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Climate warming negatively affects plant water-use efficiency in a seasonal hydroperiod wetland

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ABSTRACT

Climate warming has substantial influences on plant water-use efficiency (PWUE), which is defined as the ratio of plant CO_2 uptake to water loss and is central to the cycles of carbon and water in ecosystems. However, it remains uncertain how does climate warming affect PWUE in wetland ecosystems, especially those with seasonally alternating water availability during the growing season. In this study, we used a continuous 10-year (2011-2020) eddy covariance (EC) dataset from a seasonal hydroperiod wetland coupled with a 15-year (2003-2017) satellite-based dataset (called PML-V2) and an in situ warming experiment to examine the climate warming impacts on wetland PWUE. The 10-year EC observational results revealed that rising temperatures had significant negative impacts on the interannual variations in wetland PWUE, and increased transpiration (E_t) rather than changes in gross primary productivity (GPP) dominated these negative impacts. Furthermore, the 15-year satellite-based evidence confirmed that, in the study region, climate warming had significant negative consequences for the interannual variations in wetland PWUE by enhancing wetland E_t. Lastly, at the leaf-scale, the light response curves of leaf photosynthesis, leaf E_t, and leaf-scale PWUE indicated that wetland plants need to consume more water during the photosynthesis process under warmer conditions. These findings provide a fresh perspective on how climate warming influences carbon and water cycles in wetland ecosystems.

1. Introduction

Plant water-use efficiency (PWUE), quantified as the ratio of ecosystem gross primary productivity (GPP) to plant transpiration (E_t), is an important indicator for assessing ecosystem responses to climate change and plays a key role in global cycles of carbon and water (Beer et al., 2009; Keenan et al., 2013; Medlyn et al., 2017). Examining the long-term changes in PWUE and its drivers will contribute substantially to predicting the fate of ecosystems under future climate conditions. For example, it has been suggested that the decreased E_t and increased PWUE can reduce water stress in terrestrial ecosystems (Mooney et al., 1991; Pan et al., 2022). Additionally, several researchers have identified that ecosystems with increasing PWUE under climate change conditions will be more likely to maintain high productivity levels (Keenan et al., 2013; Cheng et al., 2017; Hutley et al., 2021). However, despite the critical role of PWUE for carbon and water cycles in ecosystems, to our knowledge, there has been no detailed investigation of the interannual variations in PWUE in wetland ecosystems, hindering our insight into the possible changes in ecosystem functions of wetlands in the context of global climate change.

Driven by climate change, the global mean temperature is projected to rise by 1-4 ℃ by the end of the 21st century (IPCC, 2013). Meanwhile, wetland ecosystems are changing rapidly under a warming climate because temperature profoundly affects almost all ecological processes, including the carbon and water cycles (Walther et al., 2002; Sun et al., 2022). Recent evidence has found that warming can significantly impact

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PWUE in different ways. Rising temperatures can enhance or inhibit GPP and E_t, further resulting in the various changes in PWUE (Niu et al., 2011; Huang et al., 2016). For instance, although a previous study has revealed rising temperatures can decrease PWUE by reducing GPP (Niu et al., 2011), another research demonstrated that the warming-induced reductions in PWUE was mainly associated with the significant increases in E_t (Huang et al., 2016). On the other hand, climate warming also has potentials to increase plant productivity (Keenan et al., 2014; Noyce et al., 2019) and reduce the water loss from plant stomata (Bonada et al., 2018; Quan et al., 2018) through direct or indirect effects, and thereby may increase PWUE. Given this, there has been little agreement on how PWUE will respond to climate warming. For wetland ecosystems, it has been previously observed that warming can have both positive and negative influences on GPP (Sun et al., 2021). Moreover, research to date has not yet determined the yearly changes in wetland E_t under climate warming conditions. Hence, there is an important gap in current knowledge about the possible changes in wetland PWUE in a changing climate.

Wetland ecosystems have a superior capacity for sequestering and storing carbon, and therefore exhibit a great potential to mitigate global climate change (Mcleod et al., 2011; Bonetti et al., 2021). Among a variety of wetland types, the seasonal hydroperiod wetland ecosystems have seasonally alternating dry periods and inundation periods due to the changes in rainfall intensity and frequency along with evapotranspiration rates (Jimenez et al., 2012; Zhao et al., 2019). In other words, unlike the permanent flooding wetlands, seasonal hydroperiod wetlands are not always "wet" during the growing season. Thus, plants in these wetland ecosystems may suffer from water scarcity as the freshwater availability that support them is becoming limited during dry periods. For instance, previous studies found that wetland plants would be affected by limited moisture supply and high soil salinity conditions during spring dry periods, resulting in weaker CO_2 sink strength at the annual scale (Chu et al., 2018; Chu et al., 2021). However, previous studies have typically ignored the possible variations in the efficiency of water use for wetland plants under climate change conditions because these studies generally consider that plants in wetlands should always have sufficient water supplies. Under a rapidly changing climate, the hydrological conditions in wetland ecosystems are expected to be shifted, for example, reductions in hydroperiod and water levels during inundation could be observed, and therefore have many ecological consequences, including alterations in ecosystem production (Schedlbauer et al., 2010; Zhao et al., 2019; Yao et al., 2022). As a result, the fate of the wetland ecosystems becomes more uncertain in a changing climate (Burkett and Kusler, 2000; Erwin, 2009).

So far, although PWUE has received much attention because it acts as the key nexus of carbon and water cycling in ecosystems, the number of studies focused on long-term changes in PWUE based on continuous in situ measurements, such as the eddy covariance (EC) observations, is extremely limited (Hu and Lei, 2021b). Making matters worse, for wetland ecosystems, there is hardly any report on the interannual variations in PWUE, let alone its responses to climate warming. Given that PWUE may play a more important role in wetland ecosystems, especially those with dry periods, as climate change continues to shift wetland hydrology, we combined multiple datasets in this study to address the above-mentioned knowledge gaps. Here, the 10-year (2011-2020) EC flux data coupled with a 15-year (2003-2017) satellite-based dataset (called PML-V2) and the data obtained from an in situ warming experiment, provides ample information to investigate the interannual variations in wetland PWUE and its responses to rising temperatures. Specifically, we aimed to address the following questions: (i) Does climate warming have significant impacts on wetland PWUE? (ii) If so, how does climate warming play its role in influencing wetland PWUE by changing GPP and\or E_t? Furthermore, there are three major hypotheses: (i) Climate warming has no significant effect on wetland PWUE. (ii) Climate warming positively affects wetland PWUE by increasing GPP and\or reducing E_t. (iii) Climate warming negatively affects wetland PWUE by decreasing GPP and\or increasing E_t. By answering these questions, we hope that our study can offer a fresh perspective on how climate change affects wetland ecosystems.

