The Heat is On: How Crops Respond to High Temperature

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Abstract

Plants are exposed to a wide range of temperatures during their life cycle and need to continuously adapt. These adaptations need to deal with temperature changes on a daily and seasonal level and with temperatures affected by climate change, and need to take into account that different organs have different optimal temperature ranges. Increasing global temperatures impact crop performance, and several physiological and developmental responses to increased temperature have been described that allow to mitigate this. In this review, we assess various developmental, physiological and biochemical responses of crops to high temperature, focusing on knowledge gained from both monocots (e.g. wheat, barley, maize, rice) and dicots (e.g. soybean or tomato). We outline several outstanding questions where crop research can exploit knowledge from model plants, such as Arabidopsis thaliana, and we highlight that studying molecular mechanisms directly in relevant crops is essential.

KEYWORDS

(High) temperature, crop, monocot, dicot, wheat, tomato, maize, rice, soybean, root, flowering, seed dormancy, shoot

1. Introduction

Plants face a wide range of temperatures during their life cycle, both on a daily and seasonal level, and need to continuously adapt (Gourdji, Sibley, & Lobell, 2013; Hatfield et al., 2011; Lobell & Gourdji, 2012; Ray, Gerber, MacDonald, & West, 2015) (**Figure 1A-B**). In addition to aboveground organs, root systems are also exposed to a soil temperature range dependent on radiation absorption, reflection and permeation, with most variation in the topsoil (Farias et al., 2018; H. Lu et al., 2020; Ren et al., 2017) (**Figure 1C**). Furthermore, due to global warming (**Figure 1D**), crops are exposed to greater variation in environmental conditions, and this has an impact on their performance (Asseng et al., 2014; Lesk, Rowhani, & Ramankutty, 2016; Liu et al., 2016; Lobell & Gourdji, 2012; Lobell, Schlenker, & Costa-Roberts, 2011; Schauberger et al., 2017; Tack, Barkley, & Nalley, 2015). The yield of staple crops (e.g. wheat, maize, rice, and soybean) already significantly dropped due to increased temperature (Lobell et al., 2011; Lobell, Sibley, & Ivan Ortiz-Monasterio, 2012; Zhao et al., 2017), and this impacts the future demands of the increasing world's population (World Resources Institute, 2018). Furthermore, it has been estimated that for each degree Celsius (°C) increase, crop production will reduce by 6% (wheat) or 10-12% (rice), thus impacting global food security further (Asseng et al., 2014; Nelson et al., 2010). In this context, nearly all the warmest years in the last 136 years have occurred since 2000 (**Figure 1D)** and temperature is predicted to increase even further in the coming decades, with up to 4.8°C by 2100 and with a likely increase of at least 1.5°C (Global Climate Change, 2020; The Intergovernmental Panel on Climate Change (IPCC), 2007).

Several physiological and developmental responses to increased temperature have been described. Heat stress is defined as the increase in temperature above a critical threshold for a period of time sufficient to cause irreversible damage to plant growth and development, even death, which is frequently occurring during a hot season. Moderately high temperature causes morphological or photosynthetic changes that together are likely to contribute to adaptive growth acclimation to otherwise detrimental high ambient temperature

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conditions (Lippmann, Babben, Menger, Delker, & Quint, 2019; Quint et al., 2016; Vu, Xu, Gevaert, & De Smet, 2019). Unlike warm temperature acclimation during vegetative development, (early) reproductive development is more vulnerable to moderately warm temperature, which directly causes grain yield reduction (Draeger et al., 2020; Hedhly, Hormaza, & Herrero, 2009). Physiological effects of high temperature on crops include protein denaturation, aggregation and degradation, degradation of chlorophyll, increased fluidity of membrane lipids, increased membrane permeability, disruption of cell organelle function, inhibition of protein synthesis, reduced rate of net photosynthesis, and cell death (Cossani & Reynolds, 2012; Los & Murata, 2004; Nagar, Singh, Arora, Dhakar, & Ramakrishnan, 2015). Furthermore, warm temperature is likely to shorten the time of growth and development of many crop species, and further affects grain number (when heat stress occurs before anthesis, at meiosis), seed size and early seed setting, accelerates senescence in photosynthetic organs and induces chlorophyll loss, thereby limiting seed setting (Asseng et al., 2014; Hatfield et al., 2011; Wang, Dinler, Vignjevic, Jacobsen, & Wollenweber, 2015; Zhao et al., 2016).

In this review, we assess various thermal responses of crops, focusing on knowledge gained from both monocots (e.g. wheat, barley, maize, rice) and dicots (e.g. soybean or tomato), at different developmental stages. These responses include architecture, photosynthesis during vegetative development, early reproductive phase (e.g. floral transition, and inflorescence, pollen and pistil development) and late generative stage (seed and fruit setting and development). Additionally, crosstalk between high temperature and biotic stresses is assessed. We discuss some molecular mechanisms underlying the physiological and developmental changes caused by moderate or critical high temperature, from which biotechnological and breeding strategies can benefit (Chen et al., 2020; Shen et al., 2019; South, Cavanagh, Liu, & Ort, 2019; Whitney, Birch, Kelso, Beck, & Kapralov, 2015).

2. Optimum temperature varies according to CROP species and developmental stage

Different plant species respond differently to the wide range of temperatures they are exposed to throughout their life cycle. Each species, shows a minimum, maximum or optimum temperature that regulates growth and that is specific for a particular developmental stage (Hatfield et al., 2011). It is obviously not surprising that the average optimal temperature for growth and developmental progression tends to be lower for the crops originating from temperate regions than for the species from subtropical or even tropical zones (**Figure 2A**).

Warm season crops (e.g. maize, rice, tomato and soybean) generally have a higher optimum temperature from emergence to the vegetative growth and development than those crops from temperate zones (e.g. wheat and barley), which are in the range of 25-32°C and 15-25°C, respectively (Ali Tahir, Nakata, Yamaguchi, Nakano, & Mukhtar Ali, 2015; Alsajri et al., 2019; Cannell, 1969; Chavan, Duursma, Tausz, & Ghannoum, 2019; Ford et al., 2016; Friend, 1965; Garmash, 2005; Hakim, Hossain, Teixeira da Silva, Zvolinsky, & Khan, 2012; Havko et al., 2020; Hemming, Walford, Fieg, Dennis, & Trevaskis, 2012; Jumrani & Bhatia, 2018; Krishnan, Ramakrishnan, Reddy, & Reddy, 2011; Liu et al., 2020; T. Lu et al., 2017; Lyu et al., 2020; Sanchez, Rasmussen, & Porter, 2014; Singh, Reddy, Reddy, & Gao, 2014; Tsai, Weng, Chen, Lin, & Tsai, 2019; Yoshida, 1973) (**Figure 2B and Table 1**).

