Effect of precipitation change on the photosynthetic performance of *Phragmites australis* under elevated temperature conditions

Linhong Teng¹, Hanyu Liu¹, Xiaonan Chu¹, Xiliang Song² and Lianhui Shi²

¹ Dezhou University, Dezhou, China
² Shandong Agricultural University, Taian, China

**ABSTRACT**

**Background:** As a fundamental metabolism, leaf photosynthesis not only provides necessary energy for plant survival and growth but also plays an important role in global carbon fixation. However, photosynthesis is highly susceptible to environmental stresses and can be significantly influenced by future climate change.

**Methods:** In this study, we examined the photosynthetic responses of *Phragmites australis* (*P. australis*) to three precipitation treatments (control, decreased 30%, and increased 30%) under two thermal regimes (ambient temperature and +4 °C) in environment-controlled chambers.

**Results:** Our results showed that the net CO₂ assimilation rate (*Pn*), maximal rate of Rubisco (*Vcmax*), maximal rate of ribulose-bisphosphate (RuBP) regeneration (*Jmax*) and chlorophyll (Chl) content were enhanced under increased precipitation condition, but were declined drastically under the condition of water deficit. The increased precipitation had no significant effect on malondialdehyde (MDA) content (*p* > 0.05), but water deficit drastically enhanced the MDA content by 10.1%. Meanwhile, a high temperature inhibited the positive effects of increased precipitation, aggravated the adverse effects of drought. The combination of high temperature and water deficit had more detrimental effect on *P. australis* than a single factor. Moreover, non-stomatal limitation caused by precipitation change played a major role in determining carbon assimilation rate. Under ambient temperature, Chl content had close relationship with *Pn* (*R² = 0.86, p < 0.01*). Under high temperature, *Pn* was related to MDA content (*R² = 0.81, p < 0.01*). High temperature disrupted the balance between *Vcmax* and *Jmax* (the ratio of *Jmax* to *Vcmax* decreased from 1.88 to 1.12) which resulted in a negative effect on the photosynthesis of *P. australis*. Furthermore, by the analysis of Chl fluorescence, we found that the xanthophyll cycle-mediated thermal dissipation played a major role in PSII photoprotection, resulting in no significant change on actual PSII quantum yield (ΦPSII) under both changing precipitation and high temperature conditions.

**Conclusions:** Our results highlight the significant role of precipitation change in regulating the photosynthetic performance of *P. australis* under elevated temperature conditions, which may exacerbate the drought-induced primary productivity reduction of *P. australis* under future climate scenarios.
INTRODUCTION

Global warming mainly caused by high levels of greenhouse gas emission is predicted to increase the air temperature by 1.1–6.4 °C in the next hundred years (Crowther et al., 2016). At the same time, extreme precipitation events like drought and waterlogging will occur more universally than ever (IPCC, 2019). The changing global climate will not only aggravate the frequency and intensity of environmental stresses but also pose serious threat to agriculture production (Hossain et al., 2021; Vaughan et al., 2018; Xin & Tao, 2021), ecosystem stability (Kanojia & Dijkwel, 2018; White et al., 2021) and terrestrial C and N cycling (Crowther et al., 2016; Li et al., 2021b). Among the environmental factors, ambient temperature and soil water content are two major abiotic factors in the limitation of plant distribution and productivity (Küsters et al., 2021; Yan, Zhong & Shangguan, 2020; Kumari et al., 2021). Their change will directly and/or indirectly influence plant physiological processes, such as resource allocation (Farfan-Vignolo & Asard, 2012; Forbesa et al., 2020), net photosynthetic rate (Shao et al., 2021; Yamori, Hikosaka & Way, 2014), carboxylation efficiency (Liu et al., 2022), photochemical efficiency of photosystem II (PSII) (Aragón-Gastélum et al., 2020; Song et al., 2016a) and water use efficiency (Liu et al., 2019), which then impact the global carbon cycling. Among all the plant physiological processes, photosynthesis plays an important role in substance metabolism (Ort et al., 2015; Zhu et al., 2020). Thus, the understand of how plant photosynthesis responses to the concurrent warming and precipitation change is necessary for plants better facing future climate change.

The high limitation on the plant carbon assimilation capacity under soil water deficient conditions has been a major reason for plant growth and crop productivity reduction (Hussain et al., 2021; Nolf et al., 2015). It is widely accepted that there are two ways in which water stress affects the photosynthesis of plants: one is the stomatal limitations, such as closing the stoma and lowering the stomatal conductance (Daryanto, Wang & Jacinthe, 2017; Talbi et al., 2020); the other is non-stomatal limitations, such as photosynthetic phosphorylation (Du et al., 2021), regeneration of ribulose-1,5-bisphosphate (RuBP) (Song et al., 2016a), activation of Rubisco and the synthesis of ATP (Ashraf & Harris, 2013; Hu et al., 2020). The stomatal limitation is generally considered as the main factor responsible for the reduction of photosynthesis under drought stress environment (Liu et al., 2005; Song et al., 2020). However, long term of drought stress may lead to the reduction of chlorophyll content (Bijanzadeh, Barati & Egan, 2022), the content of Rubisco (Gadzinowska et al., 2021), the maximum Rubisco carboxylation rate and potential maximum rate of electron transport for RuBP regeneration (Song et al., 2016a), resulting in the decline of the plants’ photosynthetic rate (He et al., 2021; Wang et al., 2019).

The photosynthesis of plants is regarded as the most sensitive process to high temperature stress (Xalxo et al., 2020). High temperature lasting for only a few minutes to
several hours will drastically damage the structure and function of photosynthetic apparatus such as thylakoid lamella and stroma, decrease the production of ATP, inhibiting a series of enzyme activities, affect the transport of photosynthetic electrons and reduce the photosynthetic rate finally (Hu et al., 2020). Heat stress can also cause photosynthesis decline through enhancing the generation of reactive oxygen species (ROS) (Hao et al., 2019), destroying the function of PSII (Jahan et al., 2021; Janka et al., 2015) suppressing the synthesis of chloroplast (Song, Wang & Lv, 2016), and inhibiting the activity of ribulose1,5-bisphosphate carboxylase/oxygenase (Rubisco) (Perdomo et al., 2017). In tomato plants, heat stress (40 °C) significantly decreased photosynthetic pigment concentrations and inhibited Rubisco accumulation resulting in a reduction of photosynthetic efficiency (Parrotta et al., 2020). Based on a 3-year study, Zhong et al. (2014) also reported that an air temperature elevation of 1.5 °C could decreased the net photosynthetic rate of Phragmites australis by 28%. In contrast, a recent study showed that increase of 4 °C significantly increased the net photosynthesis rate, transpiration rate, leaf temperature and chlorophyll content in leaves of lettuce by 114.9%, 65.5%, 7.1% and 9.8%, respectively (Ouyang et al., 2020). Although an emerging pool of knowledge shows that plant photosynthesis was noticeable affected by heat stress, the mechanism of the photoinhibition caused by high temperature is still need further research.

Coastal wetlands account for 0.22–0.34% of global land surface (Fennessy, 2014) and act as “blue carbon” resources due to the relatively high net primary productivity and low organic matter decomposition rate (Drake et al., 2015; Zhong et al., 2016). It is estimated that 13–17.2 Pg of carbon were stored in coastal wetlands (Hiraishi et al., 2014). However, coastal wetlands are also potential source of global greenhouse gases (Hsieh et al., 2020). The climate change increased the release rate of carbon in the CO₂ and CH₄ through organic matter decomposition and decreased the amount of carbon stored in coastal wetlands. It is found that a 1.5 °C temperature enhancement could result in the gas emissions released form wetlands increase by 37.5% (Liu et al., 2020). As plant photosynthesis is the major way of carbon fixation in coastal wetlands, keep the photosynthesis at a high rate under climate change conditions is essential for global carbon cycling. Phragmites australis (P. australis) belonging to the Poaceae family, is the main constructive and dominant plants in coastal wetlands of China and plays an important role in maintaining the ecosystem function (Guan et al., 2017). Their spatial distribution is mainly limited by air temperature change and soil water deficit. The research on P. australis’s photosynthetic characteristics in response to rising temperature and changing precipitation pattern can provide a theoretical basis for dealing with climate change in coastal wetlands. This main aims of the work were to investigate the photosynthetic responses of P. australis to precipitation change under elevated temperature conditions. Specifically, three key research questions were addressed in the paper: (1) Are there any negative or positive influences of temperature and precipitation change on photosynthetic performance of P. australis? (2) What are the physiological mechanisms of precipitation change and high temperature affecting the carbon assimilation of P. australis? (3) What are the protection mechanisms of P. australis to avoid damage caused by environmental stress?
MATERIALS AND METHODS

Plant culture and experimental design
The experiment was carried out at the Dezhou University, Shandong Province, China. The seeds of *P. australis* and soils were obtained from the costal wetland in Kenli, Dongying, China. The soil sample site has a northern subtropical marine monsoon climate. The annual average temperature and precipitation which obtained from the Kenli Meteorological Station of the China Meteorological Administration (37°35′ N, 118°33′ E; elevation 85 m) in the past 10 years (2010–2019) were 12 °C and 552 mm, respectively. About 70–74% of the annual precipitation is concentrated from July to September.

