Interactive Effects of Elevated CO₂ Concentration and Irrigation on Photosynthetic Parameters and Yield of Maize in Northeast China

Fanchao Meng¹,², Jiahua Zhang¹,³*, Fengmei Yao⁴, Cui Hao¹

¹ Institute of Eco-Environment and Agro-Meteorology, Chinese Academy of Meteorological Sciences, Beijing, China, ² College of Atmospheric Science, Nanjing University of Information Science & Technology, Nanjing, China, ³ Key Laboratory of Meteorological Science, Institute of Remote Sensing and Digital Earth, Chinese Academy of Sciences, Beijing, China, ⁴ Key Laboratory of Computational Geodynamics, Chinese Academy of Sciences, Beijing, China

Abstract

Maize is one of the major cultivated crops of China, having a central role in ensuring the food security of the country. There has been a significant increase in studies of maize under interactive effects of elevated CO₂ concentration ([CO₂]) and other factors, yet the interactive effects of elevated [CO₂] and increasing precipitation on maize has remained unclear. In this study, a manipulative experiment in Jinzhou, Liaoning province, Northeast China was performed so as to obtain reliable results concerning the later effects. The Open Top Chambers (OTCs) experiment was designed to control contrasting [CO₂] i.e., 390, 450 and 550 µmol·mol⁻¹, and the experiment with 15% increasing precipitation levels was also set based on the average monthly precipitation of 5–9 month from 1981 to 2010 and controlled by irrigation. Thus, six treatments, i.e. C₃₉₀W₀, C₄₅₀W₀, C₅₅₀W₀, C₃₉₀W₁₅%, C₄₅₀W₁₅%, and C₅₅₀W₁₅% were included in this study. The results showed that the irrigation under elevated [CO₂] levels increased the leaf net photosynthetic rate (Pₚₙ) and intercellular CO₂ concentration (Cᵢ) of maize. Similarly, the stomatal conductance (Gₛ) and transpiration rate (Tₑ) decreased with elevated [CO₂], but irrigation has a positive effect on increased of them at each [CO₂] level, resulting in the water use efficiency (WUE) higher in natural precipitation treatment than irrigation treatment at elevated [CO₂] levels. Irradiance-response parameters, e.g., maximum net photosynthetic rate (Pₚₙ₉₉) and light saturation points (LSP) were increased under elevated [CO₂] and irrigation, and dark respiration (Rₙ) was increased as well. The growth characteristics, e.g., plant height, leaf area and aboveground biomass were enhanced, resulting in an improved of yield and ear characteristics except axle diameter. The study concluded by reporting that, future elevated [CO₂] may favor to maize when coupled with increasing amount of precipitation in Northeast China.

Introduction

The CO₂ concentration ([CO₂]) in the atmosphere is about 390 µmol·mol⁻¹ as a consequence of fossil fuel combustion and deforestation, which is predicted to reach 550 µmol·mol⁻¹ by the middle of this century [1]. Elevated [CO₂] is an important abiotic factor, and has significant fertilization effects on crops. Extensive previous studies have reported that elevated [CO₂] significantly improved water use efficiency, lower transpiration rate, shorten maize growth period, and increased plant height, leaf number, leaf area, growth rate and yield [2–12]. In addition, the increasing of atmospheric [CO₂] affects precipitation balance, which can change the seasonal precipitation distribution [13]. It has been estimated that this effect would bring about a 10% increase or decrease in water resources at different areas [14]. The global annual average precipitation increase is about 2% since the beginning of the 20th century [15–16], and this rise over the area of 30°–85°N has shown a 7%–12% increase [17]. It has been predicted that the rainfall decrease will be noticed in middle-and-lower regions of Yangtze River (24° N–34° N, 100° E–122° E), while the rain belts are likely to move towards north of China and precipitation would increase in Northeast China in the future [18]. The crop growth of Northeast China will likely be affected by both elevated [CO₂] and increasing precipitation, which are important abiotic factors that directly or indirectly affect crop growth, physiological processes and productivity. Thus, it is necessary to understand the interactive effects of elevated [CO₂] and increasing precipitation on crop growth in Northeast China under future climate change.

In fact, lots of studies have been focused on the interactive effects of elevated [CO₂] and other environmental factors on plant growth. The study of the interactive effects of elevated [CO₂] and temperature indicated that the effects on photosynthesis and growth in C₄ species are obvious [19–22]. FACE (Free Air Carbon-dioxide Enrichment) and chamber experiment have demonstrated that the interactive effects of elevated [CO₂] and
Elevated \([\text{CO}_2]\) and Irrigation on Photosynthesis and Yield of Maize

drought stress have an increase in the leaf water-use efficiency [23–24], and more recent evidence shows that maize will benefit from the increase in \([\text{CO}_2]\) under drought condition [25–29]. Also, the studies of the interactive effects of elevated \([\text{CO}_2]\) and light on plant found that high light have a great effect on net photosynthesis in condition of elevated \([\text{CO}_2]\) [30–31]. Regarding the interactive effects of elevated \([\text{CO}_2]\) and Ozone (\(\text{O}_3\)), studies showing that elevated \([\text{CO}_2]\) inhibits adverse effects of \(\text{O}_3\) and increased trees seedling stem diameters at low \(\text{O}_3\) [32–35]. Moreover, the interactive effects of elevated \([\text{CO}_2]\) and soil nutrition have been investigated. For example, the studies of the interactive effects of elevated \([\text{CO}_2]\) and nitrogen (N) indicated that there is a positive \(\text{CO}_2\timesN\) interaction for grain yield of rice [36–39], while the research on the interactive effects of elevated \([\text{CO}_2]\) and potassium (K) found that plants grown under elevated \([\text{CO}_2]\) are more sensitive to K deficiency with higher leaf critical K levels [39]. Further, there are lots of studies involving the interactive effects of elevated \([\text{CO}_2]\) and other factors (e.g., NaCl-salinity, plant diversity) have been reported [40–41]. However, the interactive effects of elevated \([\text{CO}_2]\) and increasing precipitation on photosynthesis and yield of maize are not well understood. In particular, there has been no detailed study evaluating the interactive effects of elevated \([\text{CO}_2]\) and increasing precipitation on photosynthesis efficiency, water use efficiency and yield of maize in Northeast China.

