
RESEARCH PAPERS

Temperature Responses of Photosynthesis and Respiration of Maize (*Zea mays*) Plants to Experimental Warming¹

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Abstract—Understanding the key processes and mechanisms of photosynthetic and respiratory acclimation of maize (*Zea mays* L.) plants in response to experimental warming may further shed lights on the changes in the carbon exchange and Net Primary Production (NPP) of agricultural ecosystem in a warmer climate regime. In the current study, we examined the temperature responses and sensitivity of foliar photosynthesis and respiration for exploring the mechanisms of thermal acclimation associated with physiological and biochemical processes in the North China Plain (NCP) with a field manipulative warming experiment. We found that thermal acclimation of A_n as evidenced by the upward shift of A_n - T was determined by the maximum velocity of Rubisco carboxylation (V_{cmax}), the maximum rate of electron transport (J_{max}), and the stomatal-regulated CO_2 diffusion process (g_s), while the balance between respiration and photosynthesis (R_d/A_g), and/or regeneration of RuBP and the Rubisco carboxylation (J_{max}/V_{cmax}) barely affected the thermal acclimation of A_n . We also found that the temperature response and sensitivity of R_d was closely associated with the changes in foliar N concentration induced by warming. These results suggest that the leaf-level thermal acclimation of photosynthesis and respiration may mitigate or even offset the negative impacts on maize from future climate warming, which should be considered to improve the accuracy of process-based ecosystem models under future climate warming.

Keywords: *Zea mays*, global warming, physiological adaptation, maize, North China Plain

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INTRODUCTION

It is well known that the optimal range for plant growth usually takes place within strict environmental conditions [1], thus the growth and production of plants may be limited by several abiotic stresses such as thermal stress [2]. Previous studies have reported that most plant species may only survive in a certain range of growth temperature, because different plants have different optimal growth temperatures [3–5]. Therefore, plants with higher optimal temperatures may benefit most from higher temperatures, and meanwhile plants with lower optimal temperatures are likely

to suffer negative impacts, and cause severe damage to plant production and/or crop yield when exposed to long-term higher temperatures such as global warming [6–8].

It has been demonstrated that the projected climate warming lead to profound impacts on global crop productivity through altering the physiological characteristics [9, 10] and biochemical traits of crops [11–13]. To understand the warming effect on the agricultural production, it is necessary to examine the biochemical and photochemical processes (photosynthesis and respiration), and the temperature response of leaf photosynthesis and respiration, which are critical to leaf development, plant growth, canopy production due to diurnal and seasonal temperature variations [14, 15]. The temperature response of photosynthesis normally follows a bell-shaped curve with an optimum

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Abbreviations: NCP—North China Plain; TNC—total non-structural carbohydrates; VPD—vapor pressure deficit; WUE—water use efficiency.

temperature [4, 16]. Previous studies have well demonstrated that plant species may adapt to temperature changes [17, 18], as indicated by the shifts in the optimal temperature and the improved photosynthetic rates at new growth temperatures [19, 20], and even different plant species may have different thermal acclimation capability [21–23]. In addition to leaf photosynthesis, the warming effect on crop was also associated with the temperature response of leaf dark respiration, which normally follows an exponential curve and commonly features the exponential increase parameter or activation energy [19]. Leaf dark respiration may also acclimate to longer-term changes in temperature [24], which is characterized by instantaneous response in the shape and/or base rate of plant respiration to growth temperature due mainly to the changes in mitochondrial abundance, protein composition, and electron transport rate [25].

Maize (*Zea mays* L.) is an economically important crop accounting for more than 30% of global cereal production. Several modeling studies have recently claimed that climate warming may decrease the maize yield in many regions all over the world [26, 27] including the North China Plain (NCP), where is one of the major regions for maize production in northern China [28] with about 40% of China's maize production [29]. This decreased maize yield in the NCP may be associated with leaf temperature response and sensitivity of photosynthesis and dark respiration of maize plants [26] under climate warming in this region. However, other studies have argued that climate warming may also lead to positive impacts on the yield of maize plants in some crop production region including the United States and China [29], because leaf photosynthesis increases with elevated temperature and reaches a maximum rate at an optimum temperature, and then declines at higher temperatures. Meanwhile, maize plants may physiologically adapt to climate warming through a shift in the optimum temperature for photosynthesis and a decline in the temperature sensitivity for dark respiration [20]. However, it is still unclear about the key processes and mechanisms determining the thermal acclimation of photosynthesis and dark respiration of plants, especially for the maize plants, one of the most important crops in the North China Plain under climate warming.

