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Diurnal temperature amplitude alters physiological and growth response of maize (*Zea mays* L.) during the vegetative stage

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ABSTRACT

Global climate models predict increase in mean daily temperature to be mainly driven by rapid increase in nighttime temperature compared to daytime temperature, leading to narrowing diurnal temperature amplitude. Higher day and night temperatures induce significant negative impact on growth and development of different crops. However, limited studies have focused on quantifying impacts associated with different diurnal temperature amplitudes maintaining the same daily mean temperature. The main objectives were to (i) quantify the impact of diurnal temperature amplitudes on the carbon balance of the plant (photosynthesis versus night respiration rate) and (ii) evaluate the significance of variable day and night temperature with a common mean on the carbohydrate composition and overall plant growth. A maize hybrid (DKC47-27RIB) was grown in controlled environments at two mean daily temperatures (30 °C and 35 °C) with three different combinations of day and night temperatures resulting in diurnal temperature amplitudes of 2 °C, 10 °C and 18 °C. After 42 days of temperature treatments, lower diurnal temperature amplitude led to a linear increase in night respiration and a linear decrease in total sugars, non-reducing sugars, starch concentrations, plant height, total leaf area and total biomass accumulation. However, there was no significant change in photosynthetic rate among the treatment combinations, while photochemical efficiency (Fv/Fm) and chlorophyll index decreased only with diurnal temperature amplitude of 18 °C and 2 °C, respectively. A significant negative relationship was found between night respiration and total biomass accumulation ($R^2 = 0.73$; $P < 0.01$), total leaf area ($R^2 = 0.82$; $P < 0.01$), specific leaf area ($R^2 = 0.21$; $P < 0.01$), non-reducing sugars ($R^2 = 0.50$; $P < 0.01$) and starch concentrations ($R^2 = 0.50$; $P < 0.01$). The results imply that narrowing diurnal temperature amplitude as a result of higher night temperature is the major driver of the negative impact on vegetative growth in maize.

1. Introduction

Global climate change models predict daily mean temperature to increase by about 1.0–3.7 °C by end of the 21st century. This change will likely be accompanied by increased frequency in heat waves and greater number of warmer nights (IPCC, 2013). Among different climate change factors, temperature is identified as one of the major drivers that affects growth, development and yield of field crops. Optimum day-time temperature and high night temperature or *vice versa* can alter normal physiological functions of crops as compared with those grown under optimum day and night temperature (Prasad et al., 2011; Shi et al., 2013; Peraudeau et al., 2015). Negative impact of high day and high night temperature stress on physiological, biochemical processes, seed-set and yield has been well documented in different crops (peanut: *Arachis hypogaea* L., Prasad et al., 2000; maize: *Zea mays* L., Karim et al., 2000; drybean: *Phaseolus vulgaris* L., Prasad et al., 2002; cotton: *Gossypium hirsutum* L., Snider et al., 2009; wheat: *Triticum aestivum* L., Prasad et al., 2011; soybean: *Glycine max* L. Merr, Djanaguiraman et al., 2013; sorghum: *Sorghum bicolor* L. Moench, Djanaguiraman et al., 2014; and rice: *Oryza sativa* L., Bahuguna et al., 2015). In maize, high day and night temperature decreased growth parameters (leaf area and biomass accumulation), photosynthetic rate, transpiration, water use efficiency and maximum quantum efficiency of PSII (Karim et al., 2000; Sinsawat et al., 2004; Ben-Asher et al., 2008). Similarly, a significant reduction in yield, photosynthetic rate, antioxidant scavenging capacity and photochemical efficiency was observed in winter wheat under high day, high night and combined high day and night temperature exposure (Narayanan et al., 2015). High and optimum day temperature combined with a range of different high night temperatures increased nighttime leaf respiration and decreased leaf chlorophyll content, gas exchange, chlorophyll fluorescence transients and pollen germination leading to lower pod set and

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reduced yield in soybean (Djanaguiraman et al., 2013). Increase in night temperature resulting in significant decrease in grain yield has also been documented in field crops grown on larger spatial or temporal scales (Peng et al., 2004; Welch et al., 2010; Lobell et al., 2012).

Mechanistically, high night temperature is known to induce increased respiration and carbon loss leading to altered sugar metabolism, lowering biomass accumulation, resulting in poor grain development and lower yield (Yin et al., 1996; Mohammed and Tarpley, 2009; Loka and Oosterhuis 2010; Djanaguiraman et al., 2013; Matsuda et al., 2014). In contrast, a non-significant effect of high night temperature on plant respiration and biomass accumulation has also been reported in tomato (*Lycopersicum esculentum* L.), soybean, lettuce (*Latuca sativa* L.) and rice (Frantz et al., 2004; Peraudeau et al., 2015). Overall, the negative impact of high day temperature stress across crops has been well established while the same with high night temperature is still unclear with contrasting responses documented in different crop species and hence warrants further investigation. In addition, most of the above studies, have quantified the response to either high day or night temperature, while narrowing diurnal temperature amplitude between day and night temperatures as a result of higher night temperature has not been systematically quantified. Although there have been studies involving combined high day and night temperature treatments (Djanaguiraman et al., 2013; Narayanan et al., 2015), these treatments have been imposed without maintaining a common mean daily temperature. Hence, deriving unbiased diurnal temperature amplitude impacts is not possible under such treatment structure.

