



**Full Length Article**

# Combined Influence of Atmospheric Warming and Elevated CO<sub>2</sub> Concentrations on Potato Physiology and Ecology in the Semi-arid Region of the Loess Plateau, China

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## Abstract

An experiment was performed to analyse combined influence of atmospheric warming and elevated CO<sub>2</sub> concentrations on the physiology, ecology of potato (*Solanum tuberosum* L.) in the semi-arid region of the Loess Plateau based on parallel observations of meteorological elements. The results showed that precipitation in the experimental region decreased from 1958 to 2016 at a rate of -12.171 mm every 10 years, the air temperature increased substantially during the past 59 years tendency rate based on linear regression was 0.417°C every 10 years, the temperature continued to increase since the 1980s and has been especially substantial since the 2000s. The net photosynthesis rate (Pn) of potato leaves treated with increased temperature (IT) combined with an elevated CO<sub>2</sub> concentration (IC) (IT+IC) was improved and was higher than those under the IT and control (CK) treatments during early growth stage. During late growth stage, Pn treated with warming and elevated CO<sub>2</sub> concentrations decreased at the highest rate. As the ambient CO<sub>2</sub> concentrations increased, leaf stomatal conductance gradually decreased, and stomatal conductance of leaves treated with warming and elevated CO<sub>2</sub> concentrations during the growth stage was lower than those of the control leaves. Leaf transpiration rates increased with warming but were highest during the early growth stage; however, during the late growth stage, the transpiration rates of the leaves treated with warming and elevated CO<sub>2</sub> concentrations were lower than those of the IT treatment and CK. The water use efficiency of leaves treated with warming and elevated CO<sub>2</sub> concentrations distinctly improved and was higher than that of the control and only warming treated leaves. The actual yield of potatoes treated with warming and elevated CO<sub>2</sub> concentrations was distinctly higher than that of the control and those treated with only warming. The yield of potatoes treated with only warming was low, and in the semi-arid region of the Loess Plateau, warming was not amenable to the expansion of potato tubers. Warming during the tuber expansion stage delayed tuber growth and caused tuber deformation. Therefore, warming combined with elevated CO<sub>2</sub> concentrations is likely to improve the Pn and water use efficiency of potato leaves, promote dry matter accumulation and increase yields. © 2020 Friends Science Publishers

**Keywords:** Potato; Climatic change; Elevated CO<sub>2</sub> concentration; Collaborative influence

## Introduction

The 5<sup>th</sup> Assessment Report of the Intergovernmental Panel on Climate Change (IPCC) (AR5) determined that global warming in the past 100 years is irrefutable (IPCC 2013). The average surface temperature of the earth increased by 0.85°C on average during the 130 years from 1880 to 2012, and the rate of temperature increase was 0.12°C·10<sup>-1</sup> during 1951~2012, which is nearly twice as fast as that since 1880. The earth has experienced three warmest 10 years since 1983~2012, and the trends and characteristics of

climate warming can be observed at nearly all places worldwide. It is estimated that the average surface temperature of the earth will continue to rise by 0.3~0.7°C during 2016~2035. Because of human activities, the concentration of CO<sub>2</sub> in the air has continually increased since 1750 and reached 391 μmol·mol<sup>-1</sup> in 2011. According to the low-emissions scenario in the Representative Concentration Pathways 4.5 (RCP4.5) when the radiation intensity is stabilized at 4.5 W·m<sup>-2</sup>, the equivalent concentration of CO<sub>2</sub> will be stabilized at approximately 650 μmol·mol<sup>-1</sup> after the year 2100 (IPCC 2013).

Stomatal conductance, transpiration rates and soil evaporation rates are affected by temperature changes; thus, crop water content circulation and evapotranspiration are influenced (Rawson 1988; Zhou *et al.* 2011). A warming experiment on potato that involved cultivation with mulching film to influence the soil and plant ecological growing microenvironment directly by improving the soil temperature and reducing moisture evaporation (Kar 2003; Wang *et al.* 2005a) revealed improved crop yield and quality (Jenkins and Gillison 1995; Lamont 2005; Luis *et al.* 2011; Wang *et al.* 2011), and the water use efficiency (WUE) increased (Wang *et al.* 2005a, b; Zhao *et al.* 2012). Similarly, an infrared radiator farm warming experiment that simulated atmospheric warming showed that potato physiology and ecology and the yield-formation processes were significantly altered (Xiao *et al.* 2013 a, b). Under a scenario of future climatic changes, warming during the tuber expansion stage will not adversely influence tuber yields under irrigation (Carolina *et al.* 2017). Because of climate warming, the potato inflorescence-forming stage in semi-arid regions has advanced by 8~9 days, the blooming stage has advanced by 4~5 days, and the potato growth period has increased in duration (Yao *et al.* 2010). Warming in the spring and autumn is good for potato growth and yields, but warming in the summer will aggravate the vulnerability of potato growth (Yao *et al.* 2013; Zhao *et al.* 2015).