Before sowing in plastic pots, the seeds of *P. australis* were sterilized by potassium permanganate solution (0.7%) for 8 min and washed with deionized water for three times. Each plastic pot (18 cm in height and 20 cm in diameter) was filled with 5.0 kg of dry soil and planted with 10 plants. The experimental soil was paddy fluvo-aquic soil, and the basic physical and chemical properties of the soil were as follows: soil pH 7.91, organic matter 9.42 g·kg⁻¹, total nitrogen 0.77 g·kg⁻¹, available phosphorus 5.92 g·kg⁻¹, and available potassium 168.72 g·kg⁻¹.

After the third leaf emerged, the seedlings were thinned to three plants per pot. There were three precipitation treatments and two temperature treatments were selected for experiment. The precipitation treatments were set as: average monthly precipitation (July to September) over 10 years (W₀); W₀ increased by 30% (W₀+30); W₀ decreased by 30% (W₀−30). The temperature treatments were set as 26.3/21.6 °C (T₀) and 30.3/25.6 °C (T₄). The treatments were set based on the monthly average temperature and rainfall during *P. australis*’s major growth stage (July to September) in the past 10 years (2010–2019). Each treatment and corresponding experiments were established in triplicates. Totally, 18 pots with healthy plants (three plants per pot) were randomly selected and placed into two environmental control chambers (RGD-500D3). The size of environmental control chamber was 750 × 660 × 2,050 mm (length × width × height). Growing conditions in the environmental control chamber were maintained as follows: 390 ppm CO₂ concentration, 1,000 µmol photons·m⁻²·s⁻¹ photosynthetic photon flux density, and 14 h photoperiod per day. All the parameter measurements were conducted after 92 days of plant growth.

Measurements

Leaf gas exchanges
Three plants from each treatment were randomly chosen from different pots for measurement. Gas exchange parameters were measured on the healthy and fully expanded leaves of *P. australis* with an open gas exchange system (CIRAS-3, PP-system, Hitchin, UK). Illumination was supplied to the leaves from a red-blue LED light source. The leaf chamber temperature, CO₂ concentration and photosynthetic photon flux density (PPFD) were controlled at 25 °C, 390 ppm and 900 µmol·m⁻²·s⁻¹, respectively.

*A/C*<sub>i</sub> curve
The measurement of *A/C*<sub>i</sub> curves was performed on the same leaves used for gas exchange parameter measurements. *A/C*<sub>i</sub> curve was measured under a light saturation level of
900 μmol·m$^{-2}$·s$^{-1}$ PPFD, and estimated using the CO$_2$ response curve of photosynthesis. The CO$_2$ gradients for A/C$_i$ curves included 390, 200, 100, 50, 390, 600, 800, 1,000 μmol·mol$^{-1}$ levels stepwise. The analysis of A/C$_i$ curve was conducted with using the plant ecophys R package, which based on the model of Farquhar, Von & Berry (1980).

**Chlorophyll fluorescence measurements**
Three areas of interest at different position of leaf were selected to calculate the fluorescence parameters. Based on the method described by Song et al. (2016b), the actual PSII quantum yield ($\Phi_{\text{PSII}}$), quantum yield of regulated energy dissipation of PSII ($\Phi_{\text{NPQ}}$), and quantum yield of nonregulated energy dissipation of PSII ($\Phi_{\text{NO}}$) were measured using an imaging-PAM fluorometer (Walz, Effeltrich, Germany). The fluorescence parameters were calculated using fellow equations described by Lazár (2015):

$$\Phi_{\text{PSII}} = (F_{m'} - F_s)/F_{m'} = \Delta F/F_{m'}$$
$$\Phi_{\text{NPQ}} = 1 - \Phi_{\text{PSII}} - 1/[NPQ + 1 + qL(F_m/F_0 - 1)]$$
$$\Phi_{\text{NO}} = 1/[NPQ + 1 + qL](F_m/F_0 - 1)$$

where $F_m$ is the maximum fluorescence in the dark-adapted state, $F_0$ is the minimum Chl fluorescence yield, $F_m'$ is the maximum fluorescence yield in the light-adapted state, $F_s$ is the Chl fluorescence during actinic illumination, $qL$ is the fraction of open PSII centers, NPQ is the non-photochemical quenching.

**Chlorophyll content**
The chlorophyll content was measured according to the method described by Hiscox & Israelstam (1979). Briefly, 0.25 g fresh leaf samples were mashed in 80% acetone (v/v) in a 4 °C refrigerator overnight. After filtered through two-layer nylon net, the extract was then centrifuged at 15,000 g for 5 min to obtain the supernatant. After determining the absorbance of the supernatant at wavelengths of 663 and 646 nm, the contents of chlorophyll a and b were calculated according to the equations of Lichtenthaler & Buschmann (2001):

Chlorophyll a = 12.25 A$_{663}$ − 2.79 A$_{647}$
Chlorophyll b = 21.50 A$_{647}$ − 5.10 A$_{663}$

**Malondialdehyde (MDA) content**
The MDA content was measured according to the thiobarbituric acid (TBA) chromogenic method described by Song, Wang & Lv (2016). Briefly, 1.0 g fresh leaf samples were homogenized with 0.1% trichloroacetic acid (TCA, 2.0 mL, pH 7.0) for 2 h an 15,000 g for 10 min. Then, 0.5 mL of supernatant was added to 1.5 mL of TBA. After the mixture was incubated in a shaking water bath at 90 °C for 20 min, the reaction was rapidly stopped by ice-water bath. These samples were centrifuged at 10,000 g for 5 min to obtain the supernatant. The absorbance of the supernatant was detected at 532, 450, and 600 nm. The amount of MDA was calculated with the following equation:

$$\text{MDA} = 6.45 \times (A_{532} - A_{600}) - 0.56 \times A_{450}$$
Statistical analysis
All statistical analyses were performed using SPSS 21.0 (SPSS Institute, Inc., Cary, NC, USA). Effects of warming and precipitation change were analyzed using one-way analysis of variance with a Duncan’s multiple range test at a 5% probability level. The linear curve fitting and graphing were performed using Origin 2021 software (Origin Lab, Northampton, MA, USA).

RESULTS
Chlorophyll content
Under both two temperature conditions (T₀ and T₄), the Chl content of P. australis was significantly affected by precipitation change. It can be seen from Table 1 that, at the condition of T₀, W₊30 caused the increase of Chl a, Chl b and Chl a+b content by 25.6%, 33.8% and 31.1%, respectively, with the Chl a/b ratio decreased by 6.6%. At the same temperature, a decreasing precipitation (W₋30) led to the decline in Chl b and Chl a+b content (10.1% and 6.2%, respectively) and the increase in Chl a/b ratio (12.2%). At a higher temperature (T₄), the adjustment of precipitation resulted in similar variations in the contents and ratios of Chl contents. Moreover, under different precipitation conditions (W₊30, W₀ and W₋30), the Chl a, Chl b and Chl a+b content at the higher temperature (T₄) decreased by 3.5–13.0%, 18.7–32.0% and 12.9–24.2%, respectively, with the Chl a/b ratio increasing by 7.6–25.3%.

