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Stomata Responses to Heat Stress

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ABSTRACT: As mean global temperatures rise, more extreme climatic phenomena like droughts and heat waves will occur more frequently. Considering this, our goal is to identify stomatal responses to high temperatures. Here, we estimate some morpho-physiological and biochemical modifications to high temperatures. Both drought and heat stress have a negative impact on carbon and other biomolecules. Plant water use efficiency Stomatal opening rates and steady-state apertures increased in response to rising temperatures. Low deficiencies and physiologically high temperatures (30°C) resulted in the biggest stomatal openings, provided that photon. The flux densities were adequate. Many species have reported decreased stomatal conductance during research with connected leaves preserved inside gas exchange cuvettes as a consequence of rising VPD. It has been persuasively shown that the VPD reaction provides an adaptive advantage. Guard cell responses to humidity were reported to change metabolically later than aperture, Since VPD typically increases with temperature, stomatal responses to temperature are difficult to distinguish from those to humidity. However, well-documented, specific stomatal responses to temperature exist. According to other researchers, Aperture maxima in the light were seen around 35°C, and at higher and lower temperatures, Aperture values decreased. The highest temperature measured, 45°C, had the greatest openings in complete darkness.

A further investigation established a correlation between closure at high temperatures and guard cell chloroplast damage. These findings confirm that guard cell chloroplasts are responsible for stomatal opening in the light, whereas opening in the dark requires oxidative phosphorylation. As a result, the temperature responses in each situation would correspond to the thermal responses of the mitochondria and chloroplasts, respectively. The majority of plants show that stomatal conductance rises with temperature, and those high ambient temperatures hinder stomatal development. Reaches a high of about 20 or 25°C, and at higher temperatures, they could show conductivity reductions. Because of how increasing leaf temperature affects intercellular CO_2 concentration, the imbalance in leaf-to-air vapour pressure, or plant water stress, stomatal conductance may decrease with temperature throughout a wide temperature range. Since many plants won't open their stomata at temperatures that are much lower than those at which they were produced, stomatal closure happens when a plant is transplanted from high to low temperatures. Temperatures above a certain point can impair the photosynthetic process. In conclusion, there are a number of places during stomatal opening where high-temperature signals may be incorporated. Stomatal opening is triggered by phototropin-mediated phosphorylation of BLUS1, which, when isolated guard cells move from the dark to the blue light, activates PM H+-ATPase channels. The protein PATROL1 is required for the insertion of AHA1 into the plasma membrane. When temperatures are high and phototropins (white light) are present, guard cells must have active PM H+-ATPase and redundant 14-3-3 protein activities in order to fully open their stomata. It has been demonstrated that guard cells combine data from temperature and light to control stomatal opening. More research is required to pinpoint the point at which these signals converge.

Keywords: Stomata, Heat Stress, Guard Cells, VPD, Stomatal Opening, Conductance.

INTRODUCTION

The frequency of more extreme climatic events, such as droughts and heat waves, will increase as mean worldwide temperatures rise. As a consequence, agriculture in areas such as the Mediterranean that are experiencing hot, dry summers where vegetation experiences photo-oxidative stress and a high evapotranspiratory demand (Haworth *et al*., 2018). Stomata are located primarily on the abaxial (lower) surface of the leaf laminae (Winkler *et al*., 1974) having 10 000 to 15 000 stomata per square centimetre, ranging in size from 10 to 13 micrograms on average to

5 microns on occasion based on how open they are (Satoh *et al.*, 1977). Plants should have acquired the ability to recognise and react to numerous stress stimuli because they live in constantly changing environments (Jia & Zhang 2008). During heat waves, certain broadleaf evergreen species will paradoxically open their stomata, which cools the leaves and prevents harmful leaf temperatures but also accelerates dehydration and increases the danger of turgor loss. Under hot, dry circumstances, plants actively increase water loss, which accelerates the process towards xylem cavitation thresholds faster than previously understood, Heat stress should be considered a primary factor causing tree death during droughts since it can play a critical role in driving droughted trees closer to mortality limits (Marchin *et al.,* 2022). We find that acute heat stress changes the expression of the transcription factors MUTE and SPCH, phosphorylates MPK3 and MPK6 to high levels, and adversely impacts stomatal differentiation. Reduced stomatal differentiation rates are the result of genetic HSP90 deficiency. Therefore, in both normal and heat-stressed settings, HSP90 chaperones protect the completion of certain stomatal differentiation processes that require these two transcription factors (Samakovli *et al.,* 2020). Weak assimilation rates are additionally a result of high temperatures, which also decrease electron capacity for transport and speed up CO_2 evolution from photorespiration and other sources (Farquhar & Sharkey 1982). Both drought and heat stress adversely affect the carbon and water efficiency of plants (Lauteri *et al*., 2014; Haworth *et al*., 2018), and as such, their combined effects on plant physiology warrant greater attention. Likewise, the amount of water that a plant can absorb from the soil increases with heat stress, after which plant functions decline (Centritto *et al.,* 2011). Here, it is demonstrated that rapid changes in a local leaf's stomatal aperture (opening or shutting) brought on by various environmental stimuli set off a ROS-dependent systemic signal that, in a matter of minutes, modifies the stomatal aperture in several systemic untreated plants.