For (cereal) crops with a winter habit, low temperature (referred to as vernalization) is, next to photoperiod, the most important environmental cue to stimulate the transition into the reproductive stage (Dixon et al., 2019; Kiss et al., 2017). Crops with a spring habit only depend on photoperiod (Gol, Tome, & von Korff, 2017). After the transition to reproductive development, the plant is more vulnerable to elevated temperature than the vegetative phase and high temperature causes yield (seed and fruit set) reduction (**Figure 2B and Table 1**) (Draeger et al., 2020; Hedhly et al., 2009). The optimum temperature range for floral development in wheat and barley under inductive photoperiod conditions is 15-20°C (Dixon et al., 2019; Draeger et al., 2020; Draeger & Moore, 2017; Ejaz & von Korff, 2017; Ford et al., 2016; Hemming et al., 2012; Oshino et al., 2007; Oshino et al., 2011), while for (sub)tropical crops this range is relatively higher (24-30°C) from the transition (double-ridge initiation or flower initiation) to pre-anthesis (**Table 1**) (Ayenan et al., 2019; Begcy et al., 2019; Dielen, Lecouvet, Dupont, & Kinet, 2001; Lyu et al., 2020; Martínez-Eixarch & Ellis, 2015; Sanchez et al., 2014; Suwa et al., 2010; Thomas & Raper, 1978; Xu, Wolters-Arts, Mariani, Huber, & Rieu, 2017).

During flowering, a temperature higher than 30-33°C increases the risk of spikelet sterility in conventional rice (Bheemanahalli et al., 2017; Jagadish, Craufurd, & Wheeler, 2007; Shi et al., 2018; Zhang et al., 2018). Male fertility is reduced in maize and soybean as the temperature rises above 28-33°C and 26-30°C, respectively (Djanaguiraman, Prasad, Boyle, & Schapaugh, 2011; Sanchez et al., 2014; Thomas & Raper, 1978; Wang, Tao, et al., 2019; Wang et al., 2020; Wiebbecke, Graham, Cianzio, & Palmer, 2012). Wheat and barley have an optimum temperature range during the flowering of around 18-21°C (Alghabari, Lukac, Jones, & Gooding, 2014; Ejaz & von Korff, 2017; Porter & Gawith, 1999; Saini, Sedgley, & Aspinall, 1983, 1984; Sakata, Takahashi, Nishiyama, & Higashitani, 2000). The optimal temperature during the generative phases of the subtropical crop tomato, encompassing most developmental stages from reproductive to fruit development, is at a relatively intermediate range (21-25°C) (Ayenan et al., 2019; Dielen et al., 2001; Goldberg, Beals, & Sanders, 1993; Paupière et al., 2017; Peet, Willits, & Gardner, 1997; Xu et al., 2017) (**Table 1**). However, the optimal temperature range for post-anthesis development, such as early seed and fruit-setting phases, in many crops is sometimes slightly lower compared to other developmental stages (Sato, Peet, & Thomas, 2002; Sehgal et al., 2018) (**Figure 2B and Table 1**). For example, the optimal range for post-anthesis development for maize is 24-29°C (Commuri & Jones, 2001; Sanchez et al., 2014) and 13-18°C for wheat and barley (Abdelrahman, Ishii, El-Sayed, & Tran, 2020; Cochrane, Paterson, & Gould, 2000; Howard et al., 2012; Kino, Pellny, Mitchell, Gonzalez-Uriarte, & Tosi, 2020; Koga et al., 2016; Wardlaw, 2002).

Soil temperature, which is several degrees lower than the air temperature (Shen, McLaughlin, Zhang, Xu, & Liang, 2018), plays an essential role in the underground root growth and development, and affects the uptake and transport of water and nutrients (Koevoets, Venema, Elzenga, & Testerink, 2016). Depending on the climate, the soil shows distinct temperature regimes. In temperate latitudes, a large majority of soil types are grouped and classified accordingly to their temperature as being mesic (mean annual temperatures: >8 °C & <15 °C), thermic (>15 & <22 °C) and hyperthermic soil (>22 °C) (USDA - Natural Resources Conservation Service, 2020). This definition solely considers mean annual temperatures, but seasonal differences may exceed ± 5°C (e.g. summer and winter). In parallel, tropical latitudes are grouped in similar categories but receive the "iso" prefix (e.g isomesic (>8°C and <15°C), isothermic (mean annual temperatures: >15°C and <22°C) or isohyperthermic (mean annual temperatures: >22 °C) and therefore, experience a narrower range of variation in between seasons (< ± 5°C). Plants develop adaptive traits to overcome limitations imposed by extreme soil temperature in their habitat (Garrett, Huynh, & North, 2010; Iversen et al., 2014; Martre, North, Bobich, & Nobel, 2002). Despite the fact that some polar plants are capable of maintaining growth under extremely low temperatures in cold soils (1-3°C), optimum root growth occurs at 12-20 °C (K. Bell & Bliss, 1978). Commonly, temperature fluctuates for the topsoil, and tends to gradually stabilize with depth (**Figure 1C**) (Aydin, Sisman, Gültekin, & Dehghan B, 2015; Chakrabarti, Singh, Kumar, Harit, & Misra, 2013; Pramanik et al., 2018). For instance, in the zone of the temperate crop wheat, the mean soil surface temperature fluctuates between 13-17°C (Chakrabarti et al., 2013). A similar top soil temperature fluctuation is observed in the zone of the tropical crop maize, but with higher absolute temperatures compared to the temperate zone (Pramanik et al., 2018; Yin et al., 2016).

Several key biochemical processes also have optimal temperatures: photosynthesis mainly depends on daytime temperature, while night-time temperature affects respiration (Dusenge, Duarte, & Way, 2019). The maximal rate of net photosynthesis is, depending on the variety, 30°C-35°C/23°C (day/night) in rice (Bahuguna, Solis, Shi, & Jagadish, 2017; Weng & Chen, 1987). In maize, relative photosynthesis reaches a maximum at 38-40°C/22-26°C, but sharply drops when the air temperature rises above 40°C (Rotundo, Tang, & Messina, 2019; Wang et al., 2020). In tomato and soybean, the maximal photosynthetic rate is at the range of 25-30°C/15°C and 28-35°C/18-22°C, respectively (Camejo et al., 2005; Djanaguiraman et al., 2011; T. Lu et al., 2017; Wiebbecke et al., 2012). In contrast, in wheat and barley, photosynthetic activity is already negatively affected when the ambient temperature is above 25°C/15°C (day/night) (Djanaguiraman, Boyle, Welti, Jagadish, & Prasad, 2018; Impa et al., 2019; Jedmowski & Bruggemann, 2015; Oukarroum, El Madidi, & Strasser, 2016; Posch et al., 2019) (**Figure 2B and Table 1**).