MDA content
Malondialdehyde (MDA) as a product of lipid peroxidation can be used as a marker for oxidative stress under environmental stress conditions. The higher MDA content indicates the stronger cell membrane lipid peroxidation. It can be seen from Fig. 1 that, under both T₀ and T₄ conditions, W₊30 had no significant effect on MDA content (p > 0.05). But W₋30 led to the significant increase of MDA by 10.1% under T₀ condition and by 9.5% under T₄ condition. At the same time, high temperature also enhanced MDA content. As shown in Fig. 1, under different precipitation conditions (W₊30, W₀ and W₋30), the MDA content in the T₄ treatment groups increased by 5.2%, 6.3% and 5.7%, respectively, compared with the T₀ treatment groups.

| Treatment | Chl a (mg/g) | Chl b (mg/g) | Chl a/b (%) | Chl a + Chl b (mg/g) |
|-----------|--------------|--------------|-------------|----------------------|
| T₀        |              |              |             |                      |
| W₊30      | 1.08 ± 0.05 a| 1.86 ± 0.08 a| 58.2 ± 0.7 b| 2.95 ± 0.13 a        |
| W₀        | 0.86 ± 0.04 b| 1.39 ± 0.02 b| 62.3 ± 1.7 b| 2.25 ± 0.06 b        |
| W₋30      | 0.86 ± 0.01 b| 1.25 ± 0.09 c| 69.9 ± 4.7 a| 2.11 ± 0.10 b        |
| T₄        |              |              |             |                      |
| W₊30      | 0.94 ± 0.01 a| 1.51 ± 0.05 a| 62.6 ± 2.4 c| 2.45 ± 0.04 a        |
| W₀        | 0.83 ± 0.02 b| 1.13 ± 0.10 b| 74.0 ± 4.4 b| 1.96 ± 0.12 b        |
| W₋30      | 0.75 ± 0.01 c| 0.85 ± 0.04 c| 87.6 ± 3.8 a| 1.60 ± 0.05 c        |

Note: Different lowercases indicate significant difference between different precipitation treatments within the same temperature treatment compared with control (p < 0.05).

Teng et al. (2022), PeerJ, DOI 10.7717/peerj.13087
Photosynthetic parameters

From Table 2, it was found that at the condition of T₀, compared to W₀, net CO₂ assimilation rate (Pₙ) in W₊3₀ treatment increased by 32.8% and in W₋3₀ treatment reduced by 18.9%, respectively. The other gas exchange parameters such as stomatal conductance (Gₛ), intercellular CO₂ concentration (Cᵢ), transpiration rate (Tᵣ) and water use efficiency (WUE) were not significantly affected by W₊3₀ or W₋3₀. At the condition of T₄, the photosynthetic parameters between W₊3₀ and W₀ showed no remarkable difference, while W₋3₀ significantly reduced the values of WUE, Pₙ, Gₛ, Cᵢ and Tᵣ by 25.2%, 52%, 14.1% and 33.0%, respectively. Under all precipitation conditions, high temperature negatively affected photosynthesis of P. australis and reduced Pₙ by 6.6∼17.4%.

The change of Pₙ as a function of increased Cᵢ in the chloroplast can be used to reflect the biochemical limitations of photosynthesis under high temperature and changing precipitation conditions. As shown in Table 2, at the condition of T₀, W₊3₀ enhanced Vₖmax and Jₖmax by 25.3% and 60.3%, while W₋3₀ caused the reduction by 34.6% and 8.2%, respectively. At the condition of T₄, W₊3₀ resulted in a significant increase of Vₖmax and Jₖmax by 63.8% and 27.3%, while W₋3₀ caused the reduction by 27.4% and 28.4%, respectively. Under W₀ and W₋3₀ conditions, T₄ significantly reduced Vₖmax by 14.5% and 5.1%, while increased Jₖmax by 4.7% and 18.4%, respectively. At the condition of W₊3₀, Vₖmax increased by 11.7% and Jₖmax decreased by 16.9% in the T₄ treatment group.

Chlorophyll fluorescence parameter

The effect of water treatments on Φₚₛᵢᵢ, Φₙₚᵢ and Φₙₒ under two temperature conditions were shown in Fig. 2. Under T₀ condition, precipitation change (W₊3₀, W₋₃₀) had no significant effect on Φₚₛᵢᵢ (p > 0.05), but drastically increased Φₙₚᵢ by 14.9% and 32.3% and reduced Φₙₒ by 13.3% and 22.7%, respectively. Under T₄ condition, Φₚₛᵢᵢ in the W₊3₀ and W₋₃₀ treatment groups increased by 8.6% and 6.8%, Φₙₒ increased by 30.3% and
21.3%, while $\Phi_{NPQ}$ decreased by 25.4% and 18.9%, respectively. Under different precipitation treatments ($W_{+30}$, $W_0$ and $W_{-30}$), compared to $T_0$, the change of $\Phi_{PSII}$ caused by $T_4$ was 29.6%, −4.1% and 9.3%, the change of $\Phi_{NPQ}$ caused by $T_4$ was −10.6%, 36.8% and −16.0%, and the change of $\Phi_{NO}$ caused by $T_4$ was 5.8%, −29.7% and 11.6%, respectively.

**Table 2** Effects precipitation change on photosynthetic parameters in leaves of *Phragmites australis* under ambient temperature ($T_0$) and high temperature ($T_4$) conditions.

| Treatment | Photosynthetic parameters | $P_n$ (μmol CO$_2$·m$^{-2}$·s$^{-1}$) | $G_s$ (μmol·mol$^{-1}$) | $C_i$ (mol H$_2$O·m$^{-2}$·s$^{-1}$) | $T_r$ (mmol·m$^{-1}$·s$^{-1}$) | WUE (μmol CO$_2$·mmol H$_2$O) | $V_{max}$ (μmol·m$^{-2}$·s$^{-1}$) | $J_{max}$ (μmol·m$^{-2}$·s$^{-1}$) |
|-----------|---------------------------|--------------------------------------|--------------------------|----------------------------------|-------------------------------|--------------------------------|--------------------------------|----------------------------------|
| $T_0$     | $W_{+30}$                 | 11.5 ± 1.0 a                         | 0.18 ± 0.03 a            | 271 ± 12 a                       | 3.5 ± 0.3 a                   | 3.3 ± 0.3 a                    | 52.0 ± 8.1 a                    | 121.0 ± 23.1 a                   |
|           | $W_0$                     | 8.6 ± 0.4 b                          | 0.14 ± 0.08 a            | 224 ± 69 a                       | 3.7 ± 1.8 a                   | 2.7 ± 1.3 a                    | 41.5 ± 1.8 b                    | 75.5 ± 11.7 ab                   |
|           | $W_{-30}$                 | 7.0 ± 0.7 c                          | 0.15 ± 0.01 a            | 303 ± 2 a                        | 3.4 ± 0.3 a                   | 2.1 ± 0.4 a                    | 27.1 ± 5.4 c                    | 69.3 ± 18.6 b                   |
| $T_4$     | $W_{+30}$                 | 9.5 ± 0.1 a                          | 0.14 ± 0.01 a            | 267 ± 2 a                        | 3.5 ± 0.1 a                   | 2.7 ± 0.1 a                    | 58.1 ± 6.5 a                    | 110.6 ± 6.0 a                   |
|           | $W_0$                     | 8.1 ± 0.7 a                          | 0.17 ± 0.03 a            | 298 ± 15 ab                      | 3.0 ± 0.3 a                   | 2.7 ± 0.01 a                   | 35.4 ± 4.6 b                    | 79.0 ± 4.1 b                    |
|           | $W_{-30}$                 | 6.0 ± 1.2 b                          | 0.08 ± 0.01 b            | 256 ± 24 b                       | 2.0 ± 0.6 b                   | 3.2 ± 1.3 a                    | 25.7 ± 3.8 b                    | 56.5 ± 10.0 b                   |

Note: Different lowercases indicate significant difference between different precipitation treatments within the same temperature treatment compared with control ($p < 0.05$).
DISCUSSION

High temperature and precipitation change as two major abiotic stresses always occur simultaneously, which threaten the sustainability of future crop production and biodiversity (Alam et al., 2021; Hosseini Sanehkoori, Pirdashti & Bakhshandeh, 2021; Küsters et al., 2021; Zhang et al., 2018). In the present study, we found that the positive effects of increased precipitation and the adverse effects of decreased precipitation on chlorophyll content, CO₂ assimilation rate, lipid peroxidation (as indicated by MDA) and the energy partitioning of PSII were significant. Meanwhile, high temperature inhibited the positive effects of increased precipitation and aggravated the adverse effects of decreased precipitation. Similarly, in the studies on Leymus chinensis (Xu & Zhou, 2011), Stipa bungeana (Song et al., 2016b), Ziziphus jujube (Jiang et al., 2020), and Robinia pseudoacacia (Yan, Zhong & Shangguan, 2020), the high temperature combined with severe drought exacerbated the adverse effects on plant growth and photosynthesis.