2. Materials and methods

2.1. Site description

This study was conducted at the Yellow River Delta, China. The Yellow River Delta provides a natural laboratory to better understand how wetland PWUE will vary in a warming climate. On the one hand, the climate in this region experienced a notable warming process (Wei et al., 2021), providing an ideal background climate for this research. On the other hand, EC records of carbon and water fluxes have exceeded a decade in this region, allowing us to quantify and examine the interannual variations in wetland PWUE. What's more, we obtained data from an in situ warming experiment (Sun et al., 2022), offering robust evidence on how experimental warming affecting on leaf-scale PWUE in the wetland. The EC site was located in the supratidal zone of the Yellow River Delta (37°45′59″ N, 118°58′51″ E; elevation: ~ 1 m), and it is a part of the EC tower group of the Yellow River Delta Ecological Research Station of Coastal Wetland, Chinese Academy of Sciences. The long-term (1961-2019) mean annual air temperature (T_{air}) is 12.66 ℃, with the mean monthly temperature being lowest in January (-2.93 ℃) and highest in July (26.30 ℃) (Wei et al., 2021). The mean annual total precipitation (PPT) is 604 mm, and about 60% of the annual PPT, influenced by a monsoon climate, falls during the summer rainy season. Wetlands in this region are mainly covered by saline and wet soils. At the study site, the soil (10 cm) has a pH of 7.8, a salinity of 0.95 ‰, and contains 14.7 g kg^{-1} total C and 0.7 g kg^{-1} total N (Han et al., 2014). The dominant vegetation species in the study site is *Phragmites australis*, which buds in mid-April, reaches a peak canopy height of about 1.7 m during summer, and begins withering in October. The maximum aboveground biomass can exceed 600 g m^{-2} during the growing season (Han et al., 2015).

2.2. Eddy covariance measurements and data processing

The turbulent fluxes of CO_2 and H_2O between the plant canopy and the atmosphere have been measured by an open-path EC system since April of 2010. The EC system was installed at the height of 2.8 m above the ground, consisting of an open-path infrared gas analyzer (IRGA, LI-7500, LI-COR Inc., Lincoln, NE, USA) measuring CO_2 and H_2O concentration and a three-dimensional sonic anemometer (CSAT-3, Campbell Scientific Inc., Logan, UT, USA) measuring wind velocity and virtual temperature. The EC system was estimated to have an approximately 90% fetch distance within 120 m upwind of the tower, so most of the recorded fluxes originated from the target region (Wei et al., 2021). More details regarding auxiliary measurements (Text S1) and data quality control have been fully described in previous papers about this site (Han et al., 2015; Chu et al., 2018). In this study, we used the evaporative fraction (EF) as a proxy of soil moisture conditions since an increase of energy allocated to evaporated water indicates a greater potential of soil on water supply (Jiang et al., 2020). EF was calculated as LE/(LE + H), where LE is the latent heat, and H is the sensible heat, ranging from 0 when fully dry to 1 when fully wet.

We gap-filled flux data and partitioned ecosystem carbon fluxes into GPP (nighttime-based method) using the 'REddyProc' package (Wutzler et al., 2018), which has been widely used in EC-based studies. In this study, a total of 45% and 40% of CO_2 and H_2O flux data were gap-filled, respectively. For ecosystem water flux, that is, evapotranspiration (ET), the total 30-min ET was converted from LE by the formula: ET = LE × (0.01800/44000) × 3600 × 0.5 (Aguilos et al., 2021). The 10-year average degree of energy balance closure (EBC) was 66 ± 7% at the study site.

2.3. Partitioning of water fluxes and calculation of PWUE

Ecosystem-scale water fluxes, ET, is the sum of biological transpiration through stomata of the leaf surface and physical evaporation from canopy intercepted water and bare soil water (Chen et al., 2014). Water loss from E_t is a physiology-based process and hence is more closely coupled with plant photosynthesis (Quan et al., 2018). Considering this, we first attempted to derive E_t data from EC-based ET. The method proposed by Wei et al. (2017), which established ecosystem-specific exponential relationships between E_t/ET and leaf area index (LAI), was applied to partition water fluxes in this research. Based on this method, wetland ecosystem E_t can be calculated as:

$$E_t = ET \times 0.65 \times LAI^{0.21} \quad (1)$$

This method has been widely applied in numerous studies previously. It only requires daily ET and LAI as the input data, with no prior assumptions about the negligible evaporation during certain dry periods. The daily LAI data used to establish the ET partitioning equation were usually derived from satellite-based products (Wei et al., 2017; Hu and Lei, 2021a). More importantly, this method was proved to have a good performance in producing reliable ET partitioning results (Hu and Lei, 2021a). The details of the calculation of daily LAI (Fig. S1) are shown in Text S2.

After the ET partitioning (Fig. S2), we used PWUE to be the ecosystem-scale water-use efficiency indicator in further analysis. Although the ecosystem-scale water-use efficiency is usually defined as the ratio of GPP and ET (i.e., WUE), there are several studies defined it as GPP/E_t (Baldocchi et al., 2021; Gu et al., 2021; Hu and Lei, 2021b), calling canopy or plant water-use efficiency (i.e., PWUE). In addition, PWUE is expected to be more associated with plant physiological controls and hence may be more sensitive to changes in climate conditions (Lavergne et al., 2019; Gu et al., 2021). The equation of PWUE is:

$$PWUE = \frac{GPP}{E_t} \quad (2)$$

Lastly, we computed canopy conductance (G_c) to help interpret the potential changes in PWUE at the study site. G_c is an integrated measure of stomatal conductance at the ecosystem level, and the algorithm of G_c based on EC datasets (Bigleaf model) has been fully documented in Knauer et al. (2018a).

2.4. Extraction of the growing season

In this research, we extracted the timing of the growing season following a GPP threshold method (Wang et al., 2019), which has advantages over other phenology monitoring methods because it can provide reliable results based on EC-observed data. A Gaussian weighted moving mean filter was firstly used to smooth the daily GPP curve (Fig. S3). After that, the timing for the start of the growing season (SOS) and the end of the growing season (EOS) were extracted from the smoothed GPP curve based on a GPP threshold (15% of the maximum daily GPP value). The SOS was then determined as the date when the smoothed GPP was greater than the GPP threshold, while the EOS was determined as the date when the smoothed GPP was less than the threshold. The same method was also applied to the satellite-based flux dataset to extract the growing season. Moreover, to examine the specific timing of warming impacts on PWUE, the entire growing season was divided into early growing season (SOS to May), peak growing season (June to August), and late growing season (September to EOS) at the study site.

2.5. Satellite-derived carbon and water fluxes

To test our results at a larger spatial scale, we used a satellite-derived dataset, called PML-V2, to probe the interannual variations in PWUE of the entire Yellow River Delta. The PML-V2 dataset estimates 8-day global carbon and water fluxes at 500 m resolution from July 2002 to December 2017 (Zhang et al., 2019). Moreover, the PML-V2 dataset uses a water-carbon coupled canopy conductance model to estimate E_t and GPP. We obtained the 8-day data of GPP and E_t from 2003 through 2017 from the PML-V2 dataset using Google Earth Engine cloud computing platform (Gorelick et al., 2017) and then applied the spline-filled method to interpolate these data to daily time resolution (Fig. S4).