The objectives of this study are to examine: (1) the temperature response and sensitivity of leaf photosynthesis and dark respiration of maize plants under field conditions; (2) the key mechanisms attributed to thermal acclimation associated with physiological and biochemical processes under future climate warming.

MATERIALS AND METHODS

Study site. This study is conducted in the Yucheng Comprehensive Experiment Station (36°40'–37°120' N, 116°22'–116°45' E; an elevation of 28 m), which is operated by the Chinese Academy of Science. This

station locates in the lower reach of the Yellow River in the North China Plain (NCP), where features a semi-arid climate with average temperature of 13.1°C, and annual precipitation of 610 mm, approximately 70% of annual precipitation occurs between June and September. The soil is consisted of 66% silt, 22% clay, and 12% sand with classified by the FAO-Uneson system. The soil chemical properties are pH 8.5, organic matter 1.47 g/kg, total N 0.9 g/kg, total P (P_2O_5) 0.2%, and total K (K_2O) 2.26%. Winter wheat (*Triticum aestivum* L.) and summer maize (*Zea mays* L.) double cropping is predominant in the NCP.

Warming experiment. The warming experiment features six 3×4 m plots with three of the plots serving as treatments and the others as control plots. The warmed plots have been heated continuously since February 4, 2010 using infrared radiators (165 \times 1.5 cm, MSR-2420, Kalglo Electronics Inc., Bethlehem, PA) suspended 2.25 m above the ground. In control plots, 'dummy' heaters with the same shape and size as the infrared radiators were also suspended 2.25 m above the ground to simulate the shading effects of the heater. The distance between control and warmed plots was approximately 5 m to avoid heating the control plot by the infrared radiator. The air and soil temperature were hourly monitored with PT 100 thermocouples (Unism Technologies Inc., China) at 2.4 m above and at the depth of 5 cm in the soil. In comparison with control plots, experimental warming increased air, soil, and canopy temperature by 1.42/1.77°C (day/night), 1.68/2.04°C (day/night), and 2.08°C (day), during maize growth period from June 24 to October 7, 2011. Soil moisture in the top 0–10 cm soil layer was also recorded with a FDS100 soil moisture sensor (Unism Technologies Inc.). During maize growing season, the mean soil moisture (% volume) in the warmed plots ($25.04 \pm 0.52\%$) was slightly lower than that in the control plots ($26.02 \pm 0.86\%$).

Field sampling. Seeds of maize (*Zea mays* L.) were exposed to a dark, cold, and wet treatment at 4°C for two days before planting to promote uniform germination. Then, they were sown in the field soil in the control and warmed plots in June 24, 2011 and both the maize seedlings in control and warmed plots grew above the soil surface in July 1, 2011. Maize plants were irrigated with below-ground water to avoid drought stress during the growing period from June 24, 2011 to October 7, 2011. Given that the ear leaf is the most important leaf for determining the crop yield, we sampled the fully expanded ear leaves of maize at the heading stage in August 24, 2011, 60 days after sowing, for the following investigations.

Gas exchange measurements. We measured foliar gas exchange using a portable photosynthesis system (LI-6400, LI-COR Inc., United States) in the heading stage of the growing season of maize plants (late August to early September) in 2011. Three fully expanded leaves were selected from each of five plants

grown in each ambient temperature or elevated temperature plot to measure the gas exchange. Ten days were required to complete all the field measurements. Light, humidity, T_{leaf} , and CO_2 concentration were independently controlled in a $2 \times 3 \text{ cm}^2$ cuvette. Given the T_{leaf} control capacity is limited ($\pm 6^\circ\text{C}$) with the factory setup of LI-6400 system, we modified the temperature control system by adding a metal block with water channel to heat or cool the peltiers, thermoelectric cooling elements. The water channels were conducted to a heating/cooling water bath, in which T_{leaf} was controlled by adding hot water or ice. This modification could control the T_{leaf} anywhere between 10 and 40°C in the field during the summer growing season.

