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Impact of light intensity and leaf temperature on photosynthesis in *Zea mays*

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This study investigates the impact of leaf temperatures (T_{leaf}) and irradiance on photosynthesis rates of maize (*Zea mays*) leaves. The research focuses on how maize plants respond to abiotic stress factors, which are crucial for determining crop growth and yield in a way to develop maize lines that are optimized for arid environments. This is crucial for improving crop productivity in areas facing high temperature and light stress, contributing to food security in challenging climates. The photosynthesis rate and stomatal conductance decreased at high irradiance while transpiration rate remained unaffected. Conversely, the photosynthesis rate declined at elevated leaf temperatures, specifically around 41°C but stomatal conductance and transpiration rates increased. These findings indicate that high T_{leaf} and irradiance significantly affect the photosynthetic performance of maize, potentially impacting plant growth and yield.

Keywords: *Zea mays*, Photosynthesis, Stomatal conductance, leaf temperature

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INTRODUCTION

Food production in the last century has been improved to meet human demand globally. The Green Revolution in the last century led to doubling of cereal production worldwide (Fischer & Edmeades, 2010; Pretty, 2008; Saville et al., 2012). These achievements are attributed to the efforts of farmers, agronomists and plant biologists. In addition, the new techniques in farming practices and plant breeding appreciably improved grain yield and quality (Mann, 1999).

However, the increase in population, concomitant with the changes in climate over the last few years, has affected food security and availability around the globe. The world population is increasing, expectedly reaching 10 billion in 2060. Due to the diversity of terrain, local climatic conditions, and the available agricultural expertise, food is not produced equally worldwide.

Furthermore, the changes in global climate, manifested as the rise in average air temperature on Earth and extreme conditions such as low or high rainfall, may cause floods or hurricanes (Sperry & Love, 2015; Vermeulen et al., 2012). In certain regions, exceedingly high temperatures prevail both day and night. For instance, in Kuwait, July sees an average maximum temperature of 45.6 °C, and the average July air temperature (the Arabian Peninsula's hottest month) hovers around 38.2 °C. Forecasts predict an annual temperature rise of 0.4 °C per decade due to Global Climate Change (UNFCC, 2012).

Therefore, cereal cultivation is hindered by various abiotic stressors (Lobell & Asner, 2003) such as soil aridity and salinity where water availability may be

diminished water potential <-1.3 MPa due to accumulation of soluble salts in the upper soil horizons. These factors can curtail plant growth by limiting water accessibility, thereby diminishing stomatal conductance (gs). To flourish in such environments, crops must possess intricate traits, including managing electrolyte uptake, compartmentalization or exclusion of ions (Sharkey & Zhang, 2010) and extraction of moisture from drying soils (Yoshida et al., 2010). Stomatal conductance regulates the exchange of gases between leaves and their surroundings, which is crucial for CO₂ assimilation. However, gs is also responsive to factors such as vapor pressure deficit (VPD), blue light, and CO₂ concentrations in the atmosphere. Elevated atmospheric VPD reduces gs; therefore, it curtail transpiration and induces loss of plant cell turgor, resulting in diminished photosynthesis rates (A) due to inadequate CO₂ entry into the mesophyll cell chloroplasts (Ocheltree et al., 2014). Reducing gs may also trigger heightened leaf temperatures (T_{leaf}) as transpiration cooling diminishes (Farquhar & Sharkey, 1982).

Moreover, water is pivotal in establishing turgor of guard cells, facilitating stomatal pore opening to enable CO₂ uptake for growth (Lobell & Asner, 2003). Turgor pressure is essential for maintaining an upright posture, particularly in herbaceous, non-woody plants like cereal crops. Without the ability to stand erect, the plant may eventually succumb to competition once a closed canopy form above. Additionally, the rate of water and nutrient ion transport via the xylem from roots to shoots is governed by guard cell turgor pressure. Consequently, acquiring mineral ions and other solutes relies on leaf

water potential (Buckley & Mott, 2013; Farquhar & Sharkey, 1982; Kim et al., 2010). Finally, water evaporation from stomatal pores cools the leaf through the great latent heat of evaporation of water (Farquhar & Sharkey, 1982).

Zea mays, commonly known as maize or corn, is one of the primary cereal crops consumed worldwide, with significant importance in food security, livestock feed, and various industrial applications. Maize is a C₄ plant utilizing a specialized photosynthetic pathway that allows for more efficient CO₂ assimilation, particularly under high light intensity and temperature conditions. The C₄ pathway involves the initial fixation of CO₂ into a four-carbon compound in mesophyll cells, which is then transported to bundle sheath cells, where CO₂ is released and refixed via the Calvin cycle. This adaptation minimizes photorespiration, enhances photosynthetic efficiency and productivity in warm climates (Crafts-Brandner & Salvucci, 2002; Lundgren et al., 2014; Sage et al., 2014).

