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REGULAR ARTICLE

Inundation depth affects ecosystem CO_2 and CH_4 exchange by changing plant productivity in a freshwater wetland in the Yellow River Estuary

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Abstract

Aims Climate change (extreme rainfall) and water management activities have led to variation in hydrological regimes, especially inundation, which may alter the function and structure of wetlands as well as wetland-atmosphere carbon (C) exchange. However, the degree to which different inundation depths (standing water depth above the soil surface) affect ecosystem CH_4 fluxes, ecosystem respiration (R_{eco}) and net ecosystem CO_2 exchange (NEE) remains uncertain in wetland ecosystems.

Methods We conducted a field inundation depth manipulation experiment (no inundation, i.e. only natural precipitation; 0, water-saturated; 5, 10, 20, 30 and 40 cm inundation depth) in a freshwater wetland of the Yellow River Delta, China. The CH_4 fluxes, R_{eco} and NEE were measured with a static chamber technique during the growing seasons (May–October) of 2018 and 2019.

Results Inundation depth significantly increased plant shoot density, above-water level leaf area index (WLAI), above-water level plant shoot height (WHeight), aboveground and belowground biomass of

Highlights

1. Variations in ecosystem CH_4 and CO_2 exchange at different inundation depths are addressed
2. Inundation depth increased the reed density, height, leaf area index and biomass
3. Ecosystem CH_4 and CO_2 exchange exhibited parabolic responses to inundation depth
4. Plant traits correlated with ecosystem C exchange under different inundation depths
5. Inundation decreased the global warming potential during the growing season

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the dominant grass *Phragmites australis* in both years. Meanwhile, inundation depth increased the CH_4 fluxes, R_{eco} (except for 0 cm) and NEE compared to no inundation, which could be attributed partly to the increased plant productivity (shoot density, WLAI, WHeight, biomass). Additionally, the CH_4 fluxes, R_{eco} or NEE exhibited parabolic responses to inundation depth. Furthermore, global warming potential (GWP) was significantly decreased under different inundation depths during the growing season, especially from 5 to 40 cm inundation depth in 2019. NEE was the largest contributor to the seasonal GWP, which indicates that the inundated wetlands are a net sink of C and have a cooling climate effect in the Yellow River Delta.

Conclusions Inundation depth substantially affects the magnitude of CH_4 fluxes, R_{eco} and NEE, which were correlated with altered plant traits in wetland ecosystems. Inundation depth could mitigate greenhouse gas emissions in the *P. australis* wetlands during the growing season. Inundation depth-induced ecosystem C exchange should be considered when estimating C sequestration capacity of wetlands due to climate change and water management activities, which will assist to accurately predict the impact of hydrological regimes on C cycles in future climate change scenarios.

Keywords Inundation depth · Plant productivity · Net ecosystem CO_2 exchange · Ecosystem respiration · Ecosystem CH_4 fluxes

Introduction

Wetlands occupy only 5–8% of the Earth′s total land surface (Mitsch and Gosselink 2007), but are widely recognized as high-carbon (C) ecosystems in the biosphere, because wetlands hold 20–30% of the estimated 1500 Pg of the global soil C pool (Nahlik and Fennessy 2016). Therefore, wetlands play an important role in regulating the C cycle at a global scale (Xiao et al. 2019). The hydrological regime is a key process in wetland ecosystems, which not only affects the structure and function of wetland ecosystems but also controls the C sink and source of wetlands (Webb and Leake 2006; Jimenez et al. 2012; Rasmussen et al. 2018). Hydrological regimes have been altered by global climate change in terrestrial ecosystems during recent years, resulting in increases in intensity and frequency of extreme rainfall, thereby increasing the risk of prolonged inundation (IPCC 2013; Trenberth 2011; Westra et al. 2014). These alterations in hydrology (e.g. inundation) increase the likelihood of changes in wetland ecosystem structure and function, affecting ecosystem C exchange (e.g. carbon dioxide (CO_2) and methane (CH_4); Han et al. 2015; Sánchez-Rodríguez et al. 2019). Thus, it is important to understand how the wetland-atmosphere C exchange responds to changes in hydrological conditions, such as inundation, which may potentially pose a large feedback to ongoing climate change (Han et al. 2015; Zhao et al. 2019).

Inundation creates anaerobic conditions in the flooded soil that exert a physiological stress on wetland plants depending on the inundation-tolerance of a species (Liu et al. 2018; Zhao et al. 2018). For less inundation-tolerant plants, this stress limits photosynthetic leaf area due to partial submergence of shoots and leaves (Schedlbauer et al. 2010; Jimenez et al. 2012). At the same time, the diffusion rate of CO_2 in water is slower than in air (Matsuda et al. 2017), which results in reduced leaf photosynthesis due to slow uptake of CO_2 into leaves. In addition, the photosynthesis of submerged leaves can be limited mainly through hindering the light transmission, especially when the above surface water is deep and/or turbid (Han et al. 2015). Moreover, inundation causes an oxygen deficiency to roots and disrupts the connection with the atmosphere (Garssen et al. 2015). Consequently, anoxic conditions inhibit root respiration and plant photosynthesis, which has a negative impact on plant growth (Sairam et al. 2008). In addition to ecosystem CO_2 uptake, inundation may also reduce ecosystem respiration. On the one hand, inundation results in partial plant stomatal closure and transpiration cessation below the water surface and restrains plant respiration (Han et al. 2015; Zhao et al. 2019) and microbial respiration, attributed to lowered diffusion of oxygen, limited aerobic microbial activity,

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C mineralization and decomposition rates (Jimenez et al. 2012; McNicol and Silver 2014). On the other hand, due to the slow diffusion rate of CO_2 in water, the diffusive boundary layer resistance could limit rates of CO_2 emission through the water surface (Han et al. 2015). Therefore, the effect of hydrological regimes on CO_2 uptake and emission are unequal, which can result in remarkable alterations in ecosystem C balance.

Wetlands often act as a net source of CH_4, especially wetland ecosystems that are inundated to a high degree, which is strongly related to the higher activity of methanogenic bacteria, lower oxidation rates and transport of CH_4 from the anaerobic zone to the atmosphere (Cheng et al. 2007; Koelbener et al. 2010; Bridgham et al. 2013). On the one hand, inundation could promote inundationtolerant plant growth, such as *Phragmites australis* and *Typha domingensis*, which provide organic substrates for methanogens by biomass decomposition and root exudation, consequently enhancing CH_4 emissions in a flooded, anaerobic environment (Cheng et al. 2007; Koelbener et al. 2010; Yang et al. 2013). Moreover, these vascular plants can transport CH_4 from the root zone to the atmosphere through dead culms, thereby bypassing the oxidizing layers and enhancing CH_4 emissions. On the other hand, aerenchyma of vascular plants can transport O_2 to the rhizosphere and promote the oxidation of CH_4 in a micro-aerobic environment under inundated conditions (Henneberg et al. 2012; Bridgham et al. 2013).