3. Growth adaptations to high temperature

While extremely high temperature (e.g. heat-shock above 40°C) can be detrimental (Camejo et al., 2006; Vara Prasad, Boote, Hartwell Allen Jr, & Thomas, 2003; Yang, Sears, Gill, & Paulsen, 2002), a milder increase in temperature can impact growth in two ways. First, warm temperature can increase the rate of growth of a given organ and proportionally decrease its growth duration without impacting the final plant body (Heschel et al., 2007; Parent & Tardieu, 2012). Second, warm temperature can accelerate growth impacting the plant body to improve evaporative cooling, increasing convection and directly avoiding heat flux from the sun (Havko et al., 2020; Rosado et al., 2019).

3.1. Coordinated growth responses

The rates of seed germination, leaf appearance, tillering or branching and leaf expansion show coordinated responses to warm temperature in crops (Parent & Tardieu, 2012), but with large variation among different cultivars from the same species (Bahuguna et al., 2014; Friend, 1965; Li, Kennedy, Huybrechts, Dochy, & Geuten, 2019). High temperature delays the start of stem elongation and results in faster stem growth rates, but without modifying total time to heading in wheat and barley (Borràs-Gelonch, Denti, B Thomas, & Romagosa, 2011; Karsai et al., 2013; Kiss et al., 2017). However, a temperature above the optimum decreases the number of leaves and tillers, as well as final stem height (Dixon et al., 2019; Hemming et al., 2012; Karsai et al., 2013). Some species, however, react differently to elevated ambient temperatures during vegetative growth. For example, soybean does not exhibit big changes during vegetative development at higher temperatures (Choi, Ban, Seo, Lee, & Lee, 2016; Lippmann et al., 2019).

3.2. Shoot architecture

In *Arabidopsis* , there is a suite of morphological changes (e.g. hypocotyl and petiole elongation, leaf hyponasty, and decreased stomatal density) induced by high ambient temperatures referred to as thermomorphogenesis (Casal & Balasubramanian, 2019; Quint et al., 2016; Vu et al., 2019). Similarly, warm temperature improves the cooling ability of tomato by promoting stomatal opening and leaf hyponasty (Havko et al., 2020). Although different crop species originating from various climates have strikingly common response curves of developmental processes over a whole temperature range (6-37), each species has its own optimum temperature range to promote maximum growth (Parent & Tardieu, 2012). The leaf and coleoptile of monocot seedlings (wheat, barley, rice and maize) or the hypocotyl of dicots (soybean and tomato) are maximally elongated at moderately high temperatures (Alsajri et al., 2019; Parent & Tardieu, 2012; Quint et al., 2016) (**Figure 3**). However, while in, for example *Arabidopsis thaliana* and tomato, these rapid architectural changes are associated with leaf cooling (Crawford, McLachlan, Hetherington, & Franklin, 2012; Havko et al., 2020; Park et al., 2019; Rosado et al., 2019), this has not been shown in economically important cereal crops.

3.3. Root system architecture

The root system is exposed to a heterogenous matrix of soil in a range of environmental conditions, including a soil temperature gradient (Lundholm, 2009; Onwuka, 2016; Ulrich et al., 2014). The responses to supraoptimum temperature include a decrease in primary root length, lateral root density and changes in angle under which roots emerge (McMichael & Quisenberry, 1993; Nagel et al., 2009; Seiler, 1998). These changes in the root system architecture impact on nutrient uptake, but also affect response effectiveness to other stresses, such as drought (Hendrick & Pregitzer, 1996). Different species show distinct optimum temperatures for root system architecture responses (Gray & Brady, 2016; Luo, Xu, Chu, He, & Fang, 2020; Walter, Silk, & Schurr, 2009) (**Table 1**). In contrast to aboveground optimum temperature responses, the root system usually shows a narrower range for suitable growth (**Table 1**). Garden pea displays a decreasing trend in primary root growth rate and lateral root development is inhibited as the temperature shifts from cold (15degC) to warm (32degC) temperature (Gladish & Rost, 1993). However, garden pea seedlings exposed to 32degC for 17 days that showed inhibition of primary root elongation, are capable of restoring root growth to a normal state when transferred to 25degC (Gladish & Rost, 1993). Similarly, soybean shows a considerable decrease in parameters related to general root growth (e.g. root surface area, cumulative root length and root volume) when submitted to a heat-temperature regime (40/32) compared to the control (30/22) (Alsajri

et al., 2019). In contrast, root secondary developmental parameters are enriched in the high temperature regime (e.g. number of root tips and root forks) (Alsajri et al., 2019). With respect to cereal crops, twenty one-day old wheat plants submitted to 36/28 (day/night regime) show a significant reduction in several root parameters when compared to the control at 25/20, such as a decrease in root biomass, shoot-to-root ratio, primary root length, root surface area and root volume (Rehman, Farooq, Asif, & Ozturk, 2019).

4. reproductive growth and development upon ambient temperature changes

Reproductive tissues and organs are developmentally more responsive to increased ambient temperature than vegetative parts (Boden, Kavanova, Finnegan, & Wigge, 2013), and some of the underlying molecular mechanisms are known.

4.1 Floral transition and development

Unlike dicots, such as *Arabidopsis*, in which the transition from the vegetative to the mature reproductive stage occurs in a shorter time, monocots (e.g. wheat and barley) show a long interval from days to weeks between first spikelet primordia formation, inside the leaf sheath up to the moment an ear is pushed out and the plant reaches the heading stage (Gauley & Boden, 2019; Gol et al., 2017). Therefore, those plants are more susceptible to supra-optimal temperature due to their long reproductive-phase establishment, leading to considerable loss of yield and grain quality (Bheemanahalli et al., 2019; Lohani, Singh, & Bhalla, 2019).

