



Research Paper

Deficit irrigation provokes more pronounced responses of maize photosynthesis and water productivity to elevated CO₂



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ABSTRACT

It is very significant to study the impact of deficit irrigation on crop growth and water use under the future scenarios with elevated CO₂ concentrations and reduced water availability. This study investigated the growth and yield differences of maize grown in a phytotron in response to elevated CO₂ concentrations under different irrigation treatments. Two irrigation treatments were carried out: regular irrigation (RI) and deficit irrigation (DI), in which the irrigation amounts were respectively 100 and 70% of evapotranspiration (*ET*), with four CO₂ concentrations (400, 550, 700, and 900 μmol mol⁻¹). Thus eight treatments, i.e. RI₄₀₀, RI₅₅₀, RI₇₀₀, RI₉₀₀, DI₄₀₀, DI₅₅₀, DI₇₀₀, and DI₉₀₀ were included in this study. Results show that, the relative reductions of stomatal conductance (*g_s*) and transpiration rate (*T_r*) in response to elevated CO₂ concentrations were higher under DI than RI, thus causing leaf temperature (*T_{leaf}*) rose higher under DI due to the transpiration cooling effect. As photosynthetic rate (*P_n*) and its physiological process were positively correlated with *T_{leaf}*, the relative increases of *P_n* and the resulting maximum leaf area index (*LAI_{max}*), total dry matter weight (*TDW*), and grain yield (*GY*) react to elevated CO₂ concentrations were higher under DI than RI, as well as the leaf water use efficiency (*WUE_L*) and water productivity (*WP*). The DI₉₀₀ treatment in which the irrigation amount was reduced by 30% only decreased the *TDW* and *GY* by 7 and 5% when compared with RI₉₀₀. The variation of *GY* was consistent with the variation of kernels per ear (*KPE*), but was not directly related to hundred-grain weight (*HGW*). The above results show that when atmospheric CO₂ concentrations rise in the future, deficit irrigation would be an effective way of saving water and would not only have a mitigating effect on water crises, but would also contribute to improving *WP*, which is more important in terms of actual production.

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1. Introduction

It is estimated that, by the end of the 21st century, atmospheric CO₂ concentration will have reached 936 μmol mol⁻¹ if we do not take measures to reduce emissions (IPCC, 2013). There have been researches about elevated CO₂ concentration effects on crops and vegetables since 1970s (Gifford, 1977, 1979; Ludlow and Wilson, 1971). The experimental equipment was mainly including enclosed chambers (Kang et al., 1996), open-top chambers (Meng et al., 2014), and free-air CO₂ enrichment technology (Leakey et al., 2006). The elevation of atmospheric CO₂ concentration would have a significant impact on crop growth (Oliver et al., 2009), because it

increases net photosynthetic rate (*P_n*), which would likely increase plant height (*H*), leaf area index (*LAI*), total dry weight (*TDW*), and grain yield (*GY*) (Ainsworth and Rogers, 2007; Kang et al., 1996; Meng et al., 2014). It would also reduce stomatal conductance (*g_s*), leading to a smaller than proportional decrease in transpiration rate (*T_r*) and total evapotranspiration (*ET*) (Allen et al., 2003; Bernacchi et al., 2007; Bunce, 2004; Vanuytrecht et al., 2012). This would ultimately mean that there would be a significant increase in the importance of water productivity (*WP*) (Idso et al., 1987; Kang et al., 2002; Li et al., 2003; Vanuytrecht et al., 2012).

Together with CO₂ concentration, the controlled variables also covered water (Kang et al., 2002), nitrogen (Li et al., 2003), temperature (Cai et al., 2016), ozone (Ainsworth, 2008), transplanting density (Lai et al., 2014), etc., among which water stress was the top factor that considered. A number of current studies have emphasized the effects of the interaction of elevated CO₂ concentration

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and water stress on crop growth, water consumption, and yield (Islam et al., 2012; Qiao et al., 2010; Saadi et al., 2015; Samarakoon and Gifford, 1996; Wall et al., 2011). The data of P_n , GY, irrigation amounts, and WUE in these references showed that elevated CO₂ concentration benefit crops more under drought conditions than well-watered conditions. A number of previous studies have also shown that elevated CO₂ concentration only affect photosynthesis and grain yield of maize, a C₄ crop, under drought conditions (Kim et al., 2007; Kimball, 2016; Leakey et al., 2006; Manderscheid et al., 2014; Rogers et al., 1983), while several other CO₂ enrichment studies with maize grown under controlled environment conditions showed an increase of C₄ photosynthesis and biomass production under sufficient water supply (Driscoll et al., 2006; Kang et al., 2002; King and Greer, 1986; Loomis and Lafitte, 1987; Morison and Gifford, 1984; Ziska and Bunce, 1997). The different results among these literatures may be due to the experimental equipments and some other experimental conditions that need further investigation.

The elevated CO₂ concentration will result in the intensity and frequency of climate extremes such as heat waves, heavy precipitation, and drought (Oliver et al., 2009), and the availability of water will rapidly decrease (IPCC, 2014). Water shortage is already a serious problem in Northwest China (Kang et al., 2002; Wang et al., 2012), and water availability will almost certainly decrease even further under climate change (IPCC, 2007; Zhao et al., 2010), posing a huge challenge for food security in the region (Kang et al., 2017). So applying water-saving irrigation method (e.g. deficit irrigation, or insufficient water supply) into that region is in urgent need in the future.

Deficit irrigation (DI) is an effective water-saving method by which to reduce water consumption used in irrigation while maintaining yield levels acceptable (Dorjia et al., 2005; Geerts and Raes, 2009; Kang et al., 2017). Although DI may reduce crop yield and total dry weight (Badr et al., 2012; Dorjia et al., 2005; Geerts and Raes, 2009; Rop et al., 2016), it also improves economic yield and fruit quality (Cantore et al., 2016; Dorjia et al., 2005), saves water, and increases WUE and WP (Badr et al., 2012; Geerts and Raes, 2009; Mitchell et al., 1991; Rop et al., 2016).

The local regular irrigation method (i.e. sufficient irrigation with 100% demand of evapotranspiration) may lead to some drought before re-irrigation. According to the above literatures it may benefit crops to some extent with elevated CO₂ concentrations in the future. But how about the deficit irrigation? The interactive impacts of elevated CO₂ concentrations (such as the projected concentration of 900 $\mu\text{mol mol}^{-1}$ under RCP 8.5 by the end of this century (IPCC, 2013)) and deficit irrigation on growth and yield of C₄ plants like maize are not yet completely unraveled and deserve further investigation. Despite there are many researches about the interactive effects of CO₂ concentration and water stress on crops, there is still a lack of experimental studies addressing the response of crops to elevated CO₂ concentrations and irrigation methods. Whether deficit irrigation still makes positive effect along with elevated CO₂ concentration or not is needed to contribute to an in-depth understanding of the changing environment and therefore of great significance in arid and semi-arid areas (Aljazairi et al., 2015; Vu and Allen, 2009).

A commonly used cultivar of maize (*Zea mays* L. cultivar Qiangsheng 51) in Northwest China has been planted for this study. Two irrigation treatments and four CO₂ concentrations have been designed in order to analyze the effects of elevated CO₂ concentrations on stomatal response, growth characteristics, yield, evapotranspiration, water use efficiency, and water productivity under regular and deficit irrigation. Our objective is to explore whether the deficit irrigation method would save water and at the same time benefit maize more than regular irrigation, thus providing a fundamental research and a reference point for irrigation

management decision in agriculture in semi-arid areas under elevated CO₂ concentrations in the future.