Leaf photosynthesis was measured at seven different temperatures between 10 and 40°C with a 5°C increment (A_n-T), whereas the light intensity kept constant at $1500 \mu\text{mol photons}/(\text{m}^2 \text{ s})$ with a red/blue LED light source, and the CO_2 concentration at $400 \mu\text{mol}/\text{mol}$. At each leaf temperature, we allowed leaf to equilibrate at $400 \mu\text{mol}/\text{mol}$ for half an hour and measured the net photosynthetic rate (A_n) for the A_n-T curve. Then, the A_n-C_i curve was also measured at the same temperature, where the CO_2 concentration was controlled at 50, 100, 150, 200, 300, 400, 600, 800, 1000, 1200, and $1400 \mu\text{mol}/\text{mol}$ under $1500 \mu\text{mol photons}/(\text{m}^2 \text{ s})$ between 10 and 40°C with a 5°C increment for each leaf. Thus, seven A_n-C_i curves were measured for each of the maize leaves in the three control and warming plots and 126 A_n-C_i curves in total were obtained for the analysis in the current study. An estimation method of Sharkey et al. (2007) was used to obtain the maximum carboxylation rate of Rubisco (V_{cmax}) and the maximum capacity of electron transport mediated ribulose biphosphate (RuBP) regeneration (J_{max}) for each observed A_n-C_i curve. Due to a relatively constant dew point of the environment, Vapor Pressure Deficit (VPD) changed inevitably along with the change of temperature, we simultaneously recorded the VPD, stomatal conductance (g_s), and transpiration rate (E) with the photosynthesis measurement. The leaf-level Water Use Efficiency (WUE) was determined by the value of the net photosynthetic rate (A_n) and transpiration rate (E) according to the formula $\text{WUE} = A_n/E$. The temperature response curve of respiration (R_d-T) for each leaf was measured after finishing the A_n-T and A_n-C_i curves. Specifically, we turned off the LED light source and meanwhile the chamber was covered with a piece of black cloth for 30 min for dark adaptation.

Biochemical composition analysis. The sampled leaves were oven-dried to constant weight at 75°C , and ground to fine powder with a ball mill (MM2, Fa. Retsch, Germany). Samples were assayed for non-structural carbohydrates according to Sage (1995). Glucose, fructose, sucrose, and starch contents were determined spectrophotometrically (UV-1750, Shi-

madzu Corp., Japan), using a glucose kit (GAHK-20, Sigma, United States). Total carbon (C) and nitrogen (N) contents in leaves were determined using an elemental analyzer (Vario Max CN; Elementar Corp., Germany).

Statistical analysis. The differences of the physiological, and biochemical variables between the warmed and control plots were tested with the analysis of variation (ANOVA) followed by Duncan's multiple range test ($P < 0.05$) using SPSS 13.0 (SPSS Inc., United States).

RESULTS

Warming Effects on Temperature Response of Leaf Photosynthesis

According to the observed A_n-T curves, we found that experimental warming significantly enhanced the maximum values of net photosynthetic rate (A_n) by about 60% ($P = 0.004$) from an average of $18.6 \mu\text{mol}/(\text{m}^2 \text{ s})$ for plants grown at ambient temperature to $29.8 \mu\text{mol}/(\text{m}^2 \text{ s})$ for plants grown at elevated temperature. Meanwhile, the optimal temperature for photosynthesis in warming condition was also significantly higher than that of maize plants grown at ambient temperature ($P < 0.05$) with an obviously shift from 29.0 to 31.0°C (Fig. 1a).

Warming Effects on Temperature Response of Leaf Dark Respiration

In contrast to photosynthesis, experimental warming marginally declined leaf dark respiration rate (R_d) and its temperature sensitivity (Q_{10}). We found that maize plants at the ambient temperature and warming treatment had similar R_d at low temperatures below 15°C . However, leaf R_d enhanced exponentially with the increase of leaf temperature for both ambient and warming ($P < 0.001$), and the leaf dark respiration rates in the ambient temperature were consistently greater than those in the warming treatment when maize plants were grown under higher temperatures over 15°C (Fig. 1b). Moreover, we also found that the Q_{10} of R_d in maize plants was also declined from 1.53 to 1.44 by experimental warming. Similar with the temperature response of dark respiration, the dark respiration and gross photosynthetic rate (A_g) ratio of maize plants grown at both the ambient and warming conditions were exponentially enhanced along with the increase of temperatures, while no significant difference in R_d/A_g was detected between the ambient and elevated temperatures ($P > 0.05$; Fig. 2).