Among cereals, maize is one of the major staple food crops with a mean optimum temperature to be 30.8 °C and the mean maximum to be 42 °C, derived through meta-analysis (Sanchez et al., 2014). The vegetative growth stage in maize and other field crops, plays a key role in determining potential crop yields and significant changes in temperature during this phase can impact yield. Recent studies have documented reduced yields in major field crops such as rice (Peraudeau et al., 2015), wheat (Narayanan et al., 2015), including maize (Karim et al., 2000; Sinsawat et al., 2004; Ben-Asher et al., 2008) when exposed to high day and or high night temperatures. However, there are no reports dealing with maize growth, physiological and biochemical functions affected by changes in diurnal temperature amplitudes. Hence our studies address a novel hypothesis in maize to varying diurnal temperature amplitudes. The main objectives were to (i) quantify the impact of diurnal temperature amplitudes on the carbon balance of the plant (photosynthesis *versus* night respiration rate) and (ii) evaluate the significance of variable day and night temperatures with a common mean on the carbohydrate composition and overall plant growth.

2. Materials and methods

2.1. Plant material and growth conditions

The research was conducted during 2014 using controlled environment facilities at the Department of Agronomy, Kansas State University, Manhattan, KS, USA. Early maturing hybrid maize plants (DKC47-27RIB, DroughtGard hybrid, Monsanto, St. Louis, MO, USA) were grown in 7 L pots (width 22 cm × height 21 cm) with Metro mix 360 growing medium (Hummert International, Topeka, KS, USA) fertilized with liquid iron (Iron 5%; Bonide products, Oriskany, NY, USA), 35 g and 4 g of Osmocote classic controlled release plant nutrients (14:14:14 NPK) and Micro max micronutrient granules (Hummert International, Topeka, KS, USA), respectively. Three seeds per pot were sown at a depth of 5 cm and four pots per treatment were maintained inside each growth chamber (Conviron Model PGR15; Winnipeg, MB, Canada). After germination, 1 g of systemic insecticide Marathon (1% Imidacloprid, 1-[(6-Chloro-3-pyridinyl) methyl]-*N*-nitro-2-imidazolidinmine; OHP Inc, Maryland, PA, USA) was applied to each pot to avoid incidence of sucking pest. The day/night temperature inside the growth chambers was maintained at 35/25 °C (daily mean temperature 30 °C), relative humidity (RH) of 60% and 12 h of photoperiod (0600 h to 1800 h) with photosynthetic active radiation (PAR) of 800 μmol m^{-2} s^{-1} at the plant canopy level using cool fluorescent lamps. A transition time of 7 h from day to night and *vice versa* was followed to replicate the diurnal temperature fluctuation under natural field conditions. Air temperature was monitored at 10 min intervals throughout the experiment using HOBO data logger (Onset UTBi-001; TidbiT v2 Temperature logger; Bourne, MA, USA). After reaching V3 growth stage (Abendroth et al., 2011; third leaf stage) plants were thinned to one plant per pot and temperatures were adjusted to two different mean daily temperature treatments (30 °C and 35 °C) with three different combinations of day and night temperatures resulting in diurnal temperature amplitude differences of 2 °C, 10 °C and 18 °C in different growth chambers. Three chambers were programmed with a mean daily temperature of 30 °C (optimum temperature for growth and development of maize) and other three chambers with mean daily temperature of 35 °C (moderately high temperature). The diurnal temperature amplitudes of 2 °C, 10 °C and 18 °C for the daily mean temperature of 30 °C was established by adjusting the day and night temperatures (°C ± SD; standard deviation) to 31 °C (±0.6)/29 °C (±0.1), 35 °C (±0.6)/25 °C (±0.1) and 39 °C (±1.1)/21 °C (±0.1). Similarly, for achieving the same amplitude differences with a daily mean temperature of 35 °C, the day and night temperatures were adjusted to 36 °C (± 0.4)/34 °C (±0.2), 40 °C (± 0.7)/30 °C (±0.1) and 44 °C (±0.5)/ 26 °C (±0.1) (Fig. 1). An independent experiment with the same hybrid, growing conditions and temperature treatments was repeated and a common set of physiological and biochemical parameters were recorded from both the experiments, after exposing the plants to 42 days of differential diurnal temperature amplitudes as mentioned above. A total of six different growth chambers were used during each experiment to expose plants to different diurnal temperature combinations mentioned above.

2.2. Leaf photosynthetic and night respiration rates

Leaf photosynthetic and night time respiration rates were recorded using a portable photosynthesis system (LI-6400 XT; LI-COR, Lincoln, NE, USA). From each temperature treatment, a minimum of six photosynthesis and night respiration measurements were recorded on the final day of treatment exposure from tagged fully expanded mature leaves between 1000 and 1015 h and 2200–2215 h (growth chamber time settings), respectively. In order to maintain equal duration of exposure to day and night temperatures, growth chamber programs were systematically adjusted to delay by 15 min from the actual time from the first chamber to last chamber, which helped to over-come the time lag between chambers, while measuring photosynthesis and leaf night respiration. This adjustment allowed us to capture the leaf photosynthesis and respiration measurements exactly after four hours' exposure to light (PAR; 800 μmol m^{-2} s^{-1}; 0600 h to 1000 h) and dark (PAR; 0 μmol m^{-2} s^{-1}; 1800–2200 h) across all treatments. The CO_2 concentration in the leaf chamber of the portable photosynthesis system was set to 400 μmol mol^{-1} and block temperature was adjusted to respective day (while measuring photosynthesis) and night (while measuring night respiration) temperature according to the growth chamber setting. The flow rate for photosynthesis measurement was 500 μmol s^{-1} and was adjusted to 100 μmol s^{-1} for measuring night respiration to