Many studies have shown that elevated CO<sub>2</sub> concentrations can promote the total biomass and yield of potato (Sicher and Bunce 1999; Wheeler *et al.* 1999; Schapendonk *et al.* 2000). For example, when CO<sub>2</sub> concentrations were 370~740 μmol·mol<sup>-1</sup> higher than ambient concentrations, the potato tuber yield increased by 27~49% (Wheeler *et al.* 1991). However, slightly adverse effects have been observed during experiments (Finnan *et al.* 2005): increased CO<sub>2</sub> supplies can accelerate leaf ageing and shorten the blooming stage (Miglietta *et al.* 1998; Lawson *et al.* 2001). Elevated CO<sub>2</sub> concentrations can lower potato leaf transpiration rates and increase photosynthesis and WUE (Ku *et al.* 1977). When CO<sub>2</sub> concentrations in an open-top chamber (OTC) were elevated by 350~700 μmol·mol<sup>-1</sup>, the canopy photosynthesis improved by 80%, but the result varied with growth stages (Schapendonk *et al.* 2000). Sicher and Bunce (1999) reported that the net photosynthesis rate in potato leaves during the whole growth period increased and was higher than that in the control leaves when the CO<sub>2</sub> concentration was elevated. The results of a controlled CO<sub>2</sub> concentration experiment showed that the total biomass, yield and WUE of potato improved when the CO<sub>2</sub> concentrations were elevated (Fleisher *et al.* 2008).

Potato (*Solanum tuberosum* L.) is planted in 157 countries worldwide, and the total yield reached 324 million tons in 2010. In China, 5.33 million ha of potatoes were planted, and the annual yield led the world by 80 million tons (Zhang *et al.* 2012). Potato is the fourth major food

crop after paddy rice, wheat and maize and is one of the most promising high-yielding crop species. Potato is tolerant to drought and arid conditions and is a particularly high-yielding crop species suitable in semi-arid regions at mid-latitudes (Zhao *et al.* 2013). Potato growth and yield formation are strongly influenced by climate warming, but studies investigating the influence of atmospheric warming combined with CO<sub>2</sub> concentrations on potato physiology, ecology and yield formation in semi-arid regions at mid-latitudes are lacking. Therefore, it is necessary to study the combined influence of elevated CO<sub>2</sub> concentrations and atmospheric warming on potato physiology and ecology, build an experimental base for potato physiology and ecology simulations, and provide a scientific reference for industrial potato development in the background of climatic change.

## Materials and Methods

### Climate and potato growth outline in the study region

The study area belongs to the semi-arid region of the Loess Plateau. The annual mean air temperature was 7.2°C, the mean air temperature in July (the hottest month) was 19.2°C, and the mean air temperature in January (the coldest month) was -7.2°C. The annual mean precipitation was 377.1 mm. The precipitation from May to October was 328.5 mm, which was 87.0% of that for the whole year. The annual mean sunshine duration was 243.7 h, and the annual mean continuous frost-free duration was 145 days.

In the study region, potato was usually planted during the first and middle ten days of May. Furthermore, the seedling stage occurred during the first and middle ten days of June, the ramifying stage occurred during the last ten days of June and during the first ten days of July, the inflorescence-forming stage occurred during the first and middle ten days of July, the blooming stage occurred during the middle and last ten days of July, and harvest occurred during the first and middle ten days of October. The whole growth period from sowing to harvest was 135~165 days. During the whole growth period, the accumulated temperature ≥ 0°C was approximately 2,729.7°C, the precipitation was approximately 346.2 mm, and the sunshine duration was approximately 1,262.1 h.

### Test design

The experiment was performed at the Dingxi Drought and Ecological Environment Experiment Station of the Lanzhou Institute of Arid Meteorology, China Meteorological Administration from April to October 2016. The experiment was performed in a new OTC to study the combined influence of atmospheric warming and elevated CO<sub>2</sub> concentrations on potato physiology and ecology. The chamber was 18 m<sup>2</sup> wide and 3 m high, and the top was open.

RCP4.5 supposed that humans tried to reduce greenhouse gas emissions, the radiation intensity stabilized at  $4.5 \text{ W}\cdot\text{m}^{-2}$ , the equivalent  $\text{CO}_2$  concentration stabilized at  $650 \mu\text{mol}\cdot\text{mol}^{-1}$  by the end of the 21<sup>st</sup> century, and the temperature increase at the surface of the earth was within  $2.0^\circ\text{C}$  (IPCC, 2013). Therefore, two treatments and one control were included in the experiment. In one treatment that included warming (IT), a temperature monitor controller was used, and the air temperature increase was controlled at  $2.0\pm 0.5^\circ\text{C}$  ( $1.5$  to  $2.5^\circ\text{C}$ ). The other treatment included both warming and an elevated  $\text{CO}_2$  concentration (IT+IC). For this treatment, a  $\text{CO}_2$  concentration monitor controller was used, and the  $\text{CO}_2$  concentration was controlled at  $650\pm 20 \mu\text{mol}\cdot\text{mol}^{-1}$ ,  $\text{CO}_2$  exposure was carried out daily during daylight. For the contrast check (CK), the ambient concentration of  $\text{CO}_2$  was approximately  $370 \mu\text{mol}\cdot\text{mol}^{-1}$ . Each treatment was repeated three times.

A local potato cultivar "New Daping" served as experimental material, and all potato seedlings were fertilized via free-air  $\text{CO}_2$  enrichment (FACE). This FACE fertilization period occurred from 07:00~18:00, and the  $\text{CO}_2$  concentration in the chamber was kept stable during the whole experimental period. The water content and fertilizer during the experimental period were constant, and the soil relative humidity ranged from 60 to 65% of field capacity during the whole experimental period, there were no restricting factors, such as plant diseases, insect pests or weeds.