The C₄ photosynthetic mechanism affords maize a competitive advantage in high-temperature environments, making it an essential crop in tropical and subtropical regions. However, the efficiency of this process is highly dependent on leaf temperature (T_{leaf}). Research has demonstrated that maize photosynthetic rate is optimal up to a T_{leaf} of approximately 38 °C, beyond which there is a marked decline in CO₂ assimilation. This decline is largely due to thermal sensitivity of the key enzymes, such as ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco) activase, which plays a critical role in the C₄ pathway. When exposed to temperatures above 38 °C, the activity of Rubisco activase is compromised, leading to a decrease in the carboxylation efficiency of Rubisco and a subsequent reduction in overall photosynthesis (Crafts-Brandner & Salvucci, 2002; Pinto et al., 2014).

The impact of temperature on maize performance and production is a critical area of study, particularly in the context of global climate change. Understanding how maize responds to thermal stress is essential for developing strategies to maintain and improve crop yield as temperature rises. Recent studies have highlighted the potential effects of temperature fluctuations on maize physiology and productivity. For instance, Casali et al. (2022) and Li et al. (2022) have explored maize genetic and physiological responses to high temperatures, identifying the key traits that could be targeted for

breeding heat-tolerant varieties. Similarly, Erenstein et al. (2022) and Fischer & Edmeades (2010) have examined broader implications of temperature changes on maize production systems, emphasizing the need for adaptive management practices to sustain maize yield in the face of climate variability. In this paper, the effect of temperature and light intensity on CO₂ assimilation by maize was investigated to find out the role of stomatal conductance in maintaining efficient photosynthesis.

MATERIALS AND METHODS

Seeds of maize (*Zea mays* L., Cultivar Katumany) were germinated on damp paper towels for 5–7 days, then transplanted on 5-liter pots containing 15% topsoil and 85% sand. Pots were supplemented with an NPK fertilizer solution which is equivalent of 0.6 mM of nitrogen (3:1:2) applied in two equal doses at the 1-week and 4-week stages. The pots were placed in a growth room with a 16/8 hour light/dark photo period and temperature of 22 °C/16 °C (day/night).

Photosynthesis measurements on maize leaves were conducted using infrared gas analyzer (IRGA; LCpro+, ADC Bioscientific Ltd., Hoddesdon, Herts., UK) equipped with a rectangular narrow leaf chamber (window area of 5.8 cm²). Mature leaves were gently placed in the leaf chamber, ensuring the entire chamber area was covered. The LCpro LED unit provided illumination, while the LCpro console controlled the CO₂ supply, air temperature and humidity.

To measure CO₂ assimilation rate (A) in response to varying light intensity, the IRGA was typically programmed to perform a Light Response (A/I) curve on the same leaf portion. All leaf chamber parameters were kept constant (Ca 380 μmol CO₂ mol⁻¹ air, humidity 5 mmol water mol⁻¹ air, constant T_{air} 23 °C), while the incident light intensity was stepwise increased from 0 to 1000 μmol photons m⁻² s⁻¹ PPFD in 12 steps. This provided leaf absorbances of 0, 9, 17, 44, 87, 174, 261, 358, 435, 522, 696, and 870 μmol m⁻² s⁻¹ PPFD.

The impact of continuous heat exposure on photosynthesis of maize leaves was assessed. In this assay, maize leaves were attached to an IRGA chamber, with leaf temperatures set at 20, 26, 30, 36, 39, and 41 (±0.4) °C. The conditions included ambient CO₂ (380 μmol CO₂ mol⁻¹ air) and saturating light (560 μmol photons m⁻² s⁻¹) for 210 minutes, during which the steady-state assimilation rate and stomatal conductance were measured.

Statistical analysis

Data were analyzed using GraphPad Prism (version 10, 2023). The ANOVA assessment was conducted

RESULTS

As absorbed irradiance increased from 0 to approximately $500 \mu\text{mol m}^{-2} \text{s}^{-1}$, the photosynthesis rate (A) progressively increased (Figure 1), reaching a peak of about $20 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$, post which assimilation rate approached a plateau across irradiances of $500\text{--}700 \mu\text{mol m}^{-2} \text{s}^{-1}$, then slightly decreased at higher irradiance. During dark (0 irradiance) the assimilation rate is $-5 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$, while A is $0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ when absorbed irradiance 8, 15 and $22 \mu\text{mol m}^{-2} \text{s}^{-1}$ photon.