Plants are therefore able to mount a systemic cell movement response, or guard cell response, which is mediated by a complex balance of hormone signaling, calcium and ROS concentrations, electric signals, and ion channel activation. This response is akin to multiple coral reef sponge cells responding in unison to a local stimulus. This kind of whole-plant systemic stomatal response most likely developed to assist land plants in becoming more fit and adapting quickly to changes in their surroundings, solidifying their position as the primary energy converters supporting life on Earth (Devireddy *et al.,* 2020). Heat increases stomatal sensitivity to drought stress when heat and drought coexist. The decrease in stomatal aperture may cause ZmSHR1's distance of action from longitudinal leaf veins to expand, protecting the plant from heat damage. This may operate to positively regulate ZmSPCHs/ZmICE1 heterodimers and raise stomatal density. Raised CO_2 levels only lessen yield losses in cases of mild drought. Understanding the impending climatic shifts and projecting the physiological and developmental stomatal responses will help to make informed decisions about the management of this crucial crop as well as predict maize output in the following years (Serna, 2022). However, when exposed to high temperatures, a buildup of heat shock proteins can help strengthen the thylakoid membranes (Heckathorn *et al.,* 1998). Reduced specificity of ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO) for CO_2 (i.e., an increase in rates of photorespiration relative to photosynthesis (PN)), lower solubility of CO_2, and reduced activity of RubisCO activase are additional methods by which heat stress can affect photosynthetic CO_2 assimilation (Jordan and Ogren 1984); Crafts-Brandner & Law (2000). Stomates' main function is to facilitate water vapour diffusion and carbon dioxide absorption by leaves, which enable the essential physiological processes of transpiration and photosynthesis. Stomatal conductance to water vapour measured with a porometer can be used to assess photosynthesis since this parameter usually correlates with CO_2 uptake by leaves (Raschke, 1975). The lower photochemistry is associated with reduced RubisCO activity during heat stress (Feller *et al.,* 1998). It would also reduce the capacity of photosystem I to act as an electron receiver for PSII, potentially exacerbating the negative impact of high temperatures on PSII (Killi *et al.,* 2017). Studies on stomatal response to temperature have often yielded contradictory results (Heath and Meidner 1957). Observed stomatal closure with increasing temperature (Hofstra and Hesketh 1969; Drake *et al.,* 1970). I found that as temperatures rose, stomata opened. Furthermore, it has been demonstrated that maximum stomatal opening occurs at moderate temperatures (Hofstra and Hesketh 1969). Heat stress may also adversely affect plant water relations by increasing Gs H_2O (Bunce, 2000). However, longer-term stomatal adaptation to growth at higher temperatures (as opposed to instantaneous increases in leaf temperature) may result in no increase in Gs H2O (Centritto *et al.,* 2011; Kaufmann, 1982). The absolute humidity differential from leaf to air (DAH) was taken into account, and it turns out that temperature is not a significant independent variable impacting conductance in conifers under field conditions. Except when the plants are developing outside of their native environments, he views temperature and water stress as secondary elements that only sometimes affect conductance. Sheriff *et al.* (1979) argue that conflict between the numerous feedback mechanisms involved in stomatal regulation could be the cause of the lack of an overall stomatal response to fluctuations in temperature.

Our objective is to identify the stomatal responses to high temperatures and the morpho-phyiological and biochemical responses of stomata towards high temperatures.