Plants exposed to environmental stresses, such as drought, extreme temperatures or their combinations, have to face several metabolic imbalances leading to oxidative damage due to ROS accumulation, resulting in detrimental secondary effects on plant organelles (Raja et al., 2020; Vurukonda et al., 2016). ROS buildup in plants can damage cell functions by causing oxidative damage, resulting in DNA nicking, amino acids and photosynthetic pigments biosynthesis inhibition, and even cell death (Nath et al., 2016; Raja et al., 2017). MDA content, a result of ROS mediated lipid peroxidation, is used as biomarker of membrane damage caused by various abiotic stresses (Morales & Munné-Bosch, 2019). In the present study, increased precipitation showed no significant effect on MDA content in leaves of P. australis, while the decreased precipitation and elevated temperature remarkable increased the MDA content. The results suggest precipitation decreased by 30% and temperature elevated by 4 °C accelerates MDA formation, resulting in serious lipid peroxidation (Morales & Munné-Bosch, 2019). Similar results were found in studies on Solanum lycopersicum (Raja et al., 2020), maize (Naz et al., 2021), and Echinacea purpurea (Hosseinpour et al., 2020). The increase in the MDA content indicates that water deficit and high temperature destroy the antioxidant defense system, generate lipid peroxidation, and cause oxidative burst and excess oxidative damage to the cell membrane in P. australis plants. The increase in lipid peroxidation is widely reported to cause oxidative damage to chloroplast organs (Sohag et al., 2020) and leads to chlorophyll degradation (Bagheri, Gholami & Baninasab, 2019). The noticeable reduction of Chl a and Chl b in the W−30 and T4 treatment supports the finding that water deficit and high temperature trigger oxidative damage to the expression of chlorophyll a-b binding protein gene (Sun et al., 2022) and the synthesis of chlorophylls (Gujjar et al., 2020), which inevitably leads to a decrease in leaf photosynthetic efficiency (Wang et al., 2019) and plant productivity (Song, Jin & He, 2019).

The response of photosynthetic capacity to the variation of soil water depends on the threshold of soil water condition. Lamptey et al. (2020) and Snider et al. (2014) proved that the photosynthetic activity will be enhanced under moderate soil water condition but be lowered under excess water or severe water deficit conditions. In the present study,
increased precipitation (W_{+30}) did not exceed the threshold of soil moisture and significantly increased the value of $P_n$. This suggests that the precipitation increased by 30% is a moderate soil water condition for the potential photosynthetic capacity of *P. australis*. The reduction of $P_n$ at the W_{-30} condition demonstrated that the severe drought stress can drastically inhibit the photosynthesis of *P. australis*. At the same time, previous studies also showed that the photosynthesis and plant growth will be limited by higher temperature above the optimum point (*Rodriguez et al., 2015*). In our study, the reduction of $P_n$ under $T_4$ condition indicated that the temperature 4 °C higher than the ambient temperature (26.3/21.6 °C) has exceeded the optimum point and is adversely to the photosynthesis of *P. australis*. However, the threshold of soil water condition and the optimum temperature point for the photosynthesis of *P. australis* are still unclear and need further investigation. It is widely accepted that the decline in $P_n$, $C_i$, $T_r$ and WUE could be attributed to decreased $G_s$ under drought and heat stress conditions (*Carvalho et al., 2019*; *Li et al., 2021a; Olorunwa, Shi & Barickman, 2021*). In this study, under ambient temperature ($T_0$) condition, the $G_s$, $C_i$, $T_r$ and WUE showed no remarkable differences in different precipitation treatments, indicating the soil water deficit is not the limiting factor in stomatal openness, water consumption (transpiration) and utilization for *P. australis* plants. On the other hand, with the increasing of temperature ($T_4$), precipitation decreased by 30% caused a remarkable reduction of $G_s$, $C_i$ and $T_r$, suggesting that higher temperature exacerbates the detrimental effect of water shortage, which is in accordance with the studies on *Xanthoceras sorbifolium* Bunge (*Du et al., 2021*), *Solanum lycopersicum* (*Raja et al., 2020*), and *Stipa bungeana* (*Song et al., 2016b*). Furthermore, drought and heat stress also cause damage to the photosynthetic apparatus as confirmed by reduced $V_{cmax}$ and $J_{max}$, as the decline in these two parameters are ascribed to a reduced number of active Rubisco molecules and a decrease of photosynthetic energy during the process of CO$_2$ assimilation (*Olorunwa, Shi & Barickman, 2021; Zhuang et al., 2020*).

The mechanisms of precipitation change affecting the carbon assimilation can be studied by stomatal limitation and non-stomatal limitation. *Song et al. (2020)* indicated that the reduction in photosynthesis of a water-stressed maize was mainly caused by stomatal limitation, whereas *Li et al. (2020)* reported that stomatal limitation did not play a major role in the change of photosynthesis of transgenic tobacco plants. The different results may be attributed to various responses from species, stress lasting time and stress intensity (*Mitchell et al., 2008; Song et al., 2020*). In our experiment, to figure out which is the main factor in limiting the photosynthesis, linear regression analysis was performed to illustrate the relationship of $P_n$ with $G_s$, $V_{cmax}$, $J_{max}$, Chl a+b content, Chl a/b ratio and MDA content under $T_0$ and $T_4$ conditions, respectively (*Fig. 3*). From the linear regression analyses, it was found there is no significant relationship between $P_n$ and $G_s$ ($p > 0.05$). But $P_n$ had a significantly positive linear correlation with $V_{cmax}$, $J_{max}$ and Chl a+b content, as well as a significantly negative linear correlation with Chl a/b ratio and MDA content. The results indicate that non-stomatal limitation caused by precipitation change plays a major role in determining the carbon assimilation rate. Similar result can be found in the research by *Xu & Zhou (2011)*, *Song et al. (2016a)*, and *Li et al. (2020)*. At the
condition of $T_0$, Chl a+b content had the closest relationship with $P_n$ ($R^2 = 0.86$, Fig. 3D) compared with other non-stomatal limitation factors. This suggests that the effect of increased precipitation on Chl content plays a major role in determining the carbon assimilation under ambient temperature condition. At the condition of $T_4$, MDA content had the closest relationship with $P_n$ ($R^2 = 0.81$, Fig. 3F) compared with other non-stomatal limitation factors. This suggests that the effect of increased precipitation on lipid peroxidation plays a major role in determining the carbon assimilation under high temperature condition.
In the present study, we found that high temperature induced the stomatal opening (increase in $G_s$, Table 2), but resulted in a decrease in carbon assimilation (decrease in $P_n$, Table 2), which is consistent with the research on *Leymus chinensis* by Xu & Zhou (2006). The response mechanism of plant photosynthesis to temperature can be studied by the balance between $V_{cmax}$ and $J_{max}$ (And & Sharkey, 1982; Song et al., 2016b). Wullschleger (1993) investigated 109 different species and concluded that there was a strong correlation between $V_{cmax}$ and $J_{max}$, which means there was a fixed balance relationship between RuBP carboxylation and regeneration in spite of the species or growth conditions. In our study, $V_{cmax}$ and $J_{max}$ showed a significant linear relationship under ambient temperature ($T_0$) condition, with the ratio of $J_{max}$ to $V_{cmax}$ being 1.88 ($p < 0.05$, Fig. 4A). However, with the increasing of temperature ($T_4$), even though there was still an obvious linear relationship between $V_{cmax}$ and $J_{max}$ ($p < 0.05$, Fig. 4B), the ratio of $J_{max}$ to $V_{cmax}$ decreased to 1.12. These results indicate that high temperature disrupted the balance between $V_{cmax}$ and $J_{max}$ resulting in a negative effect on the photosynthesis of *P. australis*. Similar results were also supported by the study of Huang et al. (2021).