At the same time that warm temperatures can accelerate (e.g. *Arabidopsis*) or delay flowering (e.g. *Brassica rapa*), it also modifies the response of the plant to photoperiod, another major factor affecting floral transition (Capovilla, Schmid, & Pose, 2014; Del Olmo, Poza-Viejo, Pineiro, Jarillo, & Crevillen, 2019). A moderately warm temperature can trigger *Arabidopsis* floral transition under non-inductive short-day (SD) conditions (Balasubramanian, Sureshkumar, Lempe, & Weigel, 2006; Vu et al., 2019), or partially hasten soybean floral initiation under non-inductive long-day (LD) (Wu et al., 2015). Differentially, elevated ambient temperature cannot compensate for photoperiod as a floral inductive signal in some species, which indicates that the effects of ambient temperature on the reproductive development are highly photoperiod-dependent (Hemming et al., 2012; Kiss et al., 2017). For wheat, barley and *Brachypodium* grown under LD conditions, warm temperatures shorten the time to floral transition (Boden et al., 2013; Dixon et al., 2018; Dixon et al., 2019; Hemming et al., 2012). In contrast, an increase in temperature delays the floral transition and development under SD condition (**Figure 4A**). In*Arabidopsis*, high temperature is able to induce the expression of flowering-promoting genes, such as *FLOWERING LOCUS T* (*FT*) under non-inductive SD (Casal & Balasubramanian, 2019; Vu et al., 2019). In contrast, transcript levels of the barley and wheat ortholog of *FLOWERING LOCUS T1* (*FT1*), do not increase upon high temperature treatments in short days (Dixon et al., 2018; Hemming et al., 2012; Kiss et al., 2017), suggesting *FT1* -independent high temperature responsiveness of flowering in cereals (Jacott & Boden, 2020). In maize, time to tasseling is advanced by higher temperature, but there is no effect on the silking time (Wang et al., 2019). Notably, rice floral meristem initiation and development benefits from its flooded cultivation, since the early reproductive stages are accomplished under water, where air high temperature is buffered, but the heading is generally accelerated by high temperature (Chen et al., 2018; Hu et al., 2015; Jagadish, Murty, & Quick, 2015).

Besides photoperiod-dependent temperature responses, vernalization regulates floral transition in winter cereal crops. *VERNALIZATION 1* (*VRN1*), a floral activator and its expression is induced under cold temperatures. The flowering repressor *VRN2* , decreased expression to reduce VRN2-regulated repression of the central flowering activator *FT1* (Huan, Mao, Chong, & Zhang, 2018; Kim, Doyle, Sung, & Amasino, 2009; Kippes et al., 2015; Oliver, Finnegan, Dennis, Peacock, & Trevaskis, 2009; Yan et al., 2006; Yan et al., 2004; Yan et al., 2003). Temperature shifts, such as those caused by climate change, hinder vernalization, which is referred to as de-vernalization (Gregory & Purvis, 1948; Mergner et al., 2020). Warm temperature-induced interruption of vernalization accelerates flowering in wheat and barley under LD photoperiod, resulting in the formation of additional spikelets due to a delay in the early stages of inflorescence development (Dixon et al., 2019; Ejaz & von Korff, 2017; Greenup et al., 2011) (**Figure 4B**).

In contrast to plastic vegetative development under high temperature, reproductive characteristics like floral

identity often show low plasticity (or phenotypic robustness / stability) against environmental fluctuation (Fal et al., 2019; Klingenberg, 2019). For instance, the rice *EXTRA GLUME 1* (*EG1*) gene, encodes predominantly mitochondria-localized functional lipase, which functions upstream of some floral identity genes (*OsMADS1* , *OsMADS6* and *OsG1*) to promote floral developmental robustness in a high temperature-dependent manner (Zhang et al., 2016).

4.2 Stamen and pistil growth and development

As many crop reproductive processes usually occur in late spring or early summer (Hedhly et al., 2009), these are more likely to be affected by high ambient temperature or heat stress than vegetative stages (Draeger & Moore, 2017). Obviously, temperature extremes or heat waves are more immediate and harmful to reproductive tissues than high ambient temperature (Draeger & Moore, 2017; Jagadish et al., 2010; Prasad & Djanaguiraman, 2014; Saini et al., 1983, 1984; Wang, Tao, et al., 2019). High temperature affects both male and female reproductive organs, such as anther development (Draeger & Moore, 2017; Yu et al., 2017), pollen formation and viability (Djanaguiraman, Prasad, Boyle, & Schapaugh, 2013; Feng et al., 2018; Gonzalo et al., 2020; Wang, Tao, et al., 2019), size of anther dehiscence for pollen dispersal (Jagadish et al., 2010; Matsui & Hasegawa, 2019), filament elongation (Sakata et al., 2010), germinative ability on the stigma (Begcy et al., 2019; Djanaguiraman et al., 2013; Endo et al., 2009; Gonzalo et al., 2020; Shi et al., 2018), pollen tube elongation in the pistil (Saini et al., 1983; Shi et al., 2018; Zhang et al., 2018), stigma receptivity and ovule viability (Hedhly, 2011), and pollen–pistil developmental synchrony that is prerequisite for pollination success (Hedhly et al., 2009; Herrero, 2003) **(Figure 4C)** . Noteworthy, all the causes of reproductive organ sterility are differentially affected by short-term or long-term high temperature exposure (Karapanos, Akoumianakis, Olympios, & Passam, 2010; Zhang et al., 2018).

The tapetum plays an important role in providing nutrients for pollen development (Shi, Cui, Yang, Kim, & Zhang, 2015; Suzuki, Takeda, Tsukaguchi, & Egawa, 2001). In rice, the leucine-rich repeat-receptor-like kinase, Thermo-Sensitive Genic Male Sterile 10 (TMS10), is essential for tapetal degeneration and pollen formation to maintain normal male fertility under high ambient temperature (Yu et al., 2017). Failure of rice pollen-stigma adhesion and germination on the stigma caused by high temperature is the result of downregulated expression of two genes, *AK106843* (encoding CYP703) and *AK106946* (encoding a GDSL type lipase), which are involved in controlling lipid components of the pollen wall in the tapetal cells (Endo et al., 2009). High temperature-induced impairment of maize pollen tube growth results from the mis-regulated expression of genes involved in the production of energy and lipids that mediate pollen tube growth (Begcy et al., 2019). In addition, rice sterility is caused by cessation of pollen tube elongation due to heat-induced reduction of endogenous auxin in pollinated pistils (Zhang et al., 2018). A sharp decrease in endogenous auxin resulting from warm temperature-induced downregulation of *YUCCA* auxin biosynthesis genes also causes male sterility in barley and *Arabidopsis* (Sakata et al., 2010). Application of auxin completely reversed male sterility (Sakata et al., 2010; Zhang et al., 2018). This is in sharp contrast with, for example, *Arabidopsis* hypocotyls where high temperature promotes auxin biosynthesis to control growth (Bellstaedt et al., 2019; Gray, Ostin, Sandberg, Romano, & Estelle, 1998).