Morpho-phyiological responses to heat stress on stomata. A fundamental issue in stomatal physiology has been the difference between stomatal responses to light and CO_2. While increasing irradiance simultaneously opens stomata and boosts inesophyll photosynthesis, which depletes intercellular CO_2, light and CO_2 both generate noticeable stomatal reactions in

intact leaves (Jarvis and Morison 1981). The obvious evidence of the specific light response of stomata, however, represents one of the most significant recent developments in stomatal physiology. Guard cells respond to light type and intensity both when they are isolated and when the leaf is whole. It is clear that photoreception originates inside guard cells, while light induces guard cell protoplasts to expand (Jewer *et al.,* 1982**;** Zeiger and Hepler 1977). The photoresponses by guard cells within the intact epidermis were intensity-dependent increases in stomatal apertures in epidermal peels exposed to light in COZ-free air (Fischer 1968**;** Travis and Mansfield 1981). Working at Duke University in 1947, C.C. Wilson documented the impact of light, temperature, and stomatal conductance affected by the atmospheric vapour deficit, initially with observations taken in the field and then in the laboratory. The work by Laboratory Wilson is notable for its three-dimensional graph, which is used by Heath & Russell (1954) for the evaluation of the results of lab tests intended to clarify how light and CO_2 interact. Wilson used leaves with empty guard cells. Similar to (Loftfield, 1921). Wilson discovered that rising temperatures led to increased stomatal opening rates and higher steady-state apertures. Wilson's conclusion was supported by future research (Meidner and Heath 1959**;** Stalfelt, 1962; Mansfield & Meyer (1966), despite the caveat that the intercellular concentration should be considered. To prevent a midday closure, both the gradient in water vapour pressure between the leaf and the atmosphere and the concentration of CO_2 must remain constant. Consequently, a theoretical model of a feedback mechanism for stomatal action was developed that included the temperature dependency of stomatal motions (Raschke, 1975). Regarding the lack of atmospheric vapour, Wilson found that for the species used, the largest stomatal openings happened at low deficits and physiologically high temperatures (30°C), provided that photon flux densities were sufficient. Moderate Starting at small atmospheric saturation deficits and temperatures, a plateau of the largest stomata opening was developed at saturating photon flux densities; this plateau was maintained at high saturation deficits with temperature. Many species have reported decreased stomatal conductance during research with connected leaves preserved inside gas exchange cuvettes as a consequence of rising VPD (Jarvis and Morison 1981). It has been persuasively shown that the VPD reaction provides an adaptive advantage (LOsch and Tenhunen 1981). Additionally, epidermal peel stomata exhibit a humidity response that is unrelated to temperature. It is obvious that, in steady-state conditions, metabolic changes in the guard cells must precede initial hydro-passive responses. The evidence that is now available suggests that peristomatic transpiration has a role in the early stages of stomatal responses to humidity. Guard cell responses to humidity were reported to change metabolically later than aperture. The conundrum presented by this apparent reversal of the paradigm explaining the regulation of stomatal motions by regulated ionic changes before water flows and turgor buildup is that it reverses the order of events. In an extreme interpretation of the issue, (Maier-Maercker 1979) hypothesised that guard cell responses are in fact regulated by hydro-passive events mediated by subsidiary (and epidermal) cells and consequent turgor changes in the epidermis. Given the undisputed data that guard cell protoplasts or guard cells from peels where other epidermal cells have been killed exhibit a wide range of reactions similar to those seen in whole leaves, the concept seems unsustainable. Therefore, the issue of how humidity affects the turgor regulation of guard cells and how that regulation is translated into metabolic changes necessary for the creation of steady-state conditions is still open (Maier-Maercker 1979). Since VPD typically increases with temperature, stomatal responses to temperature are difficult to distinguish from those to humidity. However, well-documented, specific stomatal responses to temperature exist (Jarvis and Morison 1981); Meidner & Mansfield 1968). According to other researchers, aperture maxima in the light were seen around 35°C, and at higher and lower temperatures, aperture values decreased. The highest temperature measured, 45°C, had the greatest openings in complete darkness (Stålfelt, 1962). A further investigation established a correlation between closure at high temperatures and guard cell chloroplast damage. These results support the idea that stomatal opening in the light is driven by guard cell chloroplasts, whereas opening in the dark is dependent on oxidative phosphorylation. Thus, the temperature responses under each circumstance would represent, respectively, the thermal reactions of the mitochondria and chloroplasts. It is yet unclear if, in addition to these temperature-dependent metabolic reactions, the guard cells also possess a specialised temperature sensor (Rogers *et al.***,** 1981)**.**