Northeast China (30°N–56°N, 120°E–135°E) is located in the middle-high latitudes and east of the Eurasian continent, which has a cultivated land area of 21.53 million \(\text{hm}^2\), accounted for 16.6% of the country’s total cultivated areas [42]. The summer is warm and short, and the annual precipitation is 400–800 mm. The precipitation from July to September is accounting for 60% of the annual precipitation. Moreover, Northeast China has fertile black soil, belonging to one of the three pieces of black soil in the world [43], hence, which is the biggest commercial grain production base and provides 30–35 million tons of commercial grain to country every year [44]. Therefore, it plays an important role to stabilize the grain market and keep sustainable development of China’s national economy. In Northeast China, maize (\(\text{Zea mays L.}\)) is the major cultivated crop, and its yield has accounted for about 1/3 of the national total maize yield [45]. The growth of maize requires more water, which yields tend to decrease if water deficit occurred during the key growing stages (e.g., silking stage) [46]. The precipitation in Northeast China can meet the water requirements of maize in most of the years, but slight drought has been discovered to occur in some of the past years. Therefore, for the rain-fed maize in Northeast China, precipitation is a very important climatic factor. If the water deficit occurred at silking stage of maize will cause disaccord flowering season, and then affect the pollination and seed formation, resulting in maize yield reduction.

To examine the interactive effects of elevated \([\text{CO}_2]\) and increasing precipitation on maize in Northeast China, we conducted an Open Top Chambers (OTCs) experiment under the combined effects of elevated \([\text{CO}_2]\) and precipitation in Jinzhou, Liaoning province during maize growing season (May to September) in 2013. Firstly, we tested the response of leaf gas exchange parameters (e.g., \(P_{\text{n}}\), \(T_{\text{c}}\)) and irradiance-response parameters (e.g., \(P_{\text{max}}\), \(L_{\text{SP}}\)) to the combined elevated \([\text{CO}_2]\) and increasing precipitation. Secondly, we examined the change in the growth parameters of maize (e.g., leaf area, aboveground biomass), yield and ear characters (e.g., ear length, ear diameter). The results of this study would be crucial for evaluating the possible consequences of climate change on crop photosynthetic capacity and yield in Northeast China, and may help inform regulatory policies to cope with the future climate change.

**Materials and Methods**

**Experimental site**

This study site is located at Jinzhou Ecological and Agricultural Meteorological Experiment Center (41°09’N, 121°10’E, 27.4 m a.s.l.) in Liaoning province of China, which is a warm temperature monsoon climate zone. The mean annual precipitation is 568.8 mm, and the mean annual temperature is 9.1°C. The annual frost-free period is approximately 180 d in duration, with an annual accumulated activity temperature is 3700°C·d. The site has typical brown soil, and the soil pH is approximately 6.3. The soil organic matter and total N are 6.41–9.43 g/kg and 0.69 g/kg, respectively [47].

**Open Top Chamber design**

Three pairs of Open Top Chambers (OTCs), each 3.5 m high with an octagonal ground surface area of 11.73 \(\text{m}^2\) were constructed. An inclined plane of 45° (inward on upper side of chambers) was provided for reducing gas escape from the top. The set up was completed in May 2011 (Fig. 1).

Additionally, the OTCs were constructed with a 5.3-m-wide buffer zone between them to prevent mutual shading. Carbon dioxide was supplied to the chambers through a pipe with pinholes connected to industrial carbon dioxide cylinders (liquid carbon dioxide, purity was 99.90%, supplied by Anjin Gas Corporation) outside the chambers. There was an exchange fan of each chamber, which mixed the entered carbon dioxide and fresh air from outside, then transported by pipe and well distributed in the entire chamber by the octagonal-pipe with holes, and the gas would discharge from the opening on top and put in air circulation. Carbon dioxide was supplied for 24 hours a day and the \([\text{CO}_2]\) was monitored by taking constant measurements with an infrared gas analyzer.

**Experimental design**

The effects of elevated \([\text{CO}_2]\) and precipitation on photosynthesis, growth, yield and ear characteristics of maize were examined in the chamber experiments. Considering the present ambient \([\text{CO}_2]\) and projected increasing \([\text{CO}_2]\) levels in next several decades from IPCC (2007) [1], three \([\text{CO}_2]\) levels were conducted with the OTC experiments including 390 \(\mu\text{mol-mol}^{-1}\) (\(C_{390}\)), 450 \(\mu\text{mol-mol}^{-1}\) (\(C_{450}\)) and 550 \(\mu\text{mol-mol}^{-1}\) (\(C_{550}\)).

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**Figure 1. View of Open Top Chambers on 21 July 2013 at Liaoning province, China.**

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According to 5–9 month average monthly precipitation in Jinzhou during 1981–2010 (see Fig. 2) and the prediction of increasing rainfall in Northeast China [18,48–49], two levels of watering including natural precipitation ($W_0$) and precipitation increased by 15% ($W_{+15}$) were designed. With this, maize, grown from seeds, was subjected to 6 different combined treatments (Table 1).

