

Plant heat stress: concepts directing future research

S.V. Krishna Jagadish^{1#}, Danielle A. Way^{2,3,4#,*} and Thomas D. Sharkey^{5,6}

¹Department of Agronomy, Kansas State University, Manhattan, KS, 66506 USA

²Department of Biology, University of Western Ontario, London, Ontario, N6A 5B7 Canada

³Nicholas School of the Environment, Duke University, Durham, NC, 27710 USA

⁴Terrestrial Ecosystem Science & Technology Group, Environmental & Climate Sciences

Department, Brookhaven National Laboratory, NY, 11973 USA

⁵ Department of Biochemistry and Molecular Biology, Michigan State University, East Lansing, MI, 48824 USA

⁶ Department of Energy Plant Research Laboratory, Michigan State University, East Lansing, MI, 48824 USA

[#]Authors contributed equally

*Corresponding author: dway4@uwo.ca

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Abstract

Predicted increases in future global temperatures require us to better understand the dimensions of heat stress experienced by plants. Here we highlight four key areas for improving our approach towards understanding plant heat stress responses. First, although the term “heat stress” is broadly used, that term encompasses heat shock, heat wave, and warming experiments, which vary in the duration and magnitude of temperature increase imposed. A greater integration of results and tools across these approaches is needed to better understand how heat stress associated with global warming will affect plants. Secondly, there is a growing need to associate plant responses to tissue temperatures. We review how plant energy budgets determine tissue temperature and discuss the implications of using leaf versus air temperature for heat stress studies. Third, we need to better understand how heat stress affects reproduction, particularly understudied stages such as floral meristem initiation and development. Fourth, we emphasize the need to integrate heat-stress recovery into breeding programs to complement recent progress in improving plant heat-stress tolerance. Taken together, we provide insights into key research gaps in plant heat stress and provide suggestions on addressing these gaps to enhance heat stress resilience in plants.

Key words – Floral meristem, Heat shock, Heat tolerance, Heat wave, Stress recovery, Tissue temperature, Warming scenarios

Introduction

Interest in plant heat stress tolerance has never been greater, driven largely by concerns of how managed and natural ecosystems will be affected by climate change. Increasing amounts of greenhouse gases result in increased energy in the atmosphere, a phenomenon termed “radiative forcing”. As a result, global mean annual temperatures are predicted to increase by 0.3-4.8 °C by 2100 (IPCC, 2014), and many areas are likely to warm above the global average. Thus, growing season temperatures, and the variability around the mean, will increase, which will alter the phenology, physiological performance, and productivity of plants (Dusenge, Duarte, & Way, 2019). Additionally, climate change is expected to lead to more frequent and severe heat waves (Hao, AghaKouchak, & Phillips, 2013), thus reducing plant survival, growth and yield (Teskey et al., 2015; Ortiz-Bobea et al., 2019).

Heat stress episodes have a wide range of effects on plant physiology and overall productivity, since they occur (or are imposed) at different temporal scales and with various levels of intensity and duration (Teskey et al., 2015; Ishimaru et al., 2016). This led to a degree of differentiation within the heat stress community, with some researchers focusing more on short-term, extreme heat shock-type experiments (often using molecular and biochemical techniques), and others concentrating more on ecological responses to longer-term warming (often focusing on physiological techniques and productivity). However, these studies all address the question of how heat stress affects plants, and an improved degree of cross-talk between these approaches is necessary if we are to fully understand how climate change will alter vegetation.

The diverse range of approaches used to investigate plant heat stress is also reflected in the diversity of ways in which heat stress is imposed on a plant. Different facilities, including

leaf chambers (Schrader, Wise, Wacholtz, Ort, & Sharkey, 2004), plant chambers and glasshouses (Jagadish et al., 2010; Dusenge, Madhavji & Way, 2020), field-based tents (Bergkamp, Impa, Asebedo, Fritz, & Jagadish, 2018), radiant heaters (Ruiz-Vera et al., 2013; Ruiz-Vera, Siebers, Drag, Ort & Bernacchi, 2015) and naturally hot summer months (Sathishraj et al., 2015) are used to quantify genetic diversity in heat tolerance, and understand physiological and molecular responses to heat stress. Although these approaches provide critical opportunities to advance heat stress research, they each address limited aspects of the heat stress response in plants (Aronson and McNulty, 2009), by altering the immediate micro-climate surrounding crops (Julia and Dingkuhn, 2013), leaves at different positions within tree canopies (Curtis, Knight, & Leigh, 2019), and even tissues within a single rice panicle (Fu et al., 2016), at different developmental stages (Shi et al., 2015). Aligning measured plant responses to changes in the micro-climate and the temperature experienced by plants will provide more reliable insights into how heat stress affects plants and help us develop strategies that can encompass heat tolerance and recovery.

Heat stress can affect plants at any point during their development, yet some stages of growth are more sensitive to heat than others. Heat stress induces strong negative impacts during the thermally-sensitive developmental periods of early establishment and of flowering and gametogenesis (Wahid, Gelani, Asiraf, & Foolad, 2007; Jagadish 2020), particularly in crops. Progress aimed towards quantifying the impact of heat stress based on plant tissue temperature would allow for improvements in addressing heat stress damage during stages such as flowering or grain-filling, or the impact on the photosynthetic machinery. The common aspect across these stages is our ability to directly relate the tissue temperature to the impact of the heat stress. However, stages such as gametogenesis and floral meristem growth, although highly sensitive to

heat stress, present an additional challenge for quantifying heat stress impacts due to their physical location within the leaf sheath (Quinones et al., 2017). This is reflected in our poor understanding of the impact of heat stress on gametogenesis and floral meristem development, despite the importance of these processes for food security in a changing climate.

Although studies involving other stresses, such as drought, have realized the importance of post-stress recovery rate as a part of an integrated strategy to develop drought-tolerant crops, heat stress studies have been less inclusive in integrating tolerance and recovery (Janni et al., 2020). Examples of differential rates of recovery and the existence of genetic diversity at the physiological (Zhang et al., 2018) and molecular levels (Liu and Bennett, 2011) in plants recovering from drought stress provide a compelling rationale for exploring and integrating recovery as a part of an integrated strategy for developing heat stress-resilient plants.

The molecular and physiological effects of heat stress on plants has been reviewed extensively in recent years (Wahid et al., 2007; Hassanuzzamann et al., 2013; Bitá & Gerats, 2013; Xu, Henry, & Sreenivasulu, 2020), and will thus not be covered here. In addition, although heat stress is often accompanied by other stresses, especially drought, the focus of this review is on heat stress experienced by plants. Therefore, taking the above knowledge gaps into consideration, this review is intended to: (i) discuss the similarities and differences between heat stress studies that vary in the duration and intensity of temperatures imposed during heat stress, i.e. heat shocks, heat waves and long-term warming scenarios; (ii) review the components that determine plant tissue temperature and emphasize the importance of framing results using tissue temperature versus ambient air temperatures; (iii) highlight the need to better address heat stress impacts on less accessible developmental stages and tissues; and (iv) emphasize the need to approach heat stress improvement in crops by integrating both higher heat tolerance and rapid

post-stress recovery. Finally, based on our current understanding, we provide suggestions for future research efforts in addressing these gaps and to develop plants that can better tolerate future warming scenarios.

Approaches, similarities and differences in heat stress responses

The study of “heat stress” in plant abiotic stress biology has a long history (MacBryde, Alderfer, & Gates, 1971; Blum 1986) and it is defined differently across studies (Fig. 1) (Wahid et al., 2007; Geange et al., 2021). The basis of these definitions varies with the temporal scale and the magnitude of temperature shift imposed on the plant (Yeh, Kaplinsky, Hu, & Charng, 2012). The stress imposed by heat on plant tissues is related to both the duration of the heat stress and the degree to which the temperature is increased during the stress, such that both longer exposure times and higher temperatures are more damaging (Colombo & Timmer, 1992; Table 1). As such, there is generally a negative relationship between how long a heat stress treatment lasts and the intensity of the heat stress conditions used in experiments (Nuttall et al., 2018).

In many molecular studies, heat stress is synonymous with “heat shock”, the short-term exposure of a plant to severe high temperature, where the stress lasts for minutes to a few hours and the air temperature increase is often 20 °C or more than the optimal temperature identified for the plant’s growth or development (Fig. 1; Mittler, Finka, & Goloubinoff, 2012). These short duration heat shock treatments (hours or shorter) are the most common form of heat stress studies on both cultivated and wild species (Geange et al., 2021). This form of heat stress induces the heat shock response, including the rapid synthesis of heat shock proteins (HSPs), molecular chaperones that help protect the cell from heat damage by stabilizing and helping refold heat-inactivated proteins (Vierling, 1991; Yadav et al., 2020). While these studies are

generally not ecologically realistic, they have allowed us to develop critical insights into the mechanisms that underlie plant sensing and tolerance of acute high temperatures (Bokszczanin, SPOT-ITN Consortium & Fragkostefanakis, 2013).

At a longer temporal scale are “heat wave” studies, which expose plants to high temperatures for hours to days, often (but not always), repeating the heat stress episode after a recovery period of days to weeks (Fig. 1; Teskey et al., 2015; Drake et al., 2018). These types of experiments are important, given that extreme events are likely to have stronger impacts on biological systems than will changes in average climate (Easterling et al., 2000; Jentsch, Kreyling & Beierkuhnlein, 2007). In heat wave experiments, the increase in air temperature is likely to be 5-10 °C above the optimum growth conditions, to mimic naturally occurring heat waves (De Boeck, Dreesen, Janssens, & Nija, 2010). However, while heat waves in the field are generally correlated with dry, sunny conditions and high evaporative demand, thus imposing some degree of drought in addition to the heat stress (De Boeck et al., 2010), heat wave experiments do not necessarily mimic these irradiance and moisture conditions (Impa et al., 2021). A similar approach is taken in many crop studies that impose a targeted one-time exposure of heat stress (ranging between a 5 and 10 °C rise in air temperature) for one or more weeks during key developmental stages such as flowering (Prasad, Bheemanahalli, & Jagadish, 2017; Chiluwal et al., 2020) and grain filling (Yang, Gu, Ding, Lu, & Lu, 2018; Impa et al., 2020; Schittenhelm, Langkamp-Wedde, Kraft, Kottamann, & Matschiner, 2020).

Lastly, climate warming experiments involve exposing plants to elevated growth temperatures for weeks to years, sometimes growing them from seed to seed under high temperatures, but usually only increase the air temperature by 2- 6 °C (Fig. 1) (Kroner and Way, 2016; Reich et al., 2018; Dusenge et al., 2020). These experiments are largely geared towards

understanding how plants will cope with the increased growing temperatures induced by climate change, and many of these studies focus on the growth, health and ecophysiology of plants. Indeed, a recent review of thermal stress studies (both for heat and cold stress) found that the most common metric of thermal damage in studies exposing plants to weeks or more of a temperature stress was the quantification of visual damage (Geange et al., 2021). Unfortunately, there has been less emphasis on assessing the molecular and metabolomic responses to long-term warming that could provide direct links with the short-term heat shock literature, though this has begun to change in recent years (Glaubitz et al., 2017; Davies, Ecroyd, Robinson, & French, 2018; Wang et al., 2020).