An illustration of the relationship between light absorbance and stomatal conductance. (gs) maize leaves are shown in Figure 2. As light absorbance increases from 0 to approximately $800 \text{mmol m}^{-2} \text{s}^{-1}$, stomatal conductance also rises, indicating a positive correlation between these variables. Initially, stomatal conductance increases sharply with absorbance, reaching a significant rate of around $200 \text{mmol m}^{-2} \text{s}^{-1}$. This trend continues, albeit at a slightly reduced rate, up to approximately $600 \text{mmol m}^{-2} \text{s}^{-1}$. Beyond this point, the increase in stomatal conductance becomes more gradual, peaking at around $700\text{--}750 \text{mmol m}^{-2} \text{s}^{-1}$. Interestingly, stomatal conductance begins to decline at higher absorbance levels above $750 \text{mmol m}^{-2} \text{s}^{-1}$, suggesting a threshold beyond which additional light does not further enhance conductance and may even have a slight inhibitory effect. The relationship between absorbance and transpiration rate in maize leaves showed in Figure 3, revealing a positive correlation that plateaus at higher absorbance levels. As absorbance increases from 0 to $500 \text{mmol m}^{-2} \text{s}^{-1}$, the transpiration rate rises sharply from approximately 1.0 to $4.0 \text{mmol m}^{-2} \text{s}^{-1}$.

The effect of leaf temperature (T_{leaf}) on the photosynthesis rate (A), stomatal conductance (gs), and transpiration rate (E). Elevated T_{leaf} typically influences these physiological processes in plants, often leading to a decline in photosynthesis rate (A) due to the increased temperature sensitivity of the photosynthetic enzymes and potential damage to the photosynthetic apparatus. Concurrently, high T_{leaf} can cause a reduction in stomatal conductance (gs) as the stomata close to minimizing water loss, thereby

restricting CO_2 uptake and further impacting photosynthetic efficiency. However, the transpiration rate (E) might exhibit a complex response; initially, it may increase with T_{leaf} due to enhanced evaporative demand, but prolonged high temperatures often result in decreased transpiration as stomata close to conserve water. These figures will elucidate the intricate interplay between T_{leaf} and these critical physiological parameters, offering insights into the plant's adaptive strategies and limitations under thermal stress conditions. This information is crucial for developing strategies to enhance plant resilience in the face of rising global temperatures and optimizing agricultural practices to sustain crop productivity.

In Figure 4, the photosynthesis rate (A) exhibits a bell-shaped response to increasing T_{leaf} . The photosynthesis rate increases from about $8.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 25°C to a peak of around $10.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 35°C . Beyond 35°C , the photosynthesis rate declines sharply, dropping to approximately $3.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 40°C . This indicates that photosynthetic efficiency improves with moderate increases in leaf temperature but declines significantly under high-temperature stress. Figure 5 shows the stomatal conductance (gs) in response to T_{leaf} . Stomatal conductance follows a parabolic trend, decreasing from about $0.08 \text{mol m}^{-2} \text{s}^{-1}$ at 25°C to a minimum of $0.04 \text{mol m}^{-2} \text{s}^{-1}$ around 27°C . It then increases, reaching a peak of approximately $0.12 \text{mol m}^{-2} \text{s}^{-1}$ at 35°C before declining again to about $0.07 \text{mol m}^{-2} \text{s}^{-1}$ at 39°C . Stomatal conductance increases again at 41°C . Figure 6 illustrates the transpiration rate (E) in relation to T_{leaf} . The transpiration rate shows an initial increase from about $1.0 \text{mmol m}^{-2} \text{s}^{-1}$ at 25°C to $2.5 \text{mmol m}^{-2} \text{s}^{-1}$ at 39°C . After a slight decrease, the rate surges sharply to $5.0 \text{mmol m}^{-2} \text{s}^{-1}$ at 41°C .

Statistical analysis, as illustrated in Figure 8, reveals highly significant effects of high leaf T_{leaf} on key physiological parameters in maize. The assimilation rate, stomatal conductance (gs), and transpiration rate all demonstrated marked changes in response to elevated T_{leaf} . Specifically, the assimilation rate significantly decreased, indicating a decline in photosynthetic efficiency under heat stress. In contrast, both stomatal conductance and transpiration rate significantly increased at higher leaf temperatures, suggesting enhanced water loss and gas exchange activity as a potential physiological response to mitigate heat stress.

