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Experimental warming enhances the carbon gain but does not affect the yield of maize (*Zea mays* L.) in the North China Plain

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ABSTRACT

Temperature response and sensitivity of photosynthesis and respiration are critical for projection of changes in the carbon exchange and net primary production of terrestrial ecosystems under global warming. Understanding the mechanisms and processes of photosynthetic and respiratory acclimation in response to warming may shed further lights on the change of crop yield in agricultural ecosystems in a warmer climate regime. We examined the temperature responses and sensitivity of net photosynthetic rate (A_n) and dark respiration (R_d) for exploring the mechanisms of thermal acclimation associated with physiological and biochemical processes affecting maize yield in the North China Plain with a field manipulative warming experiment. We found that warming substantially enhanced the carbon gain of maize plants through facilitating CO_2 diffusion from ambient air to chloroplasts by altering stomatal structure and spatial distribution pattern, and benefitting CO_2 assimilation efficiency with smaller vascular bundles and bigger chloroplasts. Moreover, we also found that acclimation of A_n to temperature (T), 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, whereas the balance between respiration and gross photosynthetic rate (R_d/A_g), and/or regeneration of RuBP and the Rubisco carboxylation (J_{max}/V_{cmax}) made little contribution to the thermal acclimation of A_n in maize plants. In addition, temperature response and sensitivity of R_d was closely associated with the changes in foliar N concentration induced by warming. As a result, experimental warming barely affected the yield and biomass of maize plants. These results suggest that the impacts of future climate warming on maize production may be mitigated or even offset by the leaf-level thermal acclimation of photosynthesis and respiration. Our findings may have important implications for improving the accuracy of process-based ecosystem models and advancing the understanding on the interactions between ecosystem functions and climate warming.

1. Introduction

It is estimated that global surface temperature may continuously increase by 1.1–6.4 °C at the end of this century depending on greenhouse gases emissions (IPCC, 2013). This projected global warming is expected to result in profound impacts on global productivity through altering the physiological characteristics (Abebe et al., 2016), biochemical traits (Yin et al., 2008; Lin et al., 2010), and anatomical structures of plants (Wassmann et al., 2009; Zheng et al., 2013a). So far, however, no consistent conclusions have been drawn on the crop yield of agricultural ecosystems in response to climate warming. For example, most studies claimed that warming will decrease crop yield (Lobell et al., 2008; Xu et al., 2016) with increased temperature having an adverse influence on net plant carbon uptake by declining leaf photosynthesis (Zhang et al., 2015) and shortening the growth stages of crops (Kim et al., 2007). By contrast, other studies suggested that the production of crops might benefit from climate warming (Thomas, 2008; Guo et al., 2010) through changes in the grain number per ear

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and the tiller number per area, or increased primary biomass production (Leuning, 1995). Meanwhile, several simulation studies also revealed that global warming may change the phenological development (Deere and Chown, 2006; Zhou et al., 2015), crop growth rates (Lobell et al., 2008), water use efficiency (Mo et al., 2009) and net primary productivity (Peraudeau et al., 2015; Tang et al., 2016), and thus affect the grain yield of crops (Gabaldón-Leal et al., 2016; Hidayati and Anas, 2016). Therefore, evaluating the impacts of experimental warming on agricultural production and exploring the underlying mechanisms that determine crop yield are crucial to accurately assessing the risk of future global warming on food supply safety.

To understand the warming effect on crop yield, it is necessary to examine the biochemical and photochemical processes such as photosynthesis and respiration, and the temperature response of leaf photosynthesis and respiration, which are critical to leaf development, plant growth, and canopy production due to diurnal and seasonal temperature variations (Lin et al., 2010). The temperature response of photosynthesis normally follows a bell-shaped curve which is characterized by the optimum temperature (Jin et al., 2011). Previous studies have well demonstrated that plant species can acclimate to temperature changes (Davidson et al., 2006), as indicated by shifts in the optimal temperature and improved photosynthetic rates at new growth temperatures (Yamori et al., 2014), and even different plant species may have different thermal acclimation capability (Niinemets et al., 2007; Xu et al., 2012). In addition to leaf photosynthesis, the warming effect on crop yield was also associated with the temperature response of leaf dark respiration, which normally follows an exponential curve and commonly features activation energy or the exponential increase parameter (Q_{10}). Leaf dark respiration can also acclimate to longer-term changes in temperature (Atkin and Tjoelker, 2003; Chi et al., 2013), which is characterized by instantaneous response in the shape and/or base rate of plant respiration to growth temperature mainly due to changes in mitochondrial abundance, protein composition, and/or electron transport rate (Armstrong et al., 2006). Investigating temperature responses and sensitivity of photosynthesis and dark respiration is not only vital in improving our knowledge on the underlying mechanisms of thermal acclimation, but also critical for identifying the thermal acclimation capability of different crops, and thus has important significance for estimating the changes in agricultural production under future climate warming (Cunningham and Read, 2002; Atkin and Tjoelker, 2003; Aspinwall et al., 2016). Maize (*Zea mays* L.) is an economically important crop all over the world, which accounts for more than 30% of global cereal production (FAO, 2014). Several studies have reported that climate warming may substantially decrease maize yield in many regions throughout the world (Hidayati and Anas, 2016; Gabaldón-Leal et al., 2016; Xu et al., 2016). The North China Plain (NCP) is one of the major regions for maize production in northern China and contributes about 40% of China's maize production (Li et al., 2011). Maize yield in the NCP may decline under climate warming from 1996 to 2100 (Piao et al., 2010), because maize yield is associated with leaf temperature response and sensitivity of photosynthesis and dark respiration (Ruiz-vera et al., 2015; Hidayati and Anas, 2016). However, some previous studies have claimed that climate warming may not universally lead to negative impacts on the yield of maize plants in some crop production regions including the United States and China (Li et al., 2011), because crops can physiologically acclimate to climate warming through a shift in the optimum temperature for photosynthesis and a decline in the temperature sensitivity for dark respiration (Yamori et al., 2014; Niles et al., 2015). Most previous studies estimated the impacts of climate warming on maize production using ecosystem process models (Blanc and Sultan, 2015; Gabaldón-Leal et al., 2016; Blanc, 2017), which, however, are failing to take into account the physiological acclimation to temperature, although temperature response and sensitivity of photosynthesis and dark respiration are crucial to crop production modeling (Garcia-Quijano and Barros, 2005; Rudnickia et al., 2017).

So far, to our knowledge, the underlying mechanisms of climate warming affecting crop production are still unclear, especially the mechanisms and processes of photosynthetic and respiratory acclimation in response to warming. Therefore, this study examined the temperature responses and sensitivity of photosynthesis and respiration for exploring the mechanisms of thermal acclimation associated with physiological and biochemical processes affecting maize yield in the North China Plain with a field manipulative warming experiment. The objectives of the current study are to: (1) examine the effects of experimental warming on the yield and biomass of maize plants; (2) investigate the temperature response and sensitivity of leaf photosynthesis and dark respiration of maize plants; (3) explore the photosynthetic and respiratory processes affecting maize yield through a field warming experiment with infrared heaters in northern China.

2. Materials and methods

2.1. Study site

We conducted this study in the Yucheng Comprehensive Experiment Station (36°40′–37°12′ N, 116°22′–116°45′ E; elevation 28 m a.s.l.) operated by the Chinese Academy of Science. This station is located in the lower reach of the Yellow River in the North China Plain (NCP), which 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, classified by the FAO-Uneson system. The soil chemical properties are pH 8.5, organic matter 14.7 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.