Three pairs of OTCs were used, and within each pair one was randomly assigned to receive the control ($390\, \text{mol} \cdot \text{mol}^{-2}$) and the others as the elevated [CO$_2$] (450 and 550 $\text{mol} \cdot \text{mol}^{-2}$). Every chamber was designed with two watering gradient (0 and +15%), and each gradients with 7 pots ($50.5\, \text{cm (diameter)} \times 32.5\, \text{cm (height)})$, producing 14 plots per treatment from June to September, respectively. It was divided into everyday average irrigation, directed into the pots in the morning and evening daily, and covering the raining days too.

The maize cultivar used in this study was Danyu 39, and now it is widely planted in Northeast China. Three maize seeds were planted in the pots using field soil on 10 May 2013, with final seeding at four-leaf stage. On 1 June, the 84 pots containing plants were moved into the chambers randomly, and each chamber contained 14 pots. Meanwhile, the levels of [CO$_2$] and water supplied were under monitored and controlled until harvest time (15 September).

Rainfall date and relative soil moisture measurements

The rainfall data were obtained from the Jinzhou weather station. The relative soil moisture (RSM) was calculated by the following equation [50]:

$$RSM(\%) = \frac{\text{soil moisture content}}{\text{soil field capacity}} \times 100\% \quad (1)$$

And the soil field capacity in this study was used the value of 21%, which according to the average value of soil field capacity in the last few years at this study site [51].

**Gas exchange measurements of maize**

Measurements were made between 8:30 a.m. and 11:30 a.m. (local time) from 24–26 July, 2013 (at the maize silking stage). Three representative plants were chosen for per treatment and the middle of the ear-leaves was measured, then the averages were taken. Gas exchange measurements were conducted using portable gas exchange systems (LI-6400, LI-Cor, Lincoln, NE, USA). The [CO$_2$] in the leaf chamber was controlled by the LI-Cor CO$_2$ injection system, and the built-in LED lamp (red/blue) supplied the irradiance. Temperature in leaf chamber was set at $30\, ^\circ\text{C}$, and the actual temperature of the leaf chamber ranged from 29 to $33\, ^\circ\text{C}$. The vapour pressure deficit on the leaf surface ($VpdL$) was between 2.9 and 3.4 kPa, and the flow control was at 500 $\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The lamp settings across the series of 2000, 1600, 1200, 1000, 800, 600, 400, 200, 150, 100, 80, 50, 20 and 0 $\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, and the measurements were recorded after equilibrium was reached. Each individual curve took approximately 30 min to complete.

$P_n$ curve fitting and analyzed of parameters were performed using the modified rectangular hyperbolic model by Ye and Yu [52–53], and its expression and correlative equations is as given below:

The soil moisture content was measured at a 0–20 cm soil depth. The soil samples of each treatment was collected and recorded as fresh weights and the samples were dried in an oven at $105\, ^\circ\text{C}$ for at least 48 hours. The soil moisture content was then measured using equation (2) given below:

$$\text{Soil moisture content(%) =} \frac{\text{fresh weight of soil} - \text{dry weight of soil}}{\text{dry weight of soil}} \times 100\% \quad (2)$$

And the soil field capacity in this study was used the value of 21%, which according to the average value of soil field capacity in the last few years at this study site [51].

**Figure 2. Monthly average precipitation during 1981–2010 years in the growing season of Maize in study area.** Gray bars indicate the regional monthly averages precipitation from 1981 to 2010, and black bars indicate increased 15% precipitation based on gray bars. doi:10.1371/journal.pone.0098318.g002
Equations (4)–(7) as described by Han et al. [54].

\[ P_n(PAR) = \frac{1 - \beta PAR}{1 + \gamma PAR} PAR - R_d \]  

(3)

where \( PAR \) is irradiance, \( \alpha \) is the initial slope of irradiance-response curve of photosynthesis when irradiance approaches to zero, \( \beta \) and \( \gamma \) are coefficients which are independent of \( PAR \), \( R_d \) is dark respiration (\( \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)). From these parameters, we can calculate \( P_{\text{max}} \) (maximum net photosynthetic rate, \( \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), \( LSP \) (light saturation point, \( \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)), \( LCP \) (light compensation point, \( \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)) and \( \varphi_c \) (quantum efficiency of the light compensation point, \( \text{mol} \cdot \text{mol}^{-1} \)) using equations (4)–(7) as described by Han et al. [54].

\[ P_{\text{max}} = \frac{1 - \beta PAR}{1 + \gamma PAR} \frac{PAR - R_d}{1} \]  

(4)

\[ \varphi_c = \frac{1 - 2\beta LCP - \beta \gamma LCP^2}{1 + \gamma LCP^2} \]  

(5)

\[ LCP = \frac{\alpha - \gamma R_d - \sqrt{(\gamma R_d - \alpha)^2 - 4\beta R_d}}{2\beta} \]  

(6)

\[ LSP = \frac{\sqrt{(\beta + \gamma) / \beta} - 1}{\gamma} \]  

(7)

Statistical analysis

In this study, statistical significance of growth and yield components was tested at 0.05 probability level \((P<0.05)\) following the DUNCAN test, performed using DPS 7.05 (Data-processing System, Zhejiang University, China). Irradiance-response curve fitting and parameter analysis based on modified rectangular hyperbolic model. The two-way analysis of variances (ANOVARs) were used to examine the interactive effects of elevated [CO2] and irrigation on growth parameters and yield of maize, and statistical significance were set at \( P<0.05 \) and \( P<0.01 \). These statistical analyses were conducted with SPSS 17.0 software (SPSS Institute Incorporated, Chicago, Illinois, USA). The standard deviation (S.D.) was calculated to compare the treatment means.