2.6. Manipulative warming experiment

The leaf-scale evidence was obtained from a manipulative warming experiment, which was established in our research station in November 2014. We used a randomized complete block design with two treatments (i.e., control and warming) and four replicates for each treatment. The plot size was 3 × 4 m, and the distance between adjacent plots was 3 m. The warming plots were heated by infrared heaters (Kalglo Electronics, Bethlehem, PA, USA) suspended 1.75 m above the ground. All the heaters have a mean radiation output of 1600 W. The warming treatment increased canopy temperature and soil temperature by approximately 1.5°C and 1.7°C, respectively. More details regarding the experimental design have been fully documented before (Sun et al., 2022). During the growing season in 2015, light response curves of leaf photosynthesis, leaf E_t, and leaf-scale plant water-use efficiency ($PWUE_{leaf}$) of the dominant species, *Phragmites australis*, were measured twice a month by an infrared gas analyzer (LI-6400, LI-COR Inc., Lincoln, NE, USA) on sunny days. $PWUE_{leaf}$ is usually defined as the ratio of photosynthetic rate to transpiration rate according to previous studies (Niu et al., 2011; Wang et al., 2020). All the measurements were conducted in the morning between 08:30 a.m. and 12:00 a.m. During the measurements, leaves were illuminated with the photosynthetically active radiation (PAR) ranging from 0 μmol m^{-2} s^{-1} to 2000 μmol m^{-2} s^{-1} using the LED light system built into the leaf chamber.

2.7. Statistical analysis

Pearson correlation analysis and stepwise linear regression were used to probe the dominant factor in regulating the interannual variations in GPP, E_t, and PWUE at the study site. Linear regressions were performed to explore other relationships, such as the relationship between T_{air} and satellite-based PWUE interannual variations. Notably, we were more interested in the yearly fluctuations in PWUE rather than its interannual trend, thereby, detrended data were used in the Pearson correlation analysis, stepwise linear regression, and linear regressions. To obtain the detrended data, we fitted a simple linear regression model (variables against years) to the data and then computed the difference between the observed value and the predicted value. These differences represented the detrended data. The paired-samples t-test was undertaken to examine warming effects on the light responses of leaf photosynthesis, E_t, and $PWUE_{leaf}$. In this study, a significance level of $P = 0.05$ was used. All statistical analyses were performed using SPSS version 28.0 (IBM SPSS Statistics for Windows, Armonk, NY, USA).

3. Results

3.1. Interannual variations in environmental variables, GPP, E_t, and PWUE in a seasonal hydroperiod wetland

The growing season global solar radiation (R_g) ranged from 199 W m^{-2} in 2011 to 228 W m^{-2} in 2018 (Fig. 1a; Table S1). T_{air} followed a similar interannual pattern with R_g (Fig. 1b). The multi-year average T_{air} was 21.02 ± 0.59 °C (CV = 3%) (Table S1), with 2011 being the coldest growing season (20.31 °C) and 2018 being the warmest one (22.02 °C). Atmospheric CO_2 concentration (C_a) exhibited an upward year-to-year variability (Fig. 1c), fluctuating between 383 ppm and 429 ppm (Table S1). The study site received mean growing season PPT of 528 ± 78 mm (CV = 15%) during the study years, ranging from 395 mm to 680

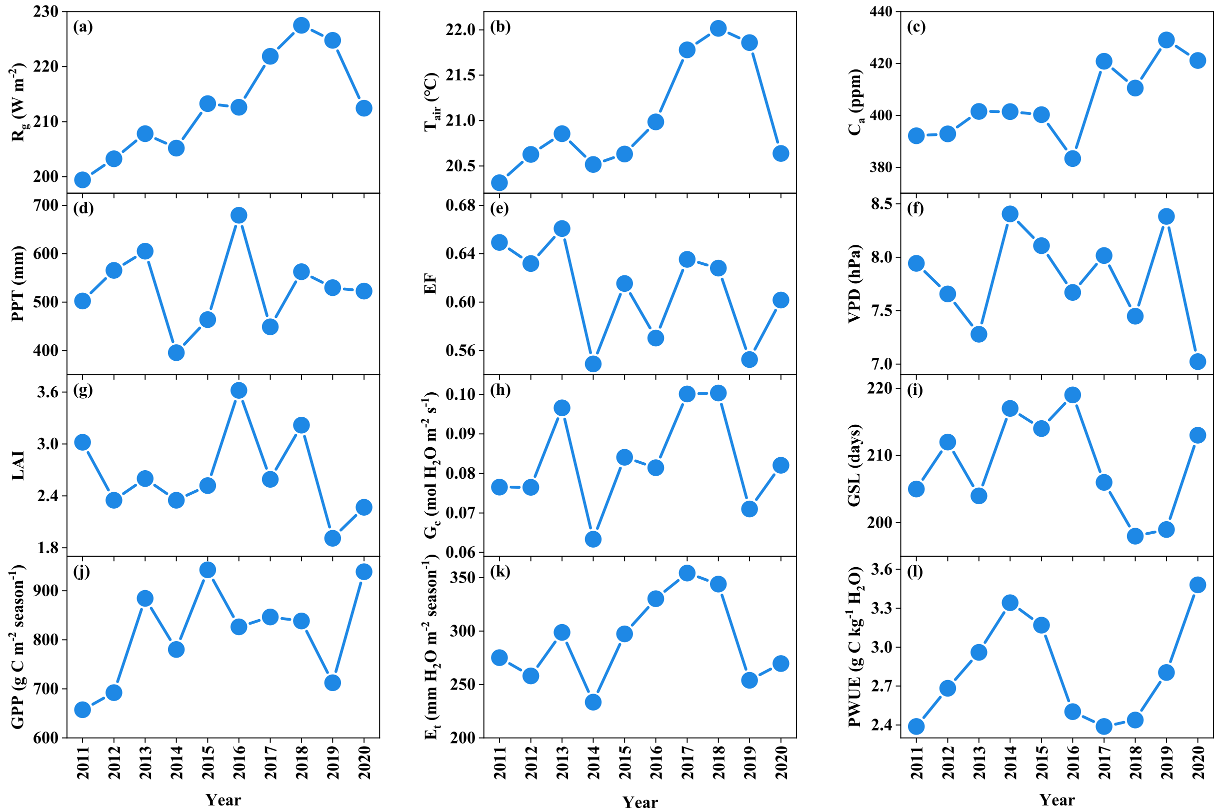

Fig. 1. Interannual variations in growing season (a) global solar radiation (R_g), (b) air temperature (T_{air}), (c) atmospheric CO_2 concentration (C_a), (d) precipitation (PPT), (e) evaporative fraction (EF), (f) vapor pressure deficit (VPD), (g) maximum leaf area index (LAI), (h) canopy conductance (G_c), (i) growing season length (GSL), (j) gross primary productivity (GPP), (k) transpiration (E_t), and (l) plant water-use efficiency (PWUE) from 2011 to 2020 in a seasonal hydroperiod wetland.

mm (Fig. 1d; Table S1). The range of the interannual variations in EF was 0.55-0.66, with a multi-year average of 0.61 ± 0.04 (CV = 6%) (Fig. 1e; Table S1). The averaged vapor pressure deficit (VPD) fluctuated between 7.02 hPa in 2020 and 8.41 hPa in 2014, with a CV of 6% (Fig. 1f; Table S1). Changes in maximum LAI, with a 10-year mean value of 2.64 ± 0.48, exhibited the largest variability (CV = 18%) among all environmental variables (Fig. 1g; Table S1). The minimum value of growing season G_c was 0.063 mol H_2O m^{-2} s^{-1} in 2014, and the maximum one was 0.100 in 2018 (Fig. 1h; Table S1). The mean growing season length (GSL) was 209 ± 7 days (CV = 3%), with 2018 experiencing the shortest growing season (198 days) and 2016 experiencing the longest one (219 days) (Fig. 1i; Table S1).