### Measured parameters and methods

The leaf net photosynthesis rate (Pn), transpiration rate (Tr), stomatal conductance (gs) and intercellular  $\text{CO}_2$  (Ci) parameters were measured from 10:00~11:30 on sunny days via a Li-6400 photosynthesis measurement system developed by LI-COR (US). The standard Li-6400 leaf chamber was used. Five representative plants with healthy and identical growth were selected in each plot. The fourth fully unfolded leaf was selected to measure the photosynthetic parameters. The light intensity (PAR) was  $1500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , and the air intake rate was  $500 \mu\text{mol}\cdot\text{mol}^{-1}$ .

Chlorophyll was measured by a SPAD-502 metre (Japan). The SPAD values were measured at the widest part of the fourth fully expanded leaf from top to bottom. Five representative plants were selected in each plot, and measurements were repeated five times for each leaf. The average value was used to represent the relative chlorophyll content of the leaf. Potato height and yield components were measured in accordance with the agrometeorological observation criterion of the China Meteorological Administration (1993).

### Statistical analyses

The climatic element rate of change tendency was

calculated as follows:  $X_i = a + bt_i$  ( $i=1, 2, n$ ) (Wei 2007). In the formula,  $X_i$  is the climatic element variable,  $t_i$  is the time corresponding to  $X_i$ ,  $a$  is the regression constant,  $b$  is the regression coefficient, and  $n$  is the number of samples.  $10b$  is the climatic element tendency rate. Statistical analyses were realized by analysis of variance, correlation analysis, linear regression analysis and nonlinear regression analysis, which calculated the related linearized coefficients and fitted the linearity and nonlinearity (Wei 2007).

## Results

### Characteristics of climate change in the experimental region

**Precipitation:** The changes in precipitation in the experimental region during 1958~2016 is shown in Fig. 1a. In the past 59 years, the annual precipitation decreased, and the decreasing precipitation tendency was  $-12.171 \text{ mm}$  ( $r=0.25$ ,  $n=59$ ,  $P=0.05$ ) every 10 years. The annual precipitation was  $377.1 \text{ mm}$  on average in the experimental region and fluctuated from  $245.7\sim 720.1 \text{ mm}$ ; the precipitation ranged from  $-34.8\sim 91.0\%$  of the percentage difference. The precipitation was high in the 1960s; the annual mean precipitation was  $447.6 \text{ mm}$ . However, the precipitation was lowest in the 1990s; the annual mean precipitation was  $365.7 \text{ mm}$ . The precipitation during the first 10 a of the 21<sup>st</sup> century was also low; the annual mean precipitation was  $375.6 \text{ mm}$ .

Winter (December ~ February of the last year) precipitation during previous years gradually increased by  $0.420 \text{ mm}$  ( $P>0.10$ ) every 10 years, but was not significant; the climatic tendencies of precipitation in the spring (March ~ May) and summer (June ~ August) were  $-1.59$  ( $P>0.10$ ) and  $-5.431 \text{ mm}$  ( $P>0.10$ ) every 10 years, respectively; these represented decreasing trends but were not significant. The climatic tendency rate of precipitation decreased by  $-5.5967 \text{ mm}$  ( $P<0.10$ ) in autumn (September ~ November) and by  $-0.117 \text{ mm}$  ( $P<0.10$ ) every 10 years during the potato growing stage (May ~ October), the latter of which was the longest period of decreasing precipitation.

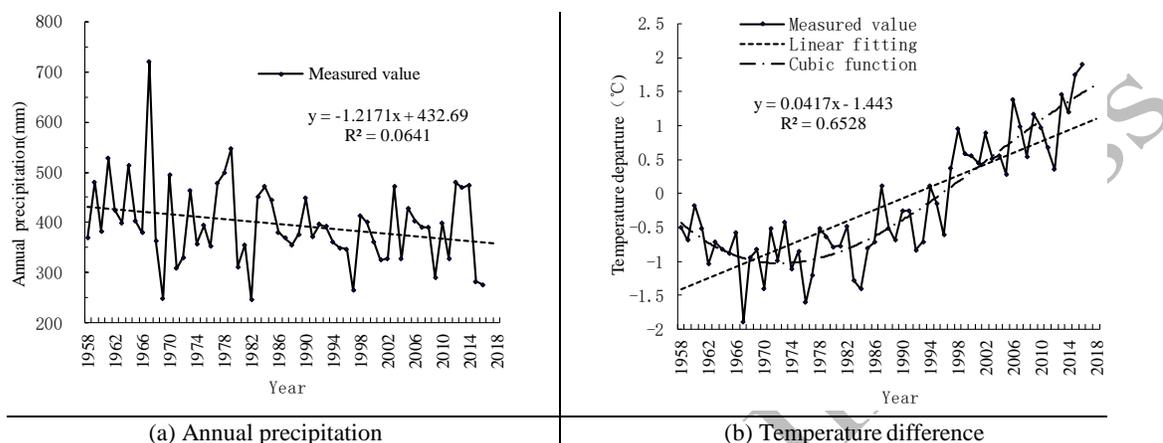
With respect to the stability of changes in precipitation, the winter precipitation difference among years was the largest and the most dynamic with coefficient of variation was 54.4%. The coefficients of variation in other seasons among years ranged from 25.9~44.8%. The annual difference in precipitation during the potato growth period was the smallest; the coefficient of variation was 20.7%. The stable period of annual changes in precipitation essentially matched the potato growth period and was the period during which the precipitation rate needed for planting potato was high.