Biochemical responses of stomata to high temperature. In the coming decades, more extreme weather-related phenomena, including heat waves and prolonged droughts, will be predicted by climate models. Instrumental measurements of hemispheric and global temperatures over the past 150 years have shown a noticeable warming trend. One effect caused by global warming has been the observed rise in heat waves. Heat has a variety of effects on plants, including one that affects how stomata form and open (Feller, 2006). High ambient temperatures inhibit stomatal production; most plants exhibit stomatal conductance increases with temperature rises up to around 20 or 25°C, and they may display conductance declines at higher temperatures (Hofstra & Hesketh 1969). Stomatal conductance may decrease with increasing temperature across a wide temperature range (Heath & Orchard (1957) because of the impact of increasing leaf temperature on intercellular CO_2 concentration (Meidner & Heath 1959), leaf-to-air vapour pressure deficit (Wuenscher and Kozlowski 1971), or plant water stress (Schulze *et al.,* 1973). Stomatal closure occurs when a plant is moved from high to low temperatures because many plants will not open their stomata at temperatures that are significantly lower than those at which they were grown (Kozlowski and Pallardy 1979). However, moving plants that are less resistant to cold temperatures from a relatively high

temperature to a chilling temperature above 0°C can cause broad stomatal openings that can last for several hours (Wilson, 1976). The process of photosynthesis is harmed by high temperatures. It has been discovered that Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) activase is heat-sensitive and plays a significant role in photosynthesis. These two factors have an impact on the Calvin cycle's activity: By the heat-sensitive enzyme Rubisco activase, active Rubisco is inactivated more quickly and reactivated more slowly (Feller, 2006). Bean (*Phaseolus vulgaris* L.) leaf segments incubated at temperatures ranging from 20 to 50°C showed varied stomatal openings, according to Feller (1996). Primary leaf segments were incubated at the specified temperature while dangling above water in the dark. The stomatal aperture was 0.66, 2.76, and 4.28 m, respectively, at incubation temperatures of 23, 30, and 35 °C after 30 min. The samples were moved from the greatest temperature to the lowest temperature (23 °C), where it was discovered that this impact was reversible (within 30 min). When 0.1 M ABA was added to the incubation media, the temperature required for stomatal opening increased. This shows that heat, which stimulates stomatal opening, and drought, which stimulates stomatal closure, interact negatively. High temperatures cause stomatal opening; therefore, there must be a compromise between leaf cooling and water use efficiency. This is crucial in cases of extreme weather, such as heat waves and droughts, which are marked by high ambient temperatures. Feller also discovered that shadowing from other plant parts or clouds can cause a portion of a leaf's lighting to alter suddenly. They discovered a difference of 10°C between bean leaves that were permanently in the shade and those that were permanently exposed to the light while simulating this circumstance. After changing the lighting, moving the leaves from the sun to the shadow (and vice versa) caused a rapid shift in temperature during the following minute. Air convection and transpiration assist in cooling the previously lit leaf on the one hand, while the energy from sunlight absorption causes the temperature within a previously shaded leaf to rise rapidly on the other. They came to the conclusion that stomata opening was a critical heat response that effectively cooled the leaf through evaporation, protecting the photosynthetic system (Feller, 2006; Kostaki *et al.* 2020). In guard cell migration brought on by high temperatures, elements related to blue light-mediated stomatal opening were required. These findings imply that routes for temperature and light signalling may interact. First, they used epidermal peel bioassays to examine stomatal reactions to high temperatures without accounting for changes in humidity. *Hordeum vulgare* L., *Commelina communis,* and Arabidopsis sp. epidermal peels all demonstrated greater stomatal opening at higher temperatures. Guard cells possess the molecular machinery required for sensing temperature changes, as demonstrated in this experiment by the epidermis' inability to receive signals from the mesophyll layer. Second, using cngc, arp6, pif4, and ft null mutants, stomatal bioassays were used to examine the participation of known high temperature signaling components. All of these mutant plants' wild-type plants possessed stomatal openings at 35 °C. When the ft mutants were kept in white light, their stomatal apertures resembled those of the wild-type plant, in contrast to the reduced stomatal opening when moved from the dark to red and blue light. These findings prompted research into the function of phototropins and BLUS1 (blue light signalling 1), a downstream target of phototropins, in high temperature-mediated stomatal opening. They discovered that phototropins had a significant role in the temperature-induced opening of the stomata. The phot 1/2 mutants have the most severely impaired stomatal aperture. According to their findings, guard cell movement can still happen in response to a temperature of 35 °C without the need for phototropin, but phototropin activation is necessary to cause full stomatal opening. Furthermore, at 35°C, blus1-3 mutants showed considerably smaller stomatal openings than wild-type plants, indicating involvement in this response. In the dark, some stomatal opening brought on by the high temperature was seen. There may be another phototropin-independent route, which would explain these results. Devireddy, Arbogast, and Mittler proposed that this reaction could be mediated by RBOHD-driven (respiratory burst oxidase protein D) ROS generation. They discovered that even in systemically untreated leaves, rapid changes in stomatal opening and closure brought about by various environmental stimuli caused a ROS-dependent systemic signal that changed the stomatal aperture within minutes (Devireddy *et al.,* 2020). Thirdly, the role of H^+-ATPase channels in the temperature-regulated stomatal response was observed. Kostaki et al. found genetic evidence suggesting that AHA1 and AHA2, isoforms of the *Arabidopsis* plasma membrane H^+-ATPase family, were required for full stomatal opening as a response to high temperature in epidermal peels (Hashimoto *et al.*, 2013). The protein PATROL1 (proton ATPase translocation control 1), which is necessary for stomatal opening in response to high temperature, low CO_2 concentration, and blue light, mediates the recruitment of AHA1 to the plasma membrane in guard cells. Investigated was the potential function of 14-3-3 proteins in AHA regulation. The plasma membrane's auto-inhibitory C-terminal region of the H+-ATPase binds to 14-3-3 proteins in reaction to blue light, promoting pumping. With potential antagonistic interactions across isoforms, the genetic study of 14-3-3 mutants has demonstrated that they contribute to high-temperature-mediated stomatal opening. In conclusion, there are a variety of locations where high-temperature signals may be integrated during stomatal opening. Stomatal opening is caused by phototropin-mediated phosphorylation of BLUS1, which in turn activates PM H+-ATPase channels when isolated guard cells migrate from the dark to the blue light. AHA1 must be inserted into the plasma membrane by the protein PATROL1. PM H+-ATPase activity and redundant 14-3-3 protein functions are necessary for guard cells to fully open their stomata at high temperatures and under the influence of phototropins (white light). Guard cells have been shown to integrate information from temperature and light to