The multi-year mean growing season GPP during the 10-year observation was 812 ± 95 g C m^{-2} $season^{-1}$ (CV = 12%), ranging between 657 g C m^{-2} $season^{-1}$ in 2011 and 943 g C m^{-2} $season^{-1}$ in 2015 (Fig. 1j; Table S1). For growing season E_t, on average, the multi-year value was 292 ± 39 mm H_2O m^{-2} $season^{-1}$ (CV = 13%), fluctuating between 233 mm H_2O m^{-2} $season^{-1}$ in 2014 and 354 mm H_2O m^{-2} $season^{-1}$ in 2017 (Fig. 1k; Table S1). Interannual variations in the ratio of the growing season GPP and E_t resulted in PWUE ranging from 2.39 g C kg^{-1} H_2O in 2011 to 3.48 g C kg^{-1} H_2O in 2020, with an average PWUE of 2.82 ± 0.39 g C kg^{-1} H_2O (CV = 14%) during the study years (Fig. 1l; Table S1).

3.2. Warming impacts on the interannual variations in PWUE in a seasonal hydroperiod wetland

According to the Pearson correlation analysis, the results revealed that R_g (*r* (Pearson correlation coefficient) = -0.66, *P* = 0.04) and T_{air} (*r* = -0.76, *P* = 0.01) had significant negative impacts on the interannual variations in PWUE, while other variables only showed weak influences (Fig. 2a). Besides, to remove collinearity between environmental variables (e.g., R_g and T_{air}), we further investigated the dominant factor for PWUE interannual variations using the stepwise regression. The findings clearly indicated that T_{air} played a predominant role in regulating PWUE interannual changes among all the explanatory variables (Fig. 2b). Nevertheless, neither of the two analysis techniques showed significant relationships between T_{air} and GPP, and E_t, on the growing season scale. We further divided the data into subsections according to the plants growth stage and found that T_{air} was significantly correlated to E_t (R^2 = 0.59, P = 0.01) and PWUE (R^2 = 0.41, P = 0.05) in the peak growing season (Fig. 2c), indicating the way of warming to reduce PWUE. For the two components of PWUE, interannual changes in E_t (R^2 = 0.47, P = 0.03) had a stronger influence on PWUE than GPP (R^2 = 0.20, P = 0.19) during the growing season (Fig. 2d). Overall, these results illustrate that warming appear to reduce wetland PWUE by promoting plants to consume more water during the photosynthesis process.

3.3. Regional-scale PWUE interannual variations in a warming climate

During the study period from 2003 to 2017, the study region experienced the warmest growing season of 21.94 ℃ in 2006, while 2003 (20.10 ℃) being the coldest one (Fig. 3a; Table S2). The range of the interannual variations in GPP and E_t was 416-533 g C m^{-2} $season^{-1}$ (CV = 6%) and 105-156 mm H_2O m^{-2} $season^{-1}$ (CV = 9%), respectively (Fig. 3b, c; Table S2). The multi-year average of PWUE was 3.41 ± 0.28 g C kg^{-1} H_2O (CV = 8%), ranging between 3.08 g C kg^{-1} H_2O in 2015 and 4.06 g C kg^{-1} H_2O in 2004 (Fig. 3d; Table S2). In addition, the interannual variations in PWUE was significantly related to E_t (R^2 = 0.34, P = 0.02) but only showed a weak relationship with GPP (R^2 = 0.04, P = 0.49) during the study years. Based on the linear regression analysis, T_{air} had a weak influence on the growing season GPP