2. Materials and methods

2.1. Experimental conditions

The experiment was conducted from May to September 2015, in the climate phytotron at Shiyanghe Experimental Station of China Agricultural University, located in Wuwei City, Gansu Province in Northwest China (N 37°52', E 102°50', altitude 1581 m) (Fig. 1). The climate phytotron consisted of four separate chambers of 3-m length by 4-m width by 2.5-m height, and was supplied with natural light. Each chamber had the same indoor equipments. The different parameters set in the phytotron, and their range of variation, are shown in Table 1. Air temperature, relative humidity, and CO₂ concentration were set automatically through a digital program timer at different time periods in a closed control cabinet (Fig. 2a). Indoor temperature was controlled by an electric heating (warming) and a compressor (cooling); relative humidity was adjusted by an ultrasonic humidifier (humidifying) and a heat transfer valve (dehumidifying); both were controlled within the accuracy range (Table 1). A CO₂ sensor was used to measure indoor CO₂ concentration, and CO₂ gas was provided by a CO₂ gas cylinder, through a pipe (Fig. 2a). When the CO₂ concentration target was set, a control system automatically calculated aeration time according to the flow rate of the CO₂ gas cylinder and the difference between the target and current CO₂ concentrations. With the consumption of CO₂ in the chamber, the above control method was repeated to maintain the target CO₂ level. Fresh air was inhaled from outside the chamber by a blower, evenly distributed throughout the chamber, from the bottom, and then extracted through the upper wall to circulate the air. The indoor wind speed was less than 0.5 m s⁻¹.

2.2. Experimental design

The maize (*Zea mays* L. cultivar Qiangsheng 51) used in the experiment was planted in plastic pots of 26.5 cm height, 21 cm and 33 cm bottom and top diameter, respectively. Three seeds were sown in each plastic pot initially and one seedling retained after emergence. The experiment was conducted in climatic chambers during the whole growth period from the date of sowing (May 7) to harvest (September 16). The pots were filled with local sandy loam soil after being air-dried, crushed, and sieved. Each pot had 18 kg of soil with a dry bulk density of 1.38 g cm⁻³ and a field water capacity of 0.27 cm³ cm⁻³. Little stones were spread over the bottom of each pot with fine sand acting as a filtration layer. The surface of the soil was then covered with fine sand and nutritive soil to reduce the impact of irrigation on the topsoil structure. The same fertilization scheme was applied in each pot, which was 1.5 g urea and 1.5 g diammonium phosphate, on May 29, June 19, July 10, July 29, and August 27. In addition, a foliar spray of 250 ml potassium dihydrogen phosphate solution was used at a concentration of 2% on May 29, June 19, July 20, and August 5.

Experimental meteorological conditions were set according to the 10-day averages of observed meteorological data from May to September of the previous six years at the experimental station; their adjustment frequencies are shown in Table 1. Natural light was utilized. The experiment consisted of two irrigation treatments, namely, regular irrigation (RI, which was similar to the local water management) and deficit irrigation (DI) in which the irrigation amounts were 100 and 70% of evapotranspiration (ET), and four CO₂ concentrations of 400 (current atmospheric CO₂ concentration), 550, 700, and 900 $\mu\text{mol mol}^{-1}$. Both regular and deficit irrigation were carried out at the same time and with the same fre-



Fig. 1. Map with Shiyanghe Experimental Station in China (The map shows only China's land area).

Table 1

The different parameters set in the phytotron, their range of variation and accuracy, and frequency of adjustment.

Parameters (unit)	Range of variation \pm accuracy	Frequency of adjustment
Temperature ($^{\circ}$ C)	$-5 \sim 40 \pm 0.1$	every 2 h from 8:00 to 20:00 each day; changed every 10 days
Relative humidity (%)	$30 \sim 95 \pm 5$	the same as temperature
CO ₂ concentration ($\mu\text{mol mol}^{-1}$)	$400 \sim 2000 \pm 50$	consistent from 8:00 to 20:00 each day in each chamber

Table 2

Irrigation water amounts for each growth stage of maize under different CO₂ concentrations and irrigation treatments. RI denotes regular irrigation, and DI denotes deficit irrigation.

CO ₂ ($\mu\text{mol mol}^{-1}$)	Irrigation regime	Irrigation amount (mm)					
		Seeding stage	Jointing stage	Heading stage	Filling stage	Maturity stage	Entire growing season
		5.7–6.25	6.26–7.18	7.19–8.7	8.8–8.26	8.27–9.16	5.7–9.16
400	RI	60	102	147	112	107	528
	DI	60	72	103	78	75	388
550	RI	60	86	124	91	94	455
	DI	60	60	87	64	66	337
700	RI	60	79	129	86	91	445
	DI	60	55	90	61	64	330
900	RI	60	85	130	98	91	464
	DI	60	60	91	69	64	344

quency in the four chambers. The crops and the corresponding CO₂ concentrations were interchanged once randomly within the four chambers in the later half maize period. There were eight treatments altogether: RI₄₀₀, RI₅₅₀, RI₇₀₀, RI₉₀₀, DI₄₀₀, DI₅₅₀, DI₇₀₀, and DI₉₀₀. Each treatment had six pot replicates placed in a row (Fig. 2b) and the two rows were switched position after each weighing. To ensure the regular emergence and growth of maize, there was no water deficit during the seedling stage, after which the deficit treatment was implemented. The experimental pots were weighed every three to four days by high precision weighing scales for the basis of the irrigation amount, and measuring cylinders were used for measuring the irrigation water manually. The irrigation amount of each growth stage is shown in Table 2.

2.3. Measurements

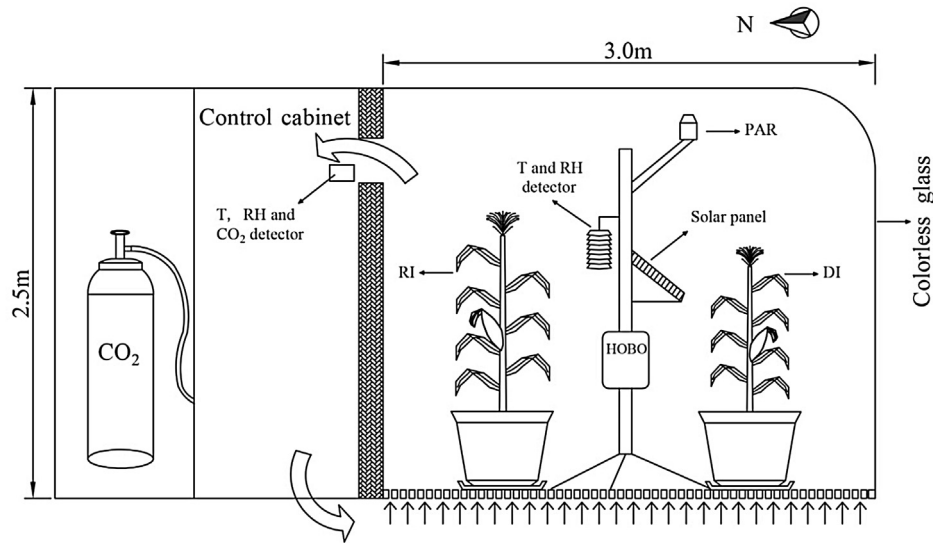
2.3.1. CO₂ concentrations

CO₂ concentrations in the chambers were monitored and recorded at 1 s intervals using the CO₂ gas sensors in the phytotron. The daily variations of the average values of four CO₂ concentrations from 8:00 to 20:00 are shown in Fig. 3a.