5.3 Seed and fruit-setting

Compared to other reproductive phases, the early seed and fruit-setting stages are more sensitive to temperature changes (**Table 1**). One of the consequences of warm temperature or heat stress is the accelerated senescence of terminal leaves, in which the majority of assimilates that are translocated to the seeds or fruit are fixed, which leads to loss of photosynthetic ability (Barlow, Christy, O'Leary, Riffkin, & Nuttall, 2015; Gourdji et al., 2013; Ishibashi, Yuasa, & Iwaya-Inoue, 2018; Marcelis & Baan Hofman-Eijer, 1993; Pimentel et al., 2015; Stratonovitch & Semenov, 2015; Suwa et al., 2010; Y. Wang et al., 2019; Xu et al., 2020). On the other hand, the expansion of tomato fruits is positively regulated by increasing temperature (10-30degC) and less related to assimilate supply. However, fruit maturity is hastened by elevated temperature, resulting in a reduction of final mean weight in tomato fruits (Adams, Cockshull, & Cave, 2001; Pearce, Grange, & Hardwick, 1993). Additionally, a shortened seed or fruit-setting duration by high temperature, also results in a significant reduction in final weight (Boden et al., 2013; Sato et al., 2002; Shi et al., 2017).

Short periods or pulses of high temperature result in uneven ripening and softness of tomato fruit, reducing the fruit quality (Mulholland, Edmondson, Fussell, Basham, & Ho, 2003). In addition, high temperature-induced inactive PHYA and PHYB1/B2 leads to the reduction of tomato fruit carotenoid content (Bianchetti et al., 2020). It is noteworthy that the effect of increased temperature (> 35degC) on ethylene production, color development, and softening is reversible (Lurie, Handros, Fallik, & Shapira, 1996).

Chromatin remodeling plays an essential role in gene expression (Eckardt, 2007; Ojolo et al., 2018), and also during high temperature-controlled seed setting (Boden et al., 2013). In *Brachypodium* , the *H2A.Z* transcript level is stable with temperature, but at high temperature H2A.Z occupation is reduced and chromatin accessibility for RNA polymerase II is increased, which upregulates the transcription of starch catabolism-related genes (e.g. *beta-amylase* (*AMY1*) and *UDP-glucose pyrophosphorylase* (*UDP-GPP*)) during the seed-setting stage and strongly reduces yield (Boden et al., 2013) **(Figure 4D)** . Additionally, *Brachypodium* seed weight and overall yield is reduced in *ACTIN-RELATED PROTEIN6* (*ARP6*) knock-down lines under high temperature, where ARP6 is required for proper H2A.Z deposition. Indeed, also in *Arabidopsis* H2A.Z is involved in temperature-dependent flowering (Kumar & Wigge, 2010), making this a more general regulatory mechanism at high temperature. In addition, alternative splicing has been shown to play an essential role in temperature sensing and adaption during seed setting (Xu et al., 2020; Zhang et al., 2014). The lower activity of *OsbZIP58* is induced by alternative splicing under high temperature and inhibits the accumulation of storage materials (such as starch and lipids) during the seed-setting stage (Xu et al., 2020). High temperature also promotes the splicing efficiency of the rice *Wx* gene to maintain proper amylose content during the seed-setting stage (Zhang et al., 2014).

5. THE ROLE OF TEMPERATURE IN seed germination

Dormancy is one of the most important factors inhibiting seed germination and hindering productivity of field crops (Bentsink & Koornneef, 2008; Yildiz et al., 2017). Survival of a dormant seed is ensured by showing apparent metabolic arrest, enduring unfavorable environmental conditions and timing germination for the correct season (Bentsink & Koornneef, 2008; Bewley, 1997; Roberts, 1972a). Even at a dormant state, seeds continuously deteriorate and are still susceptible to a wide range of environmental fluctuations, such as temperature, moisture content and oxygen pressure, lately influencing seed viability (Ellis & Roberts, 1980a, 1980b; Owen & Ashton, 1956; Roberts, 1972b). Specifically, seed exposure to warm temperatures for a long period of time may act as catalyzer for dehydration (Berjak & Pammenter, 2013; Silva, 1998; Syeda, Khan, & Mohmand, 2000). For instance, rice and wheat seeds exposed to warm temperatures, 40degC for 40 days and 37-50degC for 12 months, respectively, show decreased longevity when compared to the control (Ellis, Hong, & Jackson, 1993; Nasreen, 1999).

The capacity to trigger seed germination at the right time is a key aspect in crop management and this is correlated with the level of seed dormancy (Benech-Arnold, Rodriguez, & Batlla, 2013). Deeply dormant seeds result in delayed germination or no germination at all even under favorable conditions, in contrast, a shallow dormant seed might exhibit pre-germination or even germinate while still attached to the mother plant, known as preharvest sprouting (Rodriguez, Barrero, Corbineau, Gubler, & Benech-Arnold, 2015; Soppe & Bentsink, 2016)(Fang & Chu, 2008; S. Liu et al., 2015). Breaking dormancy and coordinating germination is also critical during malt production, in which barley seeds undergo germination triggering processes (K. Shu et al., 2015; Ullrich, Han, & Jones, 1997). Although preharvest sprouting is highly species and genotype-dependent, it is mostly observed after exposing plants to a rainfall or high moisture air conditions, but also occurs upon exposing the plants to high temperatures during the grain ontogenesis stage (**Figure 4E**). During grain ontogenesis, low temperatures produce higher level of seed dormancy and better physiological mature seeds than control temperatures (Nyachiro, Clarke, DePauw, Knox, & Armstrong, 2002).