Warming Effects on V_{cmax} , J_{max} , and $J_{\text{max}}/V_{\text{cmax}}$ Ratio

Both the maximum carboxylation rate (V_{cmax}) and the maximum electron transport rate (J_{max}) were gen-

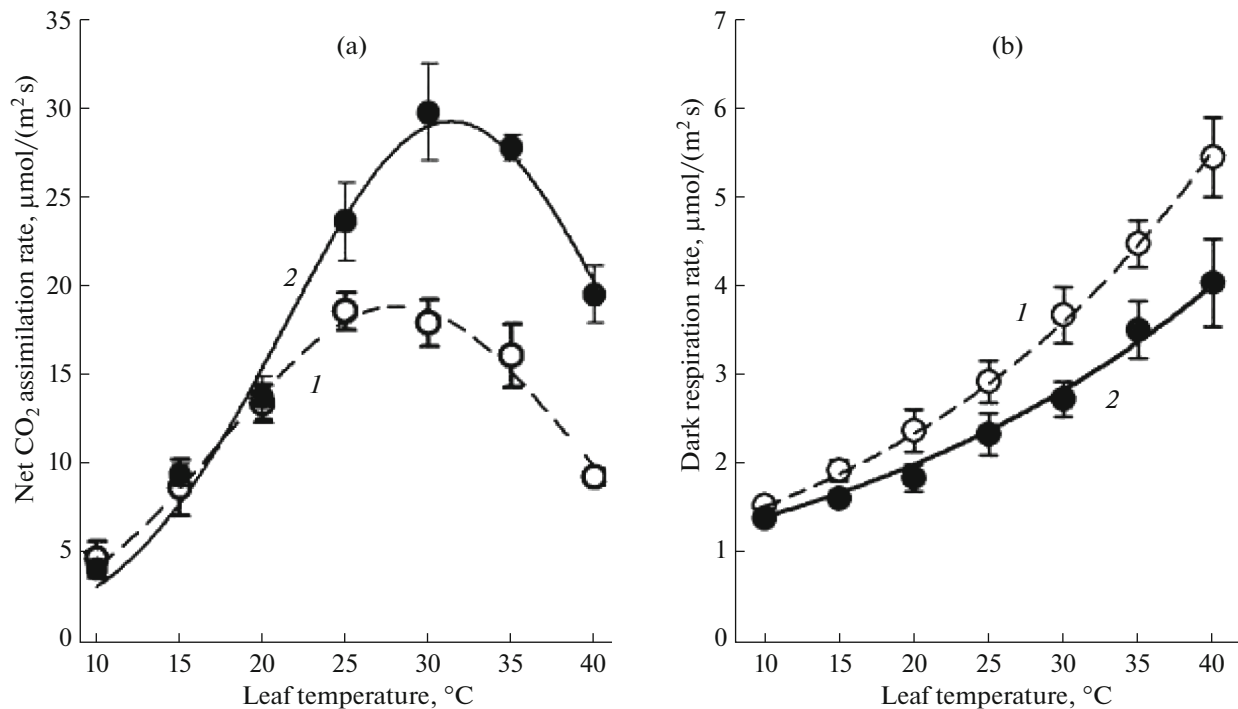


Fig. 1. Net CO₂ assimilation rate (A_n) and dark respiration rate (R_d) of maize plant at control or warming condition. (a) Control ($T_{\text{opt}} = 29.0^{\circ}\text{C}$); warming ($T_{\text{opt}} = 31.0^{\circ}\text{C}$); $P = 0.004$; (b) control ($Q_{10} = 1.53$); warming ($Q_{10} = 1.44$); $P < 0.001$. 1—control; 2—warming.