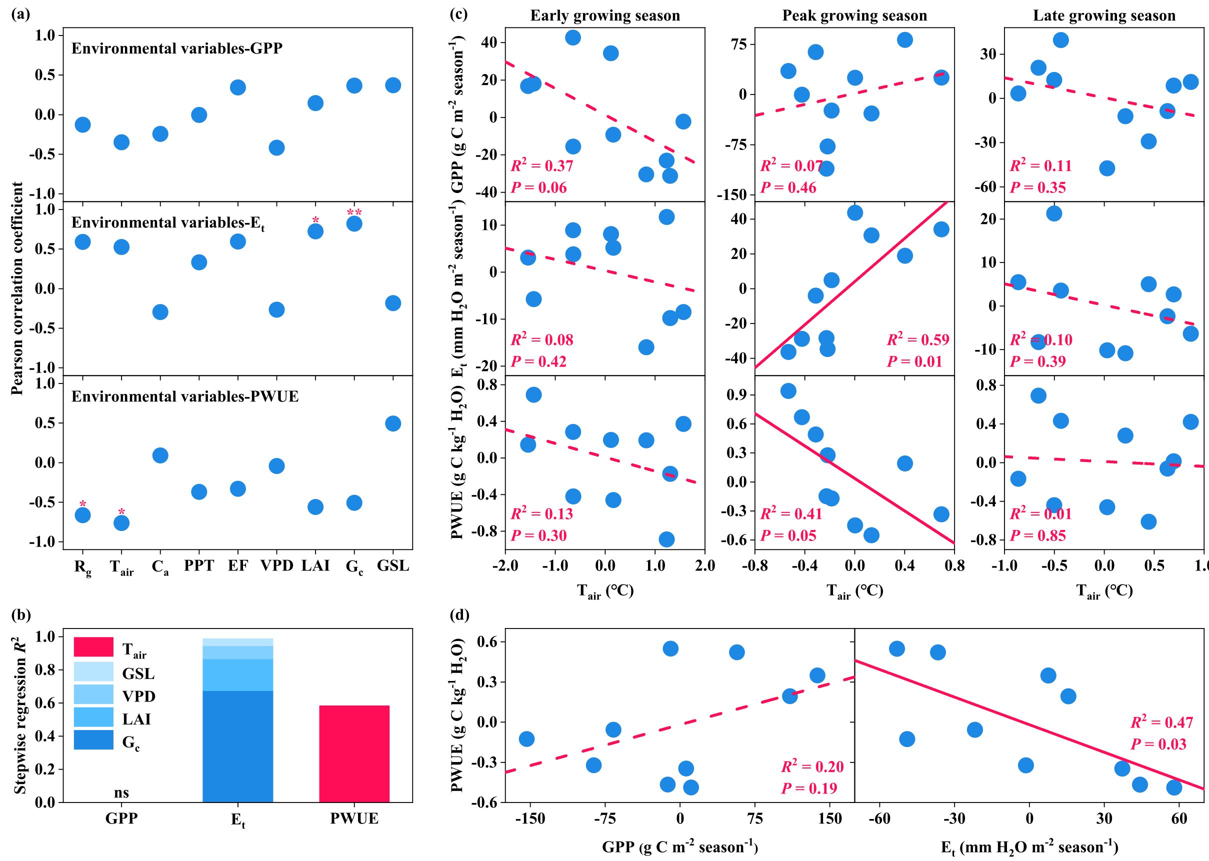

Fig. 2. (a) Pearson correlation analysis between the interannual variations in growing season gross primary productivity (GPP), transpiration (E_t), and plant water-use efficiency (PWUE) and their potential environmental drivers in a seasonal hydroperiod wetland. R_g, global solar radiation; T_{air}, air temperature; C_a, atmospheric CO_2 concentration; PPT, precipitation; EF, evaporative fraction; VPD, vapor pressure deficit; LAI, leaf area index; G_c, canopy conductance; GSL, growing season length. * $P < 0.05$; ** $P < 0.01$. (b) The relative contribution of environmental variables to the interannual variations in growing season GPP, E_t, and PWUE. Stepwise linear regression was used to isolate the significant ($P < 0.05$) predictors. The "ns" means no significant predictors were found in the stepwise linear regression. (c) Linear relationships between T_{air} and GPP, E_t, and PWUE in the early growing season, peak growing season, and late growing season. Solid lines indicate significant linear regressions ($P < 0.05$) while dashed lines indicate the regressions are not significant ($P > 0.05$). (d) Interannual variations in growing season PWUE as functions of GPP and E_t. All the data were detrended in this section.

interannual variations ($R^2 = 0.19$, $P = 0.11$; Fig. 3e) and a significant positive impact on the yearly changes in E_t ($R^2 = 0.62$, $P < 0.001$; Fig. 3f). Last, a significant negative correlation between T_{air} and PWUE ($R^2 = 0.33$, $P = 0.03$) was observed over the study years (Fig. 3g). In agreement with the EC-based findings, the results in this section indicate that the warming-induced increases in E_t dominated the reduction of wetland PWUE.

3.4. Effects of warming on light responses of leaf photosynthesis, E_t, and $PWUE_{leaf}$

Light response curves of leaf photosynthesis, E_t, and $PWUE_{leaf}$ in both control and warming plots increased rapidly with rising PAR until approximately 500 μmol m^{-2} s^{-1} (Fig. 4a-c). Then, the changes of photosynthesis and $PWUE_{leaf}$ tended to be flat while E_t continued to increase rapidly. The positive effect of experimental warming on leaf photosynthesis was pronounced when PAR exceeded 200 μmol m^{-2} s^{-1}, and then the differences in leaf photosynthesis (the value in warming plots minus it in control plots) fluctuated between 0.26 μmol CO_2 m^{-2} s^{-1} and 0.62 μmol CO_2 m^{-2} s^{-1} over the process of light response (Fig. 4d). The differences in E_t were relatively large (0.15-0.21 mmol H_2O m^{-2} s^{-1}) under moderate PAR levels (100-1000 μmol m^{-2} s^{-1}), while the small differences in E_t (< 0.1 mmol H_2O m^{-2} s^{-1}) were found under low and high PAR conditions (Fig. 4e). $PWUE_{leaf}$ in warming plots was always lower than it in control plots when PAR exceeded 50 μmol m^{-2} s^{-1}, the largest difference was -0.31 μmol CO_2 mmol^{-1} H_2O (Fig. 4f). As a result, compared to the control plots, experimental warming significantly promoted photosynthesis ($P = 0.01$) and E_t ($P < 0.001$) on the leaf scale (Fig. 4a, b). $PWUE_{leaf}$ in warming plots was significantly lower ($P < 0.001$) than it in control plots (Fig. 4c). Leaf-scale evidence again confirmed that wetland plants need to consume more water during the photosynthesis process under warmer conditions.

3.5. Site comparisons: effects of warming on PWUE in various ecosystems

In this section, we collected several long-term EC datasets to examine the effects of rising temperatures on PWUE in various ecosystems (Text S3). Annual T_{air} in all sites showed overall increasing trends during the study period (Fig. 5a-d). The multi-year mean value of PWUE was 3.16 ± 0.33 g C kg^{-1} H_2O in the tropical rainforest (9 years), 3.80 ± 0.28 g C kg^{-1} H_2O in the oak savanna (18 years), 3.7 ± 0.6 g C kg^{-1} H_2O in the crop site with winter wheat (15 years), and 4.4 ± 0.8 g C kg^{-1} H_2O in the crop site with summer maize (Fig. 5e-g; Table S3). The other two wetland sites showed 7-year mean PWUE values of 3.55 ± 0.40 g C kg^{-1} H_2O (US-MYB) and 2.06 ± 0.15 g C kg^{-1} H_2O (US-TW1), respectively (Fig. 5h; Table S3). Meanwhile, PWUE exhibited pronounced year-to-year variability with CV ranging from 7% in the oak savanna site to 18% in the crop site with summer maize. Regression results revealed a significant negative impact ($R^2 = 0.21$, $P = 0.03$) of T_{air} on PWUE in wetland sites (Fig. 5l), while other correlations were relatively weak (P