Results

Rainfall data and relative soil moisture

The variations of 5–9 month average monthly precipitation in Jinzhou during 1981–2010 are as shown in this work (Fig. 2). The work indicated that the amount of rainfall was maximum in July (176.93 mm) and less in May (57.43 mm).

The relative soil moisture of irrigation treatment was higher than that of the natural precipitation treatment at each [CO2] level (Fig. 3). The range of relative soil moisture in irrigation treatment was about 68.55%–69.84% and that of natural precipitation was about 56.68%–58.32%. According to the national standard of the Classification of Meteorological Drought (GB/T20481-2006) [50], we can see that the natural precipitation treatments are in-fact under slight drought.

Photosynthetic gas exchange parameters of maize

According to previous studies, the relationship between photosynthetic rate and irradiance could be well described by modified rectangular hyperbolic model [52]. This model was used to obtain the irradiance-response curve (Fig. 5 A), with \( R^2>0.99 \)

### Table 1. Treatments performed in OTCs.

| Treatments          | Description                                                                 |
|---------------------|-----------------------------------------------------------------------------|
| C390W15%            | Elevated [CO2] concentration (390 \text{\mu mol mol}^{-1}) and Increased 15% of precipitation |
| C390W0(CK)          | Elevated [CO2] concentration (390 \text{\mu mol mol}^{-1}) and Natural precipitation |
| C450W0(CK)          | Elevated [CO2] concentration (450 \text{\mu mol mol}^{-1}) and Natural precipitation |
| C550W0(CK)          | Elevated [CO2] concentration (550 \text{\mu mol mol}^{-1}) and Natural precipitation |
| C390W15%            | Ambient [CO2] concentration (390 \text{\mu mol mol}^{-1}) and Increased 15% of precipitation |
| C390W0(CK)          | Ambient [CO2] concentration (390 \text{\mu mol mol}^{-1}) and Natural precipitation |

It was obtained by dry weight. Before weighing, three plants from each treatment were separated into stem, leaf and grain. This was as a result of the need to shrivel it in oven at 105°C for 45 min and drying to constant weight at 85°C for at least 48 h.

At maturity stage, ten plants of each treatment were harvested for the yield components. The grains from each ear of maize were threshed by hand after air dried and weighed. The measured ear characteristics include: ear length, ear diameter, ear weight, 100-kernel weight, rows per ear, kernel number, shelled kernels, bare-tip length and axle diameter. The yield of each plant was calculated by 14% moisture content of grain.

During sampling, three representative plants of each treatment were randomly selected for measurement.

Growth and harvesting of maize

Maize growth stages were recorded throughout the growing season. The plant height, ear height, stem diameter, leaf area and aboveground biomass were measured at the silking stage of the maize. Leaf area of each plant was determined with long-width coefficient method (length × width × 0.75). Aboveground biomass
for all treatments, meanwhile the characteristic parameters were calculated from table 2. From the comparison between $P_n$ of experimental value and model predicted value (Fig. 4), it could be seen that there was a good agreement between them.

Figure 5 showed the dynamic changes of $P_n$, $T_r$, $WUE$, $G_s$ and $C_i$ with $PAR$ increased during silking stage of maize under interactive effects of elevated [CO2] and irrigation. With increased of $PAR$, $P_n$ curves of six treatments increased with elevated [CO2] and irrigation. Similarly, when $PAR$ is above 1500 μmol·m$^{-2}$·s$^{-1}$, $P_n$ curves closed to saturation and becomes stable. The order of six treatments were: $C_{550W+15%}>C_{450W+15%}>C_{550W0}>C_{390W+15%}>C_{450W0}>C_{390W0}$ (Fig. 5A); Whereas all the $T_r$ curves decreased with elevated [CO2], and were much lower in natural precipitation than irrigation treatment at each [CO2] level (Fig. 5B). $WUE$ showed higher values with elevated [CO2], and natural precipitation treatment showed higher than irrigation treatment at elevated [CO2] levels (Fig. 5C). However, $G_s$ curves showed opposite trend. The $G_s$ curves were lower with elevated [CO2] and rose with irrigation at the same [CO2] levels (Fig. 5D). There were high trends of $C_i$ under elevated [CO2], and the irrigation treatments were higher with the increased amounts in $PAR$ at each [CO2] level (Fig. 5E).

The $P_n$ curves were fitted and the parameters were generated by the modified rectangular hyperbolic model. The parameter $P_{nmax}$ of the ear-leaves for maize was increased by 12.43%, 19.80% and 29.70% under irrigation conditions above the natural precipitation at 390, 450 and 550 μmol·mol$^{-1}$ [CO2] levels, respectively. $Q_c$ was not affected by irrigation and elevated [CO2] (Table 2). Irrigation increased $LSP$ by 8.25%, 7.60% and 9.97% at 390, 450 and 550 μmol·mol$^{-1}$ [CO2] levels, respectively, but $LCP$ increased by 38.73%, 15.81% and 42.92%, and $R_d$ increased by 42.71%, 33.93% and 41.81% under the same conditions (Table 2).