erally enhanced with the increase of leaf temperature in maize plants grown at control and warming plots (Fig. 3). Although the V_{cmax} was not statistically different between the ambient and warming plots from 10 to 25 $^{\circ}\text{C}$, the V_{cmax} values in warming conditions were significantly lower than those in ambient plots with the

temperature increasing from 25 to 40 $^{\circ}\text{C}$ ($P = 0.02$). By contrast, experimental warming marginally decreased the average temperature sensitivity (Q_{10}) of V_{cmax} from 2.56 to 2.47 (Fig. 3a). Unlike V_{cmax} , the temperature response of J_{max} followed a bell-shaped curve with the peak J_{max} value appearing at 31.8 and 34.5 $^{\circ}\text{C}$, respectively, for the control and warming plots (Fig. 3b). Meanwhile, our result also showed that the difference between the two optimal temperatures of J_{max} was statistically significant ($P = 0.02$). In addition, the $J_{\text{max}}/V_{\text{cmax}}$ ratio declined quadratically with the increase of leaf temperature for both the ambient and elevated temperatures (Fig. 3c). We also found that experimental warming barely affected the $J_{\text{max}}/V_{\text{cmax}}$ ratio of maize plants ($P = 0.14$).

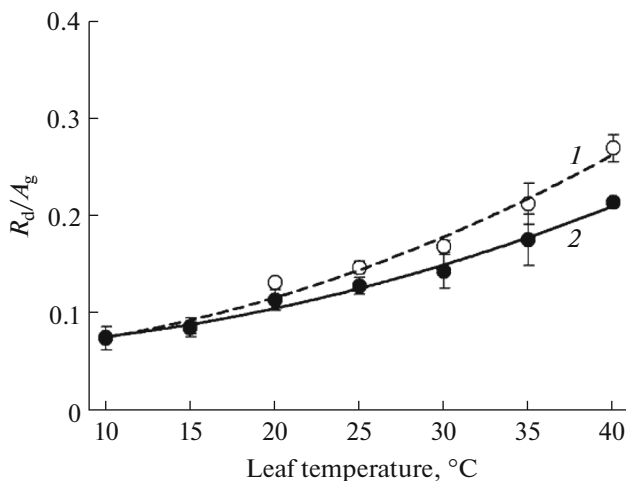


Fig. 2. Warming effects on the response of R_d/A_g ratio (balance between dark respiration and gross CO₂ assimilation) to elevated leaf temperature. 1—control; 2—warming. $P > 0.05$.

Warming Effects on g_s , E , and WUE

We found that the stomatal conductance (g_s) of maize plants in response to experimental warming featured typically bell-shaped curves under both the ambient and warming conditions (Fig. 4a), and warming dramatically shifted the optimal temperature for g_s from 20.9 to 26.4 $^{\circ}\text{C}$ ($P = 0.002$). However, the temperature response of leaf transpiration rates (E) shared linear relationship to growth temperature, and the E was substantially increased from 1.92 to 9.56 $\text{mmol}/(\text{m}^2 \text{ s})$ for warming plots and from 1.63 to 6.99 $\text{mmol}/(\text{m}^2 \text{ s})$ for