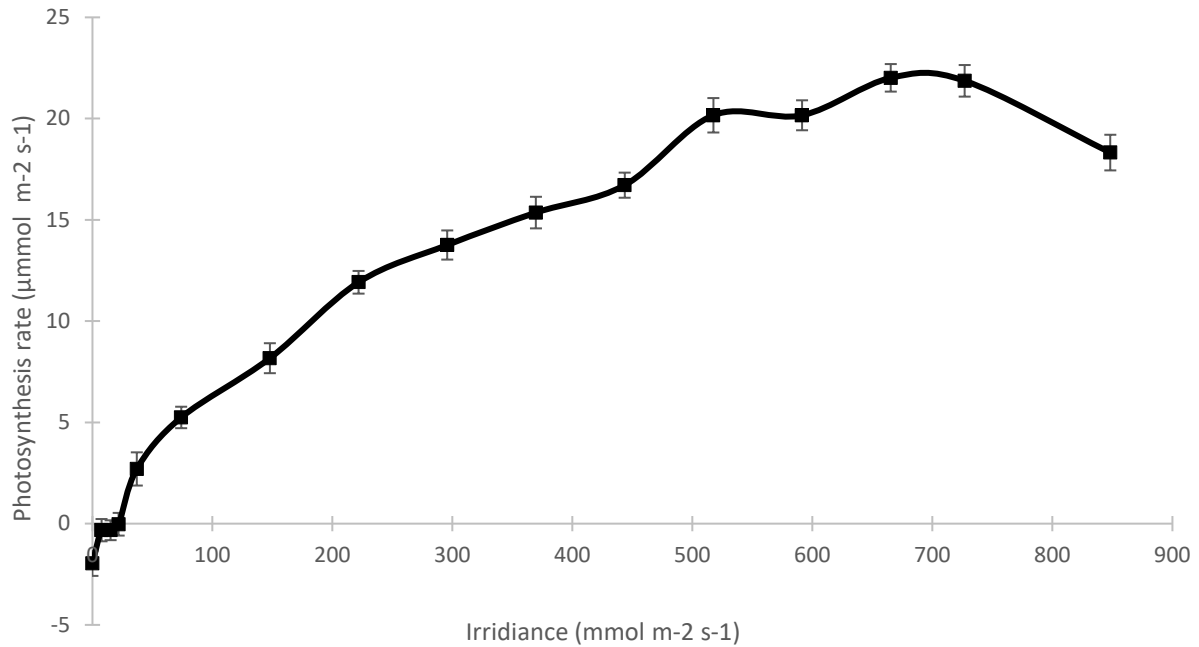


Figure 1. The photosynthesis rate of maize leaf in response to changing absorbance. All leaf chamber parameters were kept constant (Ca 380 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air, humidity 5 mmol mol^{-1} air, constant T_{air}), while the incident light intensity was gradually adjusted from 0 to 1000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ PPFD in 15 steps. Each data point is the average (\pm SE) of 7 biological replicate, the p-value: 3.34×10^{-18} .