Growth and development of maize

Plant height, ear height, stem diameter, leaf area and aboveground biomass of maize all had increasing trend under elevated [CO2] and irrigation, while $C_{390W0}$ always at its lowest value (Fig. 6). Plant height of $C_{550W+15%}$, $C_{450W+15%}$ and $C_{390W+15%}$ were significantly higher than $C_{390W0}$, $C_{450W0}$ and $C_{390W0}$ by 5.28%, 4.60% and 5.86%, respectively ($P<0.05$; Fig. 6A), while ear height were higher by 5.69%, 3.34% and 5.50%, respectively, and the same trend as plant height ($P<0.05$;
Fig. 6B). There were no significant differences of stem diameter for all treatments at silking stage, but C390W0 was observed to be low \( (P<0.05; \text{Fig. } 6C) \). There was a significant interactive effect for elevated \([\text{CO}_2]\) and irrigation in plant height \( (P<0.05; \text{Table } 4) \), but no significant interactive effects in ear height and stem diameter \( (P>0.05; \text{Table } 4) \). Irrigation significantly increased the leaf area by 12.04\%, 9.90\% and 7.75\% at 390, 450 and 550 \( \mu\text{mol mol}^{-1} \) \([\text{CO}_2]\) levels, respectively \( (P<0.05; \text{Fig. } 6D) \). In addition, irrigation significantly increased aboveground biomass by 16.66\%, 10.75\% and 7.65\% at 390, 450 and 550 \( \mu\text{mol mol}^{-1} \) \([\text{CO}_2]\) levels, respectively \( (P<0.05; \text{Fig. } 6E) \). The interactive effects of elevated \([\text{CO}_2]\) and irrigation were highly significant in leaf area \( (P<0.05; \text{Table } 4) \) and aboveground biomass \( (P<0.05; \text{Table } 4) \).

Yield and ear characteristics of maize

The study also revealed that when irrigation was compared with the natural precipitation at 390, 450 and 550 \( \mu\text{mol mol}^{-1} \) \([\text{CO}_2]\) levels, significantly increased the seed yield by 17.48\%, 14.91\% and 8.39\%, respectively \( (P<0.05; \text{Table } 3) \). Following from the above, economic coefficient showed a significant increase that was higher in irrigation than natural precipitation at each \([\text{CO}_2]\) level \( (P<0.05; \text{Table } 4) \). There were significant interactive effects of elevated \([\text{CO}_2]\) and irrigation on maize seed yield \( (P<0.05; \text{Table } 4) \) and biological yield \( (P<0.01; \text{Table } 4) \).

The maize ear characteristics showed significant differences in six treatments under elevated \([\text{CO}_2]\) and irrigation \( (P<0.05; \text{Table } 5) \). Irrigation increased 100-kernel weight by 10.59\%, 8.20\% and 5.19\% at 390, 450 and 550 \( \mu\text{mol mol}^{-1} \) \([\text{CO}_2]\) respectively, whereas that of shriveled kernels decreased by 16.66\%, 10.75\% and 7.65\% at 390, 450 and 550 \( \mu\text{mol mol}^{-1} \) \([\text{CO}_2]\) levels, respectively \( (P<0.05; \text{Table } 5) \). Also, rows per ear increased, but there was no difference among the six treatments. Maize ear length, ear diameter and ear weight were all significantly increased under irrigation, whereas axe diameter showed increasing trend at 390, 450 and 550 \( \mu\text{mol mol}^{-1} \) \([\text{CO}_2]\) levels \( (P<0.05) \). However, there was no noteworthy difference for bare-tip length \( (P<0.05; \text{Table } 5) \).

Table 2. Parameters of irradiance-response curves of maize under effects of elevated \([\text{CO}_2]\) and different irrigation.

| Treatments               | \( \rho_{\text{max}} \) (\( \mu\text{mol m}^{-2} \text{s}^{-1} \)) | \( \text{LSP} \) (\( \mu\text{mol m}^{-2} \text{s}^{-1} \)) | \( \text{LCP} \) (\( \mu\text{mol m}^{-2} \text{s}^{-1} \)) | \( \psi_e \) (\( \text{mol mol}^{-1} \)) | \( R_d \) (\( \mu\text{mol m}^{-2} \text{s}^{-1} \)) | \( R^2 \) |
|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|--------------------------|------|
| C390W15%                 | 36.8702                  | 1884.3777                | 94.8387                  | 0.0544                   | 5.1268                   | 0.997|
| C390W0(CKI)              | 32.7945                  | 1740.8274                | 68.3083                  | 0.0530                   | 3.5925                   | 0.998|
| C450W15%                 | 35.3561                  | 1768.8612                | 62.8339                  | 0.0483                   | 3.0519                   | 0.994|
| C450W0(CKI)              | 29.5133                  | 1650.8724                | 54.2541                  | 0.0417                   | 2.2788                   | 0.997|
| C550W15%                 | 32.0309                  | 1643.9243                | 66.9802                  | 0.0469                   | 3.1668                   | 0.993|
| C550W0(CKI)              | 24.6966                  | 1501.2016                | 46.8651                  | 0.0482                   | 2.2332                   | 0.992|

Abbreviations are: \( \rho_{\text{max}} \) - maximum net photosynthetic rate, \( \text{LSP} \) - light saturation point, \( \text{LCP} \) - light compensation point, \( \psi_e \) - quantum efficiency of the light compensation point, \( R_d \) - dark respiration.