2.2. Field warming experiment

The field warming experiment features six 3 m × 4 m plots with 3 of the plots serving as treatments and the other 3 plots as control (3 replicates). A 5-m buffer was established between the plots to reduce disturbances. The warmed plots have been heated continuously since 4 February 2010 using infrared radiators (165 cm × 1.5 cm, electric power 2000 W, 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 plots by the infrared radiators. The air and soil temperature were hourly monitored with PT100 thermocouples (Unism Technologies Incorporated, Beijing, China) at 2.4 m above and at a 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 24 June to 7 October 2011. Soil moisture in the top 0–10 cm soil layer was recorded with a FDS100 soil moisture sensor (Unism Technologies Incorporated, Beijing, China). During maize growing season, the mean soil moisture (% volume) in the warmed plots (25.04 ± 0.52%, mean ± SD) was slightly lower than that in the control plots (26.02 ± 0.86%).

2.3. Field sampling

Seeds of maize (*Zea may* L.) were exposed to a dark, cold, and wet treatment at 4 °Cfor 2 days before planting to promote uniform germination. Then, they were sown in the field soil in the control and warmed plots on 24 June 2011 and both the maize seedlings in control and warmed plots grew above the soil surface on 1 July 2011. Maize plants were irrigated with below-ground water to avoid drought stress during the growing period from 24 June 2011 to 7 October 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 on 24 August 2011, 60 days after sowing, for the following investigations.

2.4. Field gas exchange measurements and sampling

We measured gas exchange in the field using a portable photosynthesis system (LI-6400, LI-COR Inc. Lincoln, Nebraska, USA) 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 leaf gas exchange (3 replicates). Light, humidity, T_{leaf}, and CO_2 concentration were independently controlled in a 2 cm × 3 cm cuvette. Given the T_{leaf} control capacity is limited (± 6 °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 connected to a heating/cooling water bath, in which T_{leaf} was controlled by adding hot water or ice. This modification could control T_{leaf} anywhere between 10 and 40 °C in the field during the summer growing season. Leaf gas exchange measurements started with the A_n–C_i curves at low T_{leaf} (10 °C) in the morning around 8:00 am and finished at high T_{leaf} (40 °C) around noon during the day. Ten days were required to complete all the leaf gas exchange measurements under field conditions.

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 was kept constant at 1500 μmol photons $m^{-2}\,s^{-1}$ with a red/blue LED light source, and the CO_2 concentration at 400 μmol mol^{-1}. At each leaf temperature, we allowed leaves to equilibrate at 400 μmol mol^{-1} for half an hour and measured the net photosynthetic rate (A_n, μmol $m^{-2}\,s^{-1}$) for the A_n–T curve. Then, the A_n–C_i curve was 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 μmol mol^{-1} under 1500 μmol photons $m^{-2}\,s^{-1}$ 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. The estimation method of Sharkey et al. (2007) was used to obtain the maximum carboxylation rate of Rubisco (V_{cmax}, μmol $m^{-2}\,s^{-1}$) and the maximum capacity of electron transport mediated ribulose bisphosphate (RuBP) regeneration (J_{max}, μmol $m^{-2}\,s^{-1}$) for each observed A_n–C_i curve. Due to a relatively constant dew point of the environment, the Vapor Pressure Deficit (VPD) changed inevitably along with the change of temperature, we simultaneously recorded the VPD, stomatal conductance (g_s, mol $m^{-2}\,s^{-1}$), and transpiration rate (T_r, mmol $m^{-2}\,s^{-1}$) with the photosynthesis measurement. The Water Use Efficiency (WUE, mmol mol^{-1}) was determined by the value of A_n and T_r, defined as A_n/T_r ratio. 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 acclimatization.

After obtaining the temperature response curves (A_n, V_{cmax}, J_{max}, g_s, WUE, and R_d), the temperature sensitivity indicators for these above photosynthetic parameters (T_{opt} for bell-shaped curves and Q_{10} for exponential curves) were fitted for each individual leaf of maize plants (Chi et al., 2013; Zhou et al., 2015).

2.5. Stomatal traits and spatial distribution pattern of stomata

We randomly selected five fully expanded ear leaves from five different maize plants at the heading stage in each of the warming and control plots (3 replicates) on 24 August 2011. To determine the stomatal and epidermal cell characteristics, we sampled impressions from the tip, middle, and base sections of the adaxial and abaxial leaf surfaces using colorless nail polish. The adaxial and abaxial epidermis of the leaves were cleaned first by a degreased cotton ball and then carefully smeared with nail varnish from the mid-area between the central vein and the leaf edge for about half an hour. The thin film (approximately 5 mm × 15 mm) was peeled off from the leaf surface and mounted on a glass slide. Then the thin film was immediately covered with a cover slip and pressured lightly with a fine-point tweezers. The imprints were observed and photographed in the laboratory with a microscope (DM2500, Leica Corp., Germany) equipped with a digital camera (DFC 300-FX, Leica Corp., Germany). Thirty separate fields of 0.16 mm^2 were analyzed in each section of the sampled leaves. Stomata and epidermal cells at the tip, middle, and base sections on each surface were counted and combined for calculating stomatal density (number per mm^2), stomatal index (SI, the ratio of stomata to epidermal cells, %), stomatal length (μm), stomatal width (μm), stomatal perimeter (μm), stomatal area (μm^2), stomatal shape index (%), and stomatal area index (%) on the adaxial surface and abaxial surface, respectively. Specifically, we took 15 images from 5 microscopic fields at each leaf section (tip, middle, and base section) on the adaxial or abaxial surfaces of the five leaves sampled from the control or warmed plots. Then we randomly selected 5 images (subsamples) from each leaf section of the adaxial or abaxial surface per leaf (5 subsamples × 3 sections × 5 leaves = 75 samples). Because the three ambient plots or the three warmed plots are the three replicates, all the data of the stomatal traits from the 5 sampled leaves (75 samples) were averaged within each plot, namely 30 samples (5 subsamples × 3 sections × 2 leaves = 30 samples) from plot 1 or plot 2 and 15 samples (5 subsamples × 3 sections × 1 leaf = 15 samples) from plot 3 in the three ambient plots or the three warmed plots. Then, we combined the subsamples of the adaxial or abaxial surfaces for estimating the stomatal characteristics for the whole leaf in the control or warmed plot (5 subsamples × 3 sections × 2 surfaces × 5 leaves = 150 samples) to measure stomatal aperture length, width, and area using Image J quantification software (NIH, USA). For visualizing and comparing the differences of stomata between the warming and control plots under scanning electron microscopy (SEM), we snapped three pieces (2 mm × 2 mm) from the middle section of each leaf with a fixative solution consisting of 2.5% (v/v) glutaraldehyde (0.1 M phosphate

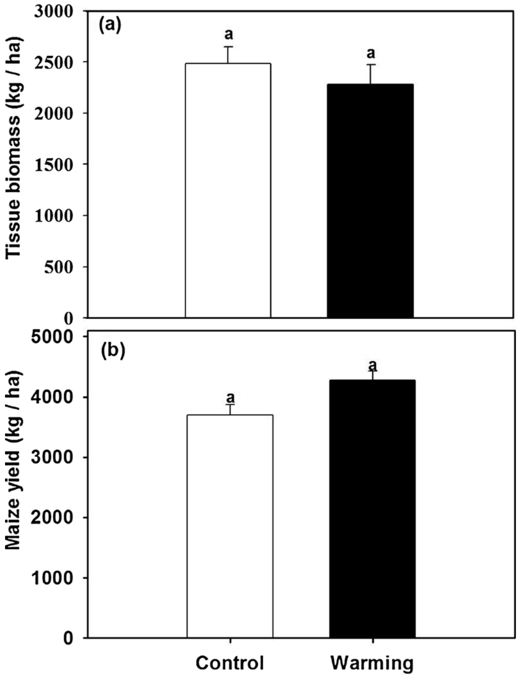

Fig. 1. Effects of experimental warming on the biomass and yield of maize. The data given are means ± standard error for 3 ambient or warmed plots.