However, there are only a few studies on the effects of inundation on ecosystem CO_2 and CH_4 exchange in different types of wetlands, and the outcomes from these studies are conflicting. For example, inundation weakened the ecosystem CO_2 sink and ecosystem respiration strength in a Florida Everglades marsh with a short-hydroperiod (Schedlbauer et al. 2010; Zhao et al. 2019) and in a supratidal wetland of the Yellow River Delta (Han et al. 2015). On the contrary, inundation increased ecosystem CO_2 sink, respiration and CH_4 fluxes with increasing vegetation biomass in a temperate fen after inundation (Minke et al. 2016). Although many studies have focused on the effects of hydrological conditions (especially groundwater table) on ecosystem CO_2 and CH_4 exchange in different wetlands (Jungkunst and Fiedler 2007; Olefeldt et al. 2017; Ratcliffe et al. 2019; Wang et al. 2017; Yang et al. 2014), less effort has been conducted to understand the effect of inundation intensity and especially different inundation depths. This suggests that more investigations are required to elucidate the regulatory mechanisms governing the influence of inundation depths on ecosystem CO_2 and CH_4 exchange in wetland ecosystems.

The Yellow River Delta is one of the most active regions of land-ocean interaction among the many river deltas in the world. The interaction of groundwater, precipitation and seawater intrusion has produced a variety of wetland types, plant communities, and ecological functions under different hydrological conditions (Han et al. 2015). During the rainy season, different inundation depths are observed, which depend on the intensity of precipitation. In recent years, the frequency and intensity of extreme rainfall have increased (Han et al. 2018), which indicates that the inundation frequency of wetlands is also increasing. Furthermore, the Chinese government has used freshwater from the Yellow River to restore the degraded wetlands in the Yellow River Delta wetlands in the past 20 years (Yang et al. 2017), which also caused more wetland soils to be inundated. These changes in inundation depth caused by extreme rainfall and water management activities may modify wetland-atmosphere CO_2 and CH_4 exchange. Therefore, we conducted a field inundation depth manipulation experiment in a freshwater wetland in the Yellow River Estuary during the growing season in 2018 and 2019. Our objectives were (1) to understand how changes in inundation depth affects plant traits and (2) to illustrate how ecosystem CO_2 and CH_4 exchange respond to changes in inundation depth.

Materials and methods

Site description

This study was carried out in the Yellow River Delta Ecological Research Station of Coastal Wetland (37°45′ 50” N, 118°59′24″ E, elevation: ~2.5 m above sea level), Chinese Academy of Sciences, which is located in Kenli County, Shandong Province, China. The site is located in supratidal wetlands of the Yellow River Delta. It has a warm-temperate and continental monsoon climate. The mean annual temperature is 12.9 °C. Annual precipitation averages 550–640 mm, ~74% of which occurs from June to September. After extreme rainfall, the wetlands are often inundated to different water levels, which will last for nearly 1–2 months. During the extreme rainfall-driven inundation, the

cumulative rainfall reached nearly 230 and 300 mm in 2018 and 2019, respectively (the weather data comes from the research station). The hydrology of the site is affected by the interactions of groundwater, precipitation and seawater. Meanwhile, the hydrology of the region is influenced by the use of freshwater from the Yellow River (Yang et al. 2017) to restore degraded wetlands in the Yellow River Delta National Nature Reserve. The groundwater table is shallow with an average depth of 1.14 m. The soil type gradually varies from fluvo-aquic to saline soil, and soil texture is mainly sandy clay loam with 6.54 g kg^{-1} soil organic matter content at 0–20 cm depth. The vegetation is relatively homogeneous and strongly dominated by common reed (*Phragmites australis*) with other associated species including *Suaeda salsa*, *Tamarix chinensis*, *Imperata cylindrica*, and *Tripolium vulgare*.

Experimental design

The experiment consisted of seven soil surface inundation depths, including control (no inundation, only natural precipitation, CK), 0 (water-saturated), 5, 10, 20, 30 and 40 cm inundation depth, respectively. Each treatment was replicated four times, and each replicate plot (2 m length × 2 m width × 0.5 m height) was separated by cement barriers at a 40 cm distance. Soil and vegetation were rarely damaged during installation of the cement barriers. There was an opaque plastic water tank (80 cm diameter and 120 cm long) at the position of 1.5 m above the ground connected to each plot with tubes. The float ball, installed at the end of the tube, controlled the water level in each plot. When the water levels fell, the valve body would sink down and the water would flow into the plot. The water could not be stopped until the water level reached the fixed inundation depth (Fig. S1). The water came from a small lake (below 1 mS cm^{-1}) near the experimental site (originally from the Yellow River which runs into the Bohai Sea) and a pump was used to pump the water into the tank after filtration to prevent the inflow of large particles and algae into the tank and tubes. There was a small hole in the wall of each plot, which was used to drain the excess water out of the plot after rain. The inundation treatments were applied from April to October of each year starting in 2017 and the vegetation of each plot was dominated by *P. australis*.

Measurements of ecosystem CO_2 and CH_4 exchange

The ecosystem C exchanges including net ecosystem CO_2 exchange (NEE), ecosystem respiration (R_{eco}) and CH_4 fluxes were all measured with an LGR Ultraportable Greenhouse Gas Analyzer (UGGA, Los Gatos Research, Inc., San Jose, USA) that measures gas concentrations continuously and automatically. The LGR analyzer was attached to transparent (NEE, CH_4 flux) and opaque (R_{eco}) cylindrical chambers (Plexiglas), which were put over patches covered by *P. australis* inside each plot. The static chambers consisted of transparent acrylic plastic with three parts: a base frame (30 cm in diameter, 10, 10, 15, 20, 30, 40, 50 cm in height for the seven treatments, respectively), a removable middle box (30 cm in diameter, 100 cm in height) and a removable top box (30 cm in diameter, 100 cm in height). The base frames were installed into the soil to 5 cm depth, with 5 cm of the frame emerging above the water surface (Wei et al. 2020), in the center of each plot in May 2018. The removable middle box was only used when the height of the vegetation was higher than 100 cm. The removable middle or top box was carefully placed on the top of the base frame and sealed with a sealing strip at the joints in order to maintain the chamber sealed during the measurement. Two battery driven fans (8 cm in diameter, 12 V) were installed inside the top of each chamber to generate turbulence inside the chamber during sampling. The gas fluxes (NEE, R_{eco}, CH_4 flux) were measured once a month in 2018, twice a month in 2019 (from 8:00 a.m. to 11:00 a.m.) during the growing season (from May to October). For each measurement, chambers were sealed for 3 min, and CO_2 and CH_4 fluxes were measured.

Measurements of shoot density, WLAI, WHeight, biomass

During the growing season, above-water level leaf area index (WLAI) of *P. australis* was measured using an ACCUPAR LP-80 ceptometer (METER Group, Pullman, WA, USA). Because the LAI is dependent on the spatial and illumination characteristics of the scanned location, four scans were made for each plot in the four cardinal directions. Consequently, the average of the four measurements was considered as the WLAI value for each plot. In addition, we measured the *P. australis* density and above-water level height (WHeight) per m^2 in the plots when measuring the ecosystem CH_4 fluxes,

R_{eco}, and NEE. The biotic factors were measured once a month in 2018 and twice a month in 2019. Before biomass harvest, the water in each plot was removed. Aboveground biomass (AGB) was clipped at the sediment surface from a 0.25 m^2 quadrat in each plot, oven dried at 65 °C for at least 2 days until no weight loss occurred anymore, and weighed. One soil core (10 cm in diameter) of 0–40 cm was excavated in each plot. The root samples from the core were washed by wet sieving under gently flowing water to remove attached soil and debris, then oven dried at 65 °C for 2 days, and weighed to determine the belowground biomass (BGB).