Chlorophyll fluorescence can be used to detect the real photosynthetic behavior of the whole plant under stress quickly (Bhagooli et al., 2021). Based on this, it is possible to evaluate both the function of photosynthetic apparatus and the effects of environmental stress on plants. Environmental stress mainly damages the photosynthetic apparatus of PSII, and PSII will adjust the rate of electron transport and photochemical efficiency in response to the weakened ability of CO$_2$ assimilation (Aragón-Gastélum et al., 2020; Hasanuzzaman et al., 2013). The damage caused by excess light energy to the system will be mitigated by heat dissipation. Water deficiency and heat stress will cause the inactivation or damage of leaf’s PSII reaction center (He et al., 2021; Mathur, Agrawal & Jajoo, 2014). This will lead to the damage of the photosynthetic apparatus and bring about the photoinhibition, which is consistent with the studies by Farfan-Vignolo & Asard (2012).
In our present research, precipitation change and high temperature had a significant effect on the photosynthesis of *P. australis*. However, how *P. australis* resists those environmental stresses to protect itself is still unknown. To solve this problem, three fluorescence parameters (\(\Phi_{\text{PSII}}\), \(\Phi_{\text{NPQ}}\) and \(\Phi_{\text{NO}}\)) based on Lake model were used to detect the partitioning of absorbed light energy and to explore the protective mechanism in PSII reaction center (Kramer et al., 2004; Li et al., 2019b). Among the three fluorescence parameters, \(\Phi_{\text{PSII}}\) (absorbed light energy utilized by PSII photochemistry) reflects the linear electron transport indirectly, \(\Phi_{\text{NPQ}}\) (thermally dissipated via \(\Delta pH\) and xanthophyll-dependent energy quenching) represents the yield of dissipation by downregulation, and \(\Phi_{\text{NO}}\) (thermally dissipated via \(\Delta pH\) and xanthophyll-dependent energy quenching) reflects the yield of other non-photochemical losses (García-Sánchez et al., 2012; Nabi et al., 2021). In Figure 2, it was found that precipitation change and high temperature had no significant effect on the value of \(\Phi_{\text{PSII}}\), suggesting that heat dissipation of the excess light energy was dissipated to the extracellular as a form of heat to protect the photosynthetic apparatus from damage caused by photoinhibition (Li et al., 2019a; Song et al., 2016b). Moreover, Figure 5 showed that there was a strong relationship \((p < 0.01)\) between \(\Phi_{\text{PSII}}\) and \(\Phi_{\text{NPQ}}\), and the correlation between \(\Phi_{\text{PSII}}\) and \(\Phi_{\text{NO}}\) were not evident \((p > 0.05)\). This suggests that the xanthophyll cycle-mediated thermal dissipation plays a major role in PSII photoprotection under changing precipitation and high temperature.
conditions, while the non-regulated quenching mechanism may play a less important role (Demmig-Adams & Adams, 2018; Stael et al., 2015). The results are opposite with the findings on plant responses to heat stress, water deficit and cold stress by other scholars (Dias et al., 2018; Osório et al., 2011; Savitch et al., 2009; Song, Wang & Lv, 2016). The possible reason is that \textit{P. australis} as the dominant species of coastal wetlands in China, having a strong ability in resisting environmental stress by dissipating excess excitation energy, which cannot be used in PSII photochemistry reaction as harmless heat through the xanthophyll cycle (Demmig-Adams et al., 1996; Lu et al., 2020; Zhang et al., 2015).

CONCLUSIONS

In conclusion, the photosynthesis of \textit{P. australis} during precipitation changing is dependent on non-stomatal limitation but not stomatal closure, which have a significant negative linear correlation with Chl a/b ratio and MDA content. At the same time, high temperature causes the biochemical limitation on photosynthesis, inhibits the positive effects of increased precipitation and aggravates the adverse effects of drought on photosynthesis of \textit{P. australis}. Even though high temperature and drought (precipitation decrease) significantly decrease the carbon assimilation rate, \textit{P. australis} still has a strong ability to protect itself from damages by transforming excess excitation energy into harmless heat. This study highlighted the significant role of precipitation change in regulating the photosynthetic performance of \textit{P. australis} under elevated temperature conditions, which may help us to better understand the mechanisms of vegetation degradation and provide knowledge basis for the restoration of the vegetation in climate sensitive regions under the background of global change.

ACKNOWLEDGEMENTS

We are grateful to Li Changjiang at Shandong Agricultural University for his assistance in the data collection and processing.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

This work was supported by the National Natural Science Foundation of China (Nos. 32000402 and 32101365) and the Fund for Doctor Research of Dezhou University, China (No. 2019xgrc26). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
National Natural Science Foundation of China: 32000402 and 32101365.
Fund for Doctor Research of Dezhou University, China: 2019xgrc26.

Competing Interests

The authors declare that they have no competing interests.
Author Contributions

- Linhong Teng conceived and designed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Hanyu Liu performed the experiments, prepared figures and/or tables, and approved the final draft.
- Xiaonan Chu performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Xiliang Song conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, and approved the final draft.
- Lianhui Shi conceived and designed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The raw measurements are available in the Supplemental File.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.13087#supplemental-information.

REFERENCES

Alam MR, Nakasathien S, Molla MSH, Islam MA, Maniruzzaman M, Sarobol MA, Vichukit V, Hassan MM, Dessoky ES, El-Ghany EMA, Brestic M, Skalicky M, Jagadish SVK, Hossain A. 2021. Kernel water relations and kernel filling traits in maize (Zea mays L.) are influenced by water-deficit condition in a tropical environment. Frontiers in Plant Science 12:717178 DOI 10.3389/fpls.2021.717178.

Aragón-Gastélum JL, Ramírez-Benítez JE, González-Durán E, González-Salvatierra C, Ramírez-Tobías HM, Flores J, Gutiérrez-Alcántara EJ, Méndez-Guzmán E, Jarquin-Gálvez R. 2020. Photochemical activity in early-developmental phases of Agave angustifolia subsp. tequilana under induced global warming: implications to temperature stress and tolerance. Flora 263:151535 DOI 10.1016/j.flora.2019.151535.

And GDF, Sharkey TD. 1982. Stomatal conductance and photosynthesis. Annual Review of Plant Physiology 33(1):317–345 DOI 10.1146/annurev.pp.33.060182.001533.

Ashraf M, Harris PJC. 2013. Photosynthesis under stressful environments: an overview. Photosynthetica 51(2):163–190 DOI 10.1007/s11099-013-0021-6.

Bagheri M, Gholami M, Baninasab B. 2019. Hydrogen peroxide-induced salt tolerance in relation to antioxidant systems in pistachio seedlings. Scientia Horticulturae 243:207–213 DOI 10.1016/j.scienta.2018.08.026.

Bijanzadeh E, Barati V, Egan TP. 2022. Foliar application of sodium silicate mitigates drought stressed leaf structure in corn (Zea mays L.). South African Journal of Botany 147:8–17 DOI 10.1016/j.sajb.2021.12.032.

Bhagooli R, Mattan-Moorgawa S, Kaullysing D, Louis YD, Gopecchund A, Ramah S, Soondur M, Pilly SS, Beesoo R, Wijayanti DP, Bachok ZB, Monráis VC, Casareto BE, Suzuki Y, Baker AC. 2021. Chlorophyll fluorescence—A tool to assess photosynthetic...
performance and stress photophysiology in symbiotic marine invertebrates and seaplants. Marine Pollution Bulletin 165(4):112059 DOI 10.1016/j.marpolbul.2021.112059.

Carvalho M, Castro I, Moutinho-Pereira J, Correia C, Egea-Cortines M, Matos M, Rosa E, Carnide V, Lino-Neto T. 2019. Evaluating stress responses in cowpea under drought stress. Journal of Plant Physiology 241(8):153001 DOI 10.1016/j.jplph.2019.153001.

Crowther TW, Todd-Brown KEO, Rowe CW, Carey JC, Machmuller MB, Snoek BL, Fang S, Zhou G, Allison SD, Blair JM, Bridgham SD, Burton AJ, Carrillo Y, Reich PB, Clark JS, Classen AT, Dijkstra FA, Elberling B, Emmett BA, Estiarte M, Frey SD, Guo J, Harte J, Jiang L, Johnson BR, Kröel-Dulay G, Larsen KS, Laudon H, Lavallee JM, Luo Y, Lupascu M, Ma LN, Marhan S, Michelsen A, Mohan J, Niu S, Pendall E, Peñuelas J, Pfeifer-Meister L, Poll C, Reynolds LL, Schmidt IK, Sistla S, Sokol NW, Templer PH, Treseder KK, Welker JM, Bradford MA. 2016. Quantifying global soil carbon losses in response to warming. Nature 540(7631):104–108 DOI 10.1038/nature20150.

Daryanto S, Wang L, Jacinthe PA. 2017. Global synthesis of drought effects on cereal, legume, tuber and root crops production: a review. Agricultural Water Management 179:18 –33 DOI 10.1016/j.agwat.2016.04.022.

Demmig-Adams B, Adams WW. 2018. An integrative approach to photoinhibition and photoprotection of photosynthesis. Environmental and Experimental Botany 154:1–3 DOI 10.1016/j.envexpbot.2018.05.006.

Demmig-Adams B, Adams WW, Barker DH, Logan BA, Bowling DR, Verhoeven AS. 1996. Using chlorophyll fluorescence to assess the fraction of absorbed light allocated to thermal dissipation of excess excitation. Physiologia Plantarum 98:253–264 DOI 10.1034/j.1399-3054.1996.809206.x.

Dias CS, Araujo L, Alves Chaves JA, DaMattia FM, Rodrigues FA. 2018. Water relation, leaf gas exchange and chlorophyll a fluorescence imaging of soybean leaves infected with Colletotrichum truncatum. Plant Physiology and Biochemistry 127:119–128 DOI 10.1016/j.plaphy.2018.03.016.

Drake K, Halifax H, Adamowicz SC, Craft C. 2015. Carbon Sequestration in Tidal Salt Marshes of the Northeast United States. Environmental Management 56(4):998–1008 DOI 10.1007/s00267-015-0568-z.