**Air temperature:** As shown in Fig. 1b, the air temperature significantly increased during the past 59 years (during 1958~2016), and the linear regression-based climatic tendency rate of the air temperature was

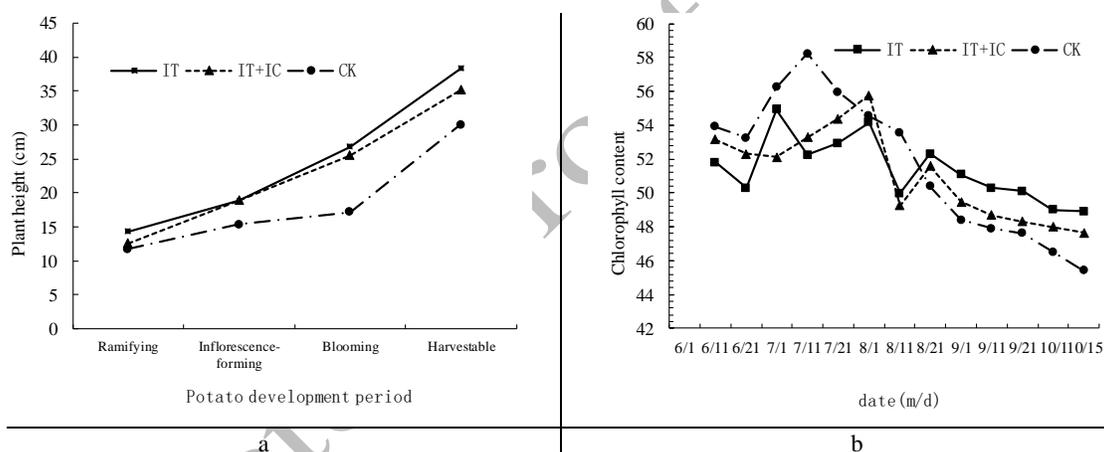
**Table 1:** Changes in plant height at different growth stages of potatoes treated with different factors

Treatment	Ramifying	Inflorescence-forming	Blooming	Harvestable
IT	14.25±1.39aA	18.83±1.21aA	26.87±4.38aA	38.30±3.73aA
IT+IC	12.55±0.90bB	18.92±1.38aA	25.46±2.49aA	35.15±3.43bA
CK	11.65±1.49bB	15.40±1.71bB	17.26±13.0bB	30.00±2.78cB

Note: a, b and c mean  $\alpha=0.05$ ; A, B and C mean  $\alpha=0.01$ ; the difference in letters between two rows means a significant difference



**Fig. 1:** Changes in annual climatic factors in the experimental region (1958–2016)



**Fig. 2:** Changes in plant height (a) and chlorophyll content (b) in potato in response to different treatments

0.417°C ( $r=0.808$ ,  $n=59$ ,  $P<0.001$ ) every 10 years. There was an inverse relation between the air temperature and the mean value during the 1960s~1980s; the values were -0.5°C in the 1960s, -0.4°C in the 1970s, -0.2°C in the 1980s, -0.5°C in the 1990s, 1.3°C in the first 10 years of the 21<sup>st</sup> century, and 1.7°C during 2011~2016. The winter warming rate was rapid in the past 59 years; the climatic tendency rate was 0.502°C ( $P<0.001$ ) every 10 years. The climatic tendency rate of autumn warming was 0.423°C ( $P<0.001$ ), which was second only to the rate during winter. The climatic tendency rate of summer warming was 0.373°C ( $P<0.001$ ), and the spring warming rate was the lowest at 0.354°C ( $P<0.001$ ) every 10 years. The climatic tendency rate of warming during the potato growth period was 0.373°C ( $P<0.001$ ) every 10 years.