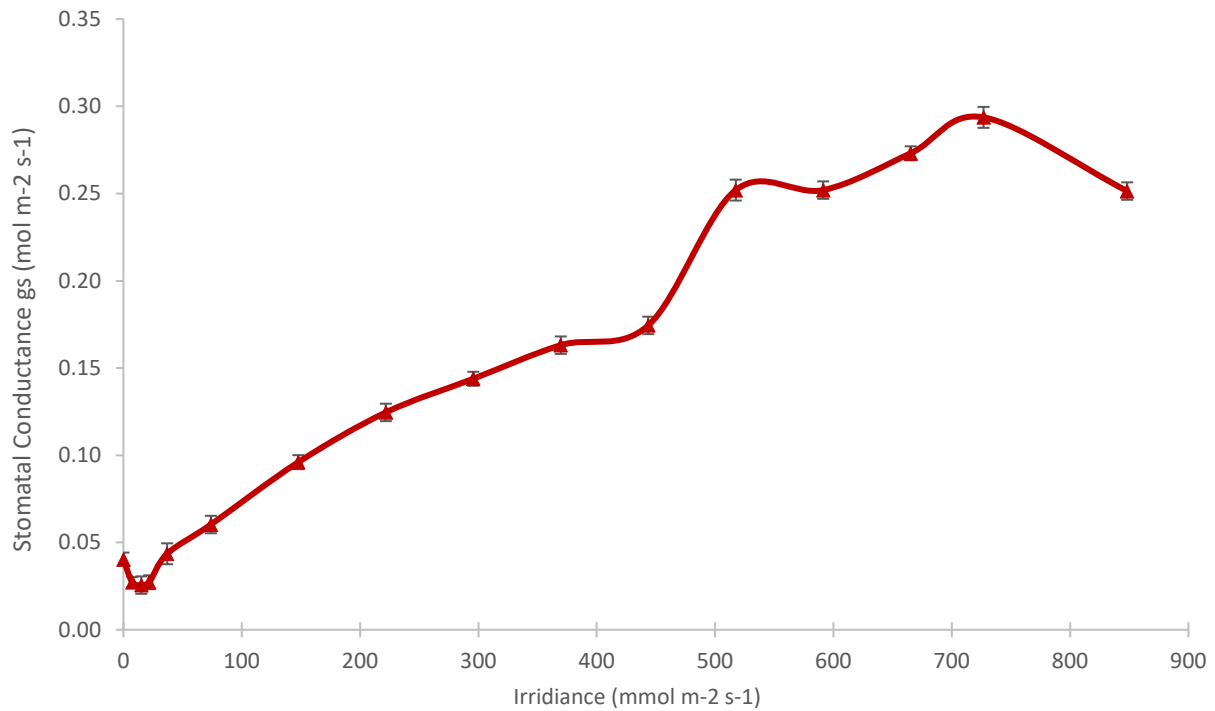


Figure 2. Stomatal conductance of maize leaf in response to changing absorbance. All leaf chamber parameters were kept constant (Ca 380 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air, humidity 5 mmol mol^{-1} air, constant T_{air}), while the incident light intensity was gradually adjusted from 0 to 1000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ PPFD in 15 steps. Each data point is the average (\pm SE) of 7 biological replicate, the p-value: 3.34×10^{-17} .

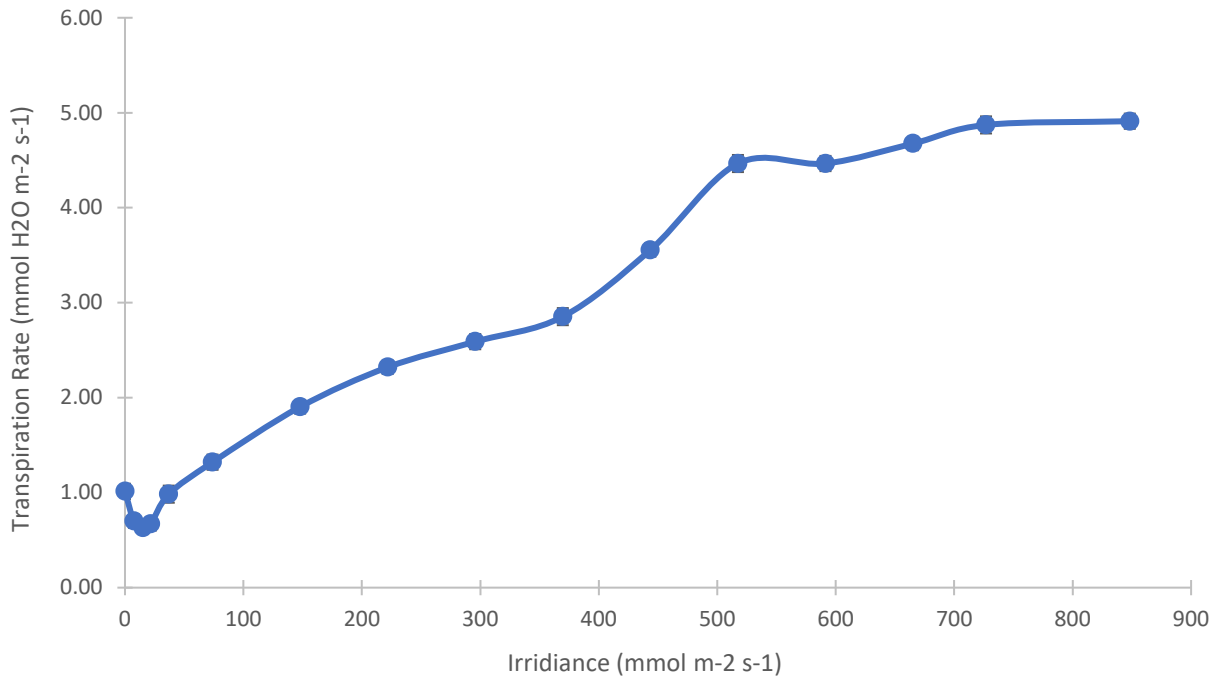


Figure 3. The transpiration rate of maize leaf is in response to changing absorbance. All leaf chamber parameters were kept constant (Ca 380 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ air, humidity 5 mmol mol^{-1} air, constant T_{air}), while the incident light intensity was gradually adjusted from 0 to 1000 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ PPFD in 15 steps. Each data point is the average (\pm SE) of 7 biological replicate, the p-value: 3.34×10^{-5} .