Global warming potential (GWP)

In the estimation of GWP, CO_2 is used as a reference gas. The CH_4 emissions are converted to the equivalent amounts of CO_2 based on the GWP value. The growing season CH_4 emission was converted to CO_2 equivalents by multiplying with a GWP factor of 28 (based on a 100-year time horizon). A positive GWP indicates a release of greenhouse gases (GHGs) to the atmosphere and a potential climate warming effect, while a negative GWP indicates GHG uptake from the atmosphere and a potential climate cooling effect (Tian et al. 2015). We calculated the GWP of the different inundation depths by using the following equation (IPCC 2013):

$$\mathrm{GWP}(CO_2\mathrm{equivalent}) = CO_2 \times 1 + CH_4 \times 28$$

Statistical analysis

In each year, NEE, R_{eco}, CH_4 fluxes, GWP and biotic factors (shoot density, WLAI, WHeight, AGB and BGB) were subjected to one-way ANOVA and significant differences between different inundation depths were examined with the Turkey's multiple range test. Multiple regressions were performed for the relationships between seasonal mean CH_4 fluxes, R_{eco}, NEE and inundation depth or biotic factors under different inundation depths. Two-way analysis of variance (ANOVA) was conducted to analyze the NEE, R_{eco}, CH_4 fluxes, GWP and biotic factors, including inundation depth, years and their interactions. In all tests, a significance level of 0.05 was used. Statistical analyses were conducted using software package SPSS version 13.0 (SPSS Inc., Chicago, IL, USA).

Results

Changes in shoot density, WLAI, WHeight and biomass under different inundation depths

Inundation depth significantly affected all biotic factors (Figs. 1 and 2 Table 1). The reed shoot density gradually increased from early April to late August, and then decreased until the end of growing season in 2018 and 2019 (Fig. S2a and b). Inundation significantly increased plant shoot density compared with the control, but there was no significant difference between the different inundation depths (Fig. 1a and b). The above-water level reed height (WHeight) gradually increased in the early growing season in 2018 and 2019, and then reached a peak in late August. After that, WHeight did not change any more (Fig. S2c and d). Inundation significantly increased WHeight relative to the control ($P < 0.05$,). The highest WHeight was 212.6 cm and 212.2 cm at 10 cm inundation depth and gradually decreased from 20 to 40 cm inundation depth in both years (Fig. 1c and d). The seasonal dynamics of above-water level leaf area index (WLAI) under different inundation depths showed a similar pattern throughout both growing seasons. The WLAI gradually increased in the early growing season, then reached a peak in late July. By August, WLAI decreased in all treatments as a consequence of leaf senescence (Fig. S2e and f). Inundation significantly increased WLAI compared to the control ($P < 0.05$) but no significant changes in WLAI were found from 10 to 40 cm inundation depth. The highest WLAI was 3.79 and 3.94 under 20 cm inundation depth in 2018 and 2019, respectively (Fig. 1e and f). Inundation significantly increased the AGB and BGB compared to the control ($P < 0.05$, Table 1), but had no significant effects from 0 to 40 cm inundation depth in either year (Fig. 2). BGB accounted for 59% and 61% of total biomass in 2018 and 2019, respectively. Overall, nonlinear relationships between WHeight, WLAI, biomass and inundation depth can be observed (Figs. 1 and 2). Additionally, there was no significant difference in shoot density, WHeight, AGB and BGB between the two years

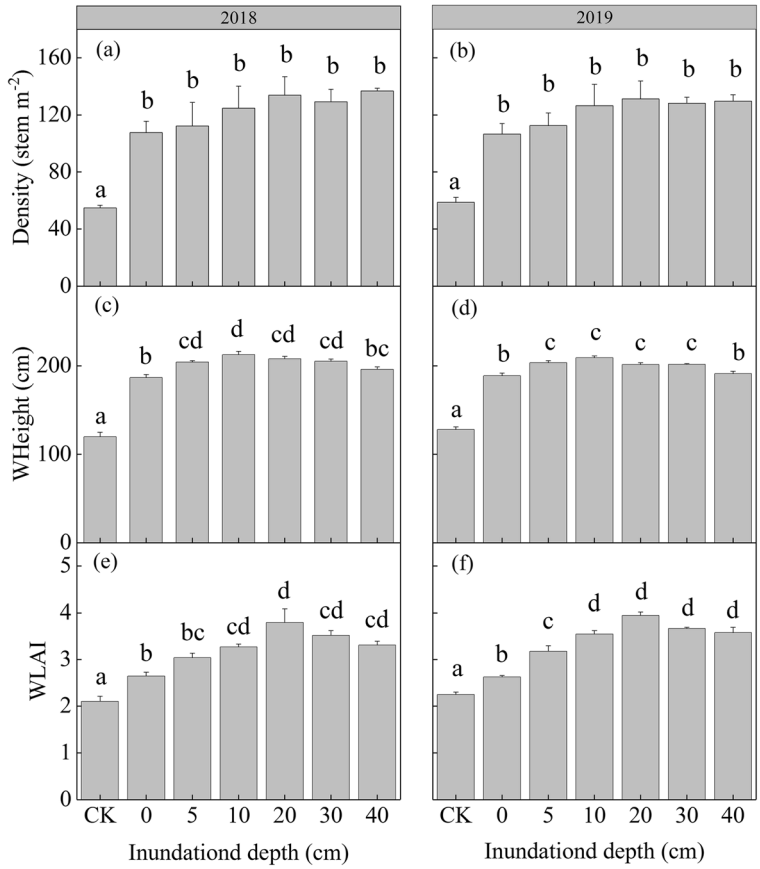

Fig. 1 Variations in (**a**, **b**) plant density, (**c**, **d**) plant height relative to water level (WHeight) and (**e**, **f**) above-water level leaf area index (WLAI) at different inundation depths during the growing season in 2018 and 2019. Data (means ± SE, $n = 4$) followed by different letters indicate significant differences ($P < 0.05$)

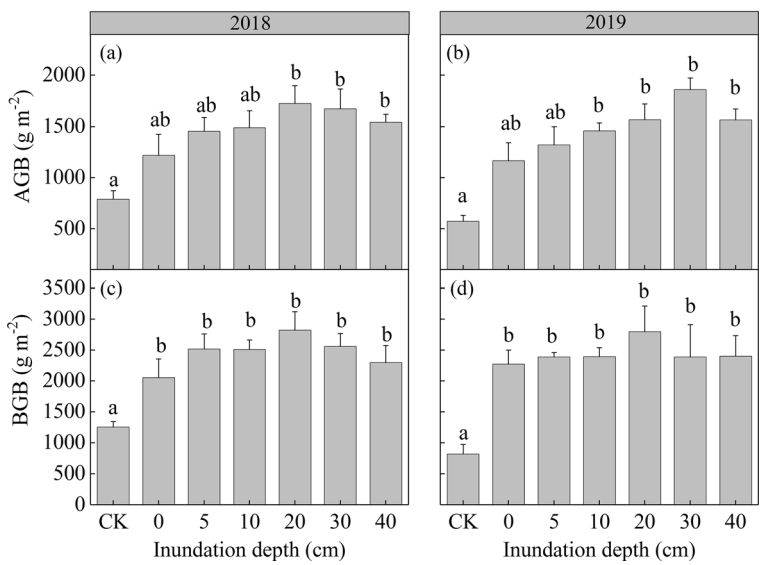

Fig. 2 Variations in (**a**, **b**) aboveground biomass (AGB) and (**c**, **d**) belowground biomass (BGB) at different inundation depths during the growing season in 2018 and 2019. Data (means ± SE, $n = 4$) followed by different letters indicate significant differences ($P < 0.05$)

