average T_a (°C)	Average VPD (kPa)
Early vegetative	≥10	18.4	0.07	4.05	0.71*	150.7	19.8	0.3
	≥5, <10	38.9	0.06	3.80	0.78*	128.3	20.8	0.3
	<5	54.2	0.05	3.79	0.92*	190.2	21.1	0.3
Peak vegetative	≥10	59.1	0.04	2.90	0.92*	63.5	28.0	0.9
	≥5, <10	74.7	0.04	2.94	0.90*	91.2	28.1	0.9
	<5	63.5	0.05	3.05	0.84*	102.6	28.0	0.9
Flowering and ripening	≥10	-	-	-	-	-	-	-
	≥5, <10	20.4	0.02	1.25	0.69*	207.7	20.1	0.6
	<5	24.2	0.02	1.23	0.68*	261.7	20.5	0.7

Note: *, *p* < 0.005.

method was used, tidal flooding resulted in reductions in daytime GPP, especially when T_a was roughly between 28 and 32 °C and PAR was > 1200 µmol m⁻² s⁻¹ over the entire vegetative growth period, as illustrated by the responses of GPP to PAR and T_a (Figs. 7 (a, b, d, e) and S1 (a, b, d, e)). This is consistent with the findings of previous research based on EC measurements (Forbrich and Giblin, 2015; Kathilankal et al., 2008; Moffett et al., 2010), and further supported by the *in situ* photosynthetic studies at the leaf scale in marshes (Kathilankal et al., 2008; Li et al., 2018). It should be noted that the A_{max} increased under tidal inundation during the vegetative growth stage (Table 1), which seems contrary to the responses of the DB VPD GPP to tidal flooding. This may be because the estimates in Table 1 did not explicitly consider the effect of T_a and VPD, while the DB VPD GPP did.

The direct tidal effects on GPP resulted from the combined effects of TWL and salinity. Although the tidal water salinity covaried strongly with the TWL, its effect on the ecosystem photosynthesis was evident, and can be supported by the facts that (1) the plant photosynthetic capacity A_{max} decreased under relatively high salinity conditions when $T_{\rm a}$ and VPD were similar, regardless of phenological stage (Table 2), and (2) the salinity had a stronger interaction with NEE and GPP relative to TWL (Fig. 5). The mechanism of the tidal effects on GPP was as follows. Saline stress, on the one hand, suppressed the activity of carboxylation enzymes in the chloroplasts of P. australis, while on the other hand, affected ion homeostasis and osmotic pressure, leading to downward Na^+ and Cl^- transport between shoot and root and ion accumulation in the shoot tissue, with decreasing K⁺ concentration in the leaves (Pagter et al., 2009). Since salt secretion is absent due to the lack of salt glands in the shoot tissues of P. australis, ion homeostasis can rarely be maintained and osmotic potential adjusted, resulting in limited photosynthetic activity as the level of salinity increased (Li et al., 2018). The influence of TWL was due to soil hypoxia or anoxia (Banach et al., 2009; Kathilankal et al., 2011; Moffett et al., 2010) as well as decreased photosynthetic leaf area (Schedlbauer et al., 2010; Jimenez et al., 2012), which lowered overall plant metabolic activity and diminished stomatal opening, consequently inhibiting photosynthesis. It should be noted that those analyses were based on either

the partitioned daytime GPP or the responses of daytime NEE to PAR, which may also incorporate potential effects of tides on $R_{\rm eco}$ implying that robust partitioning of net CO₂ fluxes into GPP and $R_{\rm eco}$ was essential for understanding the environmental controls on plant photosynthesis, as the tidal effects on GPP and $R_{\rm eco}$ could be different in the magnitude and sensitivity.