Despite the differences in how researchers use these different approaches to tackle the question of plant heat stress, the mechanisms of how plants cope with heat stress across different studies can show considerable overlap. A key feature in heat stress studies, irrespective of the approach followed, is enhanced thermotolerance in plants exposed to heat stress (see Table 1). It has long been known that exposing plants to a non-lethal high temperature exposure, which is termed “priming”, induces acquired thermotolerance, increasing the plants’ performance and survival under a subsequent heat shock episode (Lin, Roberts, & Key, 1984; Vierling, 1991; Charng et al., 2007; Wang et al., 2012; Lin et al., 2014; Yonghui et. al., 2018). But this phenomenon is not limited to short-term heat shock events. Indeed, both simulated heat waves and long-term climate warming studies have found that plants exposed to warmer temperatures have higher thermotolerance to a subsequent heat stress event (Shi et al., 2015; Srikanthbabu et al., 2002). This acquired thermotolerance is most often evident when examining metrics such as electrolyte leakage (an indicator of membrane damage) (Way & Sage, 2008; Chi, Fung, Liu, Hsu, & Charng, 2009), the heat tolerance of the maximum photochemical efficiency of

photosystem II (F_v/F_m) (Table 1), and either seed or seedling viability (Chen, Burke, Xin, Xu, & Velten, 2006; Perez et al., 2009).

Heat stress often also leads to the production of reactive oxygen species (ROS) in plant tissues (Huang, Ullah, Zhou, Yi, & Zhao, 2019; Suzuki & Katano, 2018). It is thought that ROS, such as hydrogen peroxide (H_2O_2), can play an important signaling role in response to stress (Mittler, 2017), but control of ROS levels can become critical for ensuring proper signaling and minimizing damage from heat stress. Recent studies show that increased air temperatures, delivered both as a +15 °C acute heat shock and a one-week +5 °C warming treatment, led to an accumulation of H_2O_2 , but also increased concentrations of ROS-scavenging enzymes, including superoxide dismutase, catalase and peroxidase, in *Arabidopsis* leaves (Wang et al., 2020). While the ROS-scavenging response was stronger in the heat-shocked leaves than in the warm-acclimated plants, the up-regulation of these similar enzymatic defenses against ROS damage indicate that both severe heat shock and longer-term moderate warming can induce similar physiological responses in plants (Wang et al., 2020). Similarly, while most research on plant HSP responses to heat stress come from heat shock experiments, plants exposed to simulated heat waves also had increased amounts of HSP70 and HSP17.6 protein (Davies et al., 2018). Taken together, these results imply that the variation in response of plants to different forms of heat stress may operate in a similar direction but at different magnitudes based on the duration and intensity of the stress imposed.

Despite the similarities in plant responses to heat stress discussed above, there are also key differences between how these three types of heat stress affect plants. In one of the few studies to directly address this phenomenon, Bauweraerts et al. (2014) exposed oak and pine seedlings to either a constant +3 °C climate warming treatment or to repeated +6 °C or +12 °C

heat waves, thus maintaining a similar average air temperature increase of 3 °C in all three treatments. The heat waves generated more severe negative effects on the plants than did the +3 °C climate warming, with the +6 °C heat wave producing less negative effects than did the more extreme but less frequent +12 °C heat waves, including a greater decrease in biomass and more extreme changes in stem allometry (Bauweraerts et al., 2014). Similarly, one week of a +5 °C day/night air warming treatment induced very different gene transcriptional, metabolic, and physiological response than did a six-hour long +15 °C heat shock in *Arabidopsis* (Wang et al., 2020). The *Arabidopsis* plants acclimated to the 5 °C warming regime had lower concentrations of H₂O₂ and lower antioxidative enzyme activity than the heat-shocked plants, though the warming treatment had a greater negative effect on leaf gas exchange than did the heat shock (Wang et al., 2020). When maize was grown at three different day/night air temperature combinations (with the same daily mean temperatures of 30 and 35 °C), plants grown under the narrower diurnal temperature amplitude treatments (and thus the highest night temperatures of 29 and 34 °C) had the lowest vegetative growth and the highest night respiration rates (Sunoj, Shroyer, Jagadish, & Prasad, 2016). While some plant responses to heat shock, heat waves, and longer-term warming may differ only by the degree to which the response is expressed during heat stress, for other biochemical and physiological responses, exposure to higher temperatures, even if over a shorter duration, appears to often induce a stronger response than does long-term moderate warming.

The similarities between many plant responses to heat stress across different stress durations and intensities points to the opportunity to better integrate the knowledge derived from heat shock experiments into climate warming studies. This includes embracing more “omics”-based techniques and other molecular tools into ecologically focused warming studies. Similarly,

exploring how well mutants and heat-tolerant lines that have been identified with short-term acute heat stresses perform under more realistic climate change scenarios would provide critical information on our ability to translate results from heat shock studies into developing climate-resilient crops and trees. However, we know relatively little about how well the results we have on heat stress tolerance in plants (which is largely derived from studies on temperate, cultivated species), applies to non-cultivated or tropical species (Geange et al., 2021). Improving our understanding of the fundamental ways in which different forms of heat stress affect a broad suite of plants, including those from natural ecosystems and regions that are already experiencing extreme heat events, will be necessary if we are to predict the effects of increasing heat stress on a global scale.

The importance of interpreting results based on tissue temperature

Irrespective of the objectives that determine the type of heat stress (either heat shock, heat wave or warming conditions) investigated, it is useful to capture temperatures experienced by the plant tissue in order to draw robust conclusions on stress-induced responses and impact. Knowing the temperature experienced by specific tissues is important for comparing findings across studies. Across the vast majority of heat stress-related studies, a predetermined level of stress is imposed, often at a target developmental stage or growth phase, to determine the physiological and molecular responses to elevated temperatures (Prasad et al., 2017; Way & Oren, 2010). In most cases, the temperatures recorded and presented, and the results interpreted are based on the imposed temperature in controlled chamber, glasshouse and field environments or the naturally-occurring hot air temperature in other field-based studies (Reich et al. 2018, Dusenke et al. 2020; Bahuguna et al., 2015; Sarwar et al., 2019). However, there are often large differences between

the ambient air temperature and the tissue temperature that the plant actually experiences (Singsaas et al., 1999; Schymanski, Or, & Zwieniecki, 2013; Shi, Ishimaru, Gannaban, Oane, Jagadish, 2015; Westreenen et al., 2020). Under sunny conditions, the canopy air temperature (60 cm below the top of the canopy) in a greenhouse with rose cuttings was 5 °C lower than the ambient air temperature at noon, while on a cloudy day it was at most 2 °C lower (Westreenen et al., 2020), while leaves at the top of an oak tree were up to 15 °C warmer than air temperature (Singsaas et al., 1999). Similarly, rice spikelet tissue temperature measured using thermocouples revealed a 0.4, 1.3 and 1.8 °C lower temperature compared to ambient air temperatures of 30, 35 and 38 °C, respectively (Jagadish et al., 2007).

Under field conditions, the ability to capture tissue temperatures has been achieved by using infra-red (IR) heating system (3-m diameter plots), wherein IR thermometers sense canopy temperature and increase tissue temperature ranging between +1.2 °C and +3 °C, compared to ambient temperature (Kimball et al., 2007). The system has been successfully used to impose stress on field grown plants, including wheat (Fang, Su, Liu, Tan & Ren, 2013 [+2 °C above ambient, leading to an 8.2% reduction in yield]) and *Zea mays* at ambient or elevated CO₂ (Ruiz-Vera et al. 2015). Rehmani et al. (2011) tested the application of the same system and imposed +1.3 °C/+2.7 °C (day/night temperature) on rice paddies during post-flowering. In order to simulate higher warming scenarios, Rehmani et al. doubled the number of IR heaters to achieve +2.7 °C/+5.7 °C (day/night) temperatures, thereby demonstrating the potential of the IR system to increase canopy temperature range to meet IPCC predictions for the 21st century. The same system, on a slightly expanded area (4-m diameter) was effectively used to increase vegetation temperatures in a tropical experimental forest in Puerto Rico (Kimball et al., 2018 [+4 °C above ambient]) and to warm the canopy and visible bare soil in an Arctic meadow of northern Norway

(Moni et al., 2019 [+3 °C]). Despite the success achieved in precise stress imposition, extremely high levels of energy demand and the limited plot size that the IR system can accommodate are major roadblocks for wider adoption and use across other disciplines such as crop breeding. Other approaches, such as a hot-blast warming facility operated on a 25 m² area, increased canopy temperature in rice paddies by 1-2 °C, and led to 4-23% and 31-62% lower grain yield across two different years (Zhang et al., 2020). Though the hot-blast facility does address the cost and space limitations raised by IR systems, the high level of interannual variability observed in yield on the same genotypes at this lower end of warming indicates the potential need for further optimization of the system.

Not only do air and tissue temperatures differ, but air and plant tissue temperatures can be highly variable over short timespans (Singsaas et al., 1999). Similarly, plant tissue temperatures and the soil temperatures surrounding the plant can also vary significantly (Fig. 2A). This variability in temperature has been addressed by reporting time-averaged values, but plants experience variable temperatures that sometimes include excursions to very high temperature that are not captured by averaged values. Given the difference between air and plant tissue temperatures, we recommend that measurements of the thermal environment in heat stress studies should include information on 1) the extent of diurnal and nocturnal variability and 2) the minimum and maximum temperature experienced by plants, since temperature averaged over even a few minutes may fail to provide important information about the heat stress variability experienced by plants.

Tissue temperature is determined by variables including soil water status, the radiation load, wind speeds, leaf morphology, the level of heat stress, and the vapor pressure deficit (Julia and Dingkuhn, 2013; Lambers and Oliveira, 2019). The three main factors that determine plant

tissue temperature are the radiative environment (R), convection (C) and latent heat loss (L) (Leuning 1989; Lambers and Oliveira, 2019). While these physical principles hold for all plant tissues, we will focus on leaves for the discussion below, and will also ignore the role of conduction and metabolic heat generation, though these can be important for certain species in some conditions (Seymour, 2010).

For radiation:

$$R = SR_{in} + LR_{in} - LR_{out} \quad (\text{Equation 1})$$

where SR_{in} is short-wave radiation ($< 3 \mu\text{m}$ wavelength) absorbed by the leaf, and LR_{in} and LR_{out} represent long-wave radiation ($> 3 \mu\text{m}$ wavelength) absorbed and emitted by the leaf, respectively. The absorption of short-wave radiation is largely determined by the intensity of solar radiation (or artificial irradiance, in controlled environments), along with leaf properties such as leaf color and leaf angle, which can modify how much short-wave radiation is absorbed (Ehleringer and Björkman, 1978; King, 1997; Falster and Westoby, 2003). Long-wave radiation exchange is primarily determined by the temperature of the leaf and its surroundings. The longwave radiation is modeled as blackbody or thermal radiation, where only leaf temperature and the temperature of the surroundings are important. Because the sun is very hot, its thermal radiation is almost exclusively at wavelengths shorter than $3 \mu\text{m}$, while leaves and their surroundings will emit at wavelengths greater than $3 \mu\text{m}$ (Fig. 3). There is very little overlap between thermal radiation in sunlight and thermal radiation of plants and their surroundings.