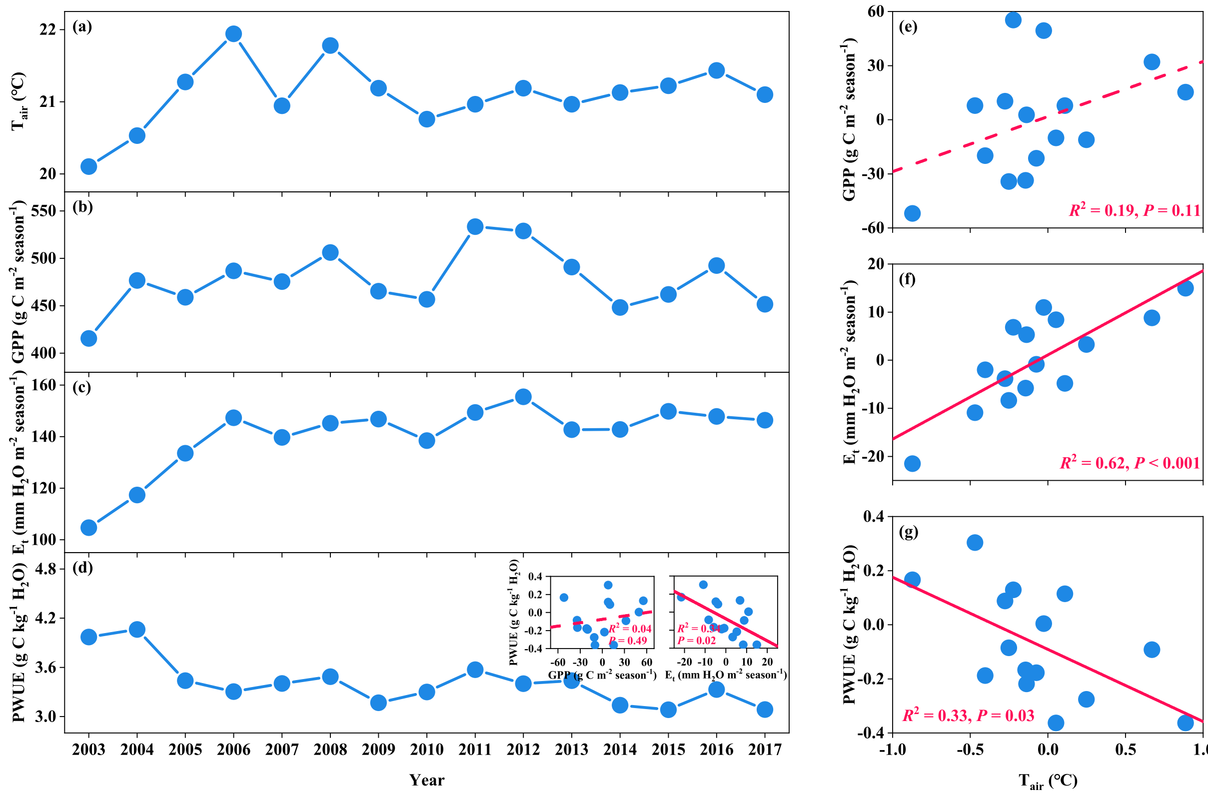

Fig. 3. (a-d) Interannual variations in growing season air temperature (T_{air}), gross primary productivity (GPP), transpiration (E_t), and plant water-use efficiency (PWUE) from 2003 to 2017 in the study region. The inserts show the interannual variations in PWUE as functions of GPP and E_t. (e-g) Linear relationships between T_{air} and GPP, E_t, and PWUE across the study period. Solid lines indicate significant linear regressions ($P < 0.05$) while the dashed lines indicate the regression are not significant ($P > 0.05$). Detrended data were used in the linear regressions.

> 0.05) across the study years (Fig. 5i-k).

4. Discussion

4.1. Ecosystem-scale PWUE in the wetland compared to other ecosystems

In light of the 10-year EC observation at the study site, wetland plants are seemed to be less efficient in water use during the photosynthesis process compared to other ecosystems. As we have shown earlier in Section 3.5, the multi-year mean PWUE obtained in this research (2.82 ± 0.39 g C kg^{-1} H_2O) was lower than the results from other long-term observations (Table S3). The same conclusion can also be drawn from a synthesized study of EC-based PWUE from 73 sites globally (Gu et al., 2021). The PWUE at our study site was close to that in woody savanna (2.62 ± 1.34 g C kg^{-1} H_2O); however, other ecosystem types, including cropland, forest, and grassland, all had higher ecosystem-scale PWUE (4.33 ± 2.37 g C kg^{-1} H_2O-6.73 ± 3.77 g C kg^{-1} H_2O). The relatively low PWUE in the wetland follows common sense—plants living in wet conditions are usually less efficient in water use (Fernández-Martínez et al., 2019). In addition to the low value, we also found that the range of the interannual changes in wetland PWUE was relatively large (CV = 14%). For instance, the PWUE interannual variations in both the tropical forest and the oak savanna had CV less than 10% (Table S3) over the 18-year and 9-year study period (Tan et al., 2015; Baldocchi et al., 2021). Taken together, the low PWUE and the large interannual variability could indicate the changes in wetland PWUE are sensitive to a changing climate (Cooley et al., 2022).

4.2. Negative impacts of climate warming on wetland PWUE

Based on several lines of evidence, we have found that climate warming had significant negative impacts on wetland PWUE (Figs. 2-4). Furthermore, our results showed that the enhancements of E_t rather than changes in GPP dominated the responses of PWUE to warming, supporting the third hypothesis in this study. This discovery illustrates that wetland plants must consume more water to maintain their productivity levels in a warming climate. To our knowledge, this is the first time these findings have ever been identified in wetland ecosystems.

High temperatures are able to enhance the biophysical driving force of E_t, for example, steepening the water vapor gradient outside the leaf, and therefore promoting more water loss through E_t (Kirschbaum and McMillan, 2018). For wet ecosystems, such as the wetland, the positive effects of warming on ecosystem E_t may be more pronounced due to the relatively high soil water availability (Quan et al., 2018). Eventually, the substantial water loss through E_t can contribute to a significant reduction in ecosystem-scale PWUE. However, the warming-induced increases in E_t was not a consistent pattern in previous studies, especially those conducted in water-limited ecosystems. Under a warmer condition, plants in dry ecosystems could suffer from water limitations and thus tend to take a “water-saving” adaptive mechanism by promoting stomatal closure to reduce E_t; meanwhile, regulated by stomatal closure, reductions in GPP could also be observed (Niu et al., 2008; Dusenge et al., 2021). For example, investigators have previously found that ecosystem-scale PWUE was reduced due to elevated temperatures and was mainly driven by the decreases in GPP (De Boeck et al., 2006; Niu et al., 2011). These results manifest different water-use strategies between plants in dry ecosystems and those in wetland ecosystems under warmer conditions. In our research, the leaf-scale evidence clearly revealed that wetland plants tend to adopt a “water-consumption” strategy in a warming climate, thus exhibiting lower PWUE (Fig. 4). In this study, we also found that the significant negative impacts of warming on PWUE were more likely to present in wetland ecosystems