Du W, Ruan C, Li J, Li H, Ding J, Zhao S, Jiang X. 2021. Quantitative proteomic analysis of Xanthoceras sorbifolium Bunge seedlings in response to drought and heat stress. Plant Physiology and Biochemistry 160:8–17 DOI 10.1016/j.plaphy.2021.01.002.

Farfan-Vignolo ER, Asard H. 2012. Effect of elevated CO2 and temperature on the oxidative stress response to drought in Lolium perenne L. and Medicago sativa L. Plant Physiology and Biochemistry 59:55–62 DOI 10.1016/j.plaphy.2012.06.014.

Farquhar GD, Von CS, Berry JA. 1980. A biochemical model of photosynthetic CO2 assimilation in leaves of C3 species. Planta 149(1):78–90 DOI 10.1007/BF00386231.

Fennessy MS. 2014. Wetland ecosystems and global change. In: Freedman B, ed. Global Environmental Change. Dordrecht: Springer Netherlands, 255–261 DOI 10.1007/978-94-007-5784-4_129.

Forbesa SJ, Cernusaka LA, Northfielda TD, Gleadowc RM, Lambertd S, Cheesman AW. 2020. Elevated temperature and carbon dioxide alter resource allocation to growth, storage and defence in cassava (Manihot esculenta). Environmental and Experimental Botany 173(3):103997 DOI 10.1016/j.envexpbot.2020.103997.

Gadzinowska J, Hura K, Ostrowska A, Hura T. 2021. Activity of the photosynthetic apparatus in dehydrated leaves of a perennial shrub Rosa rubiginosa L. with different levels of drought.
memory. *Environmental and Experimental Botany* **187**:104493
DOI 10.1016/j.envexpbot.2021.104493.

García-Sánchez M, Korbee N, Pérez-Ruzafa IM, Marcos C, Domínguez B, Figueroa FL, Pérez-Ruzafa Á. 2012. Physiological response and photoacclimation capacity of *Caulerpa prolifera* (Forsskål) J.V. Lamouroux and *Cymodocea nodosa* (Ucria) Ascherson meadows in the Mar Menor lagoon (SE Spain). *Marine Environmental Research* **79**(4):37–47
DOI 10.1016/j.marenvres.2012.05.001.

Guan B, Yu J, Hou A, Han G, Wang G, Qu F, Xia J, Wang X. 2017. The ecological adaptability of *Phragmites australis* to interactive effects of water level and salt stress in the Yellow River Delta. *Aquatic Ecology* **51**(1):107–116
DOI 10.1007/s10452-016-9602-3.

Gujjar RS, Banyen P, Chuekong W, Worakan P, Roytrakul S, Supaibulwatana K. 2020. A synthetic cytokinin improves photosynthesis in rice under drought stress by modulating the abundance of proteins related to stomatal conductance, chlorophyll contents, and rubisco activity. *Plants* **9**(9):1106
DOI 10.3390/plants9091106.

Hao L, Guo L, Li R, Cheng Y, Huang L, Zhou H, Xu M, Li F, Zhang X, Zheng Y. 2019. Responses of photosynthesis to high temperature stress associated with changes in leaf structure and biochemistry of blueberry (*Vaccinium corymbosum* L.). *Scientia Horticulturae* **246**:251–264
DOI 10.1016/j.scienta.2018.11.007.

Hasanuzzaman M, Nahar K, Alam MM, Roychowdhury R, Fujita M. 2013. Physiological, biochemical, and molecular mechanisms of heat stress tolerance in plants. *International Journal of Molecular Sciences* **14**(5):9643–9684
DOI 10.3390/ijms14059643.

He W, Yan K, Zhang Y, Bian L, Mei H, Han G. 2021. Contrasting photosynthesis, photoinhibition and oxidative damage in honeysuckle (*Lonicera japonica* Thunb.) under iso-osmotic salt and drought stresses. *Environmental and Experimental Botany* **182**(7):104313
DOI 10.1016/j.envexpbot.2020.104313.

Hiraishi T, Krug T, Tanabe K, Srivastava N, Baasansuren J, Fukuda M, Troxler TG. 2014. 2013 Supplement to the 2006 IPCC guidelines for national greenhouse gas inventories: wetlands. Switzerland: IPCC.

Hiscox JD, Israelstam GF. 1979. A method for the extraction of chlorophyll from leaf tissue without maceration. *Canadian Journal of Botany* **57**(12):1332–1334
DOI 10.1139/b79-163.

Hossain A, Skalicky M, Brestic M, Maitra S, Alam MA, Syed MA, Hossain J, Sarkar S, Saha S, Bhadra P, Shankar T, Bhatt R, Chaki AK, Sabagh AE, Islam T. 2021. Consequences and mitigation strategies of abiotic stresses in wheat (*Triticum aestivum* L.) under the changing climate. *Agronomy* **11**(2):214
DOI 10.3390/agronomy11020241.

Hosseini Sannehkooi F, Pirdashti H, Bakhshandeh E. 2021. Quantifying water stress and temperature effects on camelina (*Camelina sativa* L.) seed germination. *Environmental and Experimental Botany* **186**:104450
DOI 10.1016/j.envexpbot.2021.104450.

Hosseinpour M, Ebadi A, Habibi H, Nabizadeh E, Jahanbakhsh S. 2020. Enhancing enzymatic and nonenzymatic response of Echinacea purpurea by exogenous 24-epibrassinolide under drought stress. *Industrial Crops & Products* **146**(4):112045
DOI 10.1016/j.indcrop.2019.112045.

Hsieh SH, Yuan CS, Le IR, Yang L, Lin HJ, Hsueh ML. 2020. In-situ measurement of greenhouse gas emissions from a coastal estuarine wetland using a novel continuous monitoring technology: comparison of indigenous and exotic plant species. *Journal of Environmental Management* **281**(1):111905
DOI 10.1016/j.jenvman.2020.111905.

Hu Y, Kang S, Ding R, Du T, Tong L, Li S. 2020. The dynamic yield response factor of alfalfa improve the accuracy of dual crop coefficient approach under water and salt stress. *Water* **12**(5):1224
DOI 10.3390/w12051224.
Huang G, Yang Y, Zhu L, Peng S, Li Y. 2021. Temperature responses of photosynthesis and stomatal conductance in rice and wheat plants. *Agricultural and Forest Meteorology* **300**(332):108322 DOI 10.1016/j.agrformet.2021.108322.

Hussain S, Ulhassan Z, Brestic M, Zivcak M, Zhou W, Allakhverdiev SI, Yang X, Safdar ME, Yang W, Liu W. 2021. Photosynthesis research under climate change. *Photosynthesis Research* **150**(1–3):5–19 DOI 10.1007/s11120-021-00861-z.

IPCC. 2019. Climate change and land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems. Available at https://www.ipcc.ch/site/assets/uploads/2019/11/SRCCCL-Full-Report-Compiled-191128.pdf.

Jahan MS, Guo S, Sun J, Shu S, Wang Y, El-Yazied AA, Alabdallah NM, Hikal M, Mohamed MHM, Ibrahim MFM, Hasan MM. 2021. Melatonin-mediated photosynthetic performance of tomato seedlings under high-temperature stress. *Plant Physiology and Biochemistry* **167**(6):309–320 DOI 10.1016/j.plaphy.2021.08.002.

Janka E, Körner O, Rosenqvist E, Ottosen CO. 2015. Using the quantum yields of photosystem II and the rate of net photosynthesis to monitor high irradiance and temperature stress in chrysanthemum (*Dendranthema grandiflora*). *Plant Physiology and Biochemistry* **90**:14–22 DOI 10.1016/j.plaphy.2015.02.019.

Jiang W, Chen L, Han Y, Cao B, Song L. 2020. Effects of elevated temperature and drought stress on fruit coloration in the jujube variety ‘Lingwuchangzao’ (Ziziphus jujube cv. Lingwuchangzao). *Scientia Horticulturae* **274**(5):109667 DOI 10.1016/j.scienta.2020.109667.

Kanojia A, Dijkwel PP. 2018. Abiotic stress responses are governed by reactive oxygen species and age. *Annual Plant Reviews Online* 1:295–326 DOI 10.1002/9781119312994.apr0611.

Kramer DM, Johnson G, Kiirats O, Edwards GE. 2004. New fluorescence parameters for the determination of QA redox state and excitation energy fluxes. *Photosynthesis Research* **79**(2):209–218 DOI 10.1023/b:pres.0000015391.99477.0d.

Kumari VV, Roy A, Vijayan R, Banerjee P, Verma VC, Nalia A, Pramanik M, Mukherjee B, Ghosh A, Reja MH, Chandran MAS, Nath R, Skalicky M, Brestic M, Hossain A. 2021. Drought and heat stress in cool-season food legumes in sub-tropical regions: consequences, adaptation, and mitigation strategies. *Plants* **10**(6):1038 DOI 10.3390/plants10061038.