For convection:

$$C = \frac{-2K_{air}(T_{leaf}-T_{air})}{B}, \quad (\text{Equation 2})$$

where K_{air} is the thermal conductivity of air, T_{leaf} and T_{air} are the leaf and air temperature, respectively, and B is the boundary thickness of the leaf. Thus, anything that alters boundary layer thickness will alter convective energy exchange. Since

$$B = 4\sqrt{d/u}, \quad (\text{Equation 3})$$

where d is leaf width in the direction of the wind, and u is wind speed, leaf morphology plays a key role in determining leaf temperature. Broad leaves can be more easily decoupled from air temperature than thin leaves, and leaf temperatures of a large, wide leaf can thus be far above or below air temperature (Vogel, 1970; Vogel, 2009). Wider leaves, therefore, can experience much higher heat stress levels under similar conditions of high irradiance and moderate wind speeds than narrow leaves (Leigh, Sevanto, Close, & Nicotra, 2017), with consequent effects on their relative physiological performances (Okajima, Taneda, Noguchi, & Terashima, 2012). In Okajima et al. (2012), reporting only the ambient environmental conditions would imply that both wide and thin leaves experienced the same degree of heat stress, when instead the difference in leaf temperatures between the two leaf morphologies (when both modeled at a similar air temperature) led to a 6-fold difference in photosynthetic rate.

The final component of leaf energy balance is latent heat exchange, which is dictated by transpiration and evaporative cooling. While latent heat exchange can warm a leaf via condensation (Leuning 1989), this effect is very unlikely to play a role in heat stress and will not be discussed here. Latent heat exchange is given by:

$$L = \lambda E = \lambda g_w (D_{leaf} - D_{air}) \quad \text{(Equation 4)}$$

where λ is the latent heat of vaporization for water, E is the transpiration rate, g_w is the conductance for water, and $(D_{leaf} - D_{air})$ is the difference in water vapor pressure between the leaf and air.

Given the high λ of water, transpiration is extremely effective at lowering leaf temperature. Plants with ample water and traits that permit high stomatal conductance (such as a high stomatal index or large stomata) can thus reduce their leaf temperature below air temperature, and do so more strongly than species with lower stomatal conductance under the same measurement conditions (Lin, Chen, Zhang, Fu, & Fan, 2017). Indeed, under an extreme heatwave treatment of four days at 43-44 °C air temperatures, *Eucalyptus parramattensis* maintained sufficiently high transpiration rates to keep most leaves just below air temperature (though some leaves reached 48-50 °C) (Drake et al., 2018). The high latent heat loss of leaves during the heat wave helped maintain leaves below severely damaging temperatures, as defined by a 50% loss of the maximum photochemical efficiency of photosystem II, despite a near complete heat stress-induced suppression of photosynthesis (Drake et al., 2018). Similarly, rice panicle temperatures varied between 9.5 °C cooler and 2 °C warmer compared to the ambient air temperature measured 2 m from the ground surface, with the differences between tissue and air temperature attributed to variation in vapor pressure deficit and associated canopy transpirational cooling (Julia and Dingkuhn, 2013). Even along a single rice panicle exposed to 40 °C ambient temperature, spikelets at the top of the panicle were >4 °C hotter than those at the bottom of the panicle (Fu et al., 2016).

An increase in air temperature, as imposed in most heat stress and warming experiments, primarily alters leaf temperature through convection (though primarily radiation in IR heater experiments). But the change in the leaf temperature dictated by a change in air temperature also depends on how radiative and latent heat exchange are altered under the growth conditions (Schymanski et al. 2013). Since exposure to heat stress can alter stomatal conductance (Dusenge et al., 2020; Wang et al., 2020), and hence latent heat loss, the difference between leaf and air temperature may vary between control plants and heat-stressed plants. Similarly, leaves from a well-watered plant with high stomatal conductance (and thus high latent heat loss) might operate well below air temperature (Drake et al. 2018), while those from plants with low stomatal conductance (such as many conifers or drought-stressed individuals) may be warmer than air temperature, especially when irradiance is high (Lin et al. 2017). Under low irradiance, such as in most growth chambers where maximum photosynthetically active radiation (PAR) levels are $\sim 250 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, leaf heating through short-wave radiation is minimal and leaf temperatures may be close to the experimentally imposed air temperature. In contrast, under field conditions, mid-summer short-wave radiation loads are high, significantly warming leaves above air temperature, such that measuring tissue temperatures is critical.

Deciphering plant heat stress responses based on ambient conditions would lead us to assume that all species and genotypes experience the same level of heat stress when exposed to the same air temperature, but they do not. This phenomenon is particularly important to consider when studying heat stress responses during the day, when shifts in stomatal conductance alter transpiration and latent heat loss, and thus leaf temperature, based on soil moisture, plant hydraulic conductance, and atmospheric vapor pressure deficit. Options such as aerial sensor-based thermal cameras in the field or Raspberry PIs for recording high-frequency tissue

temperatures under controlled environment chamber experiments need to be better explored to establish standard protocols and develop tools to routinely associate physiological responses to *in situ* tissue temperature. When these are not available, the use of thermocouples (Shi et al., 2015) or handheld infrared thermometers (Deva, Urban, Challinor, Falloon, & Svitakova, 2020) to measure tissue temperature on representative plants in the study can help assess the degree to which the treatment air temperature has been translated into a change in plant tissue temperature. Reporting tissue temperatures will both improve our knowledge of the actual temperatures that lead to heat stress and enable more direct comparisons between studies that use different methods for imposing heat stress.

Developmental stage is a crucial determinant of plant vulnerability to heat

The developmental stage at which a plant is exposed to heat stress strongly affects the overall plant response. Regardless of the plant functional type, two of the most heat-susceptible phases in a plant's life cycle are the early seedling stage and the reproductive period.

The early seedling stage is a vulnerable phase under heat stress in all plants. Poorly-developed roots restrict the ability to take up water for latent heat loss. In addition, short seedlings sit in the Earth's boundary layer (the thin layer of still air immediately adjacent to the ground surface, analogous to the leaf boundary layer; Villagarcía et al., 2007), minimizing the potential for convective cooling but still allowing for high radiative energy input. In reforestation sites, the bare, dark soil can produce extreme temperatures at seedling height, inhibiting growth and killing seedlings (Grossnickle, 2000). Indeed, at a site with maximum air temperatures of near 30 °C, air temperatures reached 45 °C at 50 mm above the soil, and a blistering 75 °C was recorded just above the soil surface (Kolb & Robberecht, 1996). Thus, not only are seedlings

susceptible to heat stress due to their small size, they can also experience much more extreme thermal conditions than larger and older plants.

Reproduction may also be equally suppressed by heat stress across different plant species and functional types. However, the implications of decreased reproduction are much more severe for annual species, and particularly annual crops, than they are for perennial plants, like trees, which can make up for a poor reproductive year in future times. Dry land crops, including sorghum, millets and wheat, encounter harsh environmental conditions during different growth and developmental stages, with heat and drought stress being the major constraints (Zampieri, Ceglar, Dentener, & Toreti A, 2017; Pfliegerer, Schleussner, Kornhuber, & Coumou, 2019). Although a combination of heat and drought stress affect crops globally, recent reports point to an increase in temperature as a primary factor affecting crop yields (Ortiz-Bobea, Wang, Carrillo, & Ault, 2019), including wheat (Tack, Barkley, & Nalley, 2015) and sorghum (Tack, Lingenfelter, & Jagadish, 2017). Comparatively, heat stress during reproductive stages is even more detrimental compared to heat stress during vegetative stages in both annual and woody perennial crops, leading to significant yield losses (Prasad et al., 2017; Hussain et al., 2019). Among the reproductive stages, gametogenesis (Begcy et al., 2019; Soltani, Weraduwage, Sharkey, & Lowry, 2019 [common bean]; Wang et al., 2019 [maize]) and flowering (Vara Prasad et al., 2000 [peanut]; Jagadish et al., 2010 [rice]; Chiluwal et al., 2020 [sorghum]; Aiqing et al., 2018, Bheemanahalli et al., 2019 [wheat]; Zinn, Tunc-Ozdemir, & Harper, 2010; Hedhly, Hormaza, & Herrero, 2008 [flowering plants]) are highly sensitive to heat stress, leading to spikelet sterility and decreased seed and fruit numbers. The above studies have used a wide range in genetic diversity, and extensively investigated the physiological, anatomical and molecular responses of heat stress during these two sensitive stages.

In contrast to the work on gametogenesis and flowering, the impact of heat stress on floral meristem development has received minimal attention (Jagadish et al., 2014). Currently, the number of studies related to heat stress impact on reproductive stages can be summarized as follows: flowering > gametogenesis > floral meristem. Floral meristem development is extremely important as the final floral (panicle) architecture and the potential floral units (spikelets) are a manifestation of changes that occur at this stage. In crops, considering that the transition from the vegetative to reproductive (floral) meristem occurs after approximately 45 to 55 days after sowing (Quinones, Mattes, Faronilo, Sudhir-Yadav, & Jagadish, 2017), the canopy cover is not sufficiently developed to cover the exposed soil surface (Fig 2A; Munns, James, Sirault, Furbank, & Jones, 2010).

Under dry land cropping systems, the soil surface temperatures during the day are significantly higher than the canopy, due to absorption and dissipation of heat by soil, as visually illustrated in Fig. 2A. A large proportion of heat absorbed by the soil surface, when radiated back towards the plant, can increase the temperature of the basal portion of the stem (Fig. 2A; Munns et al., 2010). Coincidentally, the floral meristem initiation in most crops occurs at the base of the stem, thereby exposing the initiation and early development of the floral meristem and spikelet differentiation to much higher temperatures than the canopy temperature due to this soil heating phenomenon. Accompanied by limited water under dry land conditions, the very early floral meristem growth and spikelet differentiation has been shown to significantly modify the morphology of field-grown rice floral meristems (Fig 2B and C; Quinones et al., 2017). Such morphological changes alter the proportion of primary and secondary branches and ultimately the final floral architecture and sink size (i.e. total number of floral units per inflorescence), leading to lower seed numbers and lower yield (Wu et al., 2016). High day and night

temperatures (under well-watered conditions) imposed from the start of panicle initiation and lasting for 15 days were correlated with reduced spikelet fertility ($r=0.58$), but the correlation was much stronger with reduced spikelets per panicle ($r=0.88$) (Wu et al., 2016). This indicates that heat stress *per se* during panicle initiation could have a similar impact on panicle architecture and size, as combined drought and heat stress. In broccoli, a significantly higher sensitivity to heat stress coincided exactly with floral initiation, resulting in unevenly sized broccoli heads, however, a similar impact was not seen when the stress was imposed either before floral initiation or after the flower buds had differentiated (Björkman and Pearson, 1998; Lin et al., 2019). These studies indicate that the level of sensitivity of floral meristems to heat stress exposure appears to be consistent with grain and vegetable crops. Apart from the cited studies, information on physiological and molecular mechanisms or pathways on how heat stress affects early floral meristem development in annual crops is very limited, and almost nothing is known about how heat stress affects these processes in trees.