We found that tidal inundation generally led to a suppression of Reco, similar to the findings of other studies (Barr et al., 2010; Knox et al., 2018; Li et al., 2014). Figs. 8, S2, S5, and S7 clearly show a reduced R_{eco} under tidal inundation at the diel scale during the peak vegetative and flowering and ripening stages. The tidal influence on $R_{\rm eco}$ can be mainly attributed to the synthetic effects of tidal water coverage and salinity (direct effect) and the temperature changes caused by flooding (indirect effect). Because the T_a under inundation was generally higher than that under non-flooded conditions, the reduction in Reco was largely attributed to the influence of higher TWLs, since T_a had an effect opposite that of TWL, a theory that was further confirmed by the near-synchronous relationship between NEE and TWL at the multi-day scale (Fig. 5). This was supported by the fact that tidal water coverage prevented gas diffusion and the flux of trapped CO₂ from the soil (Guo et al., 2009; Han et al., 2015). It is therefore reasonable to argue that tidal submergence suppressed the sensitivity of $R_{\rm eco}$ to temperature.

Inconsistent with the discussion above, however, the derived temperature sensitivities (E_0) of the NB R_{eco} under tidal inundation were higher than those under non-inundation conditions (Table 3 and Fig. S6), similar to the findings of Knox et al. (2018). This is likely due to the fact that the lateral transports of carbon fluxes, namely dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), and particulate organic carbon (POC), formed non-negligible uncertainties in the flux measurements by the EC technique (Gao et al., 2020; Wang et al., 2016; Yan et al., 2008). If the CO₂ in tidal water is greater (less) than atmospheric CO₂, then the fluxes will dissolve in (be released from) the tidal water, leading to an extra carbon source/sink that interferes with the EC measurements. Moreover, there were some inconsistences between the R_{eco} estimates in Table 1 and the DB VPD R_{eco} (Figs. S4 and S5), which were likely due to the fact that the former did not consider the

Table 3

Comparison of parameters rb and E_0 for Eq. (S1) and R^2 fitted to half-hourly nighttime data of NEE and T_a , and the average, minimum, and maximum of T_a with and without tidal inundation during the early vegetative, peak vegetative, and flowering and ripening stages at the study site.

Period	Tidal inundation	rb	E_0	R^2	The mean, min, and max of $T_{\rm a}$ (°C)
Early vegetative	No	3.9 (3.7, 4.1)	87.8 (34.0, 141.6)	0.009	16.0, 7.6, 23.3
	Yes	4.1 (3.6, 4.6)	10.4 (-94.9, 115.8)	0.0002	17.5, 7.3, 24.8
Peak vegetative	No	2.0 (1.8, 2.1)	205 (173, 237)	0.17*	24.3, 17.7, 29.3
	Yes	1.8 (1.5, 2.1)	252 (182, 321)	0.16*	25.0, 18.2, 29.3
Flowering and ripening	No	1.1 (1.0, 1.2)	397 (367, 426)	0.35*	22.8, 13.1, 29.0
	Yes	0.7 (0.6, 0.9)	556 (473, 640)	0.41*	24.3, 14.7, 29.0

Note: *, p < 0.005.



Fig. 8. Averaged diel variations of NEE (blue), the DB VPD R_{eco} (red), the DB VPD GPP (blue), T_a (red), PAR (blue), and VPD (red) during tidal (darker lines) and non-tidal (lighter lines) inundation periods under (a–c) offshore (180–360°) and (d–f) onshore (0–180°) wind conditions during the peak vegetative stage. The error bars represent standard errors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4

Comparison of parameters A_{max} and α for Eq. (S2) and R^2 fitted to half-hourly daytime data of NEE and PAR during tidal and non-tidal inundation periods under offshore (180–360°) and onshore (0–180°) wind conditions during the peak vegetative stage at the study site.

Wind direction	Tidal inundation	A _{max}	α	R _{eco}	R^2
Offshore	No	64.9	0.06	4.18	0.86*
	Yes	75.0	0.05	3.99	0.73*
Onshore	No	63.4	0.06	4.05	0.85*
	Yes	69.1	0.06	4.12	0.70*

Note: *, *p* < 0.005.

effects of $T_{\rm a}$ and VPD on the flux partitioning, whereas the latter did. This implies that in the future, the tidal effect must be included in the flux partitioning algorithm for tidal wetlands.