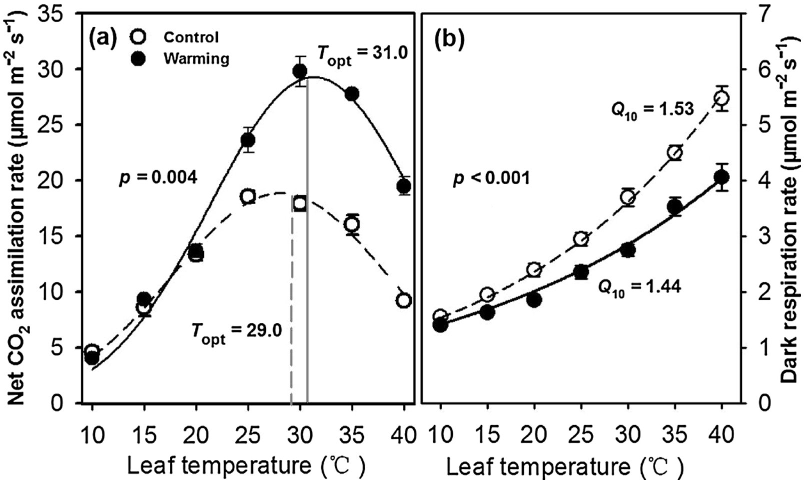

Fig. 2. Net CO$_2$ assimilation rate (A_n) and dark respiration rate (R_d) of maize at control or warming condition. The data given are means ± standard error for 3 ambient or warmed plots.

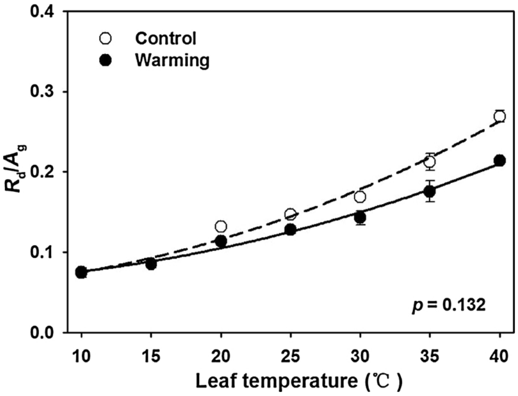

Fig. 3. Warming effects on the response of R_d/A_g ratio (balance between dark respiration and gross CO$_2$ assimilation) to elevated leaf temperature. The data given are means ± standard error for 3 ambient or warmed plots.

buffer, pH 7.0). Samples were stored at 4 °C and transported to the laboratory as soon as possible. Then the samples were washed six times with the same buffer and post fixed in 1% (v/v) osmium tetroxide for 3 h at room temperature. After being washed with the same buffer, leaf tissues were passed through an ethanol dehydration series. Then the samples were critical point-dried, mounted on stubs, and coated with gold in a high-vacuum vaporisation unit. Samples were examined and photographed at 10 kV under a Quanta 200 scanning electron microscope (FEI Corp, USA).

2.6. Anatomical measurements and ultrastructure observation

We used the same ear leaves for further anatomical observations and measurements. The internal anatomy of the selected leaves was assessed on leaf sections harvested from the middle of the leaf and prepared for light microscope observation as described by Sage and Williams (1995). Images of leaf cross-sections were used to estimate leaf anatomical features using Image J software (NIH, USA). Leaf mesophyll thickness was measured between epidermal layers at five points in each cross-section and the interveinal distance was measured between two adjacent vascular bundles (Pengelly et al., 2010). The percentage of the leaf cross-section covered by mesophyll or vascular tissue was determined by laying a grid of 200 random points over cross-sections of images and calculating the proportion of points falling on mesophyll or vascular cells (McKown and Dengler, 2007; Riyadh et al., 2007).

For visualizing the ultrastructure of cellular organelles, we took the

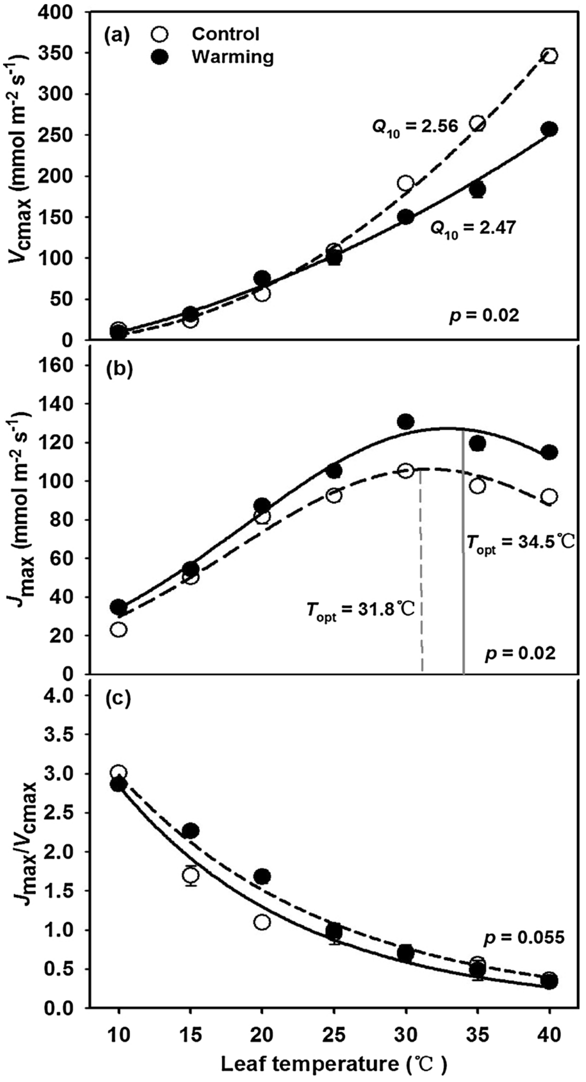

Fig. 4. Warming effects on the responses of maximum rate of Rubisco carboxylation (V_{cmax}), the maximum rate of photosynthetic electron transport (J_{max}), and the balance between J_{max} and V_{cmax} (J_{max}/V_{cmax}) to leaf temperature. The data given are means ± standard error for 3 ambient or warmed plots.