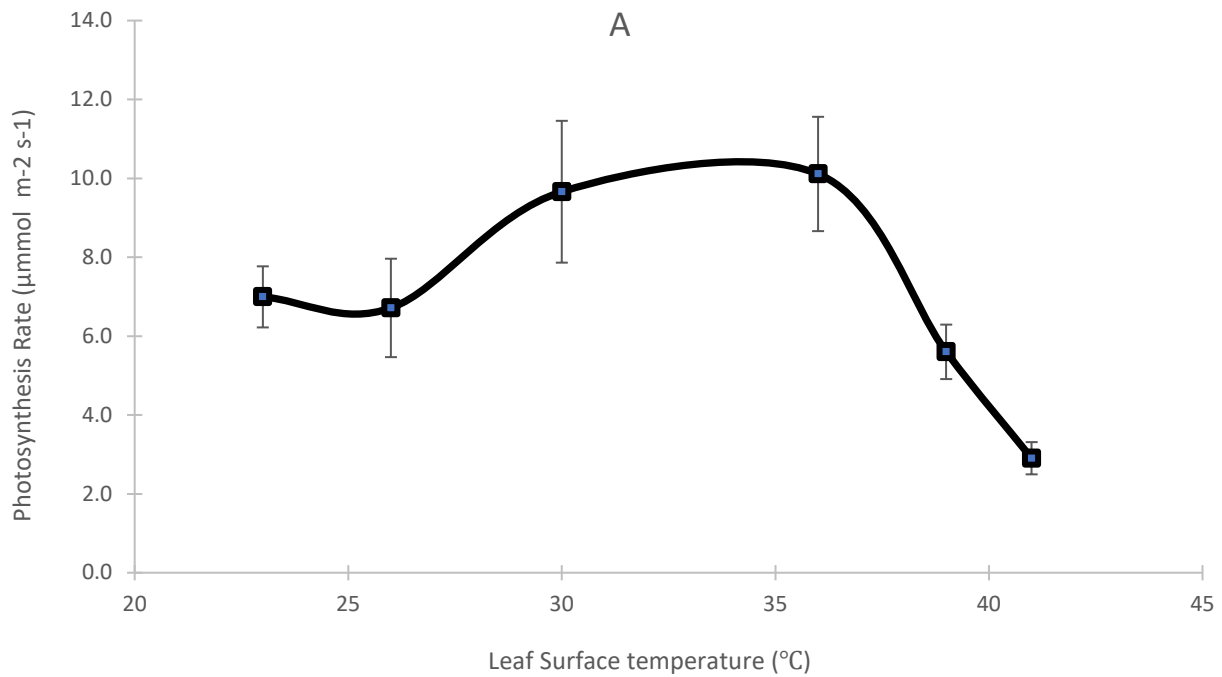


Figure 4. The effect of T_{leaf} on the photosynthesis rate (A) of maize leaves. Each data point is the average (\pm SE) $n=5$ for 23 $^{\circ}\text{C}$ and 25 $^{\circ}\text{C}$, $n=9$ for 30 $^{\circ}\text{C}$, $n=12$ for 36 $^{\circ}\text{C}$, $n=21$ for 39 $^{\circ}\text{C}$, $n=12$ for 41 $^{\circ}\text{C}$ biological replicate, ($p < 0.000018$).