Table 1 Results (F values) of two-way ANOVA on the effects of Inundation depth (ID), year (Y) and their interactions on plant shoot density, above-water level leaf area index (WLAI), plant height relative to water level (WHeight), aboveground biomass (AGB) and belowground biomass (BGB), ecosystem CH_4 fluxes (CH_4), ecosystem respiration (R_{eco}), net ecosystem CO_2 exchange (NEE) and Global warming potential (GWP)

Effect	Density	WLAI	WHeight	AGB	BGB	CH_4	R_{eco}	NEE	GWP
ID	15.12***	54.38***	213.84***	9.36***	7.18***	26.32***	28.82***	39.26***	9.88***
Y	0.02	6.97*	0.65	0.65	0.27	147.36***	61.68***	388.48***	382.8***
ID × Y	0.06	0.36	1.50	0.21	0.24	4.91**	0.74	9.55**	11.61***

and no significant interactive effect between inundation depth and year (Table 1).

Effects of inundation depth on ecosystem CO_2 and CH_4 exchange

The CH_4 fluxes, R_{eco} and NEE showed distinct seasonal patterns under different inundation depths during the growing season in 2018 and 2019 (Fig. S3). Ecosystem CH_4 fluxes gradually increased during the early growing season, and then reached a peak in August and rapidly declined thereafter (Fig. S3a and b). With the *P. australis* canopy fully developed, R_{eco} and NEE reached a peak in late July in both years under the different inundation depths. From August to October, the R_{eco} and NEE rapidly decreased with the decrease of solar radiation, temperature and WLAI (Fig. S3c–f).

Inundation depth significantly affected the magnitudes of CH_4 fluxes, R_{eco} and NEE in 2018 and 2019 (Fig. 3). The CH_4 fluxes, R_{eco} and NEE exhibited a parabolic curve against the inundation depth (Fig. 4). Compared to the control, inundation significantly increased CH_4 fluxes ($P < 0.05$), but affected CH_4 fluxes from 10 to 40 cm inundation depth to a minor degree (Fig. 3a and b). Inundation significantly increased R_{eco} in both years relative to the control ($P < 0.05$), except for 0 cm inundation depth, while only minor differences in R_{eco} were found from 5 to 40 cm inundation depth in 2018, and among 5, 20, 30 and 40 cm inundation depth in 2019 (Fig. 3c and d). Inundation significantly increased NEE during the growing season in both years ($P < 0.05$). However, inundation depth had little effect on NEE among 5, 10 and 20 cm inundation depth in 2018, and among 5, 10, 20, 30 and 40 cm inundation depth in 2019 (Fig. 3e and f). In addition, the CH_4 fluxes in 2018 were higher than those in 2019, whereas R_{eco} and NEE in 2018 were lower than those in 2019 ($P < 0.001$; Table 1). The inundation depth of 40 cm had the highest, albeit still negative, GWP and the inundation depth of 5 cm resulted in the lowest GWP (closely followed by 10 cm) during the growing season in 2018, while there was little difference in GWP among the other inundation depths (Fig. 5a). During the growing season in 2019, inundation significantly decreased GWP compared to the control. However, only minor differences in GWP were found from 5 to 40 cm inundation depths, which overall decreased with increasing inundation depth (Fig. 5b). Our study also showed that NEE was the largest contributor to total seasonal GWP during the growing season in the Yellow River Delta (Table S1). In addition, the GWP in 2018 was much lower than that in 2019 (Fig. 5).

Relationships between ecosystem CO_2 and CH_4 exchange and WLAI, WHeight, and biomass

NEE was negatively, and R_{eco} was positively correlated with the WLAI under different inundation depths during the growing season in 2018 and 2019 ($P < 0.05$), whereas there was no significant relationship between CH_4 fluxes and WLAI (Fig. 6). Additionally, CH_4 fluxes, R_{eco} and NEE were significantly related to WHeight during the growing season in both years (Fig. 7). CH_4 fluxes and R_{eco} showed a weak, but significant, positive correlation with AGB in both years (Fig. 8a–g), while BGB was only positively correlated with CH_4 fluxes in 2018 (Fig. 8b). NEE had a weak, but significant, negative correlation with AGB, but only in 2018 (Fig. 8k).

Discussion

Effects of inundation depth on plant growth

Inundation regime is regarded an important hydrological factor affecting plant species diversity and

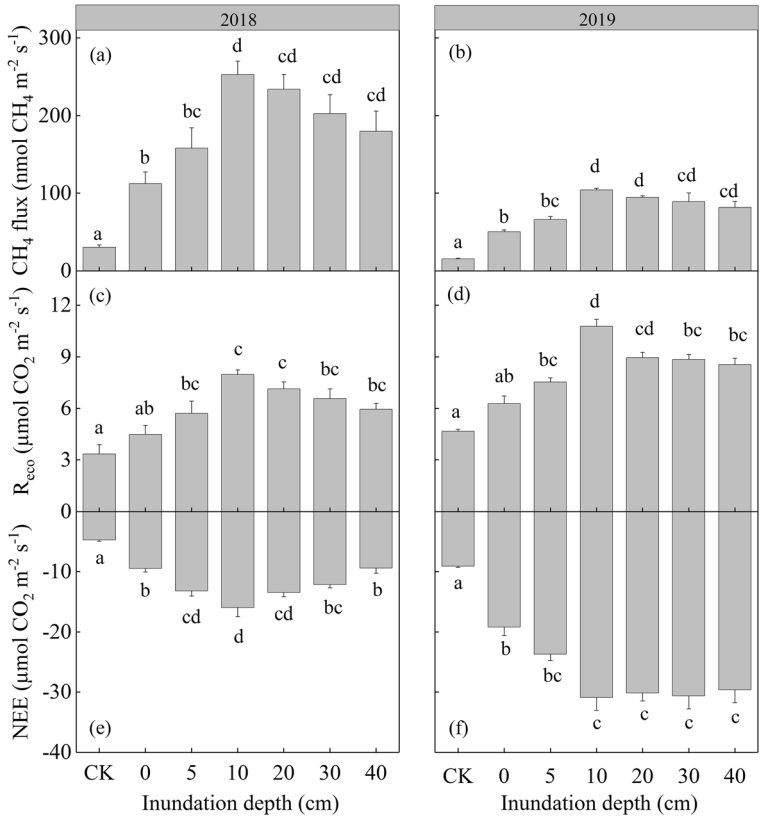

Fig. 3 Variations in (**a**, **b**) CH_4 fluxes, (**c**, **d**) ecosystem respiration (R_{eco}) and (**e**, **f**) net ecosystem CO_2 exchange (NEE) at different inundation depths during the growing season in 2018 and 2019 (means ± SE, n = 4). Different letters indicate significant differences between inundation depths ($P < 0.05$)