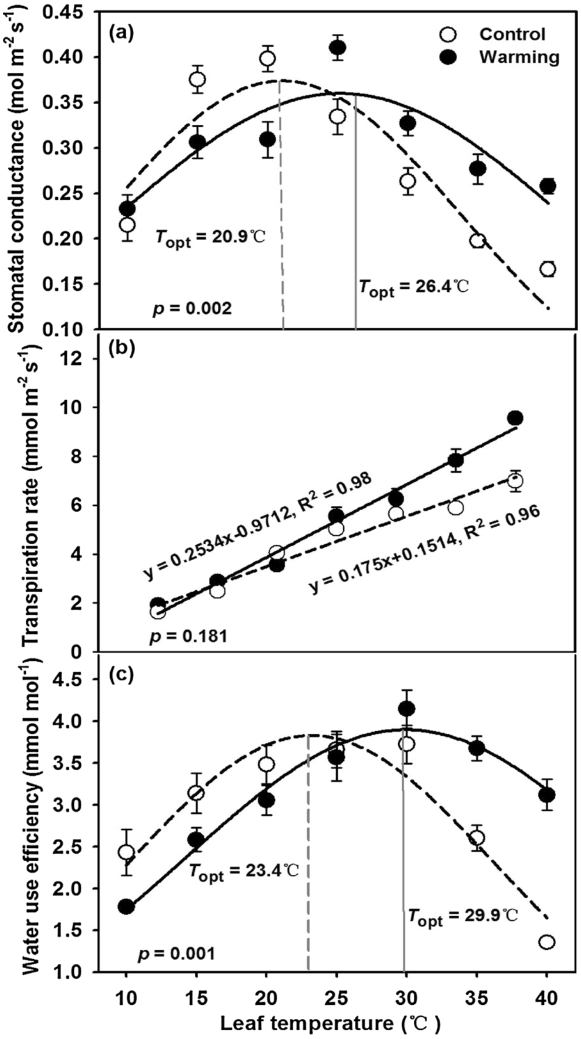

Fig. 5. Stomatal conductance, transpiration rates, and water use efficiency of maize at control or warming condition. The data given are means ± standard error for 3 ambient or warmed plots.

advantage of the transmission electron microscope. Samples were dissected from five fully expanded ear leaves and immediately fixed in 2.5% (v/v) glutaraldehyde (0.1 M phosphate buffer, pH 7.0) for 2 h at 4 °C. Then the samples were washed four times with the same buffer and post fixed in 1% osmium tetroxide for 3 h. After being washed with the same buffer, leaf tissues were passed through an ethanol dehydration series, and then infiltrated and embedded in Spurr's resin. Sections were cut using an LKB-V ultramicrotome (LKB, Bromma, Sweden). Thin sections were stained with uranyl acetate and lead citrate, then observed and photographed under a transmission electron microscope (JEOL Ltd, Tokyo, Japan).

2.7. Biochemical composition analysis

The five sampled leaves from ambient or warming plots were oven-dried to constant weight at 75 °C, and ground to fine powder with a ball mill (MM2, Fa. Retsch, Haan, Germany). Samples were assayed for non-structural carbohydrates ($mg\,g^{-1}$ dry weight) according to Hendrix (1993) and Way and Sage (2008). Glucose, fructose, sucrose, and starch concentrations were determined spectrophotometrically (UV-1750, Shimadzu Corp., Tokyo, Japan) using a glucose assay kit (GAHK-20, Sigma, St Louis, MO, USA). Foliar nitrogen (N) concentration ($mg\,g^{-1}$ dry weight) was determined using an elemental analyzer (Vario Max CN; Elementar Corp., Germany).

2.8. Measuring plant biomass and yield

We obtained the biomass and yield (kg/ha) of the three warming plots and the three control plots by harvesting and de-potting all maize plants on 7 October 2011. The grain seed and the biomass (leaves plus stem and root) of all maize plants were removed with scissors, placed in paper bags, and oven-dried at 80 °C for 24 h before the measurement of dry biomass using an electronic scale with a precision of 0.1 g.

2.9. Statistical analysis

We used the one-way analysis of variance (ANOVA) followed by Duncan's multiple range test ($p < .05$) to analyze the effects of warming on anatomical and biochemical variables as well as maize biomass and yield. Moreover, the optimal temperature (T_{opt}) of A_n, J_{max}, g_s, and WUE as well as the temperature sensitivity (Q_{10}) of R_d and V_{cmax} were tested with the two-way ANOVA. In addition, the differences of the balance between J_{max} and V_{cmax} (J_{max}/V_{cmax}), the balance between R_d and A_g (R_d/A_g), as well as transpiration rate between the warmed and control plots were tested with the two-way Repeated Measures ANOVA (RM ANOVA) using temperature and control/warming treatment as two factors. We also tested the interaction effect between temperature (repeated factor) and control/warming treatment (grouping factor) in the RM ANOVA. The statistical analysis was performed with SPSS 13.0 (SPSS Inc., Chicago, IL, USA).

3. Results

3.1. Warming effects on the yield and biomass of maize

Experimental warming barely affected the tissue biomass and yield of maize (Fig. 1). Experimental warming slightly decreased the tissue biomass of maize plants by 8.2% from 2484 to 2280 kg per hectare (ha). By contrast, the maize yield was slightly increased by 15.6% from 3698 to 4275 kg per ha by experimental warming. However, biomass and yield of maize plants were not significantly different between the ambient and elevated temperatures (ANOVA, all $p > .05$; Fig. 1).

3.2. Warming effects on temperature responses of leaf photosynthesis and respiration

According to the observed A_n–T curves, experimental warming significantly enhanced the maximum values of net photosynthetic rate (A_n) by about 60% (ANOVA, $p = .004$) from an average of 18.6 $\mu mol\,m^{-2}\,s^{-1}$ for plants grown at ambient temperature to 29.8 $\mu mol\,m^{-2}\,s^{-1}$ 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 (ANOVA, $p < .05$) with an obvious shift from 29.0 °C to 31.0 °C (Fig. 2a). In contrast to photosynthesis, experimental warming declined leaf dark respiration rate (R_d) and its temperature sensitivity (Q_{10}). 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 treatments (ANOVA, $p < .001$), and the leaf dark respiration rates in the warming treatment were consistently lower than those in ambient temperature (Fig. 2b). Moreover, 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 ambient and warming conditions were exponentially enhanced along with the increase of temperature, while no significant difference in R_d/A_g was detected between the ambient and elevated temperatures (RM ANOVA, $p = .132$; Fig. 3). We also checked the interaction between temperature and warming treatment, and no statistically significant interaction was found between temperature and