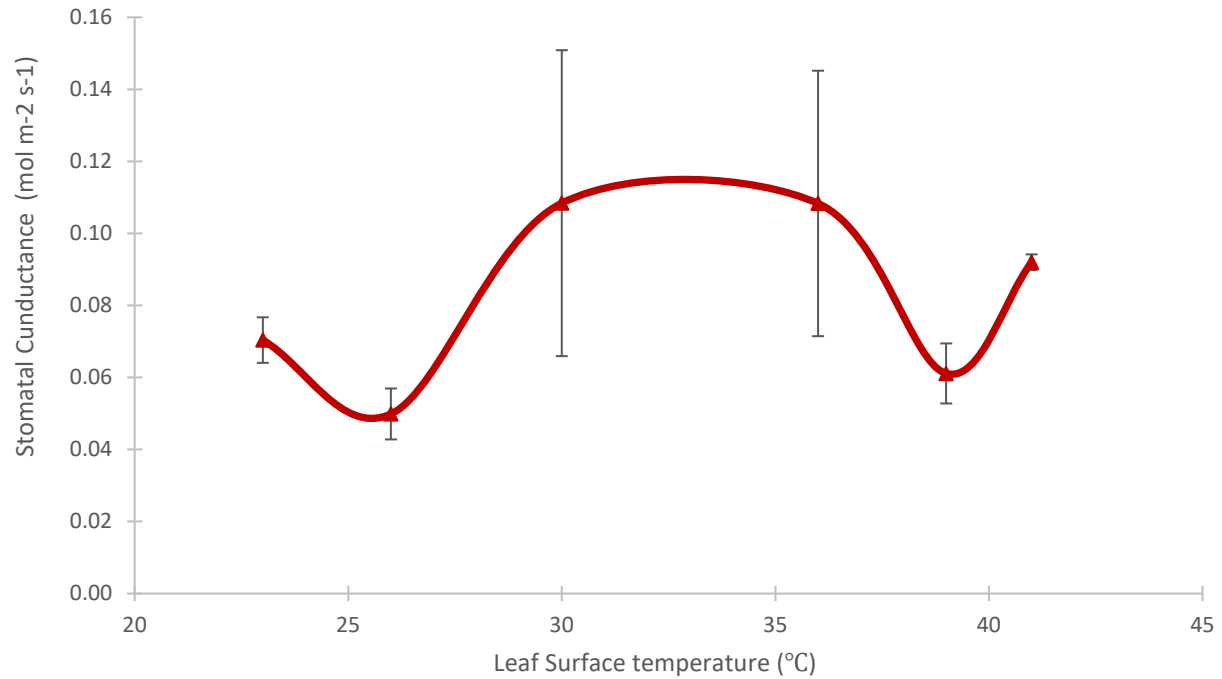


Figure 5. The effect of (T_{leaf}) on stomatal conductance (gs) in maize leaves. Each data point is the average (\pm SE) $n=5$ for 23°C and 25°C, $n=9$ for 30°C, $n=12$ for 36°C, $n=21$ for 39°C, $n=12$ for 41°C biological replicate, ($p=0.330932$).