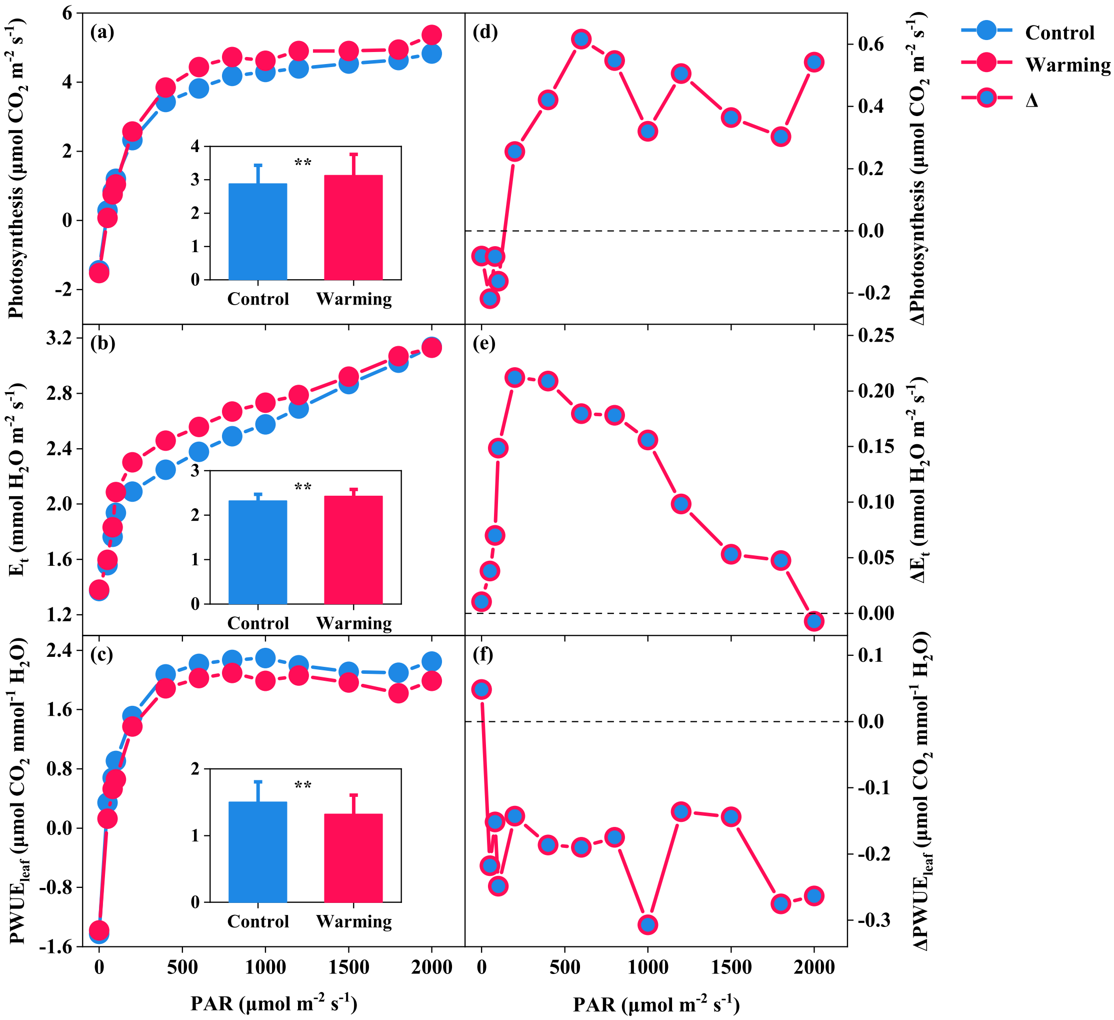

Fig. 4. (a-c) Light response curves of leaf photosynthesis, leaf transpiration (E_t), and leaf-scale plant water-use efficiency ($PWUE_{leaf}$) in the control and warming plots. PAR, photosynthetically active radiation. Insert panels show the mean values of leaf photosynthesis, E_t, and $PWUE_{leaf}$. Error bars represent standard error across replicates (n = 4). ** $P < 0.01$. (d-f) Differences in the light response curves of leaf photosynthesis, E_t, and $PWUE_{leaf}$ between control and warming plots. Differences (Δ) were calculated as the mean value in warming plots minus it in control plots.

compared to drier terrestrial ecosystems (Fig. 5). These results demonstrated the distinct responses of wetland PWUE to climate change in contrast to terrestrial ecosystems.

The significant negative impacts of warming on wetland PWUE can also be related to the distinct sensitivities of ecosystem GPP and E_t to meteorological factors. It has been previously shown that the water lost through E_t was more closely associated with meteorological drivers than GPP (Cooley et al., 2022). Moreover, according to our EC observations, at least during the study years, we did not find significant influential factors for the interannual variations in growing season GPP (Fig. 2a, b). Although climate warming is expected to stimulate ecosystem net carbon uptake under wet conditions (Quan et al., 2019), the linkage between T_{air} and the yearly changes in GPP was weak based on EC observations (Fig. 2a) and the regional-scale evidence (Fig. 3e). The absence of the strong relationships between GPP and the environmental drivers we selected can be partly interpreted by the hydrological regimes in wetlands, for instance, the episodic flooding events (Han et al., 2015). It has been proved that both the average water level during inundation period and the length of inundation period determined the interannual variations in GPP in a seasonal hydroperiod wetland (Zhao et al., 2019). At our study site, because of the intensifying rainfall pulse during the summer rainy season, surface flooding was often observed, and the flooding duration can last at least 1-2 months each year (Wei et al., 2021). Thereby, the potential promoting effects of warming on GPP were seemed to be overshadowed by the impacts of flooding events in the wetland.

4.3. Limitations and implications

This study is one of the first attempts to examine the interannual variations in PWUE in wetlands. Nevertheless, this work is still subject to some limitations. For example, an unclosed energy balance could reduce the accuracy of PWUE estimates (Knauer et al., 2018b). Still, in fact, this limitation is unavoidable for wetland sites and can be attributed to the energy storage terms that are subject to flooding conditions (Huang et al., 2019; Eichelmann et al., 2022). Fortunately, according to a previous study (Lavergne et al., 2019), EBC non-closure probably does not affect the estimated interannual trend in PWUE as the yearly changes in the residual (R_n (net radiation) - LE - H) were not significant ($R^2 = 0.17$, $P = 0.24$; data not shown) at our study site. Moreover, for ET partitioning, although multiple methods have been developed to partition EC-based ecosystem ET, each of them has advantages and limitations. However, the uncertainties may be difficult to avoid as long as the EC-based ET was partitioned into E_t. Further work, which can take these limitations into account, will need to be undertaken to improve PWUE investigations in wetland ecosystems.