Küsters J, Pötsch EM, Resch R, Gierus M. 2021. The effect of summer water stress on the nutritive value of orchard grass (*Dactylis glomerata* L.) in permanent grassland under increased temperature and elevated atmospheric CO$_2$. *Ecological Indicators* **125**(3–4):107566 DOI 10.1016/j.ecolind.2021.107566.

Lamptey S, Li L, Xie J, Coulter JA. 2020. Tillage system affects soil water and photosynthesis of plastic-mulched maize on the semiarid Loess Plateau of China. *Soil and Tillage Research* **196**(1–2):104479 DOI 10.1016/j.still.2019.104479.

Lazár D. 2015. Parameters of photosynthetic energy partitioning. *Journal of Plant Physiology* **175**(89):131–147 DOI 10.1016/j.jplph.2014.10.021.

Li J, Zhao S, Yu X, Du W, Li H, Sun Y, Sun H, Ruan C. 2021a. Role of Xanthoceras sorbifolium MYB44 in tolerance to combined drought and heat stress via modulation of stomatal closure and ROS homeostasis. *Plant Physiology and Biochemistry* **162**:410–420 DOI 10.1016/j.plaphy.2021.03.007.

Li P, Zhu Y, Song X, Song F. 2020. Negative effects of long-term moderate salinity and short-term drought stress on the photosynthetic performance of *Hybrid Pennisetum*. *Plant Physiology and Biochemistry* **155**:93–104 DOI 10.1016/j.plaphy.2020.06.033.
Li L, Konkel J, Jin VL, Schaeffer SM. 2021b. Conservation management improves agroecosystem function and resilience of soil nitrogen cycling in response to seasonal changes in climate. *Science of the Total Environment* 779:146457 DOI 10.1016/j.scitotenv.2021.146457.

Li Y, Song H, Zhou L, Xu Z, Zhou G. 2019a. Tracking chlorophyll fluorescence as an indicator of drought and rewatering across the entire leaf lifespan in a maize field. *Agricultural Water Management* 211:190–201 DOI 10.1016/j.agwat.2018.09.050.

Li Y, Zhang T, Zhang Z, He K. 2019b. The physiological and biochemical photosynthetic properties of Lycium ruthenicum Murr in response to salinity and drought. *Scientia Horticulturae* 256:108530 DOI 10.1016/j.scienta.2019.05.057.

Lichtenthaler HK, Buschmann C. 2001. Chlorophylls and carotenoids: measurement and characterization by UV-VIS spectroscopy. *Current Protocols in Food Analytical Chemistry* 1(1):F4.3.1–F4.3.8 DOI 10.1002/0471142913.faf0403s01.

Liu B, Liang J, Tang G, Wang X, Liu F, Zhao D. 2019. Drought stress affects on growth, water use efficiency, gas exchange and chlorophyll fluorescence of Juglans rootstocks. *Scientia Horticulturae* 250(9):230–235 DOI 10.1016/j.scienta.2019.02.056.

Liu F, Jensen CR, Shahanzari A, Andersen MN, Jacobsen SE. 2005. ABA regulated stomatal control and photosynthetic water use efficiency of potato (*Solanum tuberosum* L.) during progressive soil drying. *Plant Science* 168(3):831–836 DOI 10.1016/j.plantsci.2004.10.016.

Liu S, Zheng Y, Ma R, Yu K, Han Z, Xiao S, Li Z, Wu S, Li S, Wang J, Luo Y, Zou J. 2020. Increased soil release of greenhouse gases shrinks terrestrial carbon uptake enhancement under warming. *Global Change Biology* 26(8):4601–4613 DOI 10.1111/gcb.15156.

Liu X, Zhang Y, Leng X, Yang Q, Chen H, Wang X, Cui N. 2022. Exploring the optimisation of mulching and irrigation management practices for mango production in a dry hot environment based on the entropy weight method. *Scientia Horticulturae* 291(4):110564 DOI 10.1016/j.scienta.2021.110564.

Lu J, Nawaz MA, Wei N, Cheng F, Bie Z. 2020. Suboptimal temperature acclimation enhances chilling tolerance by improving photosynthetic adaptability and osmoregulation ability in watermelon. *Horticultural Plant Journal* 6(1):4–60 DOI 10.1016/j.hpj.2020.01.001.

Mathur S, Agrawal D, Jajoo A. 2014. Photosynthesis: response to high temperature stress. *Journal of Photochemistry and Photobiology B: Biology* 137(2):116–126 DOI 10.1016/j.jphotobiol.2014.01.010.

Mitchell PJ, Veneklaas EJ, Lambers H, Burgess SSO. 2008. Leaf water relations during summer water deficit: differential responses in turgor maintenance and variation in leaf structure among different plant communities in south-western Australia. *Plant, Cell & Environment* 31(12):1791–1802 DOI 10.1111/j.1365-3040.2008.01882.x.

Morales M, Munné-Bosch S. 2019. Malondialdehyde: facts and artifacts. *Plant Physiology* 180(3):1246–1250 DOI 10.1104/pp.19.00405.

Nabi A, Parwez R, Aftab T, Khan MMA, Naeem M. 2021. Triacontanol protects *Mentha arvensis* L. from nickel-instigated repercussions by escalating antioxidant machinery, photosynthetic efficiency and maintaining leaf ultrastructure and root morphology. *Journal of Plant Growth Regulation* 40:1594–1612 DOI 10.1007/s00344-020-10208-y.

Nath M, Bhatt D, Prasad R, Gill SS, Anjum NA, Tuteja N. 2016. Reactive oxygen species generation-scavenging and signaling during plant-arbuscular mycorrhizal *Piriformospora indica* interaction under stress condition. *Frontiers in Plant Science* 7(906):1574 DOI 10.3389/fpls.2016.01574.

Naz R, Sarfraz A, Anwar Z, Yasin M, Nosheen A, Keyani R, Roberts TH. 2021. Combined ability of salicylic acid and spermidine to mitigate the individual and interactive effects of...
drought and chromium stress in maize (*Zea mays* L.). *Plant Physiology and Biochemistry* **159**:285–300 DOI 10.1016/j.plaphy.2020.12.022.

Nolf M, Creek D, Duursma R, Holtum J, Mayr S, Choat B. 2015. Stem and leaf hydraulic properties are finely coordinated in three tropical rain forest tree species. *Plant, Cell & Environment* **38**(12):2652–2661 DOI 10.1111/pce.12581.

Olorunwa J, Shi A, Barickman TC. 2021. Varying drought stress induces morpho-physiological changes in cowpea (*Vigna unguiculata* L.) genotypes inoculated with *Bradyrhizobium japonicum*. *Plant Stress* **2**(2):100033 DOI 10.1016/j.stress.2021.100033.

Ouyang Z, Tian J, Yan X, Shen H. 2020. Effects of different concentrations of dissolved oxygen or temperatures on the growth, photosynthesis, yield and quality of lettuce. *Agricultural Water Management* **228**:105896 DOI 10.1016/j.agwat.2019.105896.

Parrotta L, Aloisi I, Faleri C, Romi M, Duca SD, Ca G. 2020. Chronic heat stress affects the photosynthetic apparatus of *Solanum lycopersicum* L. cv Micro-Tom. *Plant Physiology and Biochemistry* **154**(11):463–475 DOI 10.1016/j.plaphy.2020.06.047.

Perdomo JA, Capó-Bauçà S, Carmo-Silva E, Galmés J. 2017. Rubisco and rubisco activase play an important role in the biochemical limitations of photosynthesis in rice, wheat, and maize under high temperature and water deficit. *Frontiers in Plant Science* **8**(1719):490 DOI 10.3389/fpls.2017.00490.

Raja V, Majeed U, Kang H, Andrabi KI, John R. 2017. Abiotic stress: interplay between ROS, hormones and MAPKs. *Environmental and Experimental Botany* **137**(4):142–157 DOI 10.1016/j.envexpbot.2017.02.010.

Raja V, Qadir SU, Alyemeni MN, Ahmad P. 2020. Impact of drought and heat stress individually and in combination on physio-biochemical parameters, antioxidant responses, and gene expression in *Solanum lycopersicum*. 3 Biotech **10**(5):208 DOI 10.1007/s13205-020-02206-4.

Rodriguez E, da Conceição Santos M, Azevedo R, Correia C, Moutinho-Pereira J, Ferreira de Oliveira JMP, Dias MC. 2015. Photosynthesis light-independent reactions are sensitive biomarkers to monitor lead phytotoxicity in a Pb-tolerant *Pisum sativum* cultivar. *Environmental Science and Pollution Research* **22**(1):574–585 DOI 10.1007/s11356-014-3375-9.