### Influence of atmospheric warming and elevated CO<sub>2</sub> concentration on potato

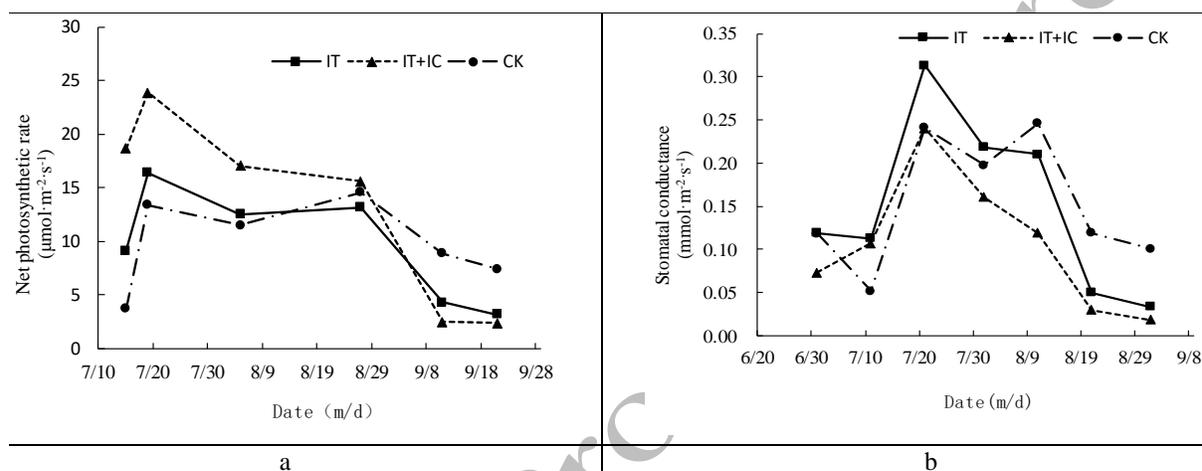
**Plant height:** Fig. 2a and Table 1 show that the height of potato plants treated with warming (IT treatment) were significantly higher than that of plants treated with warming and elevated CO<sub>2</sub> concentrations (IT+IC treatment), and that of the CK ( $P<0.01$ ) at the ramifying stage. In addition, the height of potato plants in the IT and IT+IC treatments was significantly higher than that of the plants in the CK treatment, which implied that the fertilization effect of CO<sub>2</sub> became increasingly distinct as the growth progressed. During the harvest stage, the potato height followed the order of IT>IT+IC>CK and was significant at 0.05 (Table 1). The difference among the three treatments was

**Table 2:** Results of the analysis of variance of the net photosynthesis in different potato treatments during the vegetative growth stage (blooming stage)

Variance source	Degrees of freedom	Sum of squares	Mean square	F value	P value
Between treatments	2	448.827	224.414	20.931	0.0001
Within treatment	20	214.430	10.722		
Total variance	22	663.257			

**Table 3:** Results of the analysis of variance of net photosynthesis in different potato treatments during the reproductive growth stage (stem expansion stage)

Variance source	Degrees of freedom	Sum of squares	Mean square	F value	P value
Between treatments	2	180.922	90.461	29.718	0.0001
Within treatment	23	70.011	3.044		
Total variance	25	250.933			

**Fig. 3:** Changes in the net photosynthesis rate (a) and stomatal conductance (b) of potato in response to different treatments

significant, which proves that increased temperature can significantly increase plant height.

**Chlorophyll content:** The chlorophyll content gradually increased as the growth progression increased. This increase followed the order of CK>IT+IC>IT during the early growth stage; it was the lowest in IT+IC on July 1 but was not significant ( $P>0.05$ ). Afterward, the chlorophyll content gradually increased and peaked on July 31; the content within the different treatments followed the order of IT+IC>CK>IT. The chlorophyll content then started to decrease with as the potato leaves aged. From August 21 to the end of harvest, the content decreased quickly as the leaves rapidly aged in the CK treatment, but the content decreased gradually as the leaves slowly aged in the IT treatment; the chlorophyll content accordingly followed the order of IT>IT+IC>CK. These results prove that the chlorophyll content was higher in the IT treatment than in the other treatments during later growth stages (Fig. 2b).

#### Influence of atmospheric warming and elevated CO<sub>2</sub> concentrations on leaf gas exchange

**Net photosynthesis rate (Pn):** The Pn in potato leaves during the vegetative growth stage and the reproductive

growth stage (the blooming stage and tuber expansion stage, respectively) followed the order: IT+IC>IT>CK. The rate of IT+IC treatment was 18.6~23.8 µmol·m<sup>-2</sup>·s<sup>-1</sup>, the rate in the IT treatment was 9.1~16.0 µmol·m<sup>-2</sup>·s<sup>-1</sup>, and the rate in the CK treatment was 3.7~13.4 µmol·m<sup>-2</sup>·s<sup>-1</sup> (Fig. 3a). The rate in the IT+IC treatment improved by 1~5 times and was, on average, 2.1 times higher than that in the CK treatment. The rate in the IT treatment improved by approximately 22 to 140% times and was, on average, 85% higher than that in the CK treatment; both rates were significant at  $P<0.01$  level (Table 2). These results showed that, during the early growth stage of potato, the atmospheric temperature was low and did not meet the most suitable temperature for potato growth. Warming compensated for the low leaf photosynthesis rate caused by low temperatures, and the rate improved in response to warming. Furthermore, because CO<sub>2</sub> concentrations increased as the temperatures increased, the raw material required for leaf photosynthesis increased under the IT+IC treatment, and the Pn further improved. Therefore, the Pn in leaves treated with warming and elevated CO<sub>2</sub> concentrations was much higher than that in the leaves of the other treatments.