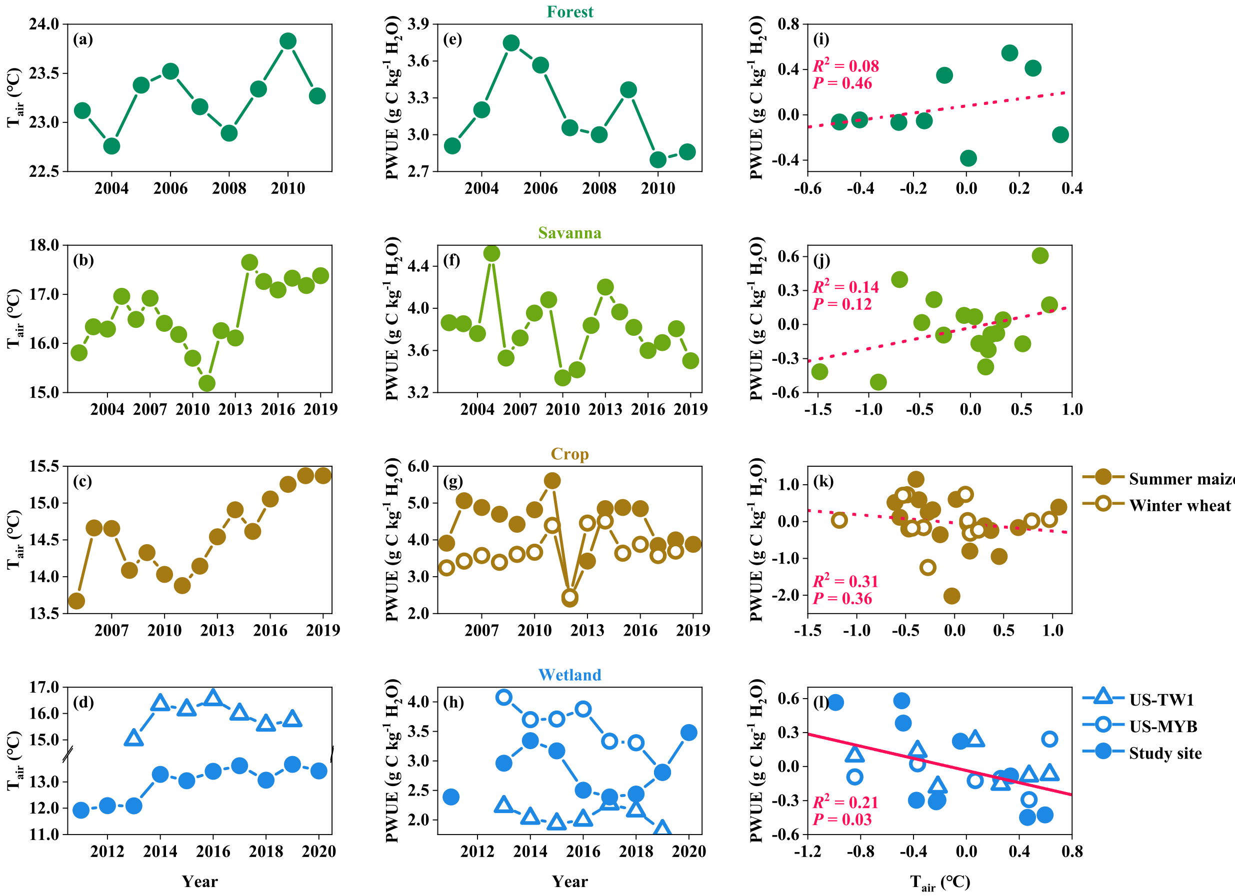

Fig. 5. Interannual variations in (a-d) annual air temperature (T_{air}) and (e-h) plant water-use efficiency (PWUE) and (i-l) the linear regressions between T_{air} and PWUE in various ecosystems. The solid line indicates a significant linear regression ($P < 0.05$) while the dashed lines indicate regressions are not significant ($P > 0.05$). The T_{air} data were obtained from the nearest weather station for each site. Detrended data were used in the linear regressions.

The findings in this study have important implications for understanding how wetland ecosystems will respond to future climate change. In this work, multiple pieces of evidence revealed the significant negative impacts of climate warming on wetland PWUE and the warming-induced more water loss by E_t dominate these negative impacts. Other wetland ecosystems, especially those with seasonal hydroperiod, may have similar responses of ecosystem-scale PWUE to climate warming. Therefore, as global temperature may continue to increase in the future (IPCC, 2013), we speculate that the reductions in wetland PWUE will compound the water stress in seasonal hydroperiod wetlands, which are not always "wet" within a year. Take the study region in this work as an example (details of data collection can be found in Text S4). The wetland ecosystems in this region experienced a significant warming process since 1980 (Fig. 6a, b). In the future, considering the most severe situation (SSP585 scenario), annual mean T_{air} will rapidly rise at a rate of 0.08 °C year^{-1} and eventually reach at an extreme high value of 19.46 °C in 2100. Due to the notable rising T_{air}, the interannual trend of PWUE is predicted to decrease according to our results in this research (Figs. 6c, d; S5), indicating wetlands in this region may suffer from increased water stress in the future. The increased water-deficit stress could have several effects on wetland ecosystems, such as shifting the structure of plant communities, decreasing wetland plant biomass, and suppressing annual CO_2 sink strength (Chu et al., 2021). Worse still, under a dramatic changing climate, a particular point to note is many of the world's wetlands are facing water scarcity due to the freshwater availability (i.e., precipitation, river discharge, and groundwater) that support them is becoming limited, may ultimately lead to wetland degradations and wetland losses (Rodell et al., 2018). Last, further studies need to be carried out in order to investigate the potential changes in wetland water use in a changing world.

5. Conclusion

In this research, multiple pieces of evidence revealed the significant negative impacts of climate warming on wetland PWUE. Specifically, the EC-based observational results revealed that rising temperatures had significant negative impacts on the interannual variations in wetland PWUE, and increased E_t rather than changes in GPP dominated these negative impacts. Furthermore, the satellite-based evidence confirmed that climate warming had significant negative consequences for the interannual variations in wetland PWUE by enhancing E_t. Lastly, the light response curves of leaf photosynthesis, leaf E_t, and $PWUE_{leaf}$ indicated that wetland plants need to consume more water during the photosynthesis process under warmer conditions. This investigation fills a gap in the research on the possible responses of PWUE in wetland ecosystems to climate warming, providing new insights into how climate warming influences carbon and water cycles in wetlands.

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.

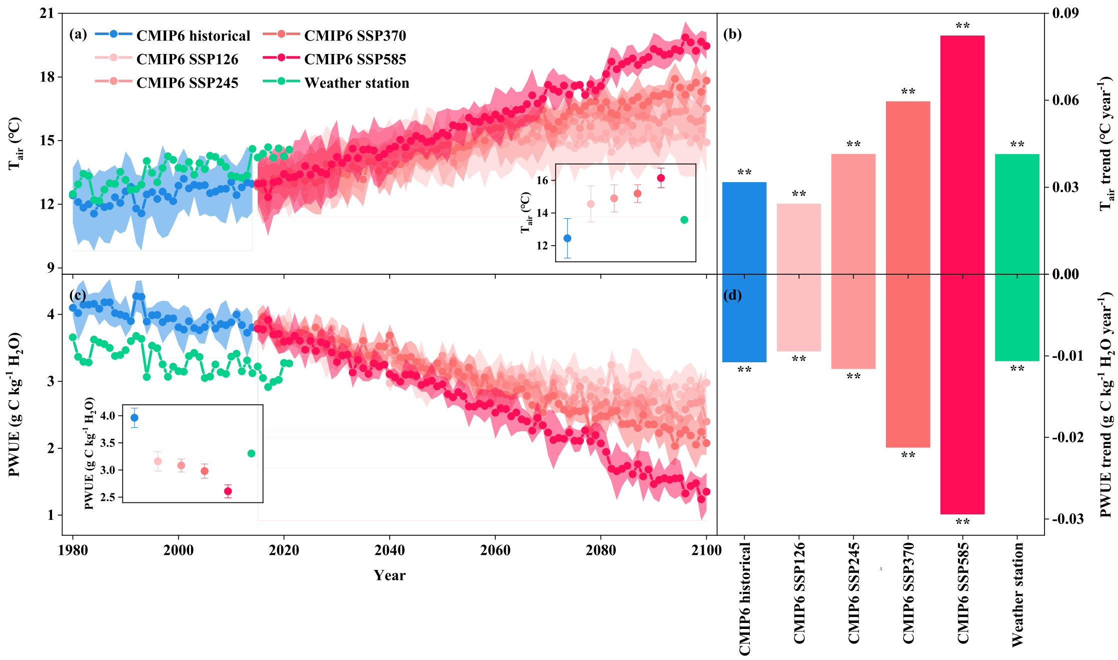

Fig. 6. Annual time series and interannual trend of (a, b) air temperature (T_{air}) and (c, d) plant water-use efficiency (PWUE) for the study region. The T_{air} data were obtained from the CMIP6 database (1980-2100) and the observations from a nearby weather station (1980-2021). Lines with shaded areas illustrate the mean and standard deviation of T_{air} simulated by four CMIP6 models under historical (1980-2014) and four future SSP scenarios (2015-2100). The PWUE time series was calculated by using the equation derived from the significant linear regression between T_{air} and satellite-based PWUE in the study region (shown in Fig. S5). The inserts in panels (a, c) show mean values of T_{air} and PWUE (mean ± standard deviation) for each dataset. Trend detection in the time series was undertaken using the non-parametric Mann-Kendall test including Sen's slope method for significance testing at $P < 0.05$. Calculated rates are given with their significance level (** $P < 0.01$).

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.watres.2023.120246.

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