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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

Yunpu Zheng[a,b], Lili Guo[a], Ruixing Hou[b], Haoran Zhou[c], Lihua Hao[a], Fei Li[a], Dongjuan Cheng[a], Zhengping Peng[d], Ming Xu[b,e,*]

[a] School of Water Conservancy and Hydropower, Hebei University of Engineering, Handan 056038, China
[b] Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, 11A Datun Road, Beijing 100101, China
[c] Department of Biology, University of Pennsylvania, Philadelphia, PA 19104, USA
[d] School of Resources and Environment Science, Hebei Agricultural University, Baoding 071001, China
[e] Center for Remote Sensing and Spatial Analysis, Department of Ecology, Evolution and Natural Resources, Rutgers University, 14 College Farm Road, New Brunswick, NJ 08901, USA

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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

* Corresponding author at: Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, 11A Datun Road, Beijing 100101, China.
E-mail address: mingxu@crssa.rutgers.edu (M. Xu).

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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