Among the genes extensively studied by having a role in germination, two of the most important players have their expression level regulated by temperature: *MOTHER OF FT AND TFL1* (*MFT*) and *DELAY OF GERMINATION 1* (*DOG1*) (Bentsink, Jowett, Hanhart, & Koornneef, 2006; Xi, Liu, Hou, & Yu, 2010). *MFT* is suggested to be the causal gene for the wheat seed dormancy QTL varying across a temperature range

(Nakamura et al., 2011). Grains from plants at seed-setting stage that were exposed to high temperatures regimes (25degC) show an abnormally low expression of *MFT* . In contrast, wheat grains matured under lower temperature (13degC) show an increased transcript level of *MFT* . In rice, *OsMFT2* knock-out lines showed preharvest sprouting under high temperature and rainy weather, whereas wild type plants and overexpression lines did not (Song et al., 2020). In parallel, *DOG1* transcript levels fluctuate according to both dormancy level and soil temperature in buried seeds, with low temperatures showing a higher level of *DOG1* than high temperatures (Footitt, Douterelo-Soler, Clay, & Finch-Savage, 2011; Graeber et al., 2014; Nakabayashi et al., 2012). *DOG1* is suggested to play a role in balancing ABA and GA levels by promoting ABA biosynthesis and GA catabolism, hormones known for promoting and breaking dormancy, respectively (P. Li, Ni, Ying, Wei, & hu, 2019; A. Yan & Chen, 2017).

In short, dormancy level and establishment during the seed maturing stages are tightly correlated to the temperature plants or seeds are exposed to. Generally, lower temperatures result in increased dormancy depth; in contrast, plants or seeds exposed to supra-optimum temperature regimes show shallow dormancy, and therefore may drive occurrence of undesirable events such as preharvest sprouting. For crops, the domestication process already resulted in selection of less dormant cultivars than the ones found in the nature (Benech-Arnold et al., 2013); however, with the warming trend observed and predicted for climate changes, seed dormancy level might decrease even more, leading to more common productivity losses and decrease in grain quality.

After dormancy is broken by exposing the seed to specific conditions, environmental factors, such as temperature, trigger physiological and biochemical processes causing the seed to germinate. Although temperature positively correlates with accelerated germination for multiple species (Barpete et al., 2015; Buriro et al., 2011), once the species-optimum temperature is reached, every increase from that point decreases germination rate rapidly (Lamichhane et al., 2019; Tyagi & Tripathi, 1983).

7. BIOCHEMICAL PROCESSES UNDER HIGH TEMPERATURE

High temperature affects several biochemical processes in plants. High day temperature impacts photosynthesis (light-dependent reactions and carbon assimilation) and photorespiration (Ahammed, Xu, Liu, & Chen, 2018; Ainsworth & Ort, 2010; Bianchetti et al., 2020; Crafts-Brandner & Salvucci, 2002; Gupta et al., 2013; Kume, Akitsu, & Nasahara, 2019; Lipova, Krchnak, Komenda, & Ilik, 2010; Nagar et al., 2015; Sharma, Andersen, Ottosen, & Rosenqvist, 2015), while respiration is mainly affected by high night temperature (Dusenge et al., 2019)**(Figure 5)** .

Rubisco activase (Rca) regulates the proportion of catalytically active Rubisco, the central photosynthetic enzyme (Bracher, Whitney, Hartl, & Hayer-Hartl, 2017; Portis Jr, 2003) **(Figure 5)** . Noteworthy, a functional *Rca* gene encodes two or more isoforms based on alternative splicing of pre-mRNA in a temperature-dependent manner. One of the isoforms is more thermotolerant in crops (Crafts-Brandner & Salvucci, 2002; Scafaro et al., 2018; Scafaro, Bautsoens, den Boer, Van Rie, & Galle, 2019; Yamori, Masumoto, Fukayama, & Makino, 2012; Yin et al., 2014).

Notably, efficient photosynthesis depends on how the Rubisco enzyme (carboxylase or oxygenase) discriminates between CO_2 and O_2 as the substrate **(Figure 5)** . Photorespiration, a major productivity limitation for C3 crops, is exacerbated as temperature increases. A decreased $[CO_2]/[O_2]$ ratio due to the reduction of stomatal conductance caused by warm temperature, results in the decreased Rubisco specificity for CO_2 relative to O_2 (Walker, VanLoocke, Bernacchi, & Ort, 2016). Compared with Rubisco, the rate of regeneration of the CO_2 acceptor ribulose 1,5-bisphosphate (RuBP) is more sensitive to higher temperature (e.g. less ATP supply caused by the impaired electron transport) (Sage, 2002). In maize, however, Rca and Rubisco activation are the major limitation to net photosynthesis (Crafts-Brandner & Salvucci, 2002).

In addition, mean night-time temperatures are rising at a faster rate than those during the daytime (Davy, Esau, Chernokulsky, Outten, & Zilitinkevich, 2017; Sadok & Jagadish, 2020), which speeds up respiration and results in crop yield and quality reduction (Coast, Šebela, Quiñones, & Jagadish, 2020; Dusenge et al., 2019; Impa et al., 2019; Impa et al., 2020; Schaarschmidt et al., 2020).

Acclimation of the above photosynthetic reactions to heat stress is significant when the temperature is elevated gradually, which, however, is less likely during sudden heat waves or intense heat stress (Posch et al., 2019; Way & Yamori, 2014). These plastic adjustments can allow plants to photosynthesize more efficiently at their new growth temperatures (Kaur, Sinha, & Bhunia, 2019; Ruiz-Vera, Siebers, Drag, Ort, & Bernacchi, 2015).

8. high temperature, A 'two-edgeD sword' in crop immunity

In addition to high temperature, plants also have to deal with biotic stresses (e.g. pathogens and pests) along their life cycle (Savary et al., 2019) and those are also affected by a shift in temperature (Bebber, Ramotowski, & Gurr, 2013). Insects propagate more at higher temperature and show increased feeding voracity across an increasing temperature range (Havko et al., 2020). In rice, high temperature contributes to bacterial blight development in field situations, and the disease severity is particularly high in the hot season (Dossa et al., 2020). For more examples related to high temperature-induced disease susceptibility we refer to a recent review (Cohen & Leach, 2020).

While plant defense mechanisms are required to ensure survival and maintain fitness, those usually come at the expense of plant growth, referred to as the "growth-defense tradeoff" (Züst & Agrawal, 2017). As thermomorphogenesis takes place by accelerating growth and development, plant immunity is profoundly affected in *Arabidposis*(Cheng et al., 2013). For instance, while PHYTOCHROME INTERACTING FACTOR 4 (PIF4), a bHLH transcription factor is stabilized and promotes temperature-mediated growth, it negatively regulates *Arabidopsis*immunity (S. Kim et al., 2020; Qiu, Li, Kim, Moore, & Chen, 2019). In addition, plant hormones linked to growth control, such as ABA, brassinosteroids and gibberellic acids, are also involved in plant-immunity pathways. Not rarely, mutants with constitutive activation of defense mechanisms impair growth (Bari & Jones, 2009; D.-L. Yang, Yang, & He, 2013). The accumulation of Heat-shock protein 90 after moderate heat stress correlates to an enhanced wound-induced JA response in tomato. Moreover, JA signaling at high temperature blocked stomata opening and hindered leaf hyponasty, having strong detrimental effects on photosynthesis and inhibiting growth (N. E. Havko et al., 2020).