2.3.2. Meteorological data

Conventional meteorological data in each chamber, including photosynthetic active radiation (PAR), air temperature (T), relative humidity (RH), and wind speed (u), were continuously observed by a portable automatic weather station (HOBO U30, Onset Com-

(a) Schematic drawing of the phytotron



(b) Experimental design

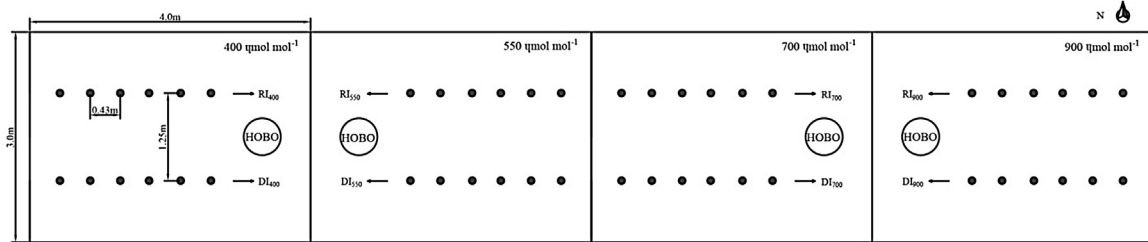


Fig. 2. Schematic drawing of the phytotron (a) and Experimental design (b) (T , daily average temperature; RH , relative humidity; PAR , photosynthetic active radiation; RI , regular irrigation; DI , deficit irrigation; $HOB0$, portable automatic weather station; ●, maize plant).

puter Corp., USA) and a multi-functional automatic anemometer (VELOCICALC 9565, TSI Inc., USA). The data were sampled every 5 s interval, and 15 min averages were calculated and recorded using a data logger. The daily average meteorological data in the chamber during the experimental period are shown in Fig. 3b.

2.3.3. Photosynthetic parameters

Stomatal conductance of water vapor diffusion (g_s), transpiration rate (T_r), leaf temperature (T_{leaf}), and net photosynthetic rate (P_n) of maize leaves were measured using a LI-6400 type photosynthesis system (Li-Cor Inc., USA). The second leaves of three representative plants undergoing the same treatment were randomly selected for measurement. The daily variations of the photosynthetic parameters of each treatment were recorded at two-hourly intervals from 8:00 to 18:00 on July 10, July 17, and August 15.

2.3.4. Crop growth and yield parameters

Three plants representative of each treatment were randomly selected to measure leaf length, maximum leaf width, and plant height using steel tapes every seven to ten days after the emergence of maize. The leaf area was calculated by summing the leaf length multiplied by the maximum leaf width and then multiplied by a conversion factor of 0.74 (Li et al., 2008). The leaf area index (LAI , $m^2 m^{-2}$) was defined as the ratio of leaf area to the soil surface area in the plastic pots. The stem dry weight (SDW), leaf dry weight (LDW), root dry weight (RDW), hundred-grain weight (HGW), ker-

nels per ear (KPE), and grain yield (GY) of maize were measured using the oven-drying method on September 16 when harvesting, and four plants representative of each treatment were selected. Specific leaf area (SLA , $cm^2 g^{-1}$) was defined as the ratio of LAI to LDW . The harvest index (HI) was defined as the ratio of GY to total dry weight (TDW).

2.3.5. Evapotranspiration

Evapotranspiration (ET) was calculated using the following water balance method, and the average of three replications.

$$ET = I + P + W - D - R - \Delta S \quad (1)$$

where ET is the crop evapotranspiration (mm), I the irrigation amount (mm), P the precipitation (mm), W the capillary rise to the root zone (mm), D the drainage from the root zone (mm), R the surface runoff (mm), and ΔS the change in soil water storage (mm).

Since the maize was grown in pots and irrigation was applied carefully, there was no surface runoff and groundwater supply. A tray was put below every pot to collect drainage or water leakage. However, there was no overly saturated water and leakage observed from the trays because the water supplements were controlled by the ET between two irrigations, and there was no rain in the chambers either. Therefore Eq. (1) can be simplified as follows:

$$ET = I - \Delta S \quad (2)$$

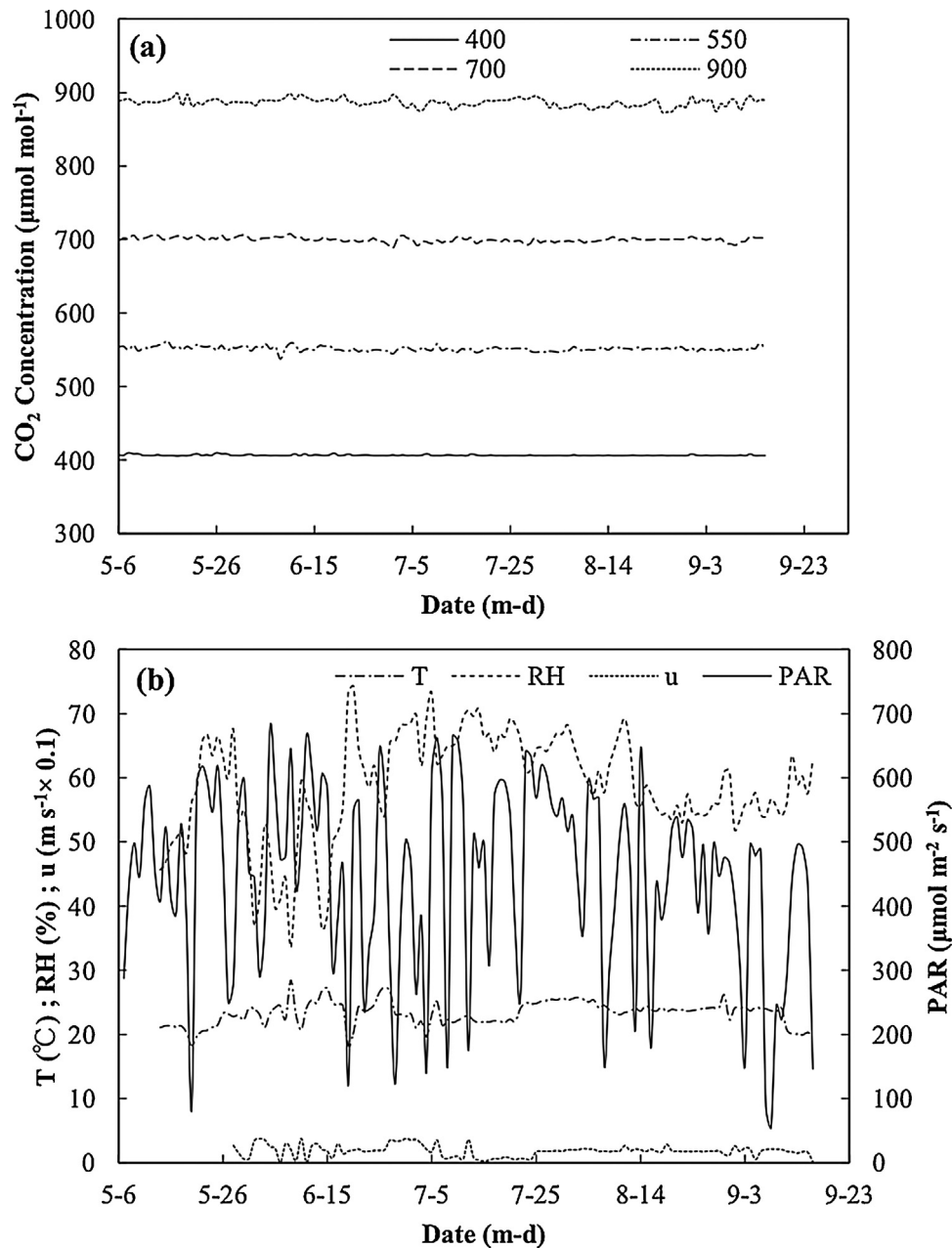


Fig. 3. Variation in the daily average of the four CO₂ concentrations from 8:00 to 20:00 (a), daily average temperature (*T*), relative humidity (*RH*), photosynthetic active radiation (*PAR*), and wind speed (*u*) in the climate chamber during the entire growth period of maize (b).