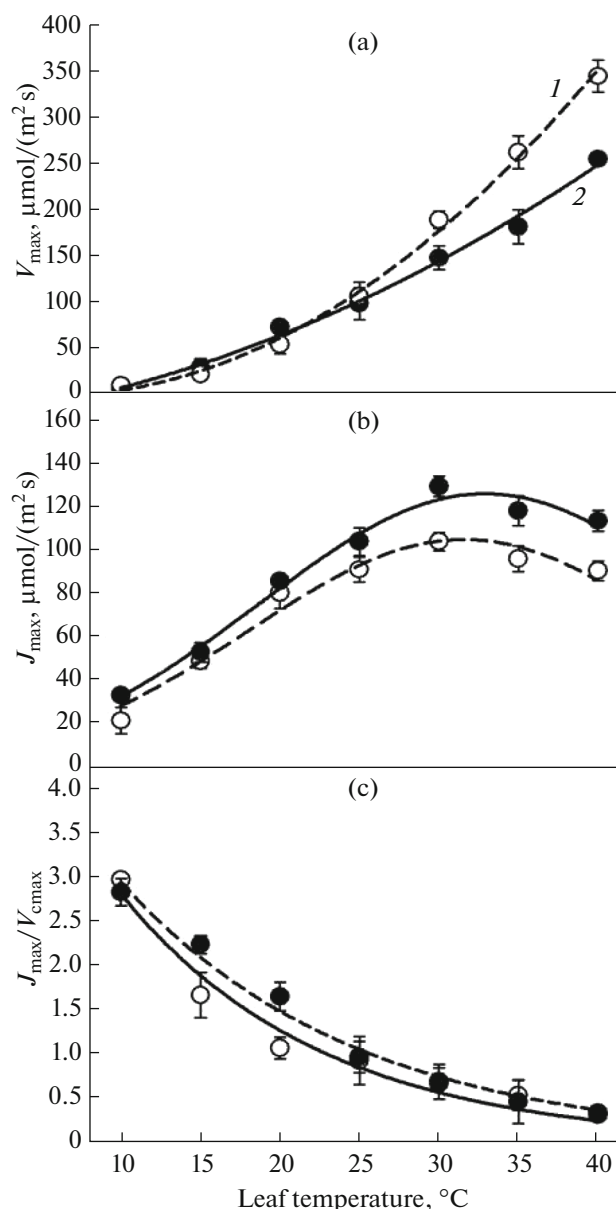


Fig. 3. Warming effects on the responses of maximum rate of Rubisco carboxylation (V_{\max}), the maximum rate of photosynthetic electron (J_{\max}) and the balance between J_{\max} and V_{\max} (J_{\max}/V_{\max}) to leaf temperature. (a) Control ($T_{10} = 2.56$); warming ($T_{10} = 2.47$); $P = 0.02$; (b) control ($T_{\text{opt}} = 31.8^\circ\text{C}$); warming ($T_{\text{opt}} = 34.5^\circ\text{C}$); $P = 0.02$; (c) $P = 0.14$. 1—control; 2—warming.

ambient plots when temperature increased from 10 to 40°C (Fig. 4b). Meanwhile, our results also showed that leaf transpiration rates in warming plots were significantly higher than those in the ambient plots ($P < 0.001$). In addition, the temperature response of WUE demonstrated typically bell-shaped curves at ambient or elevated temperatures (Fig. 4c). Experimental warming significantly enhanced the optimal temperature from 23.4 to 29.9°C ($P = 0.001$).