Recently, an interesting phenomenon has been documented in barley wherein $\sim 17\%$ of daily water loss was from stomata on the leaf sheath (Sadok, Lopez, Zhang, Tamang, & Muelhbauer, 2020). Previous findings show that the temperature perceived by the developing panicle enclosed within the leaf sheath can differ depending on the developmental stage. In rice, panicles exposed to stress during earlier developmental stages recorded lower internal tissue temperatures than the surrounding air (Shi et al., 2015), while just before heading, rice panicles tend to have a similar, or even higher temperatures than the ambient air (Lawas, Bheemanahalli, Solis, Jagadish, 2018). This discovery opens up new research directions to optimize sheath stomatal density as a potential means to alter the plant's microclimate, with the aim of protecting floral meristem development and gametogenesis from heat stress damage (Fig. 4).

During early growth stages, the negative impact of high soil temperature (Fig. 2a) on rooting characteristics, including root architecture, anatomy and hydraulic conductance, cannot be ruled out. Current information related to heat stress and roots is mostly obtained from controlled environment studies. For example, hydroponically-grown tomato seedlings exposed to six days of moderate to severe root temperature (32 to 39 °C) resulted in reduced nutrient uptake (Giri, Heckathorn, Misha & Krause, 2017). In more recent studies, high air temperatures increased the root length and mass ratio in primary roots and the root length and surface area in primary lateral roots in maize seedlings (Vescio, Abenavoli & Sorgona, 2021); in contrast, heat stress during flowering suppressed root morphological traits in oilseed rape genotypes (Wu, Shah, Duncan & Ma, 2020). These inconsistent findings indicate that heat stress impact on rooting characteristics varies based on stress intensity, stage and also crop species, warranting further investigations. Further, the limitations of considering air temperatures (instead of plant tissue temperatures) while investigating heat stress impact on aboveground plant parts has been extensively detailed in the previous section and there is similarly a difference between soil temperatures compared to air temperature, particularly between the soil surface and deeper soil layers (Reynolds & Ewing 1989; Shati, Prakash, Norouzi & Blake, 2018; Ostmeyer et al., 2020). Hence, we strongly recommend recording soil temperatures to reliably associate soil microclimate with heat stress impacts on root biology. In summary, information on the impact of heat stress on root biology in plants is very limited and largely remains a “black box” in field-grown plants.

Heat stress exposure during later reproductive developmental stages, such as gametogenesis and flowering, leads to spikelet sterility and lower yield, while heat stress during floral meristem development cuts back on the overall sink size and hence operates via a different

route through which an irreversible yield reduction occurs. A practical advantage for studying heat stress impacts during flowering is that the easy accessibility of the inflorescence allows for imposing appropriate phenotyping methods, with accuracy at the desired target stage. Unlike flowering, gametogenesis and the floral meristem stages are embedded within the stem vegetative tissue, significantly reducing the ability and accuracy of identifying the developmental stage, thereby lowering the repeatability of quantifying stress impact at the target stage. Hence, innovative phenotyping methods including image or sensor-based phenotyping tools that can enhance the accuracy of stress impact detection during floral meristem initiation and spikelet differentiation are essential to address this knowledge gap in crop science (Fig. 4).

Heat tolerance and recovery are equally important

Studies on heat stress, either using controlled environment chambers or field conditions, are generally aimed at enhancing “tolerance”, a widely accepted target to protect plants from future warming scenarios. In contrast to warming experiments, plants are not exposed to heat shocks and heat waves for their entire growth period, but rather transiently, allowing the plants to recover from the stress impact (Rueher, Gast, Weber, Daug, & Arneth, 2016; Schymanski et al. 2013; Way, Schnitzler, Monson, & Jackson, 2011). Although identifying mechanisms and traits that help plants tolerate these brief episodes of stress is important for breeding and selecting climate-resilient plants, similar information on crops’ ability to overcome the damage caused by heat shocks or waves once the stress is released is very limited. This is of particular relevance to effects of heat on reproduction. A heat wave could block reproduction (and in many cases this means loss of yield) or could only delay reproduction and seed set, perhaps until after the heat wave. There is very little information addressing this issue.

Unlike heat stress, drought stress studies have been actively pursuing both tolerance and recovery strategies, simultaneously at the physiological and molecular level, to minimize the stress' impact during the vegetative (Abid et al., 2018 [wheat], Zhang, Lei, Lai, Zhao, & Song, 2018 [maize]), reproductive and grain-filling stages (Lawas et al., 2019 [rice]). The physiological processes in crops that were affected by moderate drought, including photosynthetic processes, reactive oxygen species levels, membrane stability, recovered completely, but this was not the case with a severe stress exposure (Abid et al., 2018; Zhang et al., 2018). Similarly, within 60 h after drought stress was released, metabolic responses in flag leaves, flowering spikelets and developing seeds returned to normal levels, although the recovery was not able to reverse the metabolic changes completely (Lawas et al., 2019). An identical response was captured with anther proteomic changes exposed to drought stress (Liu & Bennett, 2011). In this study, 14 and 13 proteins were significantly altered under drought stress in the sensitive rice genotype IR64 and the tolerant Moroberekan, respectively, with none of the proteins reverting to normal in IR64 but 10 proteins reverted back to normal levels after rewatering in Moroberekan. The study by Liu & Bennett (2011) provides evidence for differentiating contrasting genotypes based on recovery at the molecular level, even in the highly sensitive reproductive tissue, while the rate of post-stress recovery is an area of research that has not been well studied yet in plants, in response to heat stress.

In comparison to drought stress, heat stress in crop plants generally leads to similar changes in physiology (Prasad et al., 2017, Cossani & Reynolds, 2012) and metabolic or transcriptome responses (Bheemanahalli et al., 2019; Begcy et al., 2019), either under high day or night temperature increases (Impa et al., 2019; Impa et al., 2020). However, none of these studies capture the extent of the reversal of physiological or molecular responses during the post-

stress recovery phase to ascertain the level of phenotypic plasticity in plants. There are some papers that address this question in trees (Ameye et al., 2012; Haldimann & Feller, 2004; Hamerlynck & Knapp, 1996; Rueher, Gast, Weber, Daug, & Arneth, 2016) and in crops, including grape leaves (Liu et al., 2012), rice seedlings (Mangrauthia et al., 2017), and recent work on the recovery of photosynthetic capacity in wheat and spinach (Chovancek, Zivcak, Brestic, Hussain & Allakhverdiev, 2021; Agrawal & Jajoo, 2021) and starch levels in cotton leaves (Loka, Oosterhuis, Baxevanos, Noulas & Hu, 2020). Additionally, post-stress photosynthetic recovery in field-grown maize and soybeans (Siebers et al., 2017; 2015) has been recorded, as has the rapid recovery of leaf total non-structural carbohydrate levels after 12 h of stress (Siebers et al., 2015). Although some studies recognize the importance of heat stress recovery, post-stress recovery has not been extensively considered to the extent that it can be effectively integrated into breeding programs. In addition, the studies noted above all measured heat stress recovery on vegetative tissue, while investigating differential levels of recovery in reproductive tissue would be an intriguing research direction, similar to observations made under drought stress (Liu & Bennett 2011). Hence, we recommend that future studies addressing heat stress consider both tolerance and recovery in the experimental design, to incorporate faster and more efficient post-stress recovery-related traits for developing robust heat resilient phenotypes for future climatic scenarios (Fig. 4).

Conclusions

Heat stress from climate change, whether imposed through long-term increases in annual mean temperature or via more frequent and extreme heat waves, is poised to reduce crop yield, and ecosystem productivity. To improve our predictions of how heat stress will affect vegetation and

improve heat stress-related breeding efforts, we outline four key areas of focus. First, a stronger integration of knowledge and tools across heat shock, heat wave, and long-term warming studies will help us identify and develop varieties and genotypes that have higher chances of success in their target environments. Sensor-based tools for measuring plant tissue temperature are now accessible and economically feasible to the extent that they can be routinely used in heat stress studies to link heat stress-tolerance and recovery mechanisms in relation to tissue temperatures. Information generated based on tissue temperature will open up new avenues for the crop modelling community to refine crop mechanistic models and enhance their prediction accuracy. Increased efforts to find alternative ways to impose and quantify heat stress impacts on tissues and developmental stages that are less accessible (for example, the floral meristem) and fully incorporating methods to integrate heat stress recovery into heat stress tolerance improvement programs is strongly recommended.

Acknowledgements

We thank Yuanyuan Wang for her help with Figures 1 and 4. We acknowledge financial support from the National Science Foundation, USA Award no. 1736192 and USDA National Institute of Food and Agriculture, hatch multistate project 1014561 to SVKJ, Kansas State University. This is contribution no. 21-143-J from the Kansas Agricultural Experiment Station. Research support for TDS comes from the MSU Plant Resilience Institute and partial salary support comes from Michigan AgBioResearch. DAW acknowledges the support of a Natural Sciences and Engineering Research Council of Canada Discovery Grant, and the United States Department of Energy contract No. DE-SC0012704 to Brookhaven National Laboratory.

Conflict of interest

Authors declare no conflict of interest

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Table 1. Declines in the maximum photochemical efficiency of photosystem II (F_v/F_m) after an acute heat stress on black spruce (*Picea mariana* (Mill.) B.S.P.) needles. Seedlings were grown under either a cool temperature regime (Cool, upper table) or a warm temperature regime (Warm, +8 °C above the cool temperature regime, lower table). The F_v/F_m was measured on samples before and after an acute heat stress, with samples exposed to a stress temperature between 37 °C and 55 °C for a stress duration between 2 minutes and 15 minutes (see Way and Sage (2008) for more details). Note that the decline in F_v/F_m is greater when the heat stress exposure temperature and/or exposure duration increase and that the warm-grown needles incur less damage to photosystem II for a given acute heat stress, indicating the acquisition of thermotolerance. Values are the means of n=2-6 sets of needles.