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Discussion

Interactive effects on photosynthetic parameters of maize

The response of plant photosynthesis to each of the environmental variables (e.g., water availability, temperature, nitrogen) associated with the elevated \([\text{CO}_2]\) has not been sufficiently understood [55–58]. The present study indicated that leaf \( P_n \) of maize improved with both elevated \([\text{CO}_2]\) and irrigation, and the curves of C390W15%, C390W0, C450W15%, C450W0 and C550W15% showed higher values than C90W0 curve (Fig 5A). The present study revealed that when irrigation was compared with natural precipitation at each \([\text{CO}_2]\) level \( (P<0.05; \text{Fig. } 5B) \). A number of other controlled environment studies [62–63] all observed the \( T_e \) decreased at elevated \([\text{CO}_2]\). It is worth mentioning, that the decrease of \( T_e \) was associated with decrease of \( G_n \) when elevated \([\text{CO}_2]\) decreased leaf \( G_n \) and caused increasing resistance from intrinsic leaf to outside, resulting in the decrease of \( T_e \) [64]. Additionally, the studies of elevated \([\text{CO}_2]\) and drought on plant reported that elevated \([\text{CO}_2]\) declined \( T_e \) in low soil moisture than high soil moisture [25,62], which in accordance with our findings. This suggested that elevated \([\text{CO}_2]\) may increased stomatal resistance and leaded to the reduce of \( T_e \) [25], but irrigation have a positive effect on stomatal opening and \( T_e \) have a increased trend in irrigation treatment compare with natural precipitation treatment at each \([\text{CO}_2]\) level. Moreover, our data indicated that \( WUE \) increased with elevated \([\text{CO}_2]\), and higher in natural precipitation treatment than irrigation treatment at elevated \([\text{CO}_2]\) levels (Fig 5C). This is in agreement with the results of previous studies, which reported elevated \([\text{CO}_2]\) have an increase trend in \( WUE \) under drought condition than well-watered condition [27,61,62,65]. Specifically, we found that the \( WUE \) have

\[ \frac{\text{CO}_2}{\text{water availability, temperature, nitrogen}} \]
a decrease trend in irrigation treatment than natural precipitation treatment at elevated [CO₂] levels, whereas the yield of that increased. This is mainly due to the increase of leaf area and biomass of crop community under elevated [CO₂] and irrigation, resulting in the increase of WUE of crop community, at last performance increase in yield of maize [25,66–69]. In our study, Gₚ increased with elevated [CO₂], whereas irrigation caused a small increase of Gₛ at each [CO₂] level (Fig 5E). However, Gₛ decreased with elevated [CO₂], and irrigation increased it greatly at each [CO₂] level (Fig 5D). Some controlled environment studies [70–72] also showing that elevated [CO₂] could cause a decrease in plant stomatal conductance (Gₛ) and partly closing of the stomata. Curtis et al. (1998) found that doubling [CO₂] average reduced Gₛ by 11% [73]. Further, the decreased Gₛ might be associated with the increase in Gₛ because a prior work showing that, Gₛ increased with rising [CO₂], wheat adjusted stomatal opening width will bring about a decrease in Gₛ so as to keep the intercellular CO₂ partial pressure to be always lower than atmospheric CO₂ partial pressure [74].

Photosynthetic parameter represented photosynthetic capacity and efficiency [75], which was usually obtained from irradiance-response model. Ye and Yu (2008) indicated that the modified rectangular hyperbolic model fitting results were quite close to the real values compare with the other models by series verification test, and the main photosynthetic parameters can be directly generated without any assumption by the model [52–53]. The model mentioned above was used and the Pₘ curves were fitted, and producing the main parameters with R²>0.99 (Table 2). Irrigation increased Pₘₘₐₓ by 12.43%, 19.8% and 29.7% at 390, 450 and 550 μmol·mol⁻¹ [CO₂] levels, respectively (Table 2). The rise in Pₘₘₐₓ has shown an improvement concerning the photosynthetic electron transport rate and photosphorylation activity. It has also shown an improvement in the photosynthetic capacity of maize. In addition, LSP increased by 9.51%, 7.15% and 8.25% under irrigation more than natural precipitation at 390, 450 and 550 μmol·mol⁻¹ [CO₂] levels, respectively (Table 2). The emergence of LSP is actually as a result of dark reactions which are able to keep up with light reactions under the intense radiation, thus restricting the increase of photosynthetic rate. However, additional irrigation under elevated [CO₂] might partly alleviate the negative effect and could promote photosynthetic capacity of maize under high light intensity. Normally, the photosynthesis reaction in a plant is very weak when in LCP, thus there was no significant effect on maize photosynthesis, even after there was a change in LCP with elevated [CO₂] and irrigation (Table 2). In addition, irrigation increased Rₛ at each [CO₂] level, which is the limiting factor for maize photosynthesis. Generally, elevated [CO₂] can cause an increase in temperature, and make plant respiration quickened, leading to increase in consumption. Thus, the net effect is an increase in Rₛ [70]. Irrigation might enhance this effect, but further researches are needed to explore the reasons.

### Interactive effects on growth of maize

The plant height increased by 5.28%, 4.60% and 5.86% under conditions of irrigation as compared with natural precipitation at 390, 450 and 550 μmol·mol⁻¹ [CO₂] levels, respectively (Fig 6A). Similar results could be found for ear height (Fig 6B), whereas stem diameter did not show any significant difference (Fig 6C). Significant interactive effects of elevated [CO₂] and irrigation were observed in plant height, whereas there was no significant interactive effects of elevated [CO₂] and irrigation in ear height and stem diameter of maize (P<0.05; Table 4). Some studies reported that leaf area of maize significantly increased under elevated [CO₂] [76–77], and this research work is in agreement with those findings (Fig 6D). In addition, irrigation increased leaf area by 12.04%, 9.90% and 7.75% at 390, 450 and 550 μmol·mol⁻¹ [CO₂] levels, respectively (Fig 6D). A similar conclusion could be found in Stipa bresilifora, in which, the leaf area increased to a maximum under conditions of elevated [CO₂] and increased precipitation of 15% [78]. Chamber studies showed that changing [CO₂] has no effect on biomass of maize and sorghum under adequate moisture conditions [79–81], and even the negative effects [82]. However, this study found that aboveground biomass of maize significantly increased by 16.66%, 10.75% and 7.65% under irrigation more than natural precipitation at 390, 450 and 550 μmol·mol⁻¹ [CO₂] levels, respectively (Fig 6E). The result is consistent with Cure’s findings [83], who reported that maize aboveground biomass increased by 7% under well-watered more than dry conditions at 550 μmol·mol⁻¹ [CO₂] in chamber (n = 4). Shi et al. (2013) observed that the aboveground biomass of Stipa bresilifora significantly increased with elevated [CO₂] and increasing precipitation [78]. Moreover, There were significant interactive effects of elevated