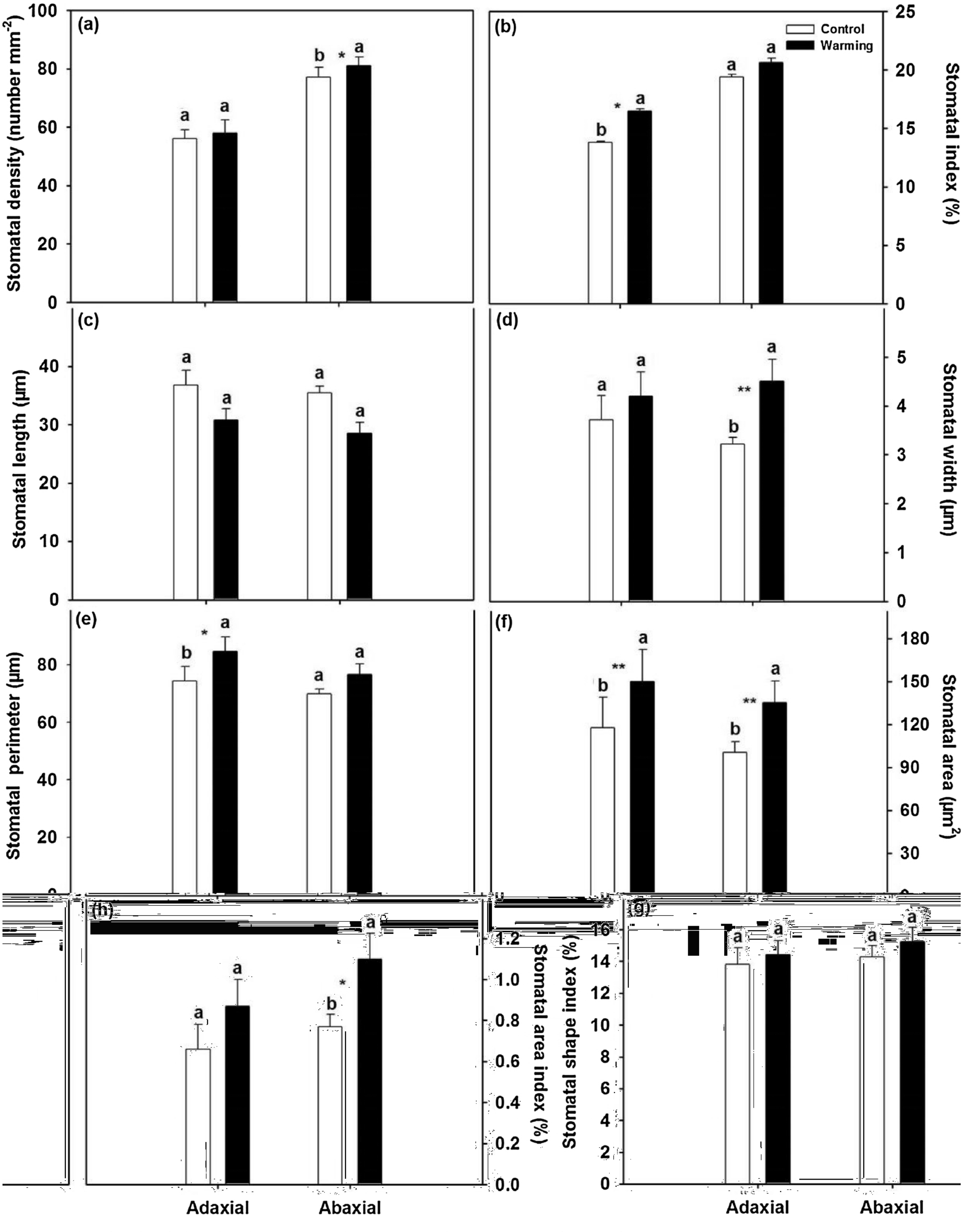

Fig. 6. Stomatal traits on the adaxial and abaxial surfaces of maize leaves at control or warming condition. Values given are means ± standard error (n = 3) for stomatal density, stomatal index, stomatal area index, stomatal shape index, stomatal length, stomatal width, stomatal perimeter, and stomatal area. Mean values were compared by the one-way analysis of variance (ANOVA) at $p < .05$. Different letters indicate $p < .05$ and the same letters indicate $p > .05$ within each leaf side.

warming treatment (RM ANOVA, $p = .538$).

3.3. Warming effects on V_{cmax}, J_{max}, and J_{max}/V_{cmax} ratio

Both the maximum carboxylation rate (V_{cmax}) and the maximum electron transport rate (J_{max}) were generally enhanced with the increase of leaf temperature in maize plants grown at control and warming plots (Fig. 4). Although V_{cmax} was not statistically different between the ambient and warming plots from 10 to 25 °C, the V_{cmax} values in warming conditions were significantly lower than those in ambient plots with the temperature increasing from 25 °C to 40 °C(ANOVA, $p = .02$). In contrast, experimental warming marginally decreased the average temperature sensitivity (Q_{10}) of V_{cmax} from 2.56 to 2.47 (Fig. 4a). Unlike V_{cmax}, the temperature response of J_{max} followed a bell-shaped curve with the peak J_{max} value appearing at 31.8 °C and 34.5 °C, respectively, for the control and warming plots (Fig. 4b). The difference between the two optimal temperatures of J_{max} was statistically significant (ANOVA, $p = .02$). The $J_{\mathrm{max}}/V_{\mathrm{cmax}}$ ratio declined

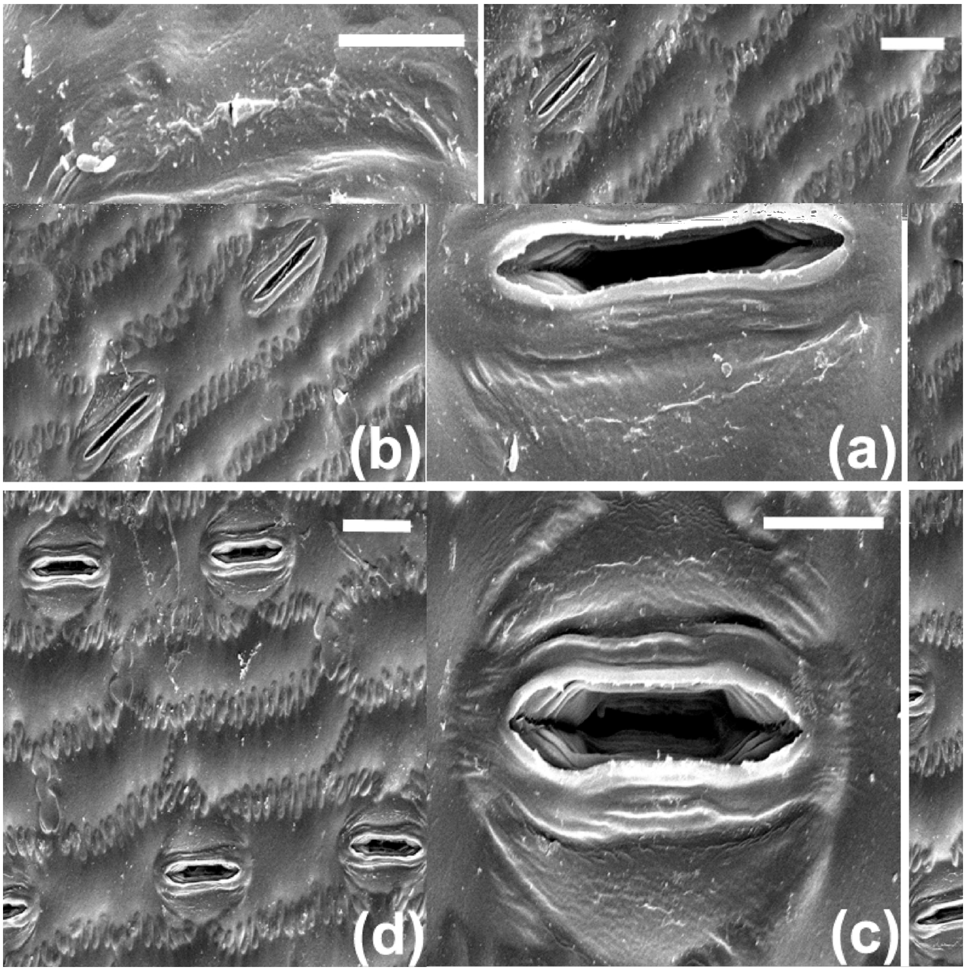

Fig. 7. Scanning electron micrographs (SEM) showing stomatal characteristics of maize leaves grown at ambient temperature (a–b) and elevated temperature (c–d). Note that shorter and wider stomatal apertures were observed on the leaves of maize grown at elevated temperature than those of their counterparts grown at ambient temperature. Bars, 10 μm (a, c) and 40 μm (b, d).

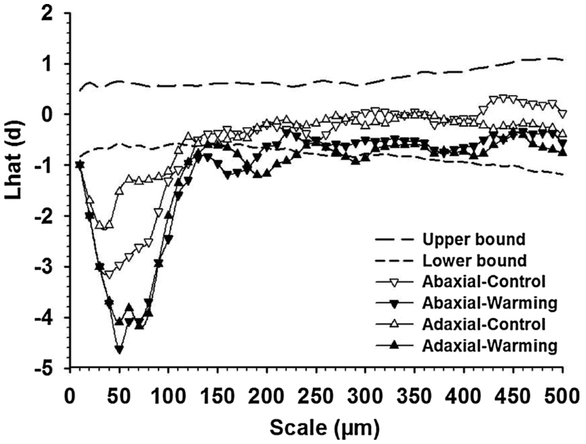

Fig. 8. Spatial pattern of stomatal distribution on leaf surfaces (middle portions of the maize). The value was obtained by averaging the Lhat (d) values of the adaxial or abaxial surface from three maize leaves. The upper and lower 95% boundaries were obtained by Monte Carlo simulation of 100 replicates.

quadratically with the increase of leaf temperature for both the ambient and elevated temperatures (Fig. 4c). Experimental warming barely affected the $J_{\max}/V_{c\max}$ ratio of maize plants (RM ANOVA, $p = .055$), and no statistical significant interaction was found between temperature and warming treatment (RM ANOVA, $p = .098$).