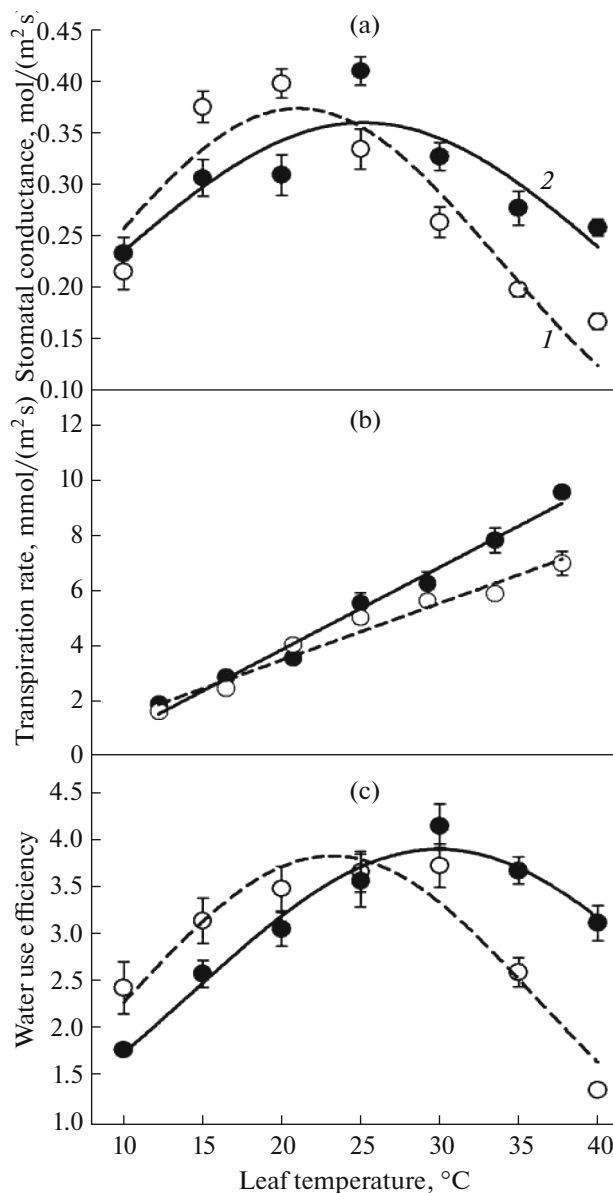


Fig. 4. Stomatal conductance, transpiration rates and water use efficiency of maize at control or warming condition. (a) Control ($T_{\text{opt}} = 20.9^\circ\text{C}$); warming ($T_{\text{opt}} = 26.4^\circ\text{C}$); $P = 0.002$; (b) control ($y = 0.175x + 0.1514$, $R^2 = 0.96$); warming ($y = 0.2534x - 0.9712$, $R^2 = 0.98$); $P < 0.001$; (c) control ($T_{\text{opt}} = 23.4^\circ\text{C}$); warming ($T_{\text{opt}} = 29.9^\circ\text{C}$); $P = 0.001$. 1—control; 2—warming.

Warming Effects on Leaf Carbohydrates

Our results showed that experimental warming sharply increased the concentrations of glucose, fructose, and sucrose by 25, 53, and 83%, respectively (Table 1). As a result, warming significantly enhanced the concentration of soluble sugars by 43.7% ($P < 0.01$). Meanwhile, we also found that the starch concentration was also substantially increased by 20% ($P < 0.05$) under warming condition, and thus experimental

Table 1. Effects of experimental warming on the content of carbohydrates and C/N ratio in maize leaf tissues

TNC, mg/g dry wt	Control	Warming	Increasing, %	<i>p</i> -value
Glucose	16.2 ± 2.7	20.2 ± 1.8	24.9	0.048
Fructose	11.4 ± 1.8	17.4 ± 0.9	52.8	0.003
Sucrose	5.1 ± 1.1	9.4 ± 1.9	83.0	0.009
Soluble sugars	32.7 ± 4.6	47.0 ± 1.4	43.7	0.001
Starch	37.5 ± 4.3	45.0 ± 3.6	20.0	0.080
TNC	69.9 ± 5.2	91.3 ± 4.5	30.8	0.006
Tissue C/N ratio, mg/g dry wt	Control	Warming	Increasing, %	<i>p</i> -value
Total carbon	436 ± 3	439 ± 3	0.8	0.18
Total nitrogen	28.5 ± 1.6	26.4 ± 0.7	−7.4	0.05
C/N ratio	15.4 ± 0.7	16.6 ± 0.3	7.8	0.03

warming significantly enhanced the Total Non-structural Carbohydrates (TNC) of maize leaves by 30.8% ($P < 0.01$; Table 1).

Warming Effects on Leaf Tissue Carbon and Nitrogen

Our results showed that experimental warming barely affected the total carbon content ($P = 0.18$), whereas substantially decreased the total nitrogen content by about 7.4% ($P = 0.05$) on a dry weight basis (Table 1). As a result, the C/N ratio was significantly increased by about 10% under warming conditions ($P = 0.03$; Table 1).

DISCUSSION

The temperature response of photosynthesis (A_n - T) normally follows a bell-shaped curve [20] which features the optimum temperature (T_{opt}), while the temperature response of leaf dark respiration (R_d - T) often follows an exponential curve, which is characterized by activation energy or the exponential increase parameter (Q_{10}). Investigating the temperature response of photosynthesis and respiration is vital in understanding thermal acclimation of plants, because the T_{opt} and sensitivity parameters may reflect the acclimation capacity of species to temperature [30]. Also, the temperature responses of photosynthesis and respiration are critical to leaf development, plant growth, and crop yield due to diurnal and seasonal temperature variations [29].

Previous studies have claimed that three major processes control the temperature response of net photosynthesis, namely the balance between photosynthesis and respiration, biochemical and photochemical processes, and stomatal constrains [5, 14, 19], which have been frequently discussed in the framework of the Farquhar Photosynthesis Model. Given that A_n is the difference between A_g and R_d ($A_n = A_g - R_d$), the temperature responses of gross CO_2 assimilation (A_g) and

leaf respiration (R_d) may directly affect the A_n - T , and thus changes in the balance between respiration and photosynthesis (R_d/A_g) may lead to the change of A_n - T . In the current study, we found that experimental warming barely affected the R_d/A_g ratio (Fig. 2), suggesting that the thermal acclimation of net photosynthesis is not attributed to the changes in R_d/A_g ratio in warmer conditions.