### Table 3. Multiple comparison on yield of maize under effects of elevated [CO₂] and irrigation.

| Treatments       | Seed yield (/g/plant) Increase compare with its CK % | Biology yield (/g/plant) Increase compare with its CK % | Economical coefficient |
|------------------|---------------------------------------------------|-----------------------------------------------------|------------------------|
| C₅₅₀W₆₁₅₆      | 336.76±2.75a                                      | 10.59                                                | 8.39                   |
| C₅₅₀W₀(CK)      | 304.52±1.01c                                     | 569.53±1.99                                         | 0.53±0.00              |
| C₅₅₀W₆₁₅₆      | 314.34±4.22b                                     | 585.81±3.84                                         | 9.30                   |
| C₅₅₀W₀(CK)      | 273.55±5.52                                      | 535.96±2.10                                         | 0.51±0.01              |
| C₅₅₀W₆₁₅₆      | 281.53±6.35                                      | 554.18±3.78                                         | 12.39                  |
| C₅₅₀W₀(CK)      | 239.64±1.09                                      | 493.09±5.54                                         | 0.49±0.00              |

The data are means ± SD (n = 3).
Different lower cases letters indicated significant difference (P<0.05).
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### Table 4. The two-way analysis of variances on growth and yield of maize between different elevated [CO2] and irrigation treatment.

| Variable                  | CO2 concentration | Irrigation | Interaction |
|---------------------------|-------------------|------------|-------------|
|                           | df    | F      | P      | df    | F      | P      | df    | F      | P      |
| Plant height              | 2     | 536.048 | 0.000  | 1     | 1105.743 | 0.000  | 2     | 6.507  | 0.012* |
| Ear height                | 2     | 9.315   | 0.002  | 1     | 26.167   | 0.000  | 2     | 0.726  | 0.498  |
| Stem diameter             | 2     | 0.988   | 0.392  | 1     | 2.454    | 0.135  | 2     | 0.020  | 0.980  |
| Leaf area                 | 2     | 622.766 | 0.000  | 1     | 777.613  | 0.000  | 2     | 4.821  | 0.029* |
| Aboveground biomass       | 2     | 58.838  | 0.000  | 1     | 137.036  | 0.000  | 2     | 4.339  | 0.038* |
| Seed yield                | 2     | 663.180 | 0.000  | 1     | 806.085  | 0.000  | 2     | 5.113  | 0.017* |
| Biology yield             | 2     | 945.868 | 0.000  | 1     | 1627.130 | 0.000  | 2     | 9.953  | 0.001**|

* and ** indicated P<0.05 and P<0.01, respectively.

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### Table 5. Change on ear characteristics of maize under effects of elevated [CO2] and irrigation.

| Treatments   | Ear length (cm) | Ear diameter (cm) | Ear weight (g) | 100-kernel weight (g) | Kernels per row (kemels/row) | Kernel number (No.) | Rows per ear (row/ear) | Shriveled kernels (kemels/ear) | Bare-tip length (cm) | Axle diameter (cm) |
|--------------|----------------|------------------|----------------|-----------------------|-------------------------------|---------------------|------------------------|-------------------------------|-----------------------|--------------------|
| C550W+15%    | 24.17±0.35a    | 6.16±0.04a       | 362.45±0.93a   | 43.97±0.21a           | 44.67±1.15a                  | 820.67±2.31a        | 16.67±1.15a            | 5.00±1.00a                      | 4.51±0.04e           | 3.80±0.31a         |
| C450W+15%    | 23.05±0.45b    | 6.03±0.04b       | 344.69±0.48b   | 42.60±0.56b           | 42.33±0.58b                  | 762.00±1.39b        | 18.00±0.01a            | 7.00±1.00d                      | 4.42±0.04e           | 3.64±0.28e         |
| C390W+15%    | 21.25±0.03c    | 5.69±0.17c       | 312.01±1.77c   | 40.40±0.75c           | 39.00±1.00c                  | 676.00±1.58c        | 17.33±1.15c            | 9.00±1.00c                      | 4.44±0.17c           | 3.55±0.26c         |
| C390W0(CK)   | 21.25±0.35d    | 5.17±0.04d       | 254.25±1.45d   | 36.53±1.31d           | 35.67±0.38d                  | 594.33±2.89d        | 16.67±1.15d            | 3.03±1.15a                      | 4.87±0.04e           | 3.54±0.28e         |

The data are means ± SD (n = 3).
Different lower cases letters (a,b,c,d,e) indicated significant difference (P<0.05).