3.4. *Warming effects on stomatal conductance, transpiration rate, and water use efficiency*

The temperature response of stomatal conductance (g_s) for maize plants under both ambient and warming conditions featured typically bell-shaped curves, and experimental warming substantially shifted the optimal temperature for g_s from 20.9 °C to 26.4 °C (ANOVA, $p = .002$; Fig. 5a). The leaf transpiration rates (T_r) enhanced linearly with the increase of temperature, increasing from 1.63 to 6.99 mmol $m^{-2} s^{-1}$ for ambient plots and from 1.92 to 9.56 mmol $m^{-2} s^{-1}$ for warming plots when temperature increased from 10 °C to 40 °C (Fig. 5b). Leaf transpiration rates in warming plots were not higher than in the ambient plots (RM ANOVA, $p = .181$), and no interaction effect was detected between temperature and warming treatment (RM ANOVA, $p = .159$). In addition, the temperature response of leaf-level Water Use Efficiency (WUE) showed typical bell-shaped curves at ambient or elevated temperatures. Experimental warming significantly enhanced the optimal temperature from 23.4 °C to 29.9 °C (ANOVA, $p = .001$; Fig. 5c).

3.5. *Warming effects on stomatal traits and spatial distribution pattern*

Experimental warming significantly increased stomatal density at the abaxial surface (Fig. 6a), while marginally increased the stomatal index by 20% at the adaxial side of maize leaves (Fig. 6b). Experimental warming barely affected the stomatal length at both the adaxial and abaxial surfaces (all $p > .05$; Fig. 6c), whereas warming significantly increased the stomatal width of abaxial surface by about 40% ($p < .01$;

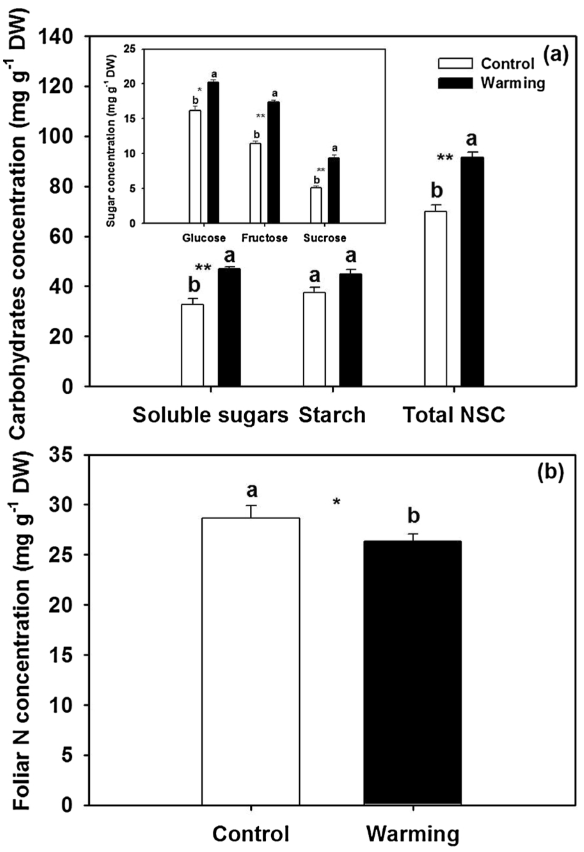

Fig. 9. Warming effects on concentrations of non-structural carbohydrates and nitrogen in maize leaves. The data given are means ± standard error for the ambient or warmed plots (n = 3).

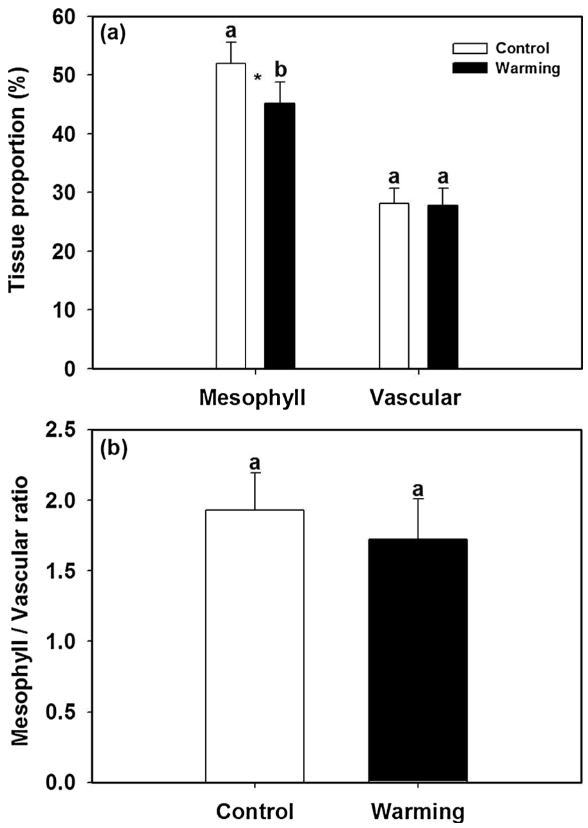

Fig. 10. Warming effects on mesophyll tissue and vascular tissue of maize plants from 3 ambient or warmed plots (n = 3).

Fig. 6d). The stomatal perimeter of adaxial surface was substantially increased by 13% ($p < .05$) under warming conditions (Fig. 6e). Also, experimental warming significantly increased the stomatal area by 27% at adaxial surface ($p < .05$) and 35% at abaxial surface ($p < .05$), respectively (Fig. 6f). As a result, experimental warming increased the stomatal area index by 43% on the abaxial surface ($p < .001$), whereas for adaxial surfaces no significant difference was detected in the stomatal area index between the ambient and elevated temperatures ($p > .05$; Fig. 6h). Stomata on both adaxial and abaxial surfaces of leaves grown at elevated temperature were shorter and wider than those leaves grown at ambient temperature (Fig. 7). The spatial pattern analysis with the Riply's K function showed that stomatal distribution on both adaxial and abaxial surfaces was highly scale-dependent under ambient and elevated temperatures (Fig. 8). On small scale (20–140 μm), stomata showed regular distribution patterns on both the adaxial and abaxial surfaces at ambient or elevated temperature (below the lower 95% envelope), and then stomata were randomly distributed with the increase of the scale up to 500 μm. Moreover, experimental warming made stomatal distribution on both the adaxial and abaxial surfaces more regular at small scales evidenced by the decreased Lhat (d) values from −2.2 to −4.2 at the adaxial surface and from −3.1 to −4.6 at the abaxial surface (Fig. 8). In addition, experimental warming also increased the threshold scale of the regular pattern from about 100–200 μm on the abaxial surface, but warming had little effect on the Lhat (d) values among of the 95% envelope, indicating that experimental warming had little impact on the random pattern of stomata at larger scales.