2.3.6. Leaf water use efficiency

Leaf water use efficiency (WUE_L) was calculated using the following formula:

$$WUE_L = \frac{P_n}{T_r} \quad (3)$$

where WUE_L is the leaf water use efficiency ($\text{mmolCO}_2 \text{ mol}^{-1} \text{H}_2\text{O}$), P_n the net photosynthetic rate ($\mu\text{molCO}_2 \text{ m}^{-2} \text{ s}^{-1}$), T_r the transpiration rate ($\mu\text{molH}_2\text{O m}^{-2} \text{ s}^{-1}$).

2.3.7. Water productivity

(*WP*) was calculated using the following formula:

$$WP = \frac{TDW}{ET} \quad (4)$$

where *WP* is the water productivity (g mm^{-1}), *TDW* the total dry weight (g), and *ET* the crop evapotranspiration (mm).

2.4. Data analysis

Microsoft Excel was used to analyze all the observed data. SPSS 21.0 software (SPSS 21.0, SPSS Inc., USA) was applied for the statistical analysis, ANOVA analysis, and the significant test of the average values of each parameter under different treatments. Although there was only one chamber of each CO₂ concentration and the pots of the same treatment were placed in a row, we interchanged the chambers at the later growth stage and switched the crop rows after each weighing, and also the observation parameters were measured randomly, so the variables can be treated as random factors. The significance level was set at 0.05.

Table 3
The effect of CO₂ concentrations on leaf temperature (T_{leaf}) under different irrigation treatments. Data in the table are the mean \pm standard error.

CO ₂ ($\mu\text{mol mol}^{-1}$)	T_{leaf} ($^{\circ}\text{C}$)	
	RI	DI
400	30.49 \pm 0.61a	30.59 \pm 0.60b
550	31.07 \pm 0.25a	31.33 \pm 0.23ab
700	31.56 \pm 0.37a	31.81 \pm 0.30ab
900	32.01 \pm 0.56a	32.32 \pm 0.44a

Means followed by the different letters (a, b, c) are significantly different at the level of $P < 0.05$, and by the same letter are not significantly different at the level of $P < 0.05$. RI denotes regular irrigation, and DI denotes deficit irrigation.

3. Results and discussion

3.1. More pronounced effects of elevated CO₂ concentrations on photosynthetic parameters of maize under deficit irrigation

The effects of different irrigation treatments and CO₂ concentrations on the stomatal conductance (g_s) and transpiration rate (T_r) of maize are shown in Fig. 4a–d. The figure shows that g_s and T_r decreased with the enrichment of CO₂ concentrations under both RI and DI. Compared with RI₄₀₀, g_s and T_r were 27 and 23% lower under DI₄₀₀; for the elevated CO₂ concentrations, g_s and T_r were 22–36 and 25–26% lower under DI when compared with RI. Relative reductions in g_s and T_r due to the DI treatment were therefore more pronounced along with elevated CO₂ concentrations.

Compared with RI₄₀₀, RI₅₅₀–RI₇₀₀–RI₉₀₀ decreased g_s by 13, 22, and 33%, and T_r by 12, 23, and 38%, respectively. Compared with DI₄₀₀, DI₅₅₀–DI₇₀₀–DI₉₀₀ decreased g_s by 8, 27, and 41%, and T_r by 16, 27, and 41%, respectively. Therefore, the relative reductions in g_s and T_r caused by elevated CO₂ concentrations were mostly higher under DI than under RI. This was because, under DI, the crop suffered from water stress, which affected the leaves and roots, so the guard cells reduced the solute in the cells by regulating their own metabolic processes to increase water potential, thus causing stomata closure (Stalfelt, 1959; Yu and Wang, 2010). Water deficit was also able to change the intracellular CO₂ concentrations (C_i) by affecting photosynthesis, plant hormones, and pH, etc., which also caused stomata closure (Schulze, 1986, 1993; Sharkey, 1984; Yu and Wang, 2010). The stomata reduction was therefore aggravated by the combined effect of deficit irrigation and elevated CO₂ concentrations. So the elevated CO₂ concentration effect on stomatal closure was higher under DI. Since stomata control is the most important way to regulate T_r (Yu and Wang, 2010), T_r had the same variation patterns as g_s .

The effect of different irrigation treatments and CO₂ concentrations on the leaf temperature (T_{leaf}) is shown in Table 3. It shows that T_{leaf} was increased along with the elevated CO₂ concentrations, but it was only significant under DI. Compared with RI₄₀₀, RI₅₅₀–RI₇₀₀–RI₉₀₀ increased T_{leaf} by 1.9, 3.5, and 5.0%, respectively. While compared with DI₄₀₀, DI₅₅₀–DI₇₀₀–DI₉₀₀ increased T_{leaf} by 2.4, 4.0, and 5.7%, respectively. Hence the relative increase in T_{leaf} caused

Table 4
The effects of CO₂ concentrations on maximum leaf area index (LAI_{max}), maximum height (H_{max}), maximum stem diameter (SD_{max}), and specific leaf area (SLA) under different irrigation treatments. Data in the table are the mean \pm standard error.

CO ₂ ($\mu\text{mol mol}^{-1}$)	LAI_{max} ($\text{cm}^2 \text{cm}^{-2}$)		H_{max} (cm)		SD_{max} (mm)		SLA ($\text{cm}^2 \text{g}^{-1}$)	
	RI	DI	RI	DI	RI	DI	RI	DI
400	6.35 \pm 0.09a	5.19 \pm 0.14c	233.70 \pm 3.75c	184.90 \pm 7.74b	20.11 \pm 0.26b	19.01 \pm 0.08b	111.83 \pm 12.33a	116.01 \pm 7.10ab
550	6.43 \pm 0.20a	5.60 \pm 0.18bc	244.85 \pm 3.33b	226.23 \pm 0.74a	20.35 \pm 0.38b	19.46 \pm 0.49b	102.20 \pm 7.47ab	118.59 \pm 2.70a
700	6.47 \pm 0.32a	6.08 \pm 0.05b	250.80 \pm 2.31ab	233.15 \pm 7.85a	20.38 \pm 0.47b	19.81 \pm 0.76b	90.32 \pm 14.19bc	98.20 \pm 9.09bc
900	6.73 \pm 0.23a	6.71 \pm 0.16a	257.23 \pm 2.62a	237.93 \pm 4.60a	22.39 \pm 0.71a	22.13 \pm 0.59a	71.70 \pm 5.86c	76.32 \pm 5.97c

Means followed by the different letters (a, b, c) are significantly different at the level of $P < 0.05$, and by the same letter are not significantly different at the level of $P < 0.05$. RI denotes regular irrigation, and DI denotes deficit irrigation.

by elevated CO₂ concentrations was higher under DI than under RI. Leaf temperature was highly correlated with T_r under most conditions (Pallas et al., 1967). And it was obvious to see that the higher T_r was shown in the markedly lower T_{leaf} , and vice versa, namely the so called transpiration cooling effect (Pallas et al., 1967). So when the elevated CO₂ concentration reduced T_r , the T_{leaf} increased. Also with the decrease in soil water in DI condition, T_r was decreasing; meanwhile, T_{leaf} rose more remarkable than that only under elevated CO₂ conditions. As T_r cannot be ignored in the changes of T_{leaf} (Cook et al., 1964; Gates, 1964) and T_r changes were more pronounced under DI, so as to the changes of T_{leaf} .