Two types of high-temperature plant resistance to *Pst* are known: high-temperature seedling plant (HTSP) resistance and high-temperature adult plant (HTAP) resistance (Chen, 2013). For HTAP resistance to*Pst* in wheat, the kinase-START gene *Yr36 (WKS1)* (Fu et al., 2009) confers non race-specific resistance to stripe rust, and its expression is upregulated at moderate-high temperatures (25 - 35 °C). However, the resistance conferred by *Yr36* is lost at low temperature (e.g. 15°C) and increases plant susceptibility to infections (Fu et al., 2009). In addition, high temperature upregulates the expression of *TaXa21* (Wang, Shang, Chen, Xu, & Hu, 2019), a leucine-rich repeat receptor-like kinase gene. The transmembrane and kinase domains of TaXa21 interact with TaWRKY76, which plays a positive role in HTSP resistance to *Pst* (Wang, H. Shang, et al., 2019; J. Wang et al., 2017). Barley plants also show HTAP resistance to stripe rust, a fungal disease common to wheat and barley (Yan & Chen, 2008).

Bacterial blight caused by *Xanthomonas oryzae pv. oryzae*(*Xoo*) leads to substantial yield loss in rice (Dossa et al., 2020). *Xa7,* one of the *Resistance* genes *(R* -genes) against pathogens (Zhang et al., 2015), effectively confers resistance to *Xoo* at high temperatures, but not at low temperature (Cohen et al., 2017; Dossa et al., 2020; Webb et al., 2010). The other way around, some biotic stresses mitigate the impairment caused by high temperature stress in crops (Anfoka et al., 2016; Mathur, Sharma, & Jajoo, 2018). However, in the field, different crops are facing different devastating bacterial or fungal diseases with changing temperature, and further molecular mechanisms on low or high temperature-triggered resistance to pathogen diseases are still elusive.

9. BIOengineering CROPS FOR HIGH TEMPERATURE TOLERANCE

Several crop bioengineering approaches have been used in recent years to improve high temperature tolerance. For example, generating a nuclear origin supplementation pathway of the D1 protein (one of the core proteins involved in PSII repair system) to enhance rice photosynthesis by maintaining the capability of PSII repairment under heat stress (Chen et al., 2020). Additionally, thermostability of Rca is considered as

a promising way to improve photosynthesis and thermotolerance for crops exposed to warmer temperature or heat stress (Scafaro et al., 2019). For example, introduction of Rca from maize into rice slightly improves the thermotolerance with respect to photosynthesis (Yamori et al., 2012), but the underlying reasons are not clear. For the rate of regeneration of the CO_2 acceptor - RuBP, overexpressing a rice sedoheptulose-1,7-bisphophate (SBPase) in rice (Feng et al., 2007) or a bifunctional cyanobacterial fructose-1,6-bisphosphatase (FBP)/SBP in soybean under elevated temperature significantly increases carbon assimilation (Kohler et al., 2017). Additionally, C2 or C4 plants suffer less net carbon loss from photorespiration due to the carbon concentrating mechanisms (Bellasio & Farquhar, 2019; Keerberg, Parnik, Ivanova, Bassuner, & Bauwe, 2014; Kennedy & Laetsch, 1974; Khoshravesh et al., 2016). It is, therefore, likely that engineering C2 or C4 photosynthesis into C3 crops could have a large impact on crop production at high temperature (Bellasio & Farquhar, 2019; Lundgren, 2020).

Since daily temperature generally peaks at noon, which overlaps with the flowering time in some crops, one of the countermeasures is an effective heat escape mechanism (Jagadish, 2020). Therefore, naturally or genetically introducing flowering traits towards cooler times of day can potentially minimize heat stress damage on reproductive organs. Some dryland crops are able to optimize their anthesis during morning or cooler evening periods under heat stress (Aiqing et al., 2018; Bheemanahalli et al., 2019). In contrast, most rice varieties need the genetic introduction of early morning flowering trait to shift their flower opening time (Bheemanahalli et al., 2017; Jagadish, 2020).

Finally, high-temperature plant resistance to fugal disease, caused by stripe rust (*Puccinia striiformis* f. sp. *Tritici,Pst*) has been successfully used to develop durable resistant wheat cultivars (Tao et al., 2020; Uauy et al., 2005; Wang, H. Shang, et al., 2019; Wang et al., 2017; J. Wang et al., 2017; J. Wang et al., 2019; Zhou et al., 2014).

10. CONCLUSIONS AND OUTLOOK

With global climate change, increasing temperature has an enormous impact on crop productivity from seedling to mature stages. Climate-smart crops will benefit from a better understanding of high temperature-associated processes. Although our knowledge on these processes has increased a lot in crops, most of the regulatory mechanisms associated with high temperature have been explored in the model plant *Arabidopsis* and are still elusive in many crops. While in some cases the knowledge gained from Arabidopsis can be translated to crops, there are also many unique aspects to crops. For example, with respect to high temperature-regulated growth it is not clear if the same cooling role from dicots can be assigned to monocot crop plants. This warrants exploring high temperature-related mechanisms directly in the relevant crop.

Understanding the molecular mechanism of how early developmental delay is regulated is an important consideration, especially given that unseasonal warm weather will disrupt vernalization significantly affecting flowering and subsequent grain production in winter crops. For example, the slow, winter-long upregulation of *VERNALIZATION INSENSITIVE 3* (*VIN3*) through NTL8 in *Arabidopsis* , provides – in addition to direct thermosensing mechanisms – a long-term biological sensing of naturally fluctuating temperatures (Zhao, Antoniou-Kourounioti, Calder, Dean, & Howard, 2020).

In addition, crop yield and quality are affected by increased respiration caused by warmer night temperature, which is likely to occur in the near future. Understanding the molecular mechanisms underlying organ sterility at high temperature is an essential countermeasure for global warming. Given the complexity of high temperature responses (growth stages, different organs, time of day, multiple sensing mechanisms, etc), it is extremely difficult to capture this in breeding approaches. Dissection of the molecular responses that occur under warm (night-time) temperatures will therefore benefit from a multi-disciplinary approach that includes physiology, developmental biology and modelling.