regulate stomatal opening. To determine the point at which these signals merge, more study is necessary (Kostaki *et al.,* 2020).

CONCLUSION AND FUTURE SCOPE

To sum up, stomata's reactions to heat stress are intricate and varied, involving both maladaptive and adaptive processes across a range of plant species. Although stomatal closure is frequently seen as a defensive mechanism to stop excessive water loss in hot weather, new studies have shown fascinating differences in stomatal behaviour, including a surprising tendency for some species to open their stomata. The complex interactions between the physiological, biochemical, and molecular mechanisms controlling stomatal regulation in the face of heat stress are highlighted by these disparate reactions. Prospective paths for clarifying the fundamental processes governing stomatal responses to heat stress remain for future study. The development of high-throughput omics technologies, including proteomics, metabolomics, and transcriptomics, presents previously untapped potential to decipher the complex gene regulatory cascades and signalling networks governing stomatal dynamics in heat-stressed environments. Furthermore, integrative methods that combine computer modelling and physiological data might offer insightful information on the emerging characteristics of stomatal behaviour and its ecological consequences in a changing climate. Moreover, there is tremendous potential for improving crop resistance to heat stress through the practical application of basic discoveries. Breeding initiatives and focused genetic engineering projects that harness genetic variability can facilitate the creation of crop varieties that are heat-tolerant and have optimal stomatal responses. Furthermore, by identifying the crucial molecular targets and signalling elements involved in heat stress adaptation, new biotechnological interventions, like synthetic biology and precision genome editing, may be developed with the goal of engineering heat-resilient stomatal traits in commercially significant crops.

To sum up, deciphering the complex reactions of stomata to heat stress advances our knowledge of how plants adapt to changing climatic conditions and presents exciting opportunities for enhancing agricultural sustainability in the context of climate change. Through the application of innovative technology and multidisciplinary methodologies, scientists can uncover novel perspectives on stomatal biology, therefore facilitating the creation of robust crop varieties that can flourish in an increasingly hotter global environment.

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Conflict of Interest. None.

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