3.6. Warming effects on carbohydrates and ultra-structures of maize leaves

Experimental warming sharply increased the concentrations of glucose, fructose, and sucrose by 25%, 53%, and 83%, respectively (Fig. 9a). As a result, warming significantly enhanced the concentration of soluble sugars by 43.7% ($p < .01$), whereas the starch concentration was barely affected ($p > 0.05$) under warming condition. Experimental warming substantially enhanced the Total Non-structural Carbohydrates (TNC) of maize leaves by 30.8% ($p < .01$; Fig. 9a). However, the foliar N concentration of maize plant was substantially declined by about 10% under warming condition ($p < .05$; Fig. 9b).

Experimental warming marginally decreased the mesophyll tissue by 13% ($p < .05$), while the vascular tissue showed no significant differences ($p > .05$) between the ambient and elevated temperatures (Fig. 10a). Meanwhile, experimental warming had little effect on the ratio of mesophyll tissue and vascular tissue, although the mesophyll–vascular ratio shared a declining trend under elevated temperature (Fig. 10b). Moreover, we also directly observed more and smaller vascular bodies in the warming treatment than in the control (Fig. 11). In addition, experimental warming barely affected chloroplast length ($p > .05$), whereas it substantially increased chloroplast width by 38.9% ($p < .01$), and thus significantly enhanced the chloroplast area by 118% ($p < .001$). Similarly, experimental warming also markedly increased the mitochondria area by 56.3% ($p < .01$; Fig. 12).

4. Discussion

4.1. Experimental warming increases carbon gain of maize plants

Experimental warming significantly enhanced the net photosynthetic rate (A_n) of maize plants by 60%, indicating that future global warming can stimulate the carbon gain of maize plants. This result is in accordance with Fan et al. (2015), who found that field experimental warming significantly increased net photosynthetic rates and substantially enhanced grain yield of winter wheat (*Triticum aestivum* L.) in the Yangtze River Basin of China in 2012–2014. However, Zhang et al.

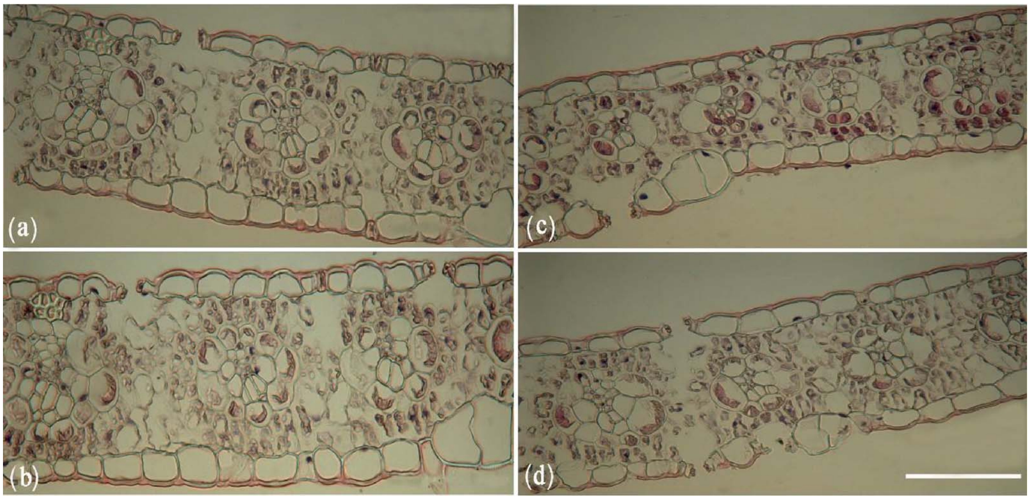

Fig. 11. Light micrographs of cross-section through leaves of maize grown at ambient temperature (a–b) and elevated temperature (c–d). Note that more and small bundle sheaths were observed in leaves of plants grown in elevated temperature. Bar, 100 µm.

(2015) reported that elevated canopy temperature (0.7 °C) marginally decreased A_n by about 10% and shortened the length of growth stage of soybean by 5 days in the North China Plain. These contradictory findings suggest that the photosynthesis of crops in response to experimental warming may depend on species/cultivars and warming intensity, and further studies should be conducted to clarify the differences.

4.2. Stomatal diffusion explains the increase of carbon gain

The stimulated A_n can be explained by the significant increases in the stomatal index, and stomatal aperture area, and thus the stomatal area index, which may benefit CO_2 diffusion from the ambient air into plant leaves. Furthermore, the maize plants in the warming plots had smaller Lhat (d) values than plants in the control plots, suggesting that experimental warming made the stomatal distribution on maize leaves more regular, which may contribute to the stimulated A_n through facilitating CO_2 diffusion from atmosphere to plant leaves by reducing the average diffusion distance (Zheng et al., 2013a; Xu, 2015). Additionally, the stomatal-regulated CO_2 diffusion process may also be associated with thermal acclimation of photosynthesis (Shpak et al., 2005). Previous studies have reported that increasing stomatal conductance (g_s) may result in an upward shift in T_{opt} of A_n (Chi et al., 2013; Zhou et al., 2015). In this study, warming significantly increased g_s and shifted the T_{opt} of g_s from 20.9 °C to 26.4 °C, which may explain the thermal acclimation of photosynthesis in response to experimental warming. This g_s response contributed to photosynthesis acclimation mainly due to changes in stomatal openness and the spatial distribution pattern of stomata under warming environments (Figs. 6–8). However, it should be noted that thermal acclimation of photosynthesis in response to warming may have a feedback on g_s through regulating the CO_2 diffusion processes from atmosphere to plants (Zhou et al., 2015).

In addition to the stomatal traits, the enhanced A_n may also be closely correlated with changes in the structure of mesophyll tissues and the feature of chloroplasts (Crawford and Wolfe, 1999; Gorsuch et al., 2010). At elevated temperature there were more and smaller vascular bundles than at ambient temperature (Fig. 11). Similar results have been reported by Yang et al. (2011), who found that warming significantly decreased vascular bundle width and vascular bundle length by 18% and 22%, respectively. These results suggest that more and smaller vascular bundles per unit leaf area may be more efficient for CO_2 assimilation under warmer conditions, because more and smaller vascular bundles can benefit the CO_2 diffusion from stomata to photosynthetic reaction sites located at vascular bundles (Yang et al., 2011). Therefore, the stimulated photosynthetic rate may be also attributed to the decreases in the size or increases in the density of the vascular bundles in maize leaves, because the higher density of vascular bundles may result in a higher rate of assimilate loading to the phloem, and this higher "sink strength" may also have a feedback on leaf photosynthesis (Nikinmaa et al., 2013). Moreover, our results also showed that experimental warming significantly increased the chloroplast size by enlarging the width and profile area of chloroplasts (Fig. 12), suggesting that the higher photosynthetic efficiency in warming conditions may also be attributed to the bigger chloroplasts in maize leaves.