Cool		Exposure temperature (°C)									
Duration	37	40	44	46	47	48	49	50	52	54	55
2 min								15			
3 min	0		9		16	8	19	43	55	63	56
5 min					13		26	25	50		47
10 min				16	30	15	28	47			
15 min				23	36	45					

Warm		Exposure temperature (°C)									
Duration	37	40	44	46	47	48	49	50	52	54	55
2 min								10			
3 min	3		11		16	17	18	23	15	32	36
5 min					10		10	26	48		47
10 min				7	18	24	43	52			
15 min				16	20						

% decrease in F_v/F_m	
	0-10
	11-20
	21-30
	31-40
	41-50
	51-60
	61-70

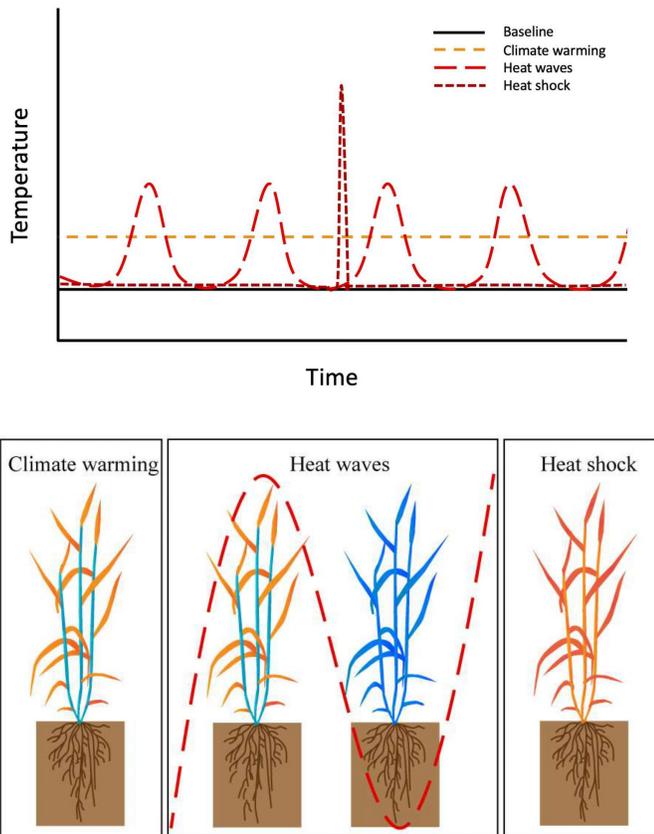


Figure 1. Upper panel: Conceptual illustration of the differences in heat stress durations and temperatures used during heat stress studies in heat shock, heat wave and warming scenarios compared to a baseline, control treatment; recovery periods are indicated in the heat shock and heat wave scenarios when the temperature returns to the baseline. Lower panel: Blue, orange and red colors indicate optimum temperature, moderate and severe high temperatures, respectively, experienced by the plant.

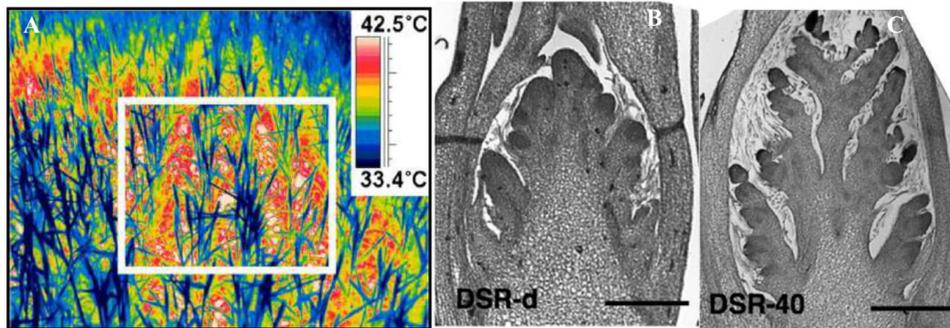


Figure 2. Infrared picture of a wheat canopy depicting a significantly higher soil surface temperature than leaf temperature (A; from Munns et al., 2010). Floral meristem morphology under direct seeded rice (DSR) without stress (B) and under drought stress equating to 40 kPa (C; from Quinones et al., 2017).

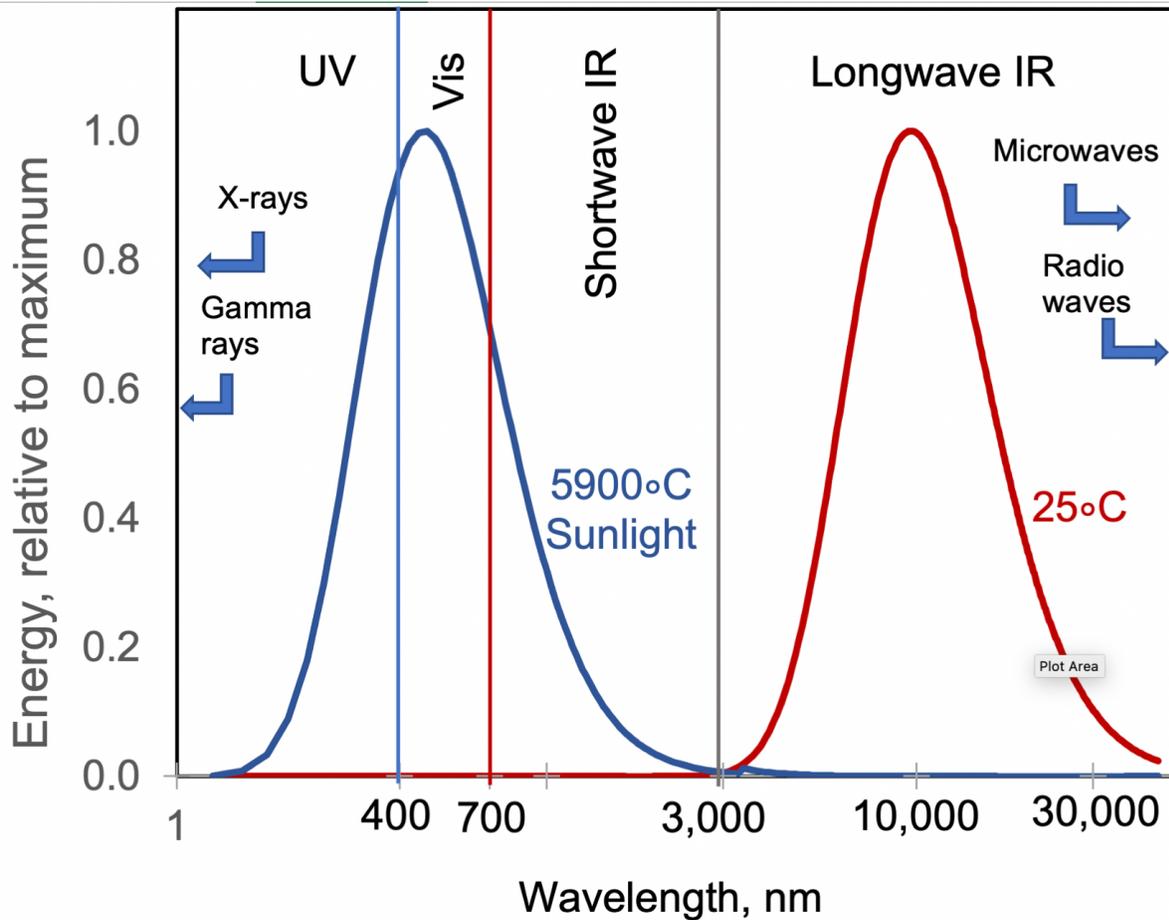


Figure 3. Relative thermal energy emission as a function of wavelength for sunlight and plants or their surroundings (25 °C as an example). Values given relative to the maximum value for each curve. The wavelength scale is logarithmic for ease of display.

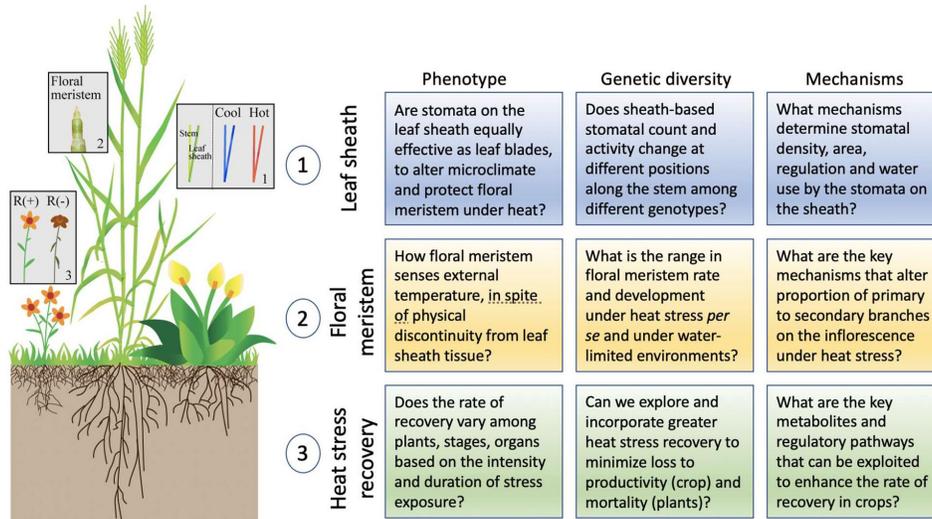


Figure 4. Major knowledge gaps related to leaf sheath temperatures (1), floral meristems (2) and recovery rates (3) under heat stress and suggestions to address these gaps to complement efforts towards developing heat tolerant plants that are better adapted to future hotter climates. Insets indicate the need to explore genetic diversity for variable leaf sheath temperatures (inset 1); floral meristems that can sustain heat stress exposures without significant negative impacts on the final inflorescence and sink size (inset 2); and rates of heat stress recovery at the organ or whole-plant level (inset 3). Inset 3: R(+) indicates a high rate of post heat-stress recovery; R(-) indicates a lack of recovery.

References

- Abid, M., Ali, S., Qi, L. K., Zahoor, R., Tian, Z., Jiang, D., Snider, J. L., & Dai, T. (2018). Physiological and biochemical changes during drought and recovery periods at tillering and jointing stages in wheat (*Triticum aestivum* L.). *Scientific Reports*, 8, 4615.
- Agrawal, D. & Jajoo, A. (2021). Study of high temperature stress induced damage and recovery in photosystem II (PSII) and photosystem I (PSI) in Spinach leaves (*Spinacia oleracea*). *Journal of Plant Biochemistry and Biotechnology*, DOI: 10.1007/s13562-020-00643-z
- Aiqing, S., Impa, S. M., Sunoj, J. V. S., Singh, K., Gill, K. S., Prasad, P. V. V., & Jagadish, S. V. K. (2018). Heat stress during flowering affects time of day of flowering, seed-set and grain quality in spring wheat (*Triticum aestivum* L.). *Crop Science*, 58, 380-392.
- Ameye, M., Wertin, T.M., Bauweraerts, I., McGuire, M.A., Teskey, R.O., Steppe, K. (2012) The effect of induced heat waves on *Pinus taeda* and *Quercus rubra* seedlings in ambient and elevated CO₂ atmospheres. *New Phytologist*, 196, 448–461.
- Aronson E. L., & McNulty S. G. (2009). Appropriate experimental ecosystem warming methods by ecosystem, objective, and practicality. *Agricultural and Forest Meteorology*, 149, 1791-1799.
- Bahuguna, R. N., Jha, J., Madan, P., Shah, D., Lawas, M. L., Khetarpal, S., & Jagadish, S. V. K. (2015). Physiological and biochemical characterization of NERICA-L 44: A novel source of heat tolerance at the vegetative and reproductive stages in rice. *Physiologia Plantarum*, 154, 543-559.
- Bauweraerts, I., Ameye, M., Wertin, T. M., McGuire, M. A., Teskey, R. O., & Steppe, K. (2014). Water availability is the decisive factor for the growth of two tree species in the occurrence of consecutive heat waves. *Agricultural and Forest Meteorology*, 189-190, 19-29.
- Begcy, K., Nosenko, T., Zhou, L. Z., Fragner, L., Weckwerth, W., & Dresselhaus, T. (2019). Male sterility in maize after transient heat stress during the tetrad stage of pollen development. *Plant Physiology*, 181, 683-700.
- Bergkamp, B., Impa, S. M., Asebedo, A. R., Fritz, A. K., & Jagadish, S. V. K. (2018). Popular winter wheat varieties response to post-flowering heat stress under controlled chambers and field-based heat tents. *Field Crops Research*, 222, 143-152.
- Berry, J., & Björkman O. (1980). Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology and Plant Molecular Biology*, 31, 491–543.
- Bheemanahalli, R., Sunoj, J. V. S., Saripalli, G., Prasad, P. V. V., Balyan, H. S., Gupta, P. K., Grant, N., Gill, K. S., & Jagadish, S. V. K. (2019). Quantifying the impact of heat stress