Fig. 4e and f show the effect of different irrigation treatments and CO₂ concentrations on net photosynthetic rate (P_n). Net photosynthetic rate increased with the enrichment of CO₂ concentration. Compared with RI₄₀₀, P_n was 24% lower under DI₄₀₀; for the elevated CO₂ concentrations, P_n was 15–20% lower under DI when compared with RI. Relative reductions in P_n due to the DI treatment were therefore weakened along with elevated CO₂ concentrations.

Compared with RI₄₀₀, RI₅₅₀–RI₇₀₀–RI₉₀₀ increased P_n by 30, 45, and 59%, respectively, while compared with DI₄₀₀, DI₅₅₀–DI₇₀₀–DI₉₀₀ increased P_n by 37, 51, and 77%, respectively. Therefore, the increased percentage of P_n caused by elevated CO₂ concentrations was higher under DI than under RI. The result was the same with those in many studies (Kang et al., 2002; Robredo et al., 2007; van der Kooi et al., 2016). This was because both water deficit and elevated CO₂ concentrations reduced the Rubisco enzyme content and activity (Vu et al., 1998), thus weakening the Calvin cycle and increasing the C_i in bundle sheath cells. At the same time, the reduced g_s caused by the two factors also increased C_i by 86 (DI₄₀₀), 94 (DI₅₅₀), 75 (DI₇₀₀), and 15 (DI₉₀₀) $\mu\text{mol mol}^{-1}$ when compared with that under RI condition with the same CO₂ concentrations (data were measured in our experiment but not shown in the tables). On the other hand, the leaf temperature rose higher under DI. It was 0.10 (DI₄₀₀), 0.26 (DI₅₅₀), 0.25 (DI₇₀₀), and 0.31 (DI₉₀₀) $^{\circ}\text{C}$ higher than under RI when CO₂ concentrations were the same (Table 3). Since P_n was positive correlated with C_i (Robredo et al., 2007), and within the optimum temperature ranges for photosynthesis at 30–40 $^{\circ}\text{C}$ (Berry and Björkman, 1980; Long, 1999; Ludlow and Wilson, 1971; Mjwara and Botha, 1993; Wardlaw, 1979), a slight increase in leaf temperature resulted in a substantial increase in the P_n of maize due to the positive effect on the photosynthetic biochemical reactions and physical processes (Ghannoum et al., 2000; Yu and Wang, 2010), the relative increase of P_n caused by elevated CO₂ concentrations was higher under DI than under RI.

3.2. More pronounced effects of elevated CO₂ concentrations on the growth and yield of maize under deficit irrigation

The effects of elevated CO₂ concentrations on the maximum leaf area index (LAI_{max}), maximum height (H_{max}), maximum stem diameter (SD_{max}), and specific leaf area (SLA) under different irrigation treatments are shown in Table 4. DI₄₀₀ decreased LAI_{max} , H_{max} , and SD_{max} by 18, 21, and 5%, respectively, but increased

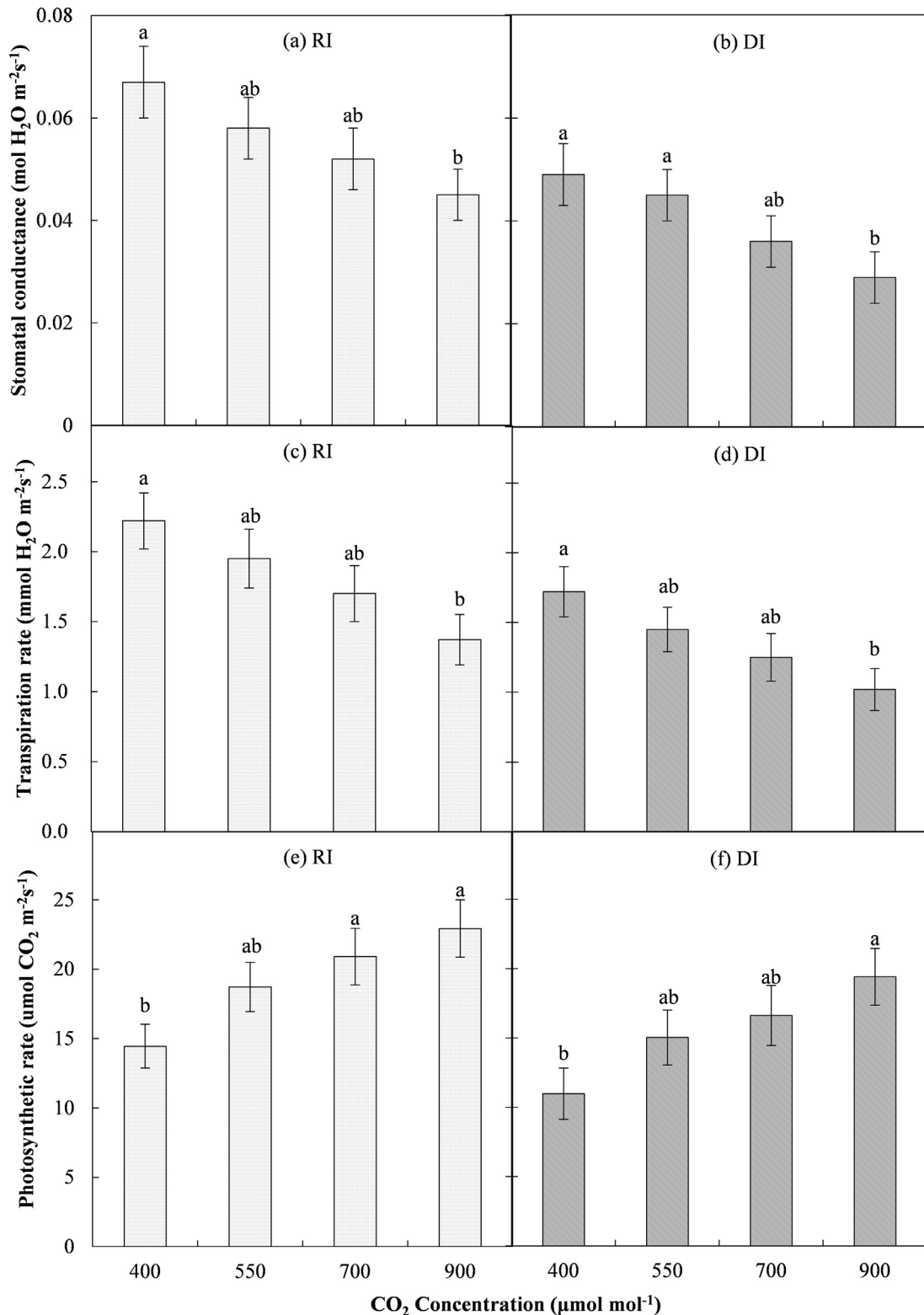


Fig. 4. The effects of CO₂ concentrations on stomatal conductance (g_s), transpiration rate (T_r), and net photosynthetic rate (P_n) under different irrigation treatments. (Data in the figure are the mean \pm standard error. Means followed by the different letters (a, b, c) are significantly different at the level of $P < 0.05$, and by the same letter are not significantly different at the level of $P < 0.05$. RI denotes regular irrigation, and DI denotes deficit irrigation).

SLA by 4% when compared with RI₄₀₀. For elevated CO₂ concentrations, DI decreased LAI_{max} , H_{max} , and SD_{max} by 0–13, 7–8, and 1–4%, but increased SLA by 6–16% when compared with RI. Relative reductions in LAI_{max} , H_{max} , and SD_{max} caused by DI were there-

fore weakened, while relative increases in SLA caused by DI were enhanced along with elevated CO₂ concentrations.