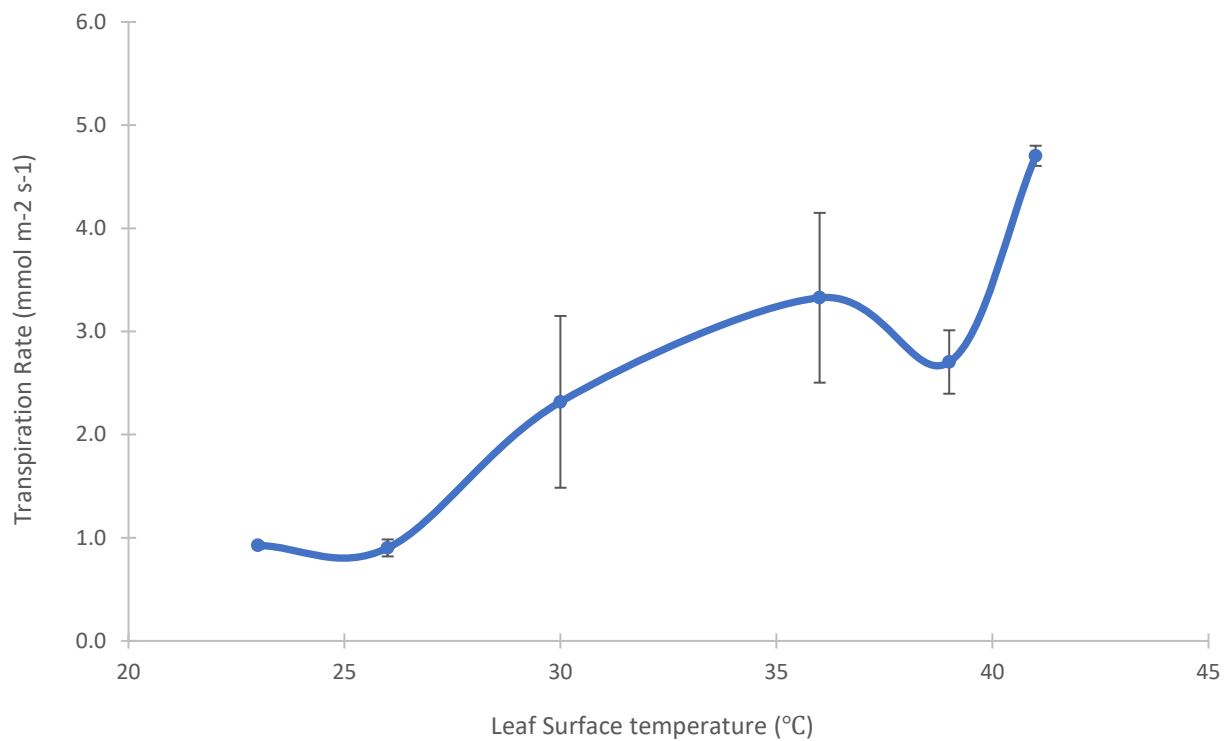


Figure 6. The effect of T_{leaf} on the transpiration rate (E) in maize leaves. Each data point is the average (\pm SE) $n=5$ for 23°C and 25°C, $n=9$ for 30°C, $n=12$ for 36°C, $n=21$ for 39°C, $n=12$ for 41°C biological replicate, ($p<0.000052$).

These findings underscore the critical impact of high leaf temperature on maize physiology, emphasizing the need for breeding programs focused on enhancing heat tolerance in maize cultivars to maintain productivity in arid environments.

DISCUSSION

The negative photosynthesis rate during darkness can be referred to respiration while the photosynthesis process has not started yet. The initial increase indicates a positive correlation between light absorption and photosynthetic activity, as higher light levels provide more energy for the photosynthetic process, enhancing carbon assimilation, which can be partially attributed to the enhanced activity of photosynthetic enzymes, such as Rubisco, which catalyzes CO₂ fixation. Higher irradiance boosts the availability of ATP and NADPH generated from the light-dependent reactions, thus improving the efficiency of the Calvin cycle (Farquhar et al., 1980). The subsequent plateau and decline at higher irradiances suggest photoinhibition, where excessive light harms the photosynthetic machinery, particularly Photosystem II, potentially due to excessive generation of reactive oxygen species (ROS) that damage cellular components (Baker, 2008; Komatsu et al., 2013). Light directly influences stomatal opening by activating photosynthesis in guard cells, which produces ATP and reducing equivalents necessary for ion transport that drives stomatal opening (Azoulay-Shemer et al., 2015), thus enhancing the transpiration rate (Lawson & Blatt, 2014). At high irradiances, stomatal conductance decreases to conserve water and limit excessive transpiration, and this role is possibly mediated by abscisic acid (ABA) signaling under stress conditions (Buckley & Schymanski, 2014). Transpiration is also affected by the plant's hydraulic system, with increased irradiance raising the demand for water transport through the xylem, which may reach its physiological limit of sap translocation (Ocheltree et al., 2014).

The present study confirms a direct effect of leaf temperature (T_{leaf}) on photosynthesis rate (A) and shows that stomata open maximally at moderate heat stress (30°C to 36°C). However, stomata close at temperatures above this range, though not enough to limit CO₂ supply to the chloroplast for photosynthesis. When T_{leaf} reaching 39°C, stomata open again, presumably to increase transpiration and reduce leaf temperature; this novel observation (Figure 6) agrees with the demonstration by Almousa (2017) on barley

(*Hordeum vulgare*). Photosynthetic enzymes like Rubisco have an optimal temperature range, where increasing temperature initially enhances enzyme activity; meanwhile excessive temperature can cause denaturation and reduce enzyme activity (Hüve et al., 2011). High temperatures induce the expression of heat shock proteins (HSPs) that assist in protein folding and protection against thermal damage. However, their capacity may be overwhelmed at very high temperatures, thereby reducing photosynthesis (Lawlor, 2002). Additionally, high temperatures increase the vapor pressure deficit (VPD), driving higher transpiration rates as part of the plant's cooling mechanism through evaporative water loss (Lawson & Blatt, 2014). At very high temperatures, transpiration increases significantly as a stress response to prevent overheating, which can result in excessive water loss and potential hydraulic failure (Hüve et al., 2011).

CONCLUSION

In conclusion, the findings emphasize the complex interplay between light intensity, temperature, and physiological processes in maize. Achieving optimal light and temperature conditions is vital for maximizing photosynthetic efficiency, stomatal conductance, and transpiration rates. Gaining insights into these dynamics is essential for developing strategies to enhance crop resilience and optimize agricultural practices. The interaction between enzymatic activity, heat shock proteins, and plant anatomical features such as stomata and xylem underscore the complexity of plant responses to environmental stressors. This comprehensive understanding is critical for improving maize productivity and sustainability under diverse environmental conditions.

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