- on pollen germination, seed-set and grain-filling in spring wheat. *Crop Science*, 59, 684-696.
- Bitá, C., & Gerats T. (2013). Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. *Frontiers in Plant Science*, 4, article 273.
- Björkman, T., & Pearson, K. J. (1998). High temperature arrest of inflorescence development in broccoli (*Brassica oleracea* var. *italica* L.). *Journal of Experimental Botany*, 49, 101-106.
- Blum A. (1986). The effect of heat-stress on wheat leaf and ear photosynthesis. *Journal of Experimental Botany*, 37, 111-118.
- Bokszczanin, K. L., Solanaceae Pollen Thermotolerance Initial Training Network (SPOT-ITN) Consortium, & Fragkostefanakis, S. (2013). Perspectives on deciphering mechanisms underlying plant heat stress response and thermotolerance. *Frontiers in Plant Science*, 4, 315.
- Chang Y. Y., Liu, H. C., Liu N. Y., Chi, W. T., Wang, C. N., Chang, S. H., & Wang T. T. (2007). A heat-inducible transcription factor, HsfA2, is required for extension of acquired thermotolerance in Arabidopsis. *Plant Physiology*, 143, 251-262.
- Chen, J., Burke, J. J., Xin, Z., Xu, C., & Velten, J. (2006) Characterization of the *Arabidopsis* thermosensitive mutant *atts02* reveals an important role for galactolipids in thermotolerance. *Plant, Cell & Environment*, 29, 1437-1448.
- Chi, W. T., Fung, R. W. M., Liu, H. C., Hsu, C. C., & Chang Y. Y. (2009) Temperature-induced lipocalin is required for basal and acquired thermotolerance in Arabidopsis. *Plant, Cell & Environment*, 32, 917-927.
- Chiluwal, A., Bheemanahalli, R., Kanaganahalli, V., Boyle, D., Perumal, R., Pokharel, M., Halilou, O., & Jagadish, S. V. K. (2020). Deterioration of ovary plays a key role in heat stress-induced spikelet sterility in sorghum. *Plant, Cell & Environment*, 43(2), 448-462.
- Chovancek, E., Zivcak, M., Brestic, M., Hussain, S. & Allakhverdiev, S. I. (2021). The different patterns of post-heat stress responses in wheat genotypes: the role of the transthylakoid proton gradient in efficient recovery of leaf photosynthetic capacity. *Photosynthesis Research*, <https://doi.org/10.1007/s11120-020-00812-0>
- Colombo S. J., & Timmer V. R. (1992) Limits of tolerance to high temperatures causing direct and indirect damage to black spruce. *Tree Physiology*, 11, 95–104.
- Cossani, C. M., & Reynolds, M. P. (2012). Physiological traits for improving heat tolerance in wheat. *Plant Physiology*, 160, 1710-1718.

- Curtis, E. M., Knight, C. A., & Leigh A. (2019). Intracanopy adjustment of leaf-level thermal tolerance is associated with microclimatic variation across the canopy of a desert tree (*Acacia papyrocarpa*). *Oecologia*, 189, 37-46.
- Davies, M., Ecroyd, H., Robinson, S. A., & French, K. (2018). Stress in native grasses under ecologically relevant heat waves. *PLoS One*, 13(10), e0204906.
- De Boeck, H. J., Dreesen, F. E., Janssens, I. A., & Nijs, I. (2010). Climatic characteristics of heat waves and their simulation in plant experiments. *Global Change Biology*, 16, 1992-2000.
- Deva, C. R., Urban, M. O., Challinor, A. J., Falloon, P., & Svitáková, L. (2020). Enhanced leaf cooling is a pathway to heat tolerance in common bean. *Frontiers in Plant Science*, 11, 19.
- Drake, J. E., Tjoelker, M. G., Vårhammar, A., Medlyn, B. E., Reich, P. B., Leigh, A., ... Barton, C. V. M. (2018). Trees tolerate an extreme heatwave via sustained transpirational cooling and increased leaf thermal tolerance. *Global Change Biology*, 24(6), 2390-2402.
- Dusenge, M.E., Duarte, A.G., & Way, D.A. (2019) Plant carbon metabolism and climate change: elevated CO₂ and temperature impacts on photosynthesis, photorespiration and respiration. *New Phytologist*, 221, 32-49.
- Dusenge, M.E., Madhavji, S., & Way, D.A. (2020) Contrasting acclimation responses to elevated CO₂ and warming between an evergreen and a deciduous boreal conifer. *Global Change Biology*, 26, 3639-3657.
- Easterling D. R., Meehl G. A., Parmesan C., Changnon S. A., Karl T. R., & Mearns L. O. (2000). Climate extremes: observations, modeling, and impacts. *Science*, 289, 2068-2074.
- Ehleringer J. R. & Björkman O. (1978). Pubescence and leaf spectral characteristics in a desert shrub, *Encelia farinosa*. *Oecologia*, 36, 151-162.
- Falster, D. S., & Westoby, M. (2003). Leaf size and angle vary widely across species: what consequences for light interception? *New Phytologist*, 158, 509-525.
- Fang, S., Su, H., Liu, W., Tan, K. & Ren, S. (2013). Infrared warming reduced winter wheat yields and some physiological parameters, which were mitigated by irrigation and worsened by delayed sowing. *PLoS ONE* 8(7): e67518.
- Fu, G., Feng, B., Zhang, C., Yang, Y., Yang, X., Chen, T., . . . Tao L. (2016). Heat stress is more damaging to superior spikelets than inferiors of rice (*Oryza sativa* L.) due to their different organ temperatures. *Frontiers in Plant Science* 7, 1637.
- Geange, S. R., Arnold, P.A., Catling, A. A, Coast, O., Cook, A. M., Gowland, K. M., Leigh, A., Notarnicola, R. F., Posch, B. C., Venn, S. E., Zhu, L., & Nicotra, A.B. (2021) The thermal tolerance of photosynthetic tissues: a global systematic review and agenda for future research. *New Phytologist* 229: 2497-2513.

- Giri, A., Heckathron, S., Mishra, S., & Krause, C. (2017). Heat stress decreases levels of nutrient-uptake and -assimilation proteins in tomato roots. *Plants*, 6(1), 6.
- Grossnickle, S. C. (2000). *Ecophysiology of Northern Spruce Species: The Performance of Planted Seeds*. NRC Research Press, Ottawa, ON, Canada. 409 pp.
- Glaubitz, U., Li, X., Schaedel, S., Erban, A., Sulpice, R., Kopka, J., Hinch D. K., & Zuther, E. (2017). Integrated analysis of rice transcriptomic and metabolomic responses to elevated night temperatures identifies sensitivity- and tolerance-related profiles. *Plant, Cell & Environment*, 40, 121-137.
- Haldimann, P., & Feller, U. (2004) Inhibition of photosynthesis by high temperature in oak (*Quercus pubescens* L.) leaves grown under natural conditions closely correlates with a reversible heat-dependent reduction of the activation state of ribulose-1,5-bisphosphate carboxylase/oxygenase. *Plant, Cell & Environment*, 27, 1169–1183.
- Hamerlynck, E., & Knapp, A.K. (1996) Photosynthetic and stomatal responses to high temperature and light in two oaks at the western limit of their range. *Tree Physiology*, 16, 557–565.
- Hao, Z., AghaKouchak A., & Phillips, T. J. (2013). Changes in concurrent monthly precipitation and temperature extremes. *Environmental Research Letters*, 8, 34014.
- Hedhly, A., Hormaza, J. I., & Herrero, M. (2008). Global warming and sexual plant reproduction. *Trends in Plant Science*, 14, 30-36.
- Huang, H., Ullah, F., Zhou, D. X., Yi, M., & Zhao, Y. (2019). Mechanisms of ROS regulation of plant development and stress responses. *Frontiers in Plant Science*, 10, 800.
- Hussain, H. A., Men, S., Hussain, S., Chen, Y., Ali, S., Zhang, S., Zhang, K., Li, Y., Liao, C., & Wang, L. (2019). Interactive effects of drought and heat stresses on morpho-physiological attributes, yield, nutrient uptake and oxidative status in maize hybrids. *Scientific Reports*, 9, 3890.
- Impa, S. M., Raju, B. R., Hein, N. T., Sandhu, J., Prasad, P. V. V., Walia, H. & Jagadish, S. V. K. (2021). High night temperature effects on wheat and rice – current status and way forward. *Plant Cell & Environment*
- Impa, S. M., Sunoj, J. V. S., Krassovskaya, I., Bheemanahalli, R., Obata, T., & Jagadish, S. V. K. (2019). Carbon balance and source-sink metabolic changes in winter wheat exposed to high night-time temperature. *Plant, Cell & Environment*, 42(4), 1233-1246.
- Impa, S. M., Vennapusa, A. R., Bheemanahalli, R., Sebela, D., Boyle, D., Walia, H., & Jagadish, S. V. K. (2020). High night temperature induced changes in grain starch metabolism alters starch, protein and lipid accumulation in winter wheat. *Plant, Cell & Environment*, 43(2), 431-447.