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[\text{CO}_2] \text{ and irrigation in leaf area (} P < 0.05; \text{ Table 4) and aboveground biomass (} P < 0.05; \text{ Table 4).}

**Interactive effects on yield and ear characteristics of maize**

The results of that elevated [CO\textsubscript{2}] increased maize yield have been indicated in previous studies. Cure \textit{et al.} (1986) reported that maize average yield increased by 27% (n = 3) by doubling [CO\textsubscript{2}] [83], while Guo (2003) indicated that maize yield might be increased by 22.80% when [CO\textsubscript{2}] levels rise up to 700 \text{mol-mol}^{-1} [84]. Long \textit{et al.} (2006) used comprehensive observation data of chamber studies (n = 14) and found out that grain yield of maize and sorghum increased by an average of 18% when [CO\textsubscript{2}] were elevated to 550 \text{mol-mol}^{-1} [CO\textsubscript{2}] levels, respectively (Table 3). This study has exhaustively shown that the maize yield of Northeast China increased by 14.15% and 27.07% with 450 and 550 \text{mol-mol}^{-1} [CO\textsubscript{2}] levels, respectively (Table 3). Additionally, irrigation significantly increased maize yield by 10.59%, 14.91% and 17.40% as compared with natural precipitation at 390, 450 and 550 \text{mol-mol}^{-1} [CO\textsubscript{2}] levels, respectively (Table 3). Similar results have been reported in previous studies [86-87], but others have reported decreases [82] or no significant change at all [79-80]. Allen (2011) predicted that management of irrigation water in a future high [CO\textsubscript{2}] world could potentially increase overall C\textsubscript{4} crop yield (in water-limited areas) [62], we agree with this idea. Moreover, biological yield has also been increased by 8.39%, 9.30% and 12.39% under irrigation more than natural precipitation at 390, 450 and 550 \text{mol-mol}^{-1} [CO\textsubscript{2}] levels, respectively (Table 3). The work also revealed that there has been significant interactive effects of elevated [CO\textsubscript{2}] and irrigation on maize seed yield (\textit{P} < 0.05; Table 4) and biological yield (\textit{P} < 0.01; Table 4). Consequently, maize economic coefficient increased in irrigation more than natural precipitation. Economic coefficient reflects the transport and store ability of crop “source” to “sink” form photosynthetic products [88]. Kirschbaum (2010) reported that plant growth response to elevated [CO\textsubscript{2}] increase with a plant’s sink capacity and nutrient status [89]. In present study, maize photosynthetic capacity was enhanced while the ear capacity was expanded under elevated [CO\textsubscript{2}] and irrigation, resulting in a more dry matter accumulation and yield increase.

Maize ear characteristics significantly changed under the interactive effects of elevated [CO\textsubscript{2}] and irrigation. 100-kernel weight and kernal number were all significantly increased under irrigation than natural precipitation at each [CO\textsubscript{2}] level (Table 5). Additionally, ear length, ear diameter and ear weight were all increased in accordance with yield, and the increase of 100-kernel weight and ear length was consistent with the study done by Wang \textit{et al.} (1996) [90]. There is a study reported that kernels per row is the main factor that will increase maize yield [91]. In this study, irrigation increased kernels per row by 9.34%, 10.44% and 8.08% at 390, 450 and 550 \text{mol-mol}^{-1} [CO\textsubscript{2}] levels, respectively, whereas rows per ear change was not remarkable (Table 5). The decreased of shriveled kernels was beneficial to yield increase. In our study, irrigation decreased shriveled kernels by 70.33%, 74.70% and 73.68% at 390, 450 and 550 \text{mol-mol}^{-1} [CO\textsubscript{2}] levels, respectively (Table 5). Optimization of the ear characteristics were reflected in an increase in yield under elevated [CO\textsubscript{2}] and irrigation. Therefore, it is necessary to irrigate with additional water for the elevated [CO\textsubscript{2}] plots of maize to compensate for photosynthesis resistance from lacking of water under elevated [CO\textsubscript{2}] condition. Moreover, bare-tile length of maize made no significant difference in all treatments, but axle diameter increased within a narrow range. The increase was by 0.28%, 0.83% and 2.13% in irrigation more than natural precipitation at 390, 450 and 550 \text{mol-mol}^{-1} [CO\textsubscript{2}] levels (Table 5). This change implied that elevated [CO\textsubscript{2}] and irrigation increased ear length, ear diameter as well as axle diameter. Thus, it can be estimated that maize yield could not be increased unlimitedly with elevated [CO\textsubscript{2}] and irrigation, but increasing the axle diameter serves as a limiting factor.

**Conclusions**

Our results demonstrated the following: 1) With elevated [CO\textsubscript{2}] and irrigation, leaf \textit{P}_\text{n} and \textit{G}_\text{i} of maize significantly increased, while elevated [CO\textsubscript{2}] brought a notable decrease in \textit{G}_\text{r} and \textit{T}_r, but irrigation have a positive effect on them, thereby increasing WUE in natural precipitation treatment than irrigation treatment at elevated [CO\textsubscript{2}] levels. 2) Irradiance-response parameters \textit{P}_\text{max} and \textit{LSP} increased more under irrigation conditions than natural precipitation at each [CO\textsubscript{2}] level. \textit{R}_2 also increased under the same conditions, and this is a limiting factor. 3) Irrigation under elevated CO\textsubscript{2} increased plant height, ear height, stem diameter, leaf area and aboveground biomass, resulting in the increase of yield. In addition, ear characteristics of maize were all superior except axle diameter. However, further study should be taken to ensure the contribution rate of elevated [CO\textsubscript{2}] and irrigation.

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**Author Contributions**

Conceived and designed the experiments: JZ. Performed the experiments: FM CH. Analyzed the data: FM FY. Contributed reagents/materials/analysis tools: FM FY. Wrote the paper: FM JZ.

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