Compared with RI₄₀₀, RI₅₅₀-RI₇₀₀-RI₉₀₀ increased LAI_{max} by 1, 2, and 6%, H_{max} by 5, 7, and 10%, and SD_{max} by 1, 1, and 11%, respectively. Compared with DI₄₀₀, DI₅₅₀-DI₇₀₀-DI₉₀₀ increased LAI_{max} by

8, 17, and 29%, H_{max} by 22, 26, and 29%, and SD_{max} by 2, 4, and 16%, respectively. Hence, the relative increases in LAI_{max} , H_{max} , and SD_{max} caused by elevated CO_2 concentrations were higher under DI than under RI. This was because the increased percentages of P_n and T_{leaf} caused by elevated CO_2 concentrations were higher under DI than under RI (see Section 3.1). Since the photosynthesis can form 90–95% of biomass (Zelitch, 1982), and a slight increase in leaf temperature between 30–35 °C was good for crop growth (Wardlaw, 1979; Watts, 1971), the relative increases in LAI_{max} , H_{max} , and SD_{max} were higher under DI.

Compared with RI_{400} , RI_{550} – RI_{700} – RI_{900} decreased SLA by 9, 19, and 36%, respectively, while compared with DI_{400} , DI_{550} – DI_{700} – DI_{900} decreased SLA by 2, 15, and 34%, respectively. The reduced percentage of SLA caused by elevated CO_2 concentrations was therefore lower under DI than under RI. Elevated CO_2 concentrations reduced SLA which was the leaf area per leaf weight, possibly because they increased P_n so that dry matter accumulation was first stored in the leaves rather than in the leaf extension within per unit leaf weight (Mamatha et al., 2014; Yelle et al., 1990). Moreover, the redistribution of excess carbohydrates into older leaves under high CO_2 concentrations contributes more to leaf weight than to leaf area, thus reducing SLA (Kimball et al., 2002). The reduced percentage of SLA caused by elevated CO_2 concentrations was lower under DI than under RI. This might have been because the absolute P_n , dry matter accumulation, and leaf area were small under DI conditions, and photosynthate was used for leaf expansion first of all rather than for storage in the per unit leaf weight to receive more light by increasing the leaf area, which was good for increasing photosynthate under disadvantage conditions. That maybe the crop ability to survive from a bad soil water environment and gain the drought tolerance. So that the reduced percentage of SLA caused by elevated CO_2 concentrations was lower under DI.

The effects of different irrigation treatments and CO_2 concentrations on the dry matter in different plant parts and the grain yield of maize are shown in Table 5. The leaf dry weight (LDW), stem dry weight (SDW), root dry weight (RDW), grain yield per plant (GY), and total dry weight (TDW) at harvest time increased under elevated CO_2 concentrations. The dry matter under DI was lower than under RI. Compared with RI_{400} , the LDW , SDW , RDW , GY , and TDW under DI_{400} was 16, 34, 25, 21, and 26% lower, respectively. While under elevated CO_2 concentrations, the LDW , SDW , RDW , GY , and TDW under DI was 6–9, 10–20, 8–15, 5–20, and 7–19% lower, respectively, when compared with RI. Therefore, the reduced percentages of GY and TDW caused by DI were weakened along with the elevated CO_2 concentrations. That was because the increased percentage of P_n caused by elevated CO_2 concentrations was higher under DI, and the fertilization effect of CO_2 concentration was more significant under DI (Leakey et al., 2006), which offset the negative effect of DI. The interesting thing was that under the CO_2 concentration of 900 $\mu\text{mol mol}^{-1}$, the reduced percentages of GY and TDW caused by DI were at their lowest and not significantly different at 5 and 7%, respectively. That may because the higher the CO_2 concentration, the greater the fertilization effect was under DI conditions. So when the irrigation amount was reduced by 30%, the DI did not significantly affect the growth of maize under elevated CO_2 concentrations. Recent studies have suggested that, in the future, as CO_2 concentrations and temperatures increase, extreme rainfall events will be more frequent in spring in Northwest China, but in summer and autumn the precipitation frequency will be reduced (Gao et al., 2015; Guo et al., 2016). Changes in precipitation patterns could lead to a mismatch between natural precipitation and the demand for water of crops, causing frequent seasonal droughts, and seriously restricting the improvement of productivity (Wang et al., 2015). In this case, applying moderate deficit irrigation to crops during the planting season could save irrigation water and decrease GY

Table 5
The effects of CO_2 concentrations on leaf dry weight (LDW), stem dry weight (SDW), root dry weight (RDW), grain yield per plant (GY), and total dry weight (TDW) when maize was harvested under different irrigation treatments. Data in the table are the mean \pm standard error.

CO_2 ($\mu\text{mol mol}^{-1}$)	LDW (g)		SDW (g)		RDW (g)		GY (g plant $^{-1}$)		TDW (g)	
	RI	DI	RI	DI	RI	DI	RI	DI	RI	DI
400	25.71 \pm 0.52c	21.55 \pm 0.28c	52.73 \pm 8.84b	34.63 \pm 2.48b	17.50 \pm 3.28b	13.10 \pm 1.05c	110.52 \pm 9.16b	86.98 \pm 9.19c	247.00 \pm 16.90c	182.83 \pm 6.00c
550	28.12 \pm 0.85bc	25.49 \pm 1.74bc	55.57 \pm 6.96ab	45.45 \pm 5.64ab	21.88 \pm 2.26ab	18.58 \pm 2.82bc	135.95 \pm 10.99ab	108.53 \pm 4.46bc	292.60 \pm 11.03bc	237.10 \pm 14.69bc
700	30.54 \pm 1.28b	28.16 \pm 2.01b	63.87 \pm 3.09ab	57.73 \pm 8.39a	23.80 \pm 2.47ab	21.45 \pm 2.32b	144.61 \pm 18.46a	125.27 \pm 19.02ab	329.50 \pm 22.53ab	287.13 \pm 34.01ab
900	35.42 \pm 1.03a	33.35 \pm 0.66a	73.95 \pm 3.58a	59.16 \pm 4.05a	28.83 \pm 3.29a	31.10 \pm 2.89a	159.28 \pm 4.82a	151.45 \pm 1.77a	359.45 \pm 14.61a	332.79 \pm 20.83a

Means followed by the different letters (a, b, c) are significantly different at the level of $P < 0.05$, and by the same letter are not significantly different at the level of $P < 0.05$. RI denotes regular irrigation, and DI denotes deficit irrigation.

slightly. This could mitigate food reduction and water crises as CO₂ concentrations increase in the future.

Table 5 also shows that, compared with RI₄₀₀, RI₅₅₀–RI₇₀₀–RI₉₀₀ increased *LDW* by 5, 21, and 40%, *SDW* by 9, 19, and 38%, *RDW* by 25, 36, and 65%, *GY* by 23, 31, and 44%, and *TDW* by 18, 33, and 46%, respectively. However, compared with DI₄₀₀, DI₅₅₀–DI₇₀₀–DI₉₀₀ increased *LDW* by 31, 67, and 71%, *SDW* by 18, 31, and 55%, *RDW* by 42, 64, and 137%, *GY* by 25, 44, and 74%, and *TDW* by 30, 57, and 82%, respectively. Accordingly, the increased percentage of dry matter caused by elevated CO₂ concentrations was higher under DI than under RI. This was due to the fact that the increased percentage of *P_n* caused by elevated CO₂ concentrations was greater under DI than under RI, resulting in a greater increase in the percentage of dry matter accumulation.