- IPCC (2014). Climate change 2014: synthesis report. In Core Writing Team, R. K. Pachauri, & L. A. Meyer (Eds.), Contribution of working groups I, II and III to the Fifth Assessment report of the Intergovernmental Panel on Climate Change. Geneva, Switzerland: IPCC.
- Ishimaru, T., Seefong, X., Nallathambi, J., Rajendran, S., Yoshimoto, M., Phoudalay, L., Benjamin, S., Hasegawa, T., Hayashi, K., Gurusamy, A., Muthurajan, R., & Jagadish, S. V. K. (2016). Quantifying rice spikelet sterility in potential heat-vulnerable regions: field surveys in southern Laos and southern India. *Field Crops Research*, 190, 3-9.
- Jagadish, S. V. K. (2020). Heat stress during flowering in cereals – effects and adaptation strategies. *New Phytologist*. 226(6), 1567-1572.
- Jagadish, S. V. K., Craufurd, P. Q. & Wheeler, T. R. (2007). High temperature stress and spikelet fertility in rice. *Journal of Experimental Botany*, 58, 1627-1635.
- Jagadish, S. V. K., Murty, M. V. R., Quick, W. P. (2014). Rice responses to raising temperatures – challenges, perspectives and future directions. *Plant Cell and Environment*, 38(9), 1686-1698.
- Jagadish, S. V. K., Muthurajan, R., Oane, R., Wheeler, T. R., Heuer, S., Bennett, J., & Craufurd, P. Q. (2010). Physiological and proteomic approaches to dissect reproductive stage heat tolerance in rice (*Oryza sativa* L.). *Journal of Experimental Botany*, 61, 143-156.
- Janni, M., Gulli, M., Maestri, E., Marmioli, M., Valliyodan, B., Nguyen, H. T., & Marmioli, N. (2020). Molecular and genetic bases of heat stress responses in crop plants and breeding for increased resilience and productivity. *Journal of Experimental Botany*, 71(13), 3780-3802.
- Jentsch A., Kreyling J., & Beierkuhnlein C. (2007) A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment*, 5, 365-374.
- Julia, C., & Dingkuhn, M. (2013). Predicting temperature induced sterility of rice spikelets requires simulation of crop-generated microclimate. *European Journal of Agronomy*, 49, 50-60.
- Kimball, B. A., Alonso-Rodríguez, A. M., Cavaleri, M. A., Reed, S. C., González, G. & Wood, T. E. (2018). Infrared heater system for warming tropical forest understory plants and soils. *Ecology and Evolution*, 8(4), 1932–1944.
- Kimball, B. A., Conley, M. M., Wang, S., Lin, X., Luo, C., Morgan, J. & Smith, D. (2007). Infrared heater arrays for warming ecosystem field plots. *Global Change Biology*, 14(2), 309-320.
- King, D. A. (1997) The functional significance of leaf angle in *Eucalyptus*. *Australian Journal of Botany*, 45, 619–639.

- Kolb, P. F., & Robberecht, R. (1996) High temperature and drought stress effects on survival of *Pinus ponderosa* seedlings. *Tree Physiology*, 16, 665–672.
- Kroner, Y., & Way D. A. (2016). Carbon fluxes acclimate more strongly to elevated growth temperatures than to elevated CO₂ concentrations in a northern conifer. *Global Change Biology*, 22, 2913-2928.
- Lambers H., & Oliveira R. S. (2019). Plant energy budgets: The plant's energy balance. In: *Plant Physiological Ecology*. Springer, p 265-278.
- Lawas, L. M. F., Bheemanahalli, R., Solis, C. A., & Jagadish, S. V. K. (2018). Sheathed panicle phenotype (cv. Sathi) maintains normal spikelet fertility and grain filling under prolonged heat stress in rice. *Crop Science*, 58(4), 1693-1705.
- Lawas, L. M. F., Erban, A., Kopka, J., Jagadish, S. V. K., Zuther, E., & Hinch, D. K. (2019). Metabolic responses of rice source and sink organs during recovery from combined drought and heat stress in the field. *GigaScience*, 8, 1-15.
- Leigh, A., Sevanto, S., Close, J. D. & Nicotra, A. B. (2017) The influence of leaf size and shape on leaf thermal dynamics: does theory hold up under natural conditions? *Plant, Cell & Environment*, 40, 237-248.
- Leuning, R. (1989) Leaf energy balances: developments and applications. *Philosophical Transactions of the Royal Society of London B*, 324, 191-206.
- Lin, C. Y., Roberts, J. K., & Key, J. L. (1984). Acquisition of thermotolerance in soybean seedlings. *Plant Physiology*, 74, 152-160.
- Lin, C. W., Fu, S. F., Liu, Y. J., Chen, C. C., Chang, C. H., Yang, Y. W., & Huang, H. J. (2019). Analysis of ambient temperature-responsive transcriptome in shoot apical meristem of heat-tolerant and heat-sensitive broccoli inbred lines during floral head formation. *BMC Plant Biology*, 19, 3.
- Lin, H., Chen, Y., Zhang, H., Fu, P., & Fan, Z. (2017). Stronger cooling effects of transpiration and leaf physical traits of plants from a hot dry habitat than from a hot wet habitat. *Functional Ecology*, 31, 2202-2211.
- Lin, M. Y., Chai, K. H., Ko, S. S., Kuang, L. Y., Lur, H. S., & Charng, Y. Y. (2014). A positive feedback loop between HEAT SHOCK PROTEIN101 and HEAT STRESS-ASSOCIATED 32-KD PROTEIN modulates long-term acquired thermotolerance illustrating diverse heat stress responses in rice varieties. *Plant Physiology*, 164, 2045–2053.
- Liu, J. X., & Bennett, J. (2011). Reversible and irreversible drought-induced changes in the anther proteome of rice (*Oryza sativa* L.) genotypes IR64 and Moroberekan. *Molecular Plant*, 4(1), 59-69.

- Liu, G. T., Wang, J. F., Cramer, G., Dai, Z.W., Duan, W., Xu, H. G., Wu, B. H., Fan, P. G., Wang, L. J., & Li, S. H. (2012). Transcriptomic analysis of grape (*Vitis vinifera* L.) leaves during and after recovery from heat stress. *BMC Plant Biology*, 12, 174.
- Loka, D. A., Oosterhuis, D. M., Baxevanos, D., Noulas, C. & Hu, W. (2020). Single and combined effects of heat and water stress and recovery on cotton (*Gossypium hirsutum* L.) leaf physiology and sucrose metabolism. *Plant Physiology and Biochemistry*, 148, 166-179.
- MacBryde, B., Alderfer, R., & Gates, D. M. (1971). Water and energy relations of plant leaves during periods of heat stress. *Oecologia Plantarum*, 6, 151-162.
- Mangrauthia, S. K., Bhogireddy, S., Agarwal, S., Prasanth, V. V., Voleti, S. R., Neelamraju, S., & Subrahmanyam, D. (2017). Genome-wide changes in microRNA expression during short and prolonged heat stress and recovery in contrasting rice cultivars. *Journal of Experimental Botany*, 68, 2399–2412.
- Mittler, R. (2017). ROS are good. *Trends in Plant Science*, 22, 11-19.
- Mittler, R., Finka, A., & Goloubinoff, P. (2012). How do plants feel the heat? *Trends in Biochemical Sciences*, 37, 118-125.
- Moni, C., Silvennoinen, H., Kimball, B.A., Fjellidal, E., Brenden, M., Burud, I., Fl, A. & Rass D. P. (2019). Controlled infrared heating of an arctic meadow: challenge in the vegetation establishment stage. *Plant Methods*, 15, 3.
- Munns, R., James, R. A., Sirault, X. R. R., Furbank, R. T., & Jones, H. G. (2010). New phenotyping methods for screening wheat and barley for beneficial responses to water deficit. *Journal of Experimental Botany*, 61(3), 3499-3507.
- Nuttall, J. G., Barlow, K. M., Delahunty, A. J., Christy, B. P. & O’Leary, G. J. (2018). Acute high temperature response in wheat. *Agronomy Journal*, 110(4), 1296-1308.
- Okajima, Y., Taneda, H., Noguchi, K., & Terashima, I. (2012). Optimum leaf size predicted by a novel leaf energy balance model incorporating dependencies of photosynthesis on light and temperature. *Ecological Research*, 27, 333-346.
- Ortiz-Bobea, A., Wang, H., Carrillo, C. M., & Ault, T. R. (2019). Unpacking the climatic drivers of US agricultural yields. *Environmental Research Letters*, 14, 064003.
- Ostmeyer, T., Bheemanahalli, R., Srikanthan, D., Bean, S., Peiris, K. H. S., Madasamy, P., Perumal, R., & Jagadish, S.V.K. (2020). Quantifying the agronomic performance of new grain sorghum hybrids for enhanced early-stage chilling tolerance. *Field Crops Research*, 258, 107955

- Perez, D. E., Hoyer, J. S., Johnson, A. I., Moody, Z. R., Lopez, J., & Kaplinsky N. J. (2009). BOBBER1 is a non-canonical Arabidopsis small heat shock protein required for both development and thermotolerance. *Plant Physiology*, 151, 241-252.
- Pfleiderer, P., Schleussner, C., Kornhuber, K., & Coumou, D. (2019). Summer weather becomes more persistent in a 2 °C world. *Nature Climate Change*, 9, 666-671.
- Prasad, P. V. V., Bhemanahalli, R., & Jagadish, S. V. K. (2017). Field crops and the fear of heat stress - opportunities, challenges, and future directions. *Field Crops Research*, 200, 114-121.
- Quinones, C., Mattes, N., Faronilo, J., Sudhir-Yadav., & Jagadish, S. V. K. (2017). Drought stress reduces grain yield by altering the floral meristem development and sink size under dry-seeded rice cultivation. *Crop Science*, 57(4), 2098-2108.
- Reich, P. B., Sendall, K. M., Stefanski, A., Rich, R. L., Hobbie, S. E., & Montgomery, R. A. (2018). Effects of climate warming on photosynthesis in boreal tree species depend on soil moisture. *Nature*, 562, 263-267.
- Rehmani, M. I. A., Zhang, J., Li, G., Ata-Ul-Karim, S. T., Wang, S., Kimball, B. A., Yan, C., Liu, Z. & Ding, Y. (2011). Simulation of future global warming scenarios in rice paddies with an open-field warming facility. *Plant Methods* 7, 41.
- Reynolds, M.P. & Ewing, E. E. (1989). Effects of high air and soil temperature stress on growth and tuberization in *Solanum tuberosum*. *Annals of Botany*, 64(3), 241-247.
- Rueher, N.K., Gast, A., Weber, C., Daub, B., & Arneth A. (2016) Water availability as dominant control of heat stress responses in two contrasting tree species. *Tree Physiology*, 36, 164-178.
- Ruiz-Vera U. M., Siebers M. H., Drag D. W., Ort D. R. & Bernacchi C. J. (2015). Canopy warming caused photosynthetic acclimation and reduced seed yield in maize grown at ambient and elevated [CO₂]. *Global Change Biology*, 21, 4237-4249.
- Ruiz-Vera U. M. Siebers M. Gray S. B. Drag D. W. Rosenthal D. M. Kimball B. A., . . . Bernacchi C. J. (2013) Global warming can negate the expected CO₂ stimulation in photosynthesis and productivity for soybean grown in the midwestern United States. *Plant Physiology*, 162, 410-423.
- Sarwar, M., Saleem, M. F., Ullah, N., Ali, S., Rizwan, M., Shahid, M. R., Alyemeni, M. N., Alamri, S. A., & Ahmad, P. (2019). Role of mineral nutrition in alleviation of heat stress in cotton plants grown in glasshouse and field conditions. *Scientific Reports* 9, 13022.
- Sadok, W., Lopez, J. R., Zhang, Y., Tamang, B. G. & Muehlbauer, G. J. (2020). Sheathing the blade: Significant contribution of sheaths to daytime and nighttime gas exchange in a grass crop. *Plant, Cell & Environment*, 43(8), 1844-1861.