4.3. Thermal acclimation of foliar photosynthesis and respiration and its effects on carbon gain

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 constraints (Atkin and Tjoelker, 2003; Zheng et al., 2013a). In the current study, experimental warming barely affected the R_d/A_g ratio, suggesting that the thermal acclimation of net photosynthesis is not attributed to the changes in R_d/A_g ratio in warmer conditions. However, our results suggest that the thermal acclimation of photosynthesis can 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 (Yamori et al., 2006; Galmés et al., 2015). This result directly supports previous conclusions 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 (Luo, 2007; Chi et al., 2013), because both the maximum velocity of Rubisco carboxylation (V_{cmax}) and the maximum rate of electron transport (J_{max}) are temperature dependent (Zhou et al., 2015), where V_{cmax} follows the Arrhenius equation and J_{max} follows a bell-shaped curve (Chi et al., 2013). In addition, experimental warming had little effect on the balance between the regeneration of RuBP and the Rubisco carboxylation (J_{max}/V_{cmax}), suggesting that N allocation between the biochemical and photochemical processes of photosynthesis has little contribution to the shift in the A_n–T curve. It has been well demonstrated that the thermal acclimation of foliar respiration may occur via the temperature-mediated change in temperature sensitivity, Q_{10} (Atkin and Tjoelker, 2003; Chi et al., 2013), which is mainly determined by the maximum enzyme activity (Luomala et al., 2003; Ethier et al., 2006), energy demand (Onoda et al., 2005; Hikosaka et al., 2006), and/or substrate availability (Campbell et al., 2007; Zheng et al., 2013b). Our results that R_d

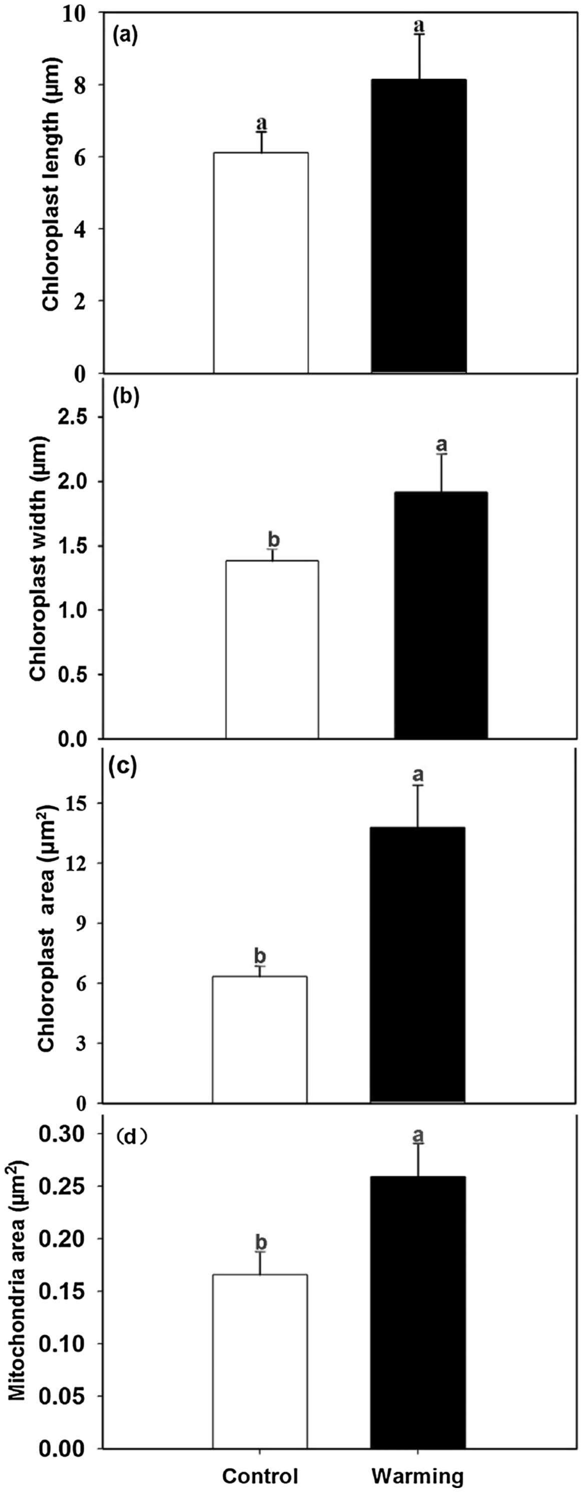

Fig. 12. Warming effects on the chloroplast and mitochondria characteristics of maize plants from 3 ambient or warmed plots (n = 3).

was sensitive to leaf temperature with the R_d–T relationship following a typical exponential curve, and that experimental warming decreased the Q_{10} of R_d, supports conclusions from previous studies that the temperature sensitivity of R_d is negatively related to leaf temperature (Mohammed and Tarpley, 2009). Earlier studies have found that the reduction of Q_{10} may be attributed to the decline in the substrate concentration under warmer conditions (Chi et al., 2013; Zhou et al., 2015). However, our results that experimental warming significantly increased the concentration of carbohydrates including starch and soluble sugars (Fig. 9) suggest 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 (Atkin and Tjoelker, 2003; Chi et al., 2013), because the N concentration is closely associated with the amounts of respiratory enzymes. Earlier results from the same warming experiment showed that experimental warming substantially decreased the foliar N concentration (Zheng et al., 2013b), 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. 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 (Atkin and Tjoelker, 2003; Davidson et al., 2006).

4.4. Relationships among thermal acclimation, carbon gain, and maize yield in response to experimental warming

Plant growth and crop yield in response to climate warming are associated with photosynthetic and respiratory acclimation to temperature (Thomas et al., 2004; Colwell et al., 2008; van Mantgem et al., 2009; Ruiz-vera et al., 2015; Abebe et al., 2016), which is characterized by the shifting capability of the optimal temperature for net photosynthesis (T_{opt}) and the sensitivity of dark respiration to temperature (Atkin and Tjoelker, 2003; van Mantgem et al., 2009; Zheng et al., 2013a; Niles et al., 2015). It has long been known that photosynthesis can acclimate to prevailing growth temperature (T_{growth}) by shifting the T_{opt} (Jin et al., 2011; Rodríguez et al., 2015). In the current study, elevating canopy temperature of maize plants by 2.08 °C resulted in a 2.0 °C shift in the T_{opt} of A_n from 29.0 to 31.0 °C (Fig. 2a), suggesting that photosynthesis of maize plants has almost fully acclimated to the two-year field experimental warming.

In addition to the thermal acclimation of photosynthesis, leaf dark respiration (R_d) and its temperature sensitivity (Q_{10}) in response to experimental warming is also vital in estimating the impacts of climate warming on maize yield (Yamori et al., 2014), because the respiratory process in response to warming may consume more photosynthetic products and change the balance between photosynthesis and respiration, thus affecting maize yield and biomass (Malcolm et al., 2006; Colwell et al., 2008; Tacarindua et al., 2013; Blanc and Sultan, 2015; Blanc, 2017). In our experiment, thermal acclimation of respiration, occurred through changes in Q_{10}, may enhance plant net carbon assimilation by reducing carbon loss under warmer climate (Atkin and Tjoelker, 2003; Yamori et al., 2014). As a result, the response of maize yield to climate warming is closely related to the R_d/A_g ratio, which indicates the balance between carbon gain, loss, and accumulation (Bunce, 2008; Chi et al., 2013; Yamori et al., 2014; Zhou et al., 2015). Our results that experimental warming at foliar level has non-linearly increased the R_d/A_g ratio suggest proportionally more carbon loss through R_d as leaf temperature increases. However, this carbon loss through R_d can be fully compensated by the increase of carbon gain as evidenced by the higher carbohydrate accumulation (TNC) in warmer conditions. It is important to note that experimental warming barely affected the maize yield and biomass in the current study. This result implied that thermal acclimation of foliar photosynthesis and respiration may positively modify the carbon balance among carbon gain, loss, and accumulation through the metabolic adjustment for compensating the negative impacts from global warming on crop yield.

5. Conclusion

Our results showed that experimental warming barely affected the maize yield of the North China Plain, although the net photosynthetic rate (A_n) was significantly increased under warming conditions. We also found that maize plants in response to warming shared apparently thermal acclimation of 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. The biochemical and photochemical processes (Rubisco carboxylation and electron transport) as well as the stomatal-regulated CO_2 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 indicate 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 models for further improving the predictions of global warming impacts on agricultural production.

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