In this study, elevated CO₂ concentrations increased *GY* and *TDW* by 24–59 and 24–64%, respectively, which was close to the results obtained by the same or similar CO₂ concentrations (Cure and Acock, 1986; Guo, 2003; Long et al., 2006; Meng et al., 2014). The changed percentages of *GY* and *TDW* were similar in the reports compiled by many researchers (Ainsworth et al., 2008; van der Kooi et al., 2016). However, the increased effects on *GY* and *TDW* caused by CO₂ enrichment differ slightly in this study when compared with the results obtained in some of the other literature on the subject. For example, the results obtained by Ziska and Bunce (1997) and Samarakoon and Gifford (1996) show that elevated CO₂ concentrations can increase the total biomass of maize in wet soil, but the effect was not significant, which differed from our conclusions. However, in a dry soil environment, *TDW* increased by 54% due to elevated CO₂ levels, which was a similar result to that given in this study. The response of *TDW* to elevated CO₂ concentrations in a dry environment or under DI treatment was very clear. The reasons for the different results in a wet environment may include the followings: (1) Our regular irrigation (RI) was conducted every three to four day according to the *ET* that consumed by the crops, it was not an absolute non-drought soil environment when compared with other literature. The crops may suffer from some slight drought periods before renewed access to irrigation, which may cause the significant results; (2) The irrigation frequency for the crops was performed more or less on a daily basis in previous studies, which was more frequent than in our study where it was carried out every three to four days. And studies have shown that *GY* and *TDW* decrease significantly with increased irrigation frequency (Tian et al., 2016); (3) This study was conducted in arid and semi-arid areas where the crop was highly dependent on water, which led to a more sensitive response to increased CO₂ concentrations; (4) Most previous studies set two constant temperatures, day and night, but we set a sine curve for the temperature during the daytime and a natural temperature at night according to the average temperature calculated at the experimental station over many years. According to the study of Hu (1963), increasing the temperature differential between day and night is beneficial to the growth and development of maize; (5) The experimental period in previous studies was short (about 30–60 days), but in this study it covered the entire growth season (about 133 days), which also resulted in a difference in biomass or yield at the final harvest. All the above explanations may cause the different result from other studies in a wet soil environment. But the increased percentages of *GY* and *TDW* caused by CO₂ enrichment under DI (or drought) are higher than under RI (or wet) is beyond doubt.

The effects of different irrigation treatments and CO₂ concentrations on hundred-grain weight (*HGW*), kernels per ear (*KPE*), and harvest index (*HI*) are shown in Table 6, in which, elevated CO₂ concentrations had no significant effects on *HGW* and *HI*, but *KPE* increased with a rise in CO₂ concentrations. There was no significant difference in terms of *HGW* between DI and RI under the same CO₂ concentration. DI₄₀₀, DI₅₅₀, DI₇₀₀, and DI₉₀₀ decreased

KPE by 21, 20, 13, and 5% respectively, however, when compared with RI under the same CO₂ concentration. The higher the CO₂ concentration, the lower the reduced percentage of *KPE* caused by DI. Compared with RI₄₀₀, RI₅₅₀–RI₇₀₀–RI₉₀₀ increased *KPE* by 23, 31, and 44%, respectively, but compared with DI₄₀₀, DI₅₅₀–DI₇₀₀–DI₉₀₀ increased it by 25, 44, and 74%. The increased percentage of *KPE* caused by elevated CO₂ concentrations was higher under DI than under RI. This accorded with the variation in *GY*, which would indicate that the variety in terms of *GY* was mainly determined by the variety in *KPE* under different irrigation and CO₂ concentration treatments, but that there was no direct relation to variations in *HGW*.

There were no significant effects in terms of elevated CO₂ concentrations on the *HI*. But DI increased *HI* by 5–15% when compared with RI, which means that DI can improve *HI*. This is consistent with many previous studies (Kang et al., 2000; Zhang et al., 1998; Zhang et al., 2008), although other studies have shown that *HI* decreases with increasing water stress (Bolaños and Edmeades, 1993; Farré and Faci, 2006; Muchow, 1989). The different results may be due to the fact that, in our experiment, the level of DI did not reach a level that could significantly reduce *HI*. This might also be due to the different dependence of *HI* on irrigation levels in different studies, where the experimental areas have different climate conditions (drought or wet). Further research is, therefore, needed on this.

3.3. More pronounced effects of elevated CO₂ concentrations on maize evapotranspiration under deficit irrigation

The effects of CO₂ concentrations on maize evapotranspiration (*ET*) under RI and DI are shown in Fig. 5. It shows that when the amount of irrigation was reduced by 30% under DI, *ET* was 30% lower than that under RI. Under both RI and DI, *ET* decreased first to a minimum value at 700 μmol mol⁻¹ and then increased with an elevation in CO₂ concentrations. This was because, although elevated CO₂ concentrations reduced *g_s* and *T_r*, they increased *LAI*, offsetting the reduction in canopy conductance caused by reduced *g_s* and *T_r* (Hileman et al., 1994; Kang et al., 1996). Wullschleger et al. (2002) also reported that the canopy conductance only decreased by 14% when *g_s* decreased by 44% due to the elevation of CO₂ concentration from 394 μmol mol⁻¹ to 538 μmol mol⁻¹. The impact of an elevated CO₂ concentration on *ET* was therefore small and, even when the CO₂ concentration reached a certain high value, *ET* increased. Oliver et al. (2009) also note that the effects of elevated CO₂ concentrations on *ET* are wide ranging and can remain at a reduced level (Cech et al., 2003; Owensby et al., 1997), or remain unchanged (Ellsworth, 1999; Qiao et al., 2010), or even increase (Tricker et al., 2009; Uddling et al., 2008).

Compared with RI₄₀₀, RI₅₅₀–RI₇₀₀–RI₉₀₀ decreased *ET* by 15, 18, and 13%, respectively, while compared with DI₄₀₀, DI₅₅₀–DI₇₀₀–DI₉₀₀ decreased *ET* by 10, 14, and 10%, respectively. Accordingly, the reduced percentage of *ET* caused by elevated CO₂ concentrations was less under DI than under RI. The result was similar to the findings of Samarakoon and Gifford (1996) and Kang et al. (2002). As mentioned previously, although the decrease in *T_r* caused by elevated CO₂ concentrations was 2–4% higher under DI than under RI, the increased percentage of *LAI* was higher (7–23%). So the offset effect of the increased *LAI* on the decreased *T_r* was more obvious. Thus, the impact of elevated CO₂ concentrations on *ET* was smaller under DI than under RI.

3.4. More pronounced effects of elevated CO₂ concentrations on water use efficiency and water productivity of maize under deficit irrigation

The effects of different irrigation treatments and elevated CO₂ concentrations on leaf water use efficiency (*WUE_L*) and water pro-

Table 6
The effects of CO₂ concentrations on hundred-grain weight (HGW), kernels per ear (KPE), and harvest index (HI) under different irrigation treatments. Data in the table are the mean ± standard error.

CO ₂ (μmol mol ⁻¹)	HGW (g)		KPE (n)		HI	
	RI	DI	RI	DI	RI	DI
400	29.28 ± 1.90a	29.72 ± 0.81a	346.13 ± 28.68b	272.42 ± 28.79c	0.41 ± 0.03a	0.47 ± 0.04a
550	31.57 ± 0.58a	32.91 ± 0.93a	425.77 ± 17.21ab	339.88 ± 13.95bc	0.43 ± 0.02a	0.46 ± 0.03a
700	32.43 ± 2.36a	32.80 ± 1.33a	452.89 ± 57.81a	392.33 ± 59.56ab	0.42 ± 0.02a	0.48 ± 0.04a
900	31.98 ± 0.54a	31.47 ± 0.98a	498.83 ± 15.10a	474.33 ± 5.55a	0.44 ± 0.02a	0.46 ± 0.02a

Means followed by the different letters (a, b, c) are significantly different at the level of $P < 0.05$, and by the same letter are not significantly different at the level of $P < 0.05$. RI denotes regular irrigation, and DI denotes deficit irrigation.