It is interesting that the daytime NEE was enhanced under tidal inundation when T_a was roughly between 28 and 32°C and PAR was > 1200 µmol m⁻² s⁻¹ during the peak vegetative stage (Fig. 6). As discussed above, both the NB and DB VPD GPP values decreased during the day in the same range as that of PAR and T_a under tidal flooding (Figs. 7 and S1), indicating that the increased net uptake of CO₂ during the peak vegetative stage could be attributed to the fact that both GPP and R_{eco} decreased, with R_{eco} decreasing to a greater extent. During the early vegetative stage, however, the opposite was true (Figs. 6, 7 and S1), reflecting the differing amounts of tidal influence on GPP and R_{eco} affected by phenological stage. Therefore, NEE responded positively or negatively to tidal flooding, depending on the magnitude of tidal suppression on GPP and R_{eco} . This finding has rarely been reported in previous research (Forbrich and Giblin, 2015; Kathilankal et al., 2008;

Knox et al., 2018; Li et al., 2014; Moffett et al., 2010).

5. Conclusions

In this study, we investigated the tidal influence on ecosystem CO_2 exchange in a *P. australis* salt marsh of an intertidal shoal in the Changjiang estuary, based on EC measurements made during 2018. The salt marsh was found to act as a strong sink for atmospheric CO_2 (NEE = -901 g C m⁻²), indicating that the study area exhibited superior performance in the net uptake of CO_2 among marsh ecosystems. We discovered that, as in most terrestrial ecosystems, PAR exerted a major controlling influence on NEE, followed by T_a and VPD at various time scales. Tides co-controlled with the main meteorological drivers, however, exerting rather strong effects on CO_2 fluxes in the tidal wetland, especially at the multi-day scale.

Regardless of which flux partitioning method was utilized, tidal inundation generally imposed inhibitory effects on GPP, which were directly attributed to TWL and salinity. The DB VPD R_{eco} was also suppressed on average under the tidal inundation condition when T_a was higher relative to the non-inundation condition, reflecting the influence of TWL on R_{eco} and the reduced sensitivity of R_{eco} to T_a . We observed a suppressed NEE under tidal inundation when T_a was roughly between 28 and 32°C and PAR was > 1200 µmol m⁻² s⁻¹ during the early vegetative stage, but an enhanced NEE in the same range as that of PAR and T_a during the peak vegetative stage. The magnitude of tidal suppression on GPP and R_{eco} resulted in the varied responses of NEE to tidal flooding.

This study not only shows the unique impact of tidal wetlands on carbon uptake, but it also represents an example of a coastal wetland in which tidal inundation promotes the net uptake of CO_2 . This

omparison of annual CO ₂ flux exchange amo	ong udal marsh ecosystems across the globe. Un	IT IOT NEE, GPP, 3	and K _{eco} : µmol m	-y				
Wetland type	Location	Latitude	Longitude	Observational period	NEE	GPP	$R_{ m eco}$	Reference
Salt marsh (P. australis)	Jiuduansha, Changjiang Delta, P.R.China	31°12′47″N	121°54'25"E	2018	- 901	1856	955	This study
Brackish marsh (Schoenoplectus and Typha)	San Francisco Bay, USA	38°12′2″N	122°1′35″W	2016	- 225			Knox et al. (2018)
Salt marsh (Spartina patens, Distichlis spicata, S.	Northeastern Massachusetts, USA			2012-2014	-337 to	806-892	546-651	Forbrich and Giblin (2015)
alterniflora)				(May-October)	- 256			
Salt marsh (P. australis, S. alterniflora, S.	Chongming, Changjiang Delta, P.R.China	31°25′-31°38′N	121°50′-122°05′E	2005-2006	-737 to			Yan et al. (2010)
mariqueter)					-518			
Brackish marsh (P. Patens)	Pointe-aux-Chenes Wildlife Management Area (WMA), LA, USA	29°30'N	90°27'W		171			Krauss et al. (2016)
Freshwater marsh (P. australis)	Liaohe Delta, China	41°08'N	121°54W	2005	-65	1257	1192	Zhou et al. (2009)

Table

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investigation provides a more holistic view of how and to what extent tidal dynamics affect CO_2 uptake, leading to a better understanding of the mechanisms and controls of coastal blue carbon, and suggests that tidal effect needs to be incorporated in the algorithm to improve flux partitioning in tidal wetlands, which contributes to the quantification of coastal blue carbon and thus climate change mitigation.

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.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2020.108108.

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