productivity in wetland ecosystems (Schile et al. 2011; Liu et al. 2018). In order to avoid the adverse effects of inundation, inundation-tolerant plants, such as *P. australis*, elongate their shoots to escape from submergence and restore leaf contact with the atmosphere (Striker et al. 2012; Voesenek et al. 2006). In the present study, inundation significantly increased WHeight of *P. australis* (Fig. 1), which indicated an escape strategy to cope with inundation. Meanwhile, inundation significantly increased shoot density, WLAI and biomass production (Figs. 1 and 2), suggesting that more energy and carbohydrates produced by photosynthesis will supplement the growth for plants to tolerate deep and long-lasting inundation (Chen et al. 2019). Additionally, BGB plays an important role in the accumulation of organic carbon in wetland ecosystems (Tripathee and Schäfer 2015). About 59 and 61% of the biomass of *P. australis* was allocated below ground under the different inundation depth. This suggests that a large part of the soil organic C may derive from roots, which will benefit long-term carbon sequestration under anaerobic conditions. Although many wetland plants can tolerate inundation, a situation in which inundation exceeds plant tolerance is not beneficial to plant growth (Xue et al. 2018). For example, plant biomass of *Bolboschoenus planiculmis* was inhibited when inundation exceeded 10 cm inundation depth (An et al. 2018). Also, more than 91 cm inundation depth significantly decreased the leaf, belowground and total biomass of *Typha domingensis* (Chen et al. 2010). However, inundation depth had little effect on biomass in either of the investigated years (Fig. 2), which indicated that *P. australis* is tolerant to a broad range of inundation conditions.

Effects of inundation depth on ecosystem CH_4 fluxes

An increase in inundation depth significantly increased ecosystem CH_4 fluxes compared to the control during the growing season in 2018 and 2019 (Fig. 3a and b). For the soil CH_4 fluxes (Fig. S4b), inundation depth (0 cm) significantly increased soil CH_4 fluxes compared to the control due to anaerobic conditions which usually enhance CH_4 production by improving anaerobic decomposition by methanogenic bacteria and limiting CH_4 oxidation in reductive conditions (Kettunen et al.

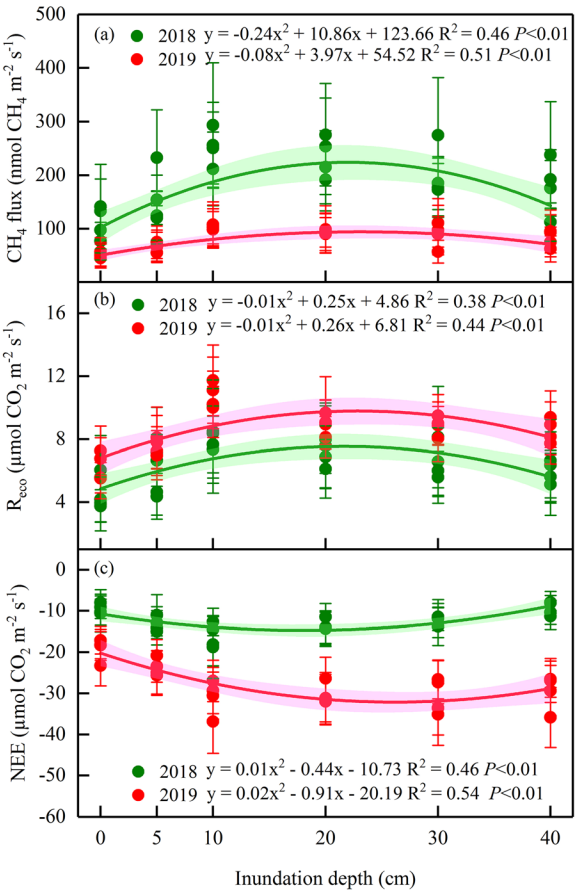

Fig. 4 Relationships between (**a**) CH_4 fluxes, (**b**) ecosystem respiration (R_{eco}) or (**c**) net ecosystem CO_2 exchange (NEE) and inundation depths in 2018 and 2019

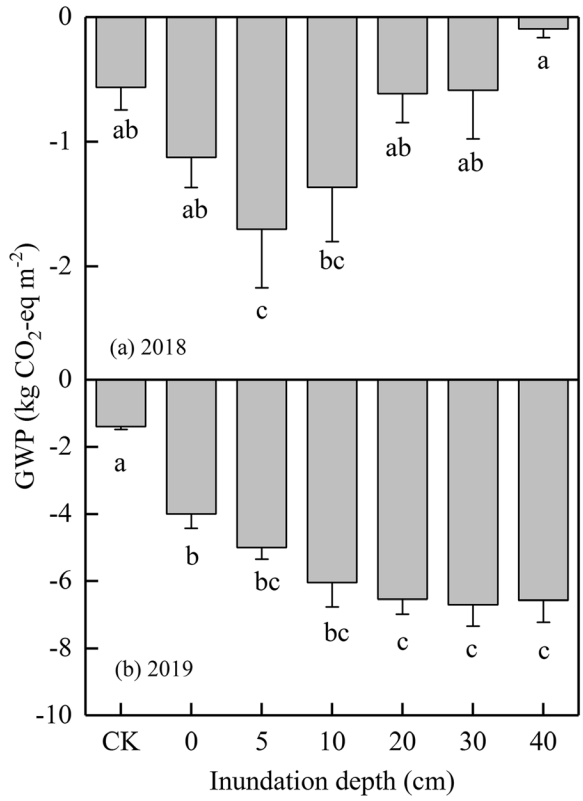

Fig. 5 Variations in global warming potential (GWP) under different inundation depths during the growing season in (**a**) 2018 and (**b**) 2019 (means ± SE, $n = 4$). Different letters indicate significant differences between inundation depths ($P < 0.05$)

1999). Other studies showed that inundation could have little effect on CH_4 fluxes as the water column can provide a diffusion barrier to the release of CH_4 from the soil or water (Cheng et al. 2007; Li et al. 2018; Wei et al. 2020). Moreover, growth of wetland plants (e.g. *P. australis*) affects soil redox conditions, resulting in increased CH_4 oxidation surrounding the rhizosphere due to enhanced turnover of root material and oxygen release (Colmer 2003; Chen et al. 2013). The aboveground and below-ground biomass at 5 cm to 40 cm inundation depths were larger than in the control (Fig. 2), which is likely to have resulted in more oxygen exudation to the surrounding rhizosphere. Thus, the more CH_4 was oxidized, the less soil CH_4 emissions under 5 to 40 cm inundation depths. Additionally, a small part of soil CH_4 could have been oxidized when passing through the water column (Boon and Lee 1997; Peacock et al. 2017). Thus, inundation depths from 5 to 40 cm probably limited soil CH_4 fluxes. Our study showed that ecosystem CH_4 fluxes were much higher than soil CH_4 fluxes in our experiment (Fig. 3 and S4), which indicate that soil CH_4 fluxes contribute little to ecosystem CH_4 fluxes. Although inundation depth limited soil CH_4 fluxes, inundation depth increased the ecosystem CH_4 fluxes compared to the control, which may partly be due to the increased shoot density, WHeight, and biomass (Fig. 1a-d, Fig. 7a and b, Fig. 8a-c).