The Rubisco carboxylation process and the RuBP regeneration process are two main biochemical and photochemical processes contributing to the thermal acclimation of photosynthesis to experimental warming [21]. Both the maximum velocity of Rubisco carboxylation (V_{cmax}) and the maximum rate of electron transport (J_{max}) are temperature dependent [16], where the V_{cmax} follows the Arrhenius equation and the J_{max} follows a bell-shaped curve [24]. A number of studies have found that the increase in the temperature sensitivity of V_{cmax} and the upward shift in the T_{opt} of J_{max} may contribute to the thermal acclimation of net photosynthesis [30]. Our results that experimental warming increased the Q_{10} of V_{cmax} from 2.47 to 2.56 (Fig. 3a) and simultaneously shifted the T_{opt} of J_{max} from 31.8 to 34.5°C (Fig. 3b), indicating that the thermal acclimation of photosynthesis may be explained by both the biochemical and photochemical processes, which is closely related to the temperature dependence of Rubisco activation status and the thermal stability of photosystem II [24]. However, we also found that experimental warming had little effect on the balance between the regeneration of RuBP and the Rubisco carboxylation (J_{max}/V_{cmax}) (Fig. 3c), suggesting that N allocation between the biochemical and photochemical processes of photosynthesis has little contribution to the shift in A_n - T curve.

In addition to biochemical limitations, the thermal acclimation of photosynthesis may also be associated with the stomatal-regulated CO_2 diffusion process [22], because changes in growth temperature may affect

CO₂ diffusivity through altering the stomatal movement and the stomatal distribution pattern on plant leaves [5]. Previous studies have reported that increasing stomatal conductance (g_s) may result in an upward shift in T_{opt} of A_n [22]. In this study, we found that warming significantly increased g_s and meanwhile shifted the T_{opt} of g_s from 20.9 to 26.4°C (Fig. 4), which may explain the thermal acclimation of photosynthesis in response to experimental warming. This g_s contributed photosynthesis acclimation due mainly to the changes in stomatal openness and the spatial distribution pattern of stomata under warming environments [5]. However, it should be noted that other environmental factors, such as warming-induced water depletion and/or change in N availability, may have interacting effects on response of CO₂ diffusion process to warming [19].

It has been demonstrated that the thermal acclimation of foliar respiration may occur via the temperature-mediated change in temperature sensitivity, Q_{10} [24], which is mainly determined by the maximum enzyme activity [19], energy demand [25] and/or substrate availability [15]. Our results that R_d was sensitive to leaf temperature with R_d - T relationship following a typical exponential curve, and experimental warming decreased the Q_{10} of R_d from 1.53 to 1.44, support conclusions from previous studies that the temperature sensitivity of R_d is negatively related to the leaf temperature [18, 19]. Earlier studies have found that the reduction of Q_{10} may be attributed to the decline in the substrate concentration under warmer condition [19, 24]. However, our results that experimental warming significantly increased the concentration of carbohydrates including starch and soluble sugars (Table 1), suggested that the substrate availability made little contribution to the decreased Q_{10} of R_d in the current study. In addition to substrate availability, the foliar N concentration induced by experimental warming may also affect the temperature sensitivity of R_d [24], because the N concentration is closely associated with the amounts of respiratory enzymes. Earlier results from the same warming experiment that experimental warming substantially decreased the foliar N concentration [25], suggesting that the decreased temperature sensitivity of R_d in the current study may be partially attributed to the declined foliar N concentration under warming environment (Table 1). It is important to note that the confounding effect of foliar N concentration with other environmental factors such as precipitation and temperature may also play a pivotal role in the “apparent” Q_{10} of R_d [18].

In conclusion, our results showed that maize plants in response to warming shared apparently thermal acclimation of the net photosynthetic rate (A_n) and leaf dark respiration (R_d) as evidenced by the upward shift of A_n - T and the declined temperature sensitivity (Q_{10}) of R_d under warmer condition. The biochemical

and photochemical processes (Rubisco carboxylation and electron transport) as well as the stomatal-regulated CO₂ diffusion process (g_s) were vital in determining the temperature response of photosynthesis, and the respiratory acclimation was closely associated with foliar N concentration. Our results also indicated that many current process-based vegetation and ecosystem models may overestimate the potential risks of climate warming on maize yield, and thus different temperature response parameters of photosynthesis and respiration should be applied to these modes for further improving the predictions of global warming impacts on agricultural production.

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