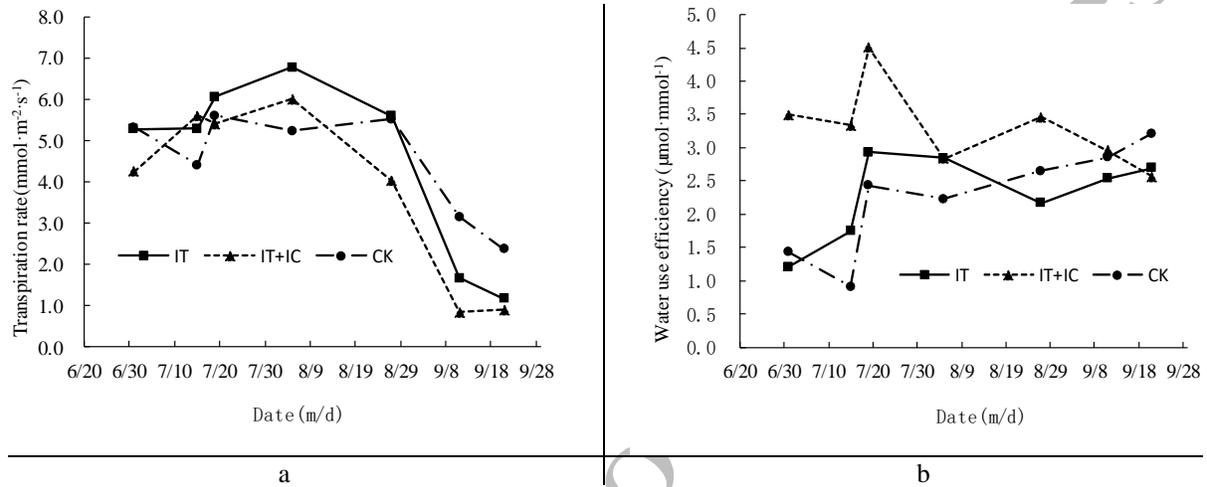
Because of warming and elevated CO<sub>2</sub> concentrations during the early stage, the potato plants grew quickly, but

**Table 4:** Results of the analysis of variance of the potato leaf transpiration rate in different treatments at the blooming stage

Variance source	Degrees of freedom	Sum of squares	Mean square	F value	P value
Between treatments	2	1.874	0.937	0.644	0.536
Within treatment	20	29.088	1.454		
Total variance	22	30.961			

**Table 5:** Results of the analysis of variance of the potato leaf transpiration rate in different treatments at the tuber expansion stage

Variance source	Degrees of freedom	Sum of squares	Mean square	F value	P value
Between treatments	2	31.210	15.605	4.315	0.025
Within treatment	25	90.411	3.616		
Total variance	27	121.622			



**Fig. 4:** Changes in the transpiration rate (a) and WUE (b) of potato in response to different treatments

during the late growth stage, the plant leaves started to age quickly; the change in net photosynthesis followed the order of CK>IT>IT+IC, and the differences were significant or extremely significant. The rate in the IT+IC treatment decreased by 210%~260% and was, on average, 70% lower than that in the CK treatment, and the decreasing rate in the IT treatment decreased by 110%~113% and was, on average, 55% lower than that in the CK treatment. These results proved that the Pn in potato leaves in the IT+IC treatment was higher than that in the other two treatments during the vegetative growth stage. During the late growth stage, the potato leaves started to age quickly because of warming and elevated CO<sub>2</sub> concentrations during the early stage, and compared with that in the potato leaves in the other treatments, the net photosynthesis in the potato leaves in the IT+IC treatment decreased more quickly, and the differences were extremely significant during the tuber expansion stage (Table 3).

**Stomatal conductance (gs):** Potato leaf gs increased but then decreased during the whole growth period (Fig. 3b). Analysis of the gs of leaves revealed that, compared with that in the CK treatment, the potato leaf gs under the IT+IC treatment decreased by 5~80% (44% on average). The gs decreased slowly in the early growth stage and quickly in the late growth stage. Compared with that in the CK

treatment, the gs in the IT+IC treatment increased by 17~46% in the early growth stage but then decreased by 9~63% (32% on average) as the duration of warming increased. Additional analyses revealed that the gs in the different treatments followed the order of IT>CK>IT+IC in the early growth stage and CK>IT>IT+IC in the late growth stage, and there was a significant or extremely significant difference among the CK, IT and IT+IC treatments. These results prove that the gs of leaves in the IT treatment is higher than that in the CK treatment during the early growth stage and lower during the late stage. The gs gradually decreased in response to elevated ambient CO<sub>2</sub> concentrations; thus, the gs of leaves in the IT+IC treatment was lower than that in the CK treatment.

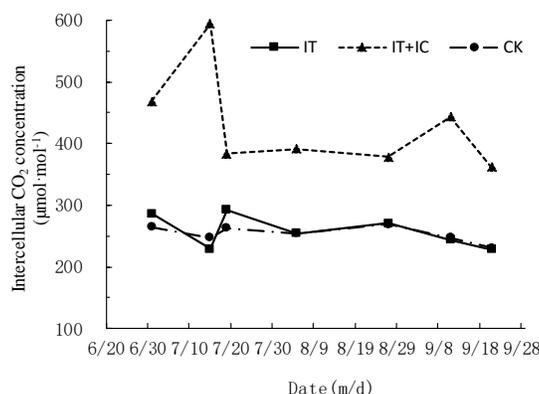
**Transpiration rate (Tr):** The transpiration rate increased as warming increased. The Tr in the IT treatment was highest, followed by that in the CK treatment and that in the IT+IC treatment. Compared with that in the CK treatment, the rate in the IT and IT+IC treatments increased by 1~12% in the early growth stage, but it decreased by 4~27% in the late growth stage (Fig. 4a). The difference in the Tr between different treatments was not significant at the blooming stage ( $p>0.05$ ; Table 4). With the advancement of the fertilization process, the differences in transpiration rates under the different treatments increased gradually. The