Savitch LV, Ivanov AG, Gudynaite-Savitch L, Huner NPA, Simmonds J. 2009. Effects of low temperature stress on excitation energy partitioning and photoprotection in *Zea mays*. *Functional Plant Biology* **36**(1):37–49 DOI 10.1071/FP08093.

Shao R, Jia S, Tang Y, Zhang J, Li H, Li L, Chen J, Guo J, Wang H, Yang Q, Wang Y, Liu T, Zhao X. 2021. Soil water deficit suppresses development of maize ear by altering metabolism and photosynthesis. *Environmental and Experimental Botany* **192**(5):104651 DOI 10.1016/j.envexpbot.2021.104651.

Snider JL, Collins GD, Whitaker J, Perry CD, Chastain DR. 2014. Electron transport through photosystem II is not limited by a wide range of water deficit conditions in field-grown
Gossypium hirsutum. Journal of Agronomy and Crop Science 200(1):77–82 DOI 10.1111/jac.12044.

Sohag AAM, Tahjib-Ul-Arif M, Brestic M, Afrin S, Sakil MA, Hossain MT, Hossain MTA. 2020. Exogenous salicylic acid and hydrogen peroxide attenuate drought stress in rice. Plant Soil and Environment 66(No. 1):7–13 DOI 10.17221/472/2019-PSE.

Song X, Zhou G, Xu Z, Lv X, Wang Y. 2016a. A self-photoprotection mechanism helps Stipa baicalensis adapt to future climate change. Scitific Reports 6(1):25839 DOI 10.1038/srep25839.

Song X, Wang Y, Lv X. 2016. Responses of plant biomass, photosynthesis and lipid peroxidation to warming and precipitation change in two dominant species (Stipa grandis and Leymus chinensis) from North China Grasslands. Ecology and Evolutation 6(6):1871–1882 DOI 10.1002/ece3.1982.

Song X, Zhou G, Xu Z, Lv X, Wang Y. 2016b. Detection of photosynthetic performance of Stipa bungeana seedlings under climatic change using Chlorophyll fluorescence imaging. Frontiers in Plant Science 6:1253–1254 DOI 10.3389/fpls.2015.01254.

Song L, Jin J, He J. 2019. Effects of severe water stress on maize growth processes in the field. Sustainability 11(18):5086 DOI 10.3390/su11185086.

Song X, Zhou G, He Q, Zhou H. 2020. Stomatal limitations to photosynthesis and their critical water conditions in different growth stages of maize under water stress. Agricultural Water Management 241(5):106330 DOI 10.1016/j.agwat.2020.106330.

Stael S, Kmiecik P, Willems P, Van Der Kelen K, Coll NS, Teige M, Van Breusegem F. 2015. Plant innate immunity—sunny side up? Trends in Plant Science 20(1):3–11 DOI 10.1016/j.tplants.2014.10.002.

Sun TT, Su ZH, Wang R, Liu R, Yang T, Zuo WT, Wen SS, Wang LQ. 2022. Transcriptome and metabolome analysis reveals the molecular mechanisms of Tamarix taklamakanensis under progressive drought and rehydration treatments. Environmental and Experimental Botany 195:104766 DOI 10.1016/j.envexpbot.2021.104766.

Talbi S, Rojas JA, Sahrawy M, Rodriguez-Serrano M, Cárdenas KE, Debouba M, Sandalio LM. 2020. Effect of drought on growth, photosynthesis and total antioxidant capacity of the saharan plant Oudeneya africana. Environmental and Experimental Botany 176(4):104099 DOI 10.1016/j.envexpbot.2020.104099.

Vaughan MM, Block A, Christensen SA, Allen LH, Schmelz EA. 2018. The effects of climate change associated abiotic stresses on maize phytochemical defenses. Phytochemistry Reviews 17(1):37–49 DOI 10.1007/s11101-017-9508-2.

Vurukonda SSKP, Vardharajula S, Shrivastava M, SkZ A. 2016. Enhancement of drought stress tolerance in crops by plant growth promoting rhizobacteria. Microbiological Research 184(10):13–24 DOI 10.1016/j.micres.2015.12.003.

Wang XM, Wang XK, Su YB, Zhang HX. 2019. Land pavement depresses photosynthesis in urban trees especially under drought stress. Science of The Total Environment 653(2):120–130 DOI 10.1016/j.scitotenv.2018.10.281.

White HJ, Caplat P, Emmerson MC, Yearsley JM. 2021. Predicting future stability of ecosystem functioning under climate change. Agriculture, Ecosystems and Environment 320(6):107600 DOI 10.1016/j.agee.2021.107600.

Wullschleger SD. 1993. Biochemical limitations to carbon assimilation in C3 plants-A retrospective analysis of the A/Ci curves from 109 species. Journal of Experimental Botany 44(5):907–920 DOI 10.1093/jxb/44.5.907.

Xalxo R, Yadu B, Chandra J, Chandrakar V, Keshavkant S. 2020. Alteration in carbohydrate metabolism modulates thermostolerance of plant under heat stress. Heat Stress Tolerance in Plants 5:77–115 DOI 10.1002/9781119432401.ch5.
Xin Y, Tao F. 2021. Have the agricultural production systems in the North China Plain changed towards to climate smart agriculture since 2000? *Journal of Cleaner Production* **299**(12):126940 DOI 10.1016/j.jclepro.2021.126940.

Xu ZZ, Zhou GS. 2006. Combined effects of water stress and high temperature on photosynthesis, nitrogen metabolism and lipid peroxidation of a perennial grass *Leymus chinensis*. *Planta* **224**(5):1080–1090 DOI 10.1007/s00425-006-0281-5.

Xu Z, Zhou G. 2011. Responses of photosynthetic capacity to soil moisture gradient in perennial rhizome grass and perennial bunchgrass. *BMC Plant Biology* **11**(11):1–11 DOI 10.1186/1471-2229-11-21.

Yamori W, Hikosaka K, Way DA. 2014. Temperature response of photosynthesis in C3, C4, and CAM plants: temperature acclimation and temperature adaptation. *Photosynthesis Research* **119**(1–2):101–117 DOI 10.1007/s11120-013-9874-6.

Yan K, Zhao S, Cui M, Han G, Wen P. 2018. Vulnerability of photosynthesis and photosystem I in Jerusalem artichoke (*Helianthus tuberosus* L.) exposed to waterlogging. *Plant Physiology and Biochemistry* **125**(3):239–246 DOI 10.1016/j.plaphy.2018.02.017.

Yan W, Zhong Y, Shangguan Z. 2020. Elevated temperature exacerbates the effects of drought on the carbon and hydraulic characteristics of Robinia pseudoacacia seedlings. *Agricultural and Forest Meteorology* **280**(4):107794 DOI 10.1016/j.agrformet.2019.107794.

Zhang W, Yu X, Li M, Lang D, Zhang X, Xie Z. 2018. Silicon promotes growth and root yield of Glycyrrhiza uralensis under salt and drought stresses through enhancing osmotic adjustment and regulating antioxidant metabolism. *Crop Protection* **107**:1–11 DOI 10.1016/j.cropro.2018.01.005.

Zhang JL, Niu JP, Duan Y, Zhang MX, Liu JY, Li PM, Ma FW. 2015. Photoprotection mechanism in the ‘Fuji’ apple peel at different levels of photooxidative sunburn. *Physiologia Plantarum* **154**(1):54–65 DOI 10.1111/ppl.12272.

Zhong Q, Gong J, Wang K, Zhang C. 2014. Effects of 3-year air warming on growth of two perennial grasses (*Phragmites australis* and *Imperata cylindrica*) in a coastal salt marsh reclaimed for agriculture. *Aquatic Botany* **117**:18–26 DOI 10.1016/j.aquabot.2014.04.001.

Zhong Q, Wang K, Lai Q, Zhang C, Zheng L, Wang J. 2016. Carbon dioxide fluxes and their environmental control in a reclaimed coastal wetland in the Yangtze Estuary. *Estuaries and Coasts* **39**(2):344–362 DOI 10.1007/s12237-015-9997-4.

Zhu B, Xie X, Meng S, Lu C, Yao Y. 2020. Sensitivity of soil moisture to precipitation and temperature over China: present state and future projection. *Science of The Total Environment* **705**(D7):135774 DOI 10.1016/j.scitotenv.2019.135774.

Zhuang J, Wang Y, Chi Y, Zhou L, Chen J, Zhou W, Song J, Zhao N, Ding J. 2020. Drought stress strengthens the link between chlorophyll fluorescence parameters and photosynthetic traits. *PeerJ* **8**(8):10046 DOI 10.7717/peerj.10046.