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AUTHOR CONTRIBUTION

T.Z., C.F.F.D.L. and I.D.S. all contributed to the concept and writing of the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

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FIGURE LEGENDS

Figure 1. Temperature exposure of plants. (A) Average monthly temperature for Ghent (Belgium) between 1982 and 2012 (data retrieved from en.climate-data.org/europe/belgium/flanders/ghent-6350/t/july-7/).**(B)** Temperature in Melle (near Ghent) on 6th- 7th May 2020 (data retrieved from www.meteo.be/nl/weer/waarnemingen/belgie). **(C)** Hourly recorded soil temperature data in Redding (California, USA) in the station WBAN 04222 at distinct depths (5, 10, 20, 50, 100 cm) in October 2018 (data retrieved from www.ncdc.noaa.gov/crn/qcdatasets.html (J. E. Bell et al., 2013)). The blue, grey, red color indicate average cool, optimum and warm temperatures for distinct root systems, respectively. **(D)**Daily recorded mean temperatures by blended stations in Belgium (10-year moving average) from 1840-2019 (data retrieved from www.ecad.eu/dailydata/index.php). The temperature difference between the lowest and highest temperature in A, B and D is indicated in red.

Figure 2. Optimal temperature for crop plants. (A) Optimal temperature range of temperate, subtropical and tropical species for aboveground and belowground organs. **(B)** Optimal temperature ranges in four main developmental phases of crops and two biochemical processes. Tomato (left) and wheat (right) are shown as a dicot and monocot crop representative, respectively. The chloroplast and mitochondrion represent photosynthesis and respiration, respectively.

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Figure 3. Growth responses of crops under high temperature. Wheat (*Triticum aestivum* var. Chinese Spring) shoot length of 14-day-old seedlings grown at indicated temperature. Scale bar: 5 cm.

Figure 4. The effect of warm temperature and heat on various stages of reproductive development. (A) Warm temperature affects the floral transition in cereal crops in a photoperiod-dependent way. Green and yellow means leaf and spikelet primordia on the apical meristem. SD / LD, short-day / long-day conditions. **(B)**Interruption of vernalization by warm temperature accelerates development of winter-habit plants, and leads to additional spikelets under long-day conditions. Grey bar with six vertical lines in the middle presents the whole life cycle of barley or wheat plants. Blue bar represents cold exposure (vernalization). Red color indicates high temperature interruption. **(C)** The effects on anther and pistil development at optimum (left grey part) and warm (right red part) ambient temperature, respectively. Top shows pollen numbers within a transverse section of the anther. Middle shows impact on anther development (filament length and anther dehiscence) and pollen numbers, and the effect on auxin levels. Bottom shows pistil with elongating pollen tubes **(D)** H2A.Z occupancy affects early seed development in a temperature-dependent way in *Brachypodium* . **(E)**Representative example of pre-harvest sprouting in rice. Image reproduced from Kai Shu, Liu, Xie, and He (2016) with permission.

Figure 5. The effect of warm temperature and heat on photosynthesis. The left (grey) and right (red) part of the leaf represent optimum and high temperature conditions, respectively. Dark and light green thylakoids indicate more or less chlorophyll, respectively. RuBisCO, ribulose-1,5-bisphosphate carboxylase/oxygenase. TCA cycle, tricarboxylic acid cycle.

TABLES

Table 1 | Optimal temperatures for indicated developmental stages and biochemical processes. The phases for

Zones
Temperate

Subtropical

Tropical

Table 1 | Optimal temperatures for indicated developmental stages and biochemical processes. The phases for

A

Aboveground Organs Belowground

B

	Temperature (°C)
Photosynthesis	
Respiration	
Seed / fruit setting	
Reproductive stage	
Vegetative stage	
Root development	

12 14 16 18 20 22 24 26 28 30 32 34 36 38 40
Temperature (°C)

Temperate (Wheat / Barley) Subtropical (Tomato) Tropical (Maize / Rice / Soybean)

14°C   19°C   24°C   29°C   34°C

A

LD

SD

B

LD

C

YUCCA
auxin

YUCCA↓
auxin ↓

D

RNAP II

ARP6

H2A.Z
(BdHTA9)

AMY1, UDP-GPP

RNA

ARP6

E
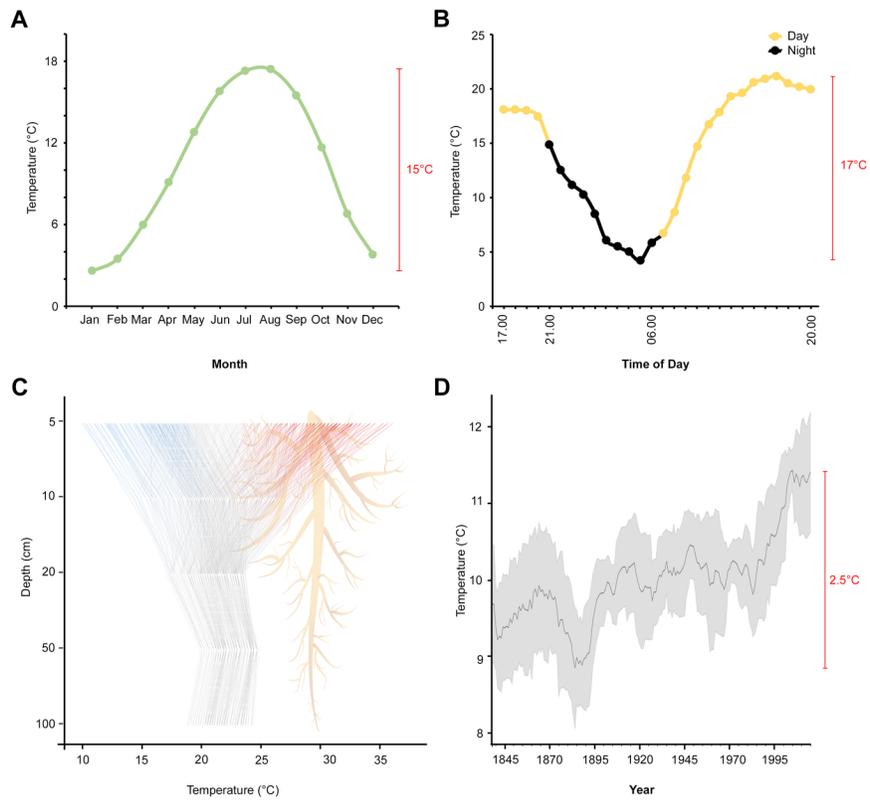