**Table 6:** Multiple comparisons (SSR method) of potato leaf transpiration rate in different treatments at the tuber expansion stage

Treatment	Mean	a=0.05	a=0.01
IT	6.4579	a	A
CK	5.8000	bc	A
IT+IC	4.0311	c	A

**Table 7:** Potato yield structure change in response to different treatments

Treatment	Potato weight per plant (g·plant <sup>-1</sup> )	Scrap potato rate (%)	Fresh stem weight (g·m <sup>-2</sup> )	Ratio of potato to stem	Theoretical yield (g·m <sup>-2</sup> )	Actual yield (kg·hm <sup>-2</sup> )
IT	81.7	1	786.89	0.84	653.69	5529.07
IT+IC	207.2	7	926.09	1.16	1168.03	8830.21
CK	133.8	1	658.51	2.32	1780.96	7820.08

**Fig. 5:** Changes in intercellular CO<sub>2</sub> concentrations in potato in response to different treatments

transpiration rate at the tuber expansion stage between the different treatments passed the significance threshold of 0.05 (Tables 5–6).

**Water use efficiency (WUE):** The leaf WUE is the amount of CO<sub>2</sub> assimilated per unit weight of water content lost to transpiration and is normally represented by the ratio of net photosynthesis to Tr, i.e., the potato leaf WUE can be calculated as follows:  $WUE = P_n/Tr$ . Under high CO<sub>2</sub> concentrations, the WUE of potato leaves was promoted by increasing the P<sub>n</sub> and decreasing the transpiration rate caused by decreasing the g<sub>s</sub>. During the blooming stage and tuber expansion stage, the potato leaf WUE increased as the CO<sub>2</sub> concentrations increased. The WUE among treatments followed the order of IT+IC>CK>IT (Fig. 4b), compared with that in the CK treatment, the average rate of WUE in the IT+IC treatment increased by 31% at the blooming stage and by 1.4 times at the tuber expansion stage. There were differences in the increase in ranges in different periods. Furthermore, compared with that in the CK treatment, the WUE in the IT treatment decreased by 15~18%. During the middle and late growth stages, the WUE followed the order of IT+IC>IT>CK. At final harvest, the WUE followed the order of CK>IT>IT+IC.

**Intercellular CO<sub>2</sub> concentration (C<sub>i</sub>):** The experimental results showed that the leaf C<sub>i</sub> in the IT+IC treatment was significantly ( $P<0.01$ ) higher than that in the IT and CK treatments. Compared with that of IT treatment, the C<sub>i</sub> in the IT+IC treatment was 31~79% higher and, on average,

54% higher, and the value was 40~83% higher and, on average, 61% higher than that in the CK treatment. Furthermore, compared with that in the CK treatment, the C<sub>i</sub> in the IT treatment was slightly higher (Fig. 5).

#### Influence of elevated CO<sub>2</sub> concentration on potato yield

Analysis of the potato yield in response to different treatments revealed that, compared with that in the CK treatment, the tuber weight per plant in the IT treatment distinctly decreased by 39% (Table 7). Furthermore, compared with that in the CK, the tuber weight per plant in the IT+IC treatment improved by 55%. Compared with that in the CK and IT treatments, the scrap potato rate in the IT+IC treatment was distinctly improved (Table 7). The changing trend of the fresh stem weight followed the order of IT+IC>IT>CK. Compared with that in the CK treatment, the weight in the IT+IC and IT treatments increased by 41 and 19%, respectively. The actual yield followed the order of IT+IC>CK>IT, and the yield in the IT treatment was lowest. The ratio of potato to stem followed the order of CK > IT+IC >IT, and the actual yield followed the order of IT+IC>CK>IT. The ratio of potato to stem under the CK increased by 1.16 and 1.14 compared with those under the IT+IC and IT treatments, respectively. Additionally, the actual yield under the IT+IC treatment increased by 60 and 13% compared with those under the IT and CK treatments, respectively.