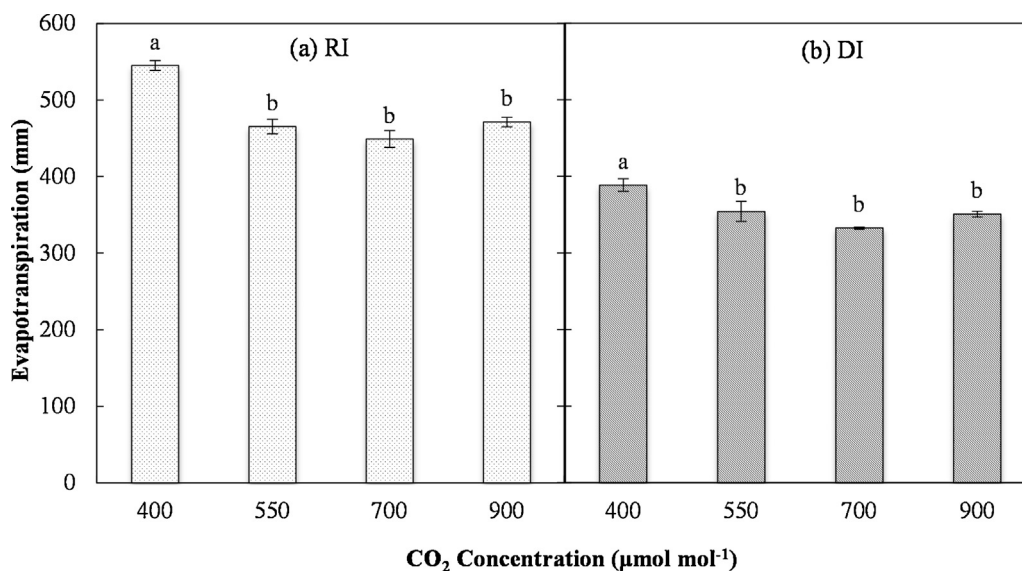


Fig. 5. The effect of CO₂ concentrations on maize evapotranspiration (ET) under different irrigation treatments. (Data in the figure are the mean ± standard error. Means followed by the different letters (a, b, c) are significantly different at the level of $P < 0.05$, and by the same letter are not significantly different at the level of $P < 0.05$. RI denotes regular irrigation, and DI denotes deficit irrigation).

Table 7
The effects of CO₂ concentrations on leaf water use efficiency (WUE_L) and water productivity (WP) of maize under different irrigation treatments. Data in the table are the mean ± standard error.

CO ₂ (μmol mol ⁻¹)	WUE _L (mmolCO ₂ mol ⁻¹ H ₂ O)		WP (g mm ⁻¹)	
	RI	DI	RI	DI
400	6.56 ± 0.49c	6.05 ± 0.64c	0.42 ± 0.00c	0.46 ± 0.03c
550	9.94 ± 0.80b	10.39 ± 1.09b	0.62 ± 0.04b	0.69 ± 0.05b
700	12.56 ± 0.97b	13.34 ± 1.28b	0.69 ± 0.08ab	0.80 ± 0.05b
900	18.72 ± 1.60a	21.23 ± 1.94a	0.79 ± 0.02a	0.93 ± 0.06a

Means followed by the different letters (a, b, c) are significantly different at the level of $P < 0.05$, and by the same letter are not significantly different at the level of $P < 0.05$. RI denotes regular irrigation, and DI denotes deficit irrigation.

ductivity (WP) are shown in Table 7. It shows that WUE_L and WP increased with the elevation of CO₂ concentrations in both irrigation treatments, so that the results were the same as the results obtained in previous studies (Idso et al., 1987; Kang et al., 2002; Leakey et al., 2006; Li et al., 2003; Meng et al., 2014; Oliver et al., 2009). Compared with RI₄₀₀, WUE_L was 8% lower with DI₄₀₀, but WP was 10% higher. As far as the elevated CO₂ concentrations were concerned, DI increased WUE_L and WP by 4–12 and 10–15%. Therefore, the increased percentages of WUE_L and WP caused by DI grew along with the elevated CO₂ concentrations.

Compared with RI₄₀₀, RI₅₅₀–RI₇₀₀–RI₉₀₀ increased WUE_L by 52, 91, and 185%, and WP by 48, 64, and 88%, respectively, while compared with DI₄₀₀, DI₅₅₀–DI₇₀₀–DI₉₀₀ increased WUE_L by 72, 120, and

251%, and WP by 50, 74, and 102%, respectively. Accordingly, the increased percentages of WUE_L and WP caused by elevated CO₂ concentrations were higher under DI than under RI. That was because at the leaf level, according to Eq. (3), when the numerator (P_n) increased and the denominator (T_r) decreased, the result (WUE_L) came out to increase. And since the increased percentage of P_n and the reduced percentage of T_r were both higher under DI than under RI (see Section 3.1), the increased percentage of WUE_L caused by elevated CO₂ concentrations was higher under DI than under RI. At the canopy level, there was a similar situation of WP to WUE_L, i.e. when the numerator (TDW) increased and the denominator (ET) decreased, the result (WP) came out to increase according to Eq. (4). The increased percentage of TDW (11–36%) was much higher

than the decreased percentage of ET (3–5%) under DI than under RI, thus the increased percentage of WP caused by elevated CO_2 concentrations was higher under DI than under RI. This was the same as the result obtained by Allen et al. (2011) using a similar CO_2 concentration.

The improvement of water use efficiency and water productivity was more significant than the improvement of P_n and yield (Chaves and Pereira, 1992), especially in the case of water deficit conditions. Water deficit reduced crop production, while increased CO_2 concentrations not only reduced water consumption, but also increased yield. The results of this study show that the increased proportion of WP caused by CO_2 enrichment was more under DI. This would provide a strong theoretical basis for conducting irrigation water management under elevated CO_2 concentrations in the future.

4. Conclusions

In this study, we explored the different effects of elevated CO_2 concentration on stomatal conductance, transpiration rate, leaf temperature, photosynthetic rate, evapotranspiration, crop growth, biomass parameters, yield parameters, leaf water use efficiency, and water productivity, among which the effect on leaf temperature was only discussed in this study, under two different irrigation methods. And the results show that the elevated CO_2 concentration would benefit maize crops more under deficit irrigation (which can save a lot of water) than regular irrigation method (which was similar to the local water management). Although the elevated CO_2 concentration and deficit irrigation decreased the absolute value of stomatal conductance and transpiration rate, but the leaf temperature increased more due to the transpiration cooling effect, then promoted the photosynthetic rate, the crop growth, and the yield, weakening the disadvantages of deficit irrigation on maize plants.

Some of our results under regular irrigation were different from those of other literature in wet soil conditions. That was because the maize grown in regular irrigation conditions may suffer from slight drought before re-irrigation and the environment was not absolutely non-water stressed. Also the irrigation frequency was quite different from other references, which may cause different results and need to be considered in the future. Whatever, our study revealed that under future climate change, deficit irrigation is not only an efficient water saving method, but also can benefit crops more with lowest yield reduction and highest water productivity.

However, the irrigation amount of this study only considered two gradients, i.e. the regular irrigation and deficit irrigation in which the irrigation amounts were 100 and 70% of evapotranspiration, respectively, which would create some limitations of the research. Also, there were no irrigation frequency, planting density, and nitrogen treatments taking into account, which are also very important factors in the crop growth periods and may cause different results when considering the CO_2 concentration effect. More consideration is needed in the future's research.

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