- Sathishraj, R., Bheemanahalli, R., Ramachandran, M., Dingkuhn, M., Muthurajan, R., & Jagadish, S. V. K. (2016). Capturing heat stress induced variability in spikelet sterility using panicle, leaf and air temperature under field conditions. *Field Crops Research*, 190, 10-17.
- Schittenhelm, S., Langkamp-Wedde, T., Kraft, M., Kottmann, L., & Matschiner, K. (2020). Effect of two-week heat stress during grain filling on stem reserves, senescence, and grain yield of European winter wheat cultivars. *Journal of Agronomy and Crop Science*, <https://doi.org/10.1111/jac.12410>
- Schrader S. M., Wise R. R., Wacholtz W. F., Ort D. R. & Sharkey T. D. (2004). Thylakoid membrane responses to moderately high leaf temperature in Pima cotton. *Plant, Cell & Environment* 27, 725-735.
- Schymanski, S. J., Or, D., & Zwieniecki, M. (2013). Stomatal control and leaf thermal and hydraulic capacitances under rapid environmental fluctuations. *PLoS One*, 8, 54231.
- Seymour, R.S. (2010). Scaling of heat production by thermogenic flowers: limits to floral size and maximum rate of respiration. *Plant, Cell & Environment*, 33, 1474-1485.
- Shati, F., Prakash, S., Norouzi, H. & Blake, R. (2018). Assessment of differences between near-surface air and soil temperatures for reliable detection of high-latitude freeze and thaw states. *Cold Regions Science and Technology*, 145, 86-92.
- Shi, W., Ishimaru, T., Gannaban, R. B., Oane, W., & Jagadish, S. V. K. (2015). Popular rice (*Oryza sativa* L.) cultivars show contrasting responses to heat stress at gametogenesis and anthesis. *Crop Science*, 55, 589-596.
- Shi, W., Lawas, L. M. F., Raju, B. R. & Jagadish, S. V. K. (2015). Acquired thermo-tolerance and trans-generational heat stress response at flowering in rice. *Journal of Agronomy and Crop Science*, 202, 309-319.
- Siebers, M. H., Slattery, R. A., Yendrek, C. R., Locke, A. M., Drag, D., Ainsworth, E. A., Bernacchi, C. J., Ort, D. R. (2017). Simulated heat waves during maize reproductive stages alter reproductive growth but have no lasting effect when applied during vegetative stages. *Agriculture Ecosystems & Environment*, 240, 162-170.
- Siebers, M. H., Yendrek, C. R., Drag, D., Locke, A. M., Acosta, L. R., Leakey, A. D. B., Ainsworth, E. A., Bernacchi, C. J., Ort, D. R. (2015). Heat waves imposed during early pod development in soybean (*Glycine max*) cause significant yield loss despite a rapid recovery from oxidative stress. *Global Change Biology*, 21(8), 3114-3125.
- Singsaas, E. L., Laporte, M. M., Shi, J. Z., Monson, R. K., Bowling, D. R., Johnson K., . . . Sharkey T.D. (1999). Leaf temperature fluctuation affects isoprene emission from red oak (*Quercus rubra*) leaves. *Tree Physiology*, 19, 917-924.

- Soltani A., Weraduwage S. M., Sharkey T. D. & Lowry D. B. (2019). Elevated temperatures cause loss of seed set in common bean (*Phaseolus vulgaris* L.) potentially through the disruption of source-sink relationships. *BMC Genomics*, 20, 312.
- Srikanthbabu, V., Krishnaprasad, B. T., Gopalakrishna, R., Savitha, M. & Udayakumar, M. (2002). Identification of pea genotypes with enhanced thermotolerance using temperature induction response technique (TIR). *Journal of Plant Physiology*, 159, 535–545.
- Sunoj, J. V. S., Shroyer, K. J., Jagadish, S. V. K., & Prasad, P. V. V. (2016). Diurnal temperature amplitude alters physiological and growth response of maize (*Zea mays* L.) during vegetative stage. *Environmental and Experimental Botany*, 130, 113-121.
- Suzuki, N., & Katano, K. (2018). Coordination between ROS regulatory systems and other pathways under heat stress and pathogen attack. *Frontiers in Plant Science*, 9, 490.
- Tack, J., Barkley, A., & Nalley, L. L. (2015). Effect of warming temperatures on US wheat yields. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 6931–6936.
- Tack, J., Lingenfelter, J., Jagadish, S. V. K. (2017). Disaggregating sorghum yield reductions under warming scenarios exposes narrow genetic diversity in US breeding programs. *Proceedings of the National Academy of Sciences of the United States of America*, 114(35), 9296-9301.
- Teskey, R., Wertin, T., Bauweraerts, I., Ameye, M., McGuire, M. A., & Steppe, K. (2015). Responses of tree species to heat waves and extreme heat events. *Plant, Cell & Environment*, 38, 1699-1712.
- Vara Prasad, P.V., Craufurd, P.Q., Summerfield, R.J., & Wheeler, T.R. (2000). Effects of short episodes of heat stress on flower production and fruit-set of groundnuts. *Journal of Experimental Botany*, 51, 777-784.
- Vescio, R., Abenavoli, M. R., & Sorgonà, A. (2021). Single and combined abiotic stress in maize root morphology. *Plants*, 10, 5.
- Vierling, E. (1991). The roles of heat shock proteins in plants. *Annual Review of Plant Physiology and Plant Molecular Biology*, 42, 579-620.
- Villagarcía, L., Were, A., Domingo, F., García, M., Alados-Arboledos, L. (2007) Estimation of soil boundary-layer resistance in sparse semiarid stands for evapotranspiration modelling. *Journal of Hydrology* 342: 173-183.
- Vogel, S. (1970). Convective cooling at low airspeeds and the shapes of broad leaves. *Journal of Experimental Botany*, 21, 91–101.

- Vogel, S. (2009) Leaves in the lowest and highest winds: temperature, force and shape. *New Phytologist*, 183, 13–26.
- Wahid A., Gelani S., Asjraf M., & Foolad M. R. (2007). Heat tolerance in plants: an overview. *Environmental and Experimental Botany*, 61, 199-223.
- Wang, L., Ma, K. B., Lu, Z. G., Ren, S. X., Jiang, H. R., Cui, J. W., Chen, G., Teng, H. J., Lam, H. M., & Jin B. (2020). Differential physiological, transcriptomic and metabolomic responses of *Arabidopsis* leaves under prolonged warming and heat shock. *BMC Plant Biology*, 20, 86.
- Wang, X., Cai, J., Liu, F., Jin, M., Yu, H., Jiang, D., Wollenweber, B., Dai, T., & Cao, W. (2012). Pre-anthesis high temperature acclimation alleviates the negative effects of post anthesis heat stress on stem stored carbohydrates remobilization and grain starch accumulation in wheat. *Journal of Cereal Science*, 55, 331–336.
- Wang, Y., Tao, H., Tian, B., Sheng, D., Xu, C., Zhou, H., Huang, S., & Wang, Pu. (2019). Flowering dynamics, pollen, and pistil contribution to grain yield in response to high temperature during maize flowering. *Environmental and Experimental Botany*, 158, 80-88.
- Way, D.A., & Oren, R. (2010) Differential responses to increased growth temperatures between trees from different functional groups and biomes: A review and synthesis of data. *Tree Physiology*, 30, 669-688.
- Way, D.A., & Sage, R.F. (2008) Elevated growth temperatures reduce the carbon gain of black spruce (*Picea mariana* (Mill.) B.S.P.). *Global Change Biology*, 14, 624-636.
- Way, D.A., Schnitzler, J.-P., Monson, R.K., & Jackson, R.B. (2011) Enhanced isoprene-related tolerance of heat- and light-stressed photosynthesis at low, but not high, CO₂ concentrations. *Oecologia*, 166, 273-282.
- Westreenen, A. V., Zhang, N., Douma, J. C., Evers, J. B., Anten, N. P. R., & Marcelis, L. F. M. (2020). Substantial differences occur between canopy and ambient climate: Quantification of interactions in a greenhouse-canopy system. *PLOS ONE*, 15(5), e0233210.
- Wu, C., Cui, K., Wang, W., Li, Q., Fahad, S., Hu, Q., Huang, J., Nie, L., & Peng, S. (2016). Heat-induced phytohormone changes are associated with disrupted early reproductive development and reduced yield in rice. *Scientific Reports*, 6, 34978.
- Wu, W., Shah, F., Duncan, R. W., & Ma, B. L. (2020). Grain yield, root growth habit and lodging of eight oilseed rape genotypes in response to a short period of heat stress during flowering. *Agricultural and Forest Meteorology*, 287, 107954.

- Xu, J., Henry, A., & Sreenivasulu, N. (2020). Rice yield formation under high day and night temperatures-A prerequisite to ensure future food security. *Plant, Cell and Environment*, 43, 1595-1608.
- Yadav, A., Singh, J., Ranjan, K., Kumar, P., Khanna, S., Gupta, M., Kumar, V., Wani, S. H., & Sirohi, A. (2020). Heat Shock Proteins: Master Players for Heat-stress Tolerance in Plants during Climate Change. In: *Heat Stress Tolerance in Plants: Physiological, Molecular and Genetic Perspectives* Eds. Wani S.H., Kumar V. pp. 189-211. John Wiley & Sons Ltd.
- Yang, H., Gu, X., Ding, M., Lu, W., & Lu, D. (2018). Heat stress during grain filling affects activities of enzymes involved in grain protein and starch synthesis in waxy maize. *Scientific Reports*, 8, 15665.
- Yeh, C. H., Kaplinsky, N. J., Hu, C., & Charng, Y. Y. (2012). Some like it hot, some like it warm: Phenotyping to explore thermotolerance diversity. *Plant Science*, 195, 10-23.
- Yonghui, F., Chuanxi, M., Zhenglai, H., Muhammad, A., Suyu, J., Tingbo, D., Wenjing, Z., Shangyu, M., Dongguo, J., & Xiao, H. (2018). Heat priming during early reproductive stages enhances thermo-tolerance to post-anthesis heat stress via improving photosynthesis and plant productivity in winter wheat (*Triticum aestivum* L.). *Frontiers in Plant Science*, 9, 805.
- Zampieri, M., Ceglar, A., Dentener, F., & Toreti, A. (2017). Wheat yield loss attributable to heat waves, drought and water excess at the global, national and subnational scales. *Environmental Research Letters*, 12, 064008.
- Zhang, X., Lei, L., Lai, J., Zhao, H., & Song, W. (2018). Effects of drought stress and water recovery on physiological responses and gene expression in maize seedlings. *BMC Plant Biology*, 18, 68.
- Zhang, Z., Yang, Z., Fahad, S., Zhang, T., Xu, W., Cui, K., Peng, S. & Huang, J. (2020). A hot-blast warming facility for simulating global warming in low-stature crop systems and its application case to assess elevated temperature effects on rice in Central China. *Plant methods*, 16, 57.
- Zinn, K. E., Tunc-Ozdemir, M., & Harper, J. F. (2010). Temperature stress and plant sexual reproduction: uncovering the weakest links. *Journal of Experimental Botany*, 61(7), 1959–1968.