## Discussion

Under the background of global warming, the eco-environment in the semi-arid region of the Northwest Loess Plateau has changed obviously, and the precipitation shows a decreasing trend of fluctuation (Yao *et al.* 2016). In contrast, the trend of temperature fluctuation is rising. In this study, the precipitation in the region showed a decreasing tendency, with a decreasing rate of -12.171 mm every 10 years, and the air temperature increased at a rate of 0.417°C every 10 years, which is consistent with existing research conclusions (Yao *et al.* 2016). CO<sub>2</sub> is the basic material for plant photosynthesis, and changes in its concentration will inevitably have an important impact on plant physiological and ecological characteristics. An elevated atmospheric CO<sub>2</sub> concentration stimulates the productivity of a broad range of agricultural crops (Kimball 1983, Lawlor and Mitchell 1991). The height of potatoes was obviously affected by the change in CO<sub>2</sub> concentration, and the height of potatoes under the IT treatment was significantly higher than those under the IT+IC and CK treatments at the ramifying stage. In addition, during the harvest stage, potato height followed the order of IT>IT+IC>CK. This proves that warming can significantly increase potato height. The content of chlorophyll in potato leaves affects the shape, yield and quality of potato, and chlorophyll content is one of the physiological indexes of potato leaves (Su *et al.* 2007). Overall, the chlorophyll content of leaves showed a downward trend during the whole growth period and reached its highest level in the mid-growth period. At the later stage of growth, the chlorophyll content under IC treatment decreased compared with that under IT treatment but increased compared with that under CK treatment. The response of different gas exchange parameters to elevated CO<sub>2</sub> was different. In the early growing season, the Pn of potato leaves under the IT+IC treatment were higher than those under the IT and CK treatments, and the results were consistent with those of Olivo *et al.* (2002). However, the increase in Pn was different; this was mainly due to the differences in potato varieties and treatments. The Pn increased under the IC treatment, which may be due to the competitiveness of the binding sites of the Rubisco enzyme, thus improving the carboxylation efficiency (Zhang *et al.* 2014). Moreover, to some extent, the inhibition of photorespiration by an elevated CO<sub>2</sub> concentration is also one of the reasons for the increase in the Pn (Drake 1997). In addition, the increase in the Pn in different growth stages was different in the present study, which is essentially consistent with existing research conclusions (Kimball *et al.* 2002). The gs of plant leaves generally decreased with increasing CO<sub>2</sub> concentrations (Bunce 2000). The change in the gs of potato leaves is sensitive to high CO<sub>2</sub> concentrations. To maintain the Ci partial pressure at a level lower than the atmospheric partial pressure, stomatal opening and closing is regulated. The gs of potato leaves decreased by an average of 44% under the IC treatment in this study, which is consistent with

the results of Olivo *et al.* (2002) and Finnan *et al.* (2005) under OTC test conditions. The Ci is related to the intensity of plant photosynthesis and is an important parameter for characterizing the physiological characteristics of plant photosynthesis (Wang *et al.* 2015). The amount of exogenous CO<sub>2</sub> absorbed by the leaves increased with an increase in the CO<sub>2</sub> concentration, which correspondingly led to an increase in CO<sub>2</sub> entering mesophyll cells. The Ci under the IT+IC treatment increased significantly, and the photosynthetic potential of the plants increased accordingly. Moreover, a decrease in gs led to an increase in resistance to water transpiration, which consequently led to a decrease in transpiration and an increase in WUE, which is of great significance for increased potato yields. Increasing the CO<sub>2</sub> concentration concurrently with temperature provided sufficient basic material for photosynthesis by potato leaves and further increased the Pn (Fleisher *et al.* 2008). WUE represents the ability of plant leaves to fix CO<sub>2</sub> under the conditions of equal water consumption and is the basic physiological parameter of water use in plant leaves (Ogutu *et al.* 2013). Under the IT+IC treatment, the WUE increased correspondingly and was greater than those under the IT and CK treatments, consistent with previous research conclusions (Carolina *et al.* 2017). Previous studies (Schapendonk *et al.* 2000) have shown that when the CO<sub>2</sub> concentration reached 350 μmol·mol<sup>-1</sup> to 700 μmol·mol<sup>-1</sup>, the average increase in tuber dry matter yield was 27%~49%; the actual potato yield in this study increased by 60% and 13% compared with those in the IT and CK treatments, respectively, which is similar to existing research conclusions (Schapendonk *et al.* 2000, Olivo *et al.* 2002). One difference in the results was that the range of increase in the potato yields was different, mainly due to differences in potato varieties and the control of the CO<sub>2</sub> concentration. The potato yield under the IT treatment decreased, mainly because potatoes are a cool-season crop. The activity of photosynthetic enzymes was affected by elevated temperature (Yao *et al.* 2013), and the photosynthesis rate decreased. Compared with the potato yield under the CK treatment, the potato yield under the IT treatment increased, mainly due to the relatively low temperature during the early stage. The increase in temperature compensated for the low-temperature-induced slow growth rate of potatoes to a certain extent, and the vegetative growth period was more vigorous for those potatoes than for potatoes under the CK treatment.

## Conclusion

The annual precipitation in the experimental region during the past 59 years tended to decrease. The air temperature tended to significantly increase and has continued to increase since the 1970s and was especially distinct in the 2000s. The plant height in the IT treatment was higher than those in both the IT+IC and CK treatments. Furthermore, the chlorophyll content of leaves was larger in the IT treatment was higher than in the other treatments during the

late growth stage. Under combined treatment of warming and elevated CO<sub>2</sub> concentration, the Pn of leaves increased. But the stimulating effect of CO<sub>2</sub> on photosynthesis gradually weakens with the development of growth process. When CO<sub>2</sub> concentration increased, The gs of leaves decreased, on the contrary, transpiration rate and water use efficiency increased. The Ci of leaves was distinctly higher than that in the leaves in the CK and IT treatments. With the increase of CO<sub>2</sub> concentration, the actual yield of potato distinctly increased. The yield of potato was low under the treatment of warming because potato is suitable for growing in cool weather, warming is not amenable to the growth of tubers, excessive warming will stop the growth of tubers. Warming and elevated CO<sub>2</sub> concentrations will stimulate the Pn and WUE of leaves, which finally result in the increase of dry matter accumulation and economic yields.

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### Author Contributions

Yao yubi, Lei jun and Niu Haiyang planned the experiments, Zhang xiuyun and Xiao guoju interpreted the results, Yao yubi and Lei jun made the write up and statistically analyzed the data and made illustrations.

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