Increased vascular plant height, shoot density and biomass would increase CH_4 emissions due to higher plant productivity (Fischer et al. 2010; Jeffrey et al. 2019). Previous studies have demonstrated that plant productivity is a good predictor of CH_4 fluxes across a wide range of wetlands (Chen et al. 2009; Fischer et al. 2010; Mozdzer and Megonigal 2013; Sun et al. 2018; Li et al. 2019). In our plots, the vegetation is relatively homogeneous and mostly dominated by *Phragmites*

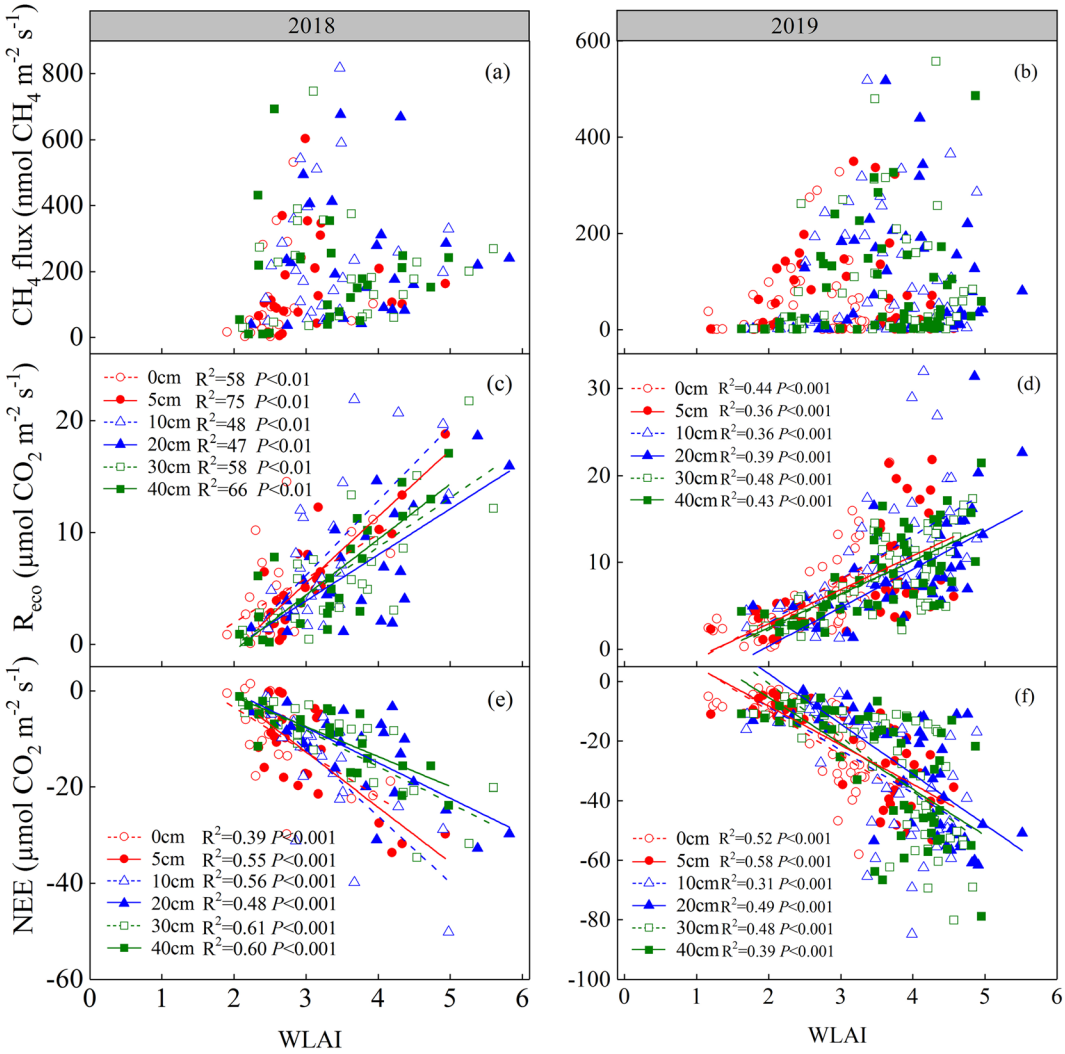

Fig. 6 Relationships between (**a**, **b**) CH_4 fluxes, (**c**, **d**) ecosystem respiration (R_{eco}) and (**e**, **f**) net ecosystem CO_2 exchange (NEE) in response to above-water level leaf area index (WLAI) under different inundation depths during the growing season in 2018 and 2019

australis, an inundation-tolerant vascular plant. Also, a significant linear relationship was found between CH_4 fluxes and WHeight or biomass (Fig. 7a and b, Fig. 8a-c). On the one hand, higher plant productivity could capture more atmospheric CO_2 and increase the production of C substrates available for methanogenesis and can thus lead to higher CH_4 production (Li et al. 2019; Cheng et al. 2007; Koelbener et al. 2010). On the other hand, the more plant biomass is produced under inundated conditions, the more aerenchyma conduits are present, suggesting that more CH_4 could bypass from the anaerobic zone to the atmosphere (Henneberg et al. 2012; Bridgham et al. 2013). This is consistent with studies in other wetlands (Chen et al. 2009; Fischer et al. 2010; Mozdzer and Megonigal 2013; Minke et al. 2016), which indicated that vascular plants play an important role in CH_4 emissions in wetland ecosystems when water levels are above the soil surface in coastal wetlands (Bridgham et al. 2013). However, there was no significant difference in CH_4 fluxes from 10 to 40 cm inundation depth (Fig. 3a and b), which was probably because inundation depth from 10 to 40 cm had no effect on shoot density and biomass (Figs. 1a and b, and 2). We also found that CH_4 fluxes in 2018 were higher than

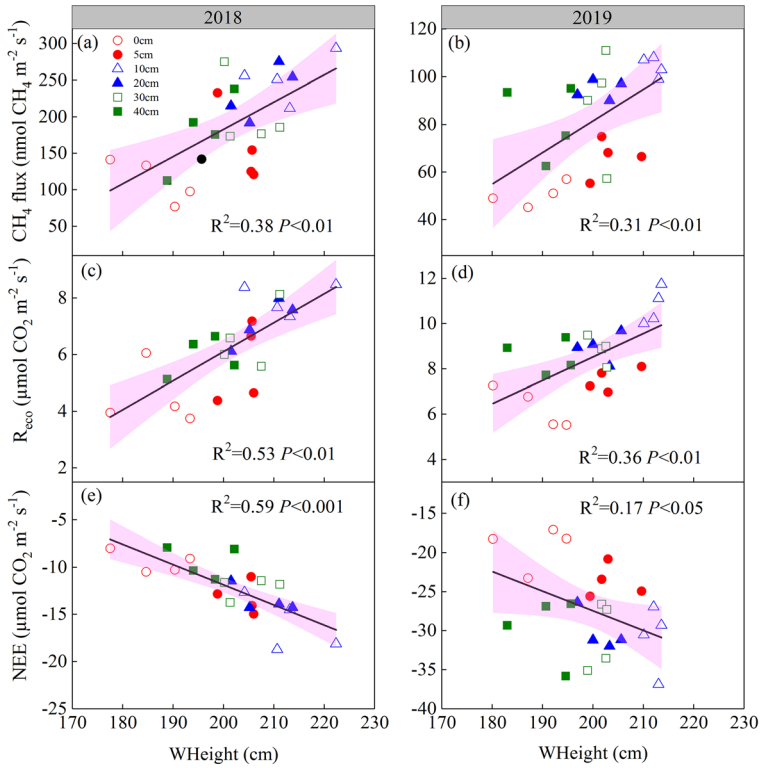

Fig. 7 Relationships between (**a**, **b**) CH_4 fluxes, (**c**, **d**) ecosystem respiration (R_{eco}) and (**e**, **f**) net ecosystem CO_2 exchange (NEE) in response to plant height relative to water level (WHeight) under different inundation depths during the growing season in 2018 and 2019. The black lines are fitted regressions, and the light pink-shaded areas around the regression lines are 95% confidence intervals

those in 2019 ($P < 0.05$, Fig. 3a and b), which was probably related to redox conditions. Under anaerobic conditions, anaerobic oxidation of methane may consume 200 Tg CH_4 per year in global wetland, decreasing the potential CH_4 emissions by over 50% (Segarra et al. 2015). Since wetland plants (e.g. *P. australis*) could transport oxygen to rhizospheres and sediments, their presence will reduce CH_4 concentrations (Jeffrey et al. 2019). Previous studies showed that CH_4 emissions were negatively related to plant biomass, which was often attributed to an increased rhizospheric oxygenation and CH_4 consumption by rhizospheric bacteria (Bhullar et al. 2013; Kao-Kniffin et al. 2010). In our study, the mean BGB in 2019 (2434 g m^{-2}) was higher than in 2018 (2318 g m^{-2}), which means that in 2019 more CH_4 was oxidized to a certain degree. Additionally, the CH_4 fluxes reached a peak in August (Fig. S3a and b), mainly because the density and WHeight reached a peak in August (Fig. S2a-d). Our study also demonstrated a clearly parabolic response of CH_4 fluxes to the gradient of inundation depth (Fig. 4a), which was not observed in previous studies (Chen et al. 2009; Minke et al. 2016). There are several potential mechanisms that could have contributed to this relationship. Firstly, an increase in inundation depth from 0 to 5 cm promoted an increase in CH_4 fluxes during the growing season, which is partly mainly because of increased plant traits with increasing inundation depth. Meanwhile, a significant positive linear correlation between WHeight and CH_4 fluxes was found (Fig. 7a and b), suggesting that the higher the WHeight, the more CH_4 emissions. Secondly, a large part of the CH_4 emissions in *P. australis* occurs close to the ground (Van Der Nat et al. 1998). For example, in a brackish-water tidal marsh of China, the main part of *P. australis* CH_4 emissions is in the base of plant, especially at a height of 0–20 cm above the ground (Tong et al. 2012). In a boreal lake, CH_4 probably escaped through the lower part of *P. australis* (<10 cm above the sediment surface) because the lacunal CH_4 concentrations were highest here (Käki et al. 2001). Inundation depth (20 to 40 cm) could inhibit the path of CH_4 emissions through the submerged plant shoots and cause a decline in CH_4 emissions. Thus, the higher WHeight was accompanied by higher CH_4 fluxes at 10 cm inundation

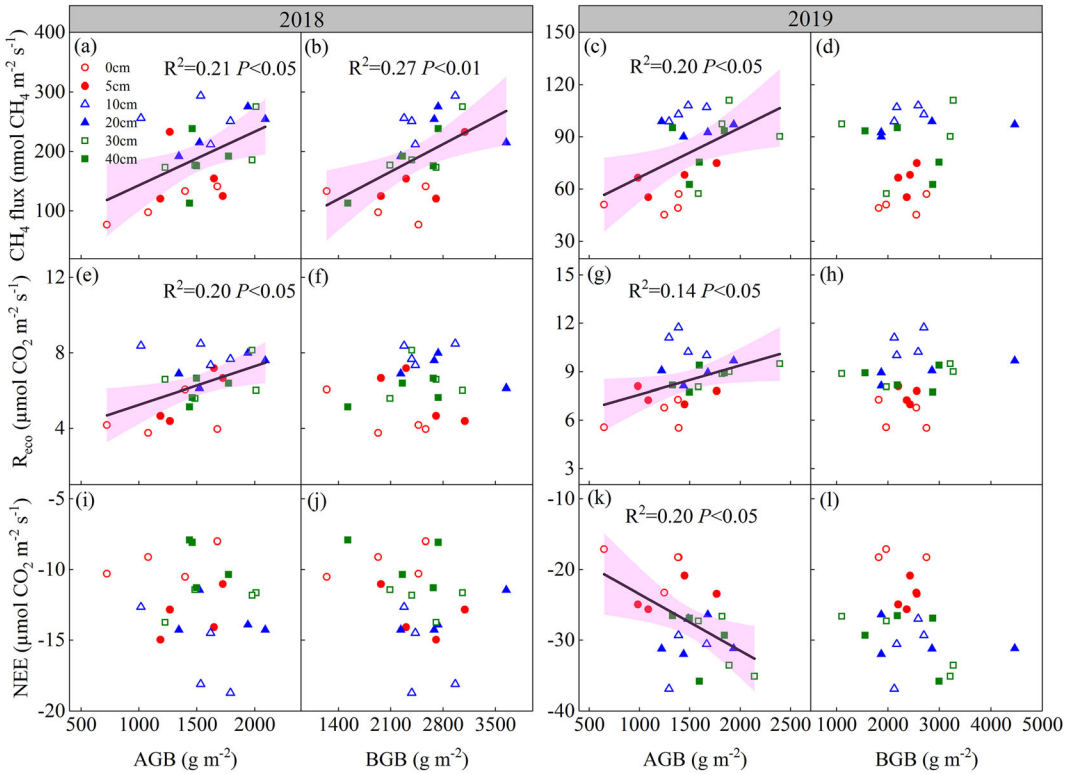

Fig. 8 Relationships between (**a**, **b**, **c**, **d**) CH_4 fluxes, (**e**, **f**, **g**, **h**) ecosystem respiration (R_{eco}) and (**i**, **j**, **k**, **l**) net ecosystem CO_2 exchange (NEE) in response to (**a**, **c**, **e**, **g**, **i**, **k**) aboveground biomass (AGB) and (**b**, **d**, **f**, **h**, **j**, **l**) belowground biomass (BGB) under different inundation depths during the growing season in 2018 and 2019. The black lines are fitted regressions, and the light pink-shaded areas around the regression lines are 95% confidence

depth, but at inundation depths from 20 to 40 cm CH_4 fluxes declined to a certain degree.

Effects of inundation depth on ecosystem CO_2 exchange

During the growing season in 2018 and 2019, the R_{eco} and NEE showed an increase as inundation depth increased compared to the control (Fig. 3c-f), which was correlated with increased WLAI, WHeight and AGB (Figs. 6c-f, 7c-f, 8e–k). The plant parts below water level had little effect on R_{eco} and NEE because the plant respiration and uptake of CO_2 for photosynthesis were limited (Jimenez et al. 2012). Thus, especially plant parts above water level are important for the ecosystem CO_2 exchange in wetland ecosystems. Plant respiration is tightly coupled to C input from the above-water level photosynthesis (Song et al. 2011; Han et al. 2012). The leaf area determines the amount of available photosynthate and the amount of light being intercepted by the vegetation, therefore the increased WLAI could enhance the uptake of CO_2 for photosynthesis on an ecosystem level (Wang et al. 2016; Acosta et al. 2017). Thus, the difference in WLAI caused by inundation depth may have been an important plant-related factor leading to the variation in R_{eco} and NEE (Han et al. 2012; Song et al. 2011). The significant correlations between R_{eco} and NEE and plant traits indicate that biotic factors are important for regulating CO_2 exchange in wetland ecosystems (Han et al. 2014; Minke et al. 2016). For example, in an Amazon floodplain wetland, NEE was increased by 20% under high water (inundated) compared to low water level, which was attributed to the higher living biomass (Morison et al. 2000). In a temperate cutover fen, R_{eco} and NEE significant increased with increasing inundation depth from 0 to 100 cm mainly due to the increased AGB (Minke et al. 2016). Previous studies reported opposite results indicating that inundation decreased R_{eco} and NEE in wetland ecosystems (Han et al. 2015; Zhao et al. 2019). The submerged plant shoots and leaves showed a reduction in the photosynthetic rates and plant respiration (Jimenez et al. 2012). In addition, the reduced R_{eco} under inundation

conditions was mainly due to the saturation of soils, subsequent oxygen limitation, and inhibition of root and soil respiration that led to lower CO_2 emissions (Han et al. 2015). However, the ecosystem CO_2 exchange can vary between different plant species. For example, Zhao et al. (2019) observed a decline in R_{eco} and NEE as inundation depth increased from 0 to 45.6 cm in a freshwater wetland dominated by sawgrass (*Cladium jamaicense* Crantz) and muhly grass (*Muhlenbergia filipes* M.A. Curtis), a weak inundation-tolerant plant. On the contrary, inundation depth (from 0 to 24 cm) enhanced R_{eco} and NEE of *Spartina alterniflora*, a stronger inundation tolerant plant (Jones et al. 2018). Therefore, the effect of inundation depth on different plant species needs to be considered in wetland ecosystems. However, there was no significant differences in R_{eco} were found from 5 to 40 cm inundation depth in 2018, among 5, 20, 30 and 40 cm inundation depth in 2019, no differences in NEE among 5, 10 and 20 cm inundation depth in 2018, and from 5 to 40 cm inundation depth in 2019 (Fig. 3c-f), which mainly due to inundation depth had little effect on plant productivity among 5 to 40 cm inundation depth (Figs. 1 and 2). Additionally, WLAI, as discussed above, plays a very important role in ecosystem CO_2 exchange. Mean WLAI values under different inundation depths in 2018 (3.26) were lower than those in 2019 (3.42) ($P < 0.05$; Table 1), which probably resulted in lower R_{eco} and NEE in 2018 than in 2019 ($P < 0.05$, Fig. 3c and f). We also found the R_{eco} and NEE reached a peak in July (Fig. S3c-f), which was mainly due to the peak of WLAI in July (Fig. S2e-f). R_{eco} and NEE exhibited a parabolic pattern against the inundation depth (Fig. 4b and c) and this nonlinear relationship has not often been reported before (Zhao et al. 2019). The majority of previous studies have only compared situations with and without inundation (Han et al. 2015; Sánchez-Rodríguez et al. 2019), but there were few studies on the effect of different inundation depths on ecosystem CO_2 exchange. In this study, we spanned a large range of inundation depths, to be able to observe a continuous response of R_{eco} and NEE to different inundation depths. We found parabolic relationship responses of R_{eco} and NEE to different inundation depths, which are likely to be induced by nonlinear changes in plant productivity. As mentioned above, the vegetation parts above water level could be important for ecosystem CO_2 exchange under different inundation depths. On the one hand, the higher the WHeight and WLAI, the higher the absorption capacity of light, the higher the uptake of CO_2 for photosynthesis and the higher plant respiration. On the other hand, the deeper the inundation (20, 30 and 40 cm), the more plant shoots and leaves were submerged, which resulted in a partial plant stomatal closure under water and a lower photosynthesis activity of submerged leaves (Schedlbauer et al. 2010; Han et al. 2015). Moreover, due to the slow diffusion rate of CO_2 in water, the diffusive boundary layer resistance could limit CO_2 emission through the water surface (Han et al. 2015). Meanwhile, CO_2 gas can dissolve in water, which suggested that the deeper the inundation, the less CO_2 efflux from water columns (Leopold et al. 2016). As a result, the R_{eco} and NEE decreased with the increase of inundation depth from 20 to 40 cm. Contrary to our results, R_{eco} and NEE linearly decreased with increasing water level from 0 to 45.6 cm in a freshwater wetland where the height of the vegetation was about 73 cm (Zhao et al. 2019). This is probably due to the fact that plant height above water level linearly decreased with the increase in water level.

Additionally, inundation depth decreased the GWP during the growing season compared to the control (Fig. 5), which suggested that relatively shallow inundation depths (5 cm in 2018 and all inundation treatments in 2019) were efficient in mitigating GHG emissions in the studied coastal wetland. The negative GWP under different inundation depths indicated that NEE was the largest contributor to the seasonal GWP, mainly because NEE values were much higher than the sum of CH_4 and R_{eco} (Table S1). Similar results have also been found in a freshwater marshland (Zhang et al. 2013) and restored deltaic wetland (Hemes et al. 2019). We also found that GWP varied greatly between 2018 and 2019, which was consistent with the results in a restored deltaic wetland (Hemes et al. 2019). This variation was due to the fact that the ecosystem C exchange showed significant differences between years. In our experiment, only the GWP of CO_2 and CH_4 fluxes were calculated, N_2O fluxes were not included. Therefore, long-term observations of all three GHGs are essential to evaluate the GWP and to better quantify wetland C sources and sinks.

Limitation of the research and outlook

Inundation depth strongly altered ecosystem CH_4 and CO_2 exchange, which was coincident with affected shoot density, height, leaf area index and biomass of

P. australis. However, the effects of abiotic factors (e.g. soil redox conditions, substrate and dissolved organic carbon) on ecosystem C exchange (especially CH_4 emissions) were not considered in our study. Meanwhile, we did not reinforce the impact of inundation duration and frequency on the C sink-source status. These limitations will increase the uncertainty about the effect of inundation regimes on ecosystem CH_4 and CO_2 exchange in freshwater wetlands in the Yellow River Estuary. Hence, future field and long-term continuous data are required to improve our knowledge on the potential impacts of hydrological regimes (inundation depth, frequency and duration) on C sequestration in wetland ecosystems.

Conclusions

This study demonstrated that ecosystem CH_4 and CO_2 exchange (CH_4 fluxes, R_{eco} and NEE) increased with increasing inundation depth in a freshwater wetland in the Yellow River Estuary, which could partly be due to the increased plant productivity (e.g. shoot density, above-water level leaf area index, plant height relative to water level and biomass) during the growing season. However, there were only minor differences in CH_4 fluxes, R_{eco} or NEE between inundation depths ranging from 10 to 40 cm, especially in 2019. The CH_4 fluxes, R_{eco} or NEE exhibited parabolic responses to inundation depth, which correlated with changing plant traits under different inundation depths. In addition, NEE was the largest contributor to total seasonal global warming potential under different inundation depths during the growing season. To understand the responses of ecosystem CH_4 and CO_2 exchange to inundation depth is important for accurately improving the ecosystem C model and it also helpful to predict the ecosystem carbon sinks or sources under the changing hydrological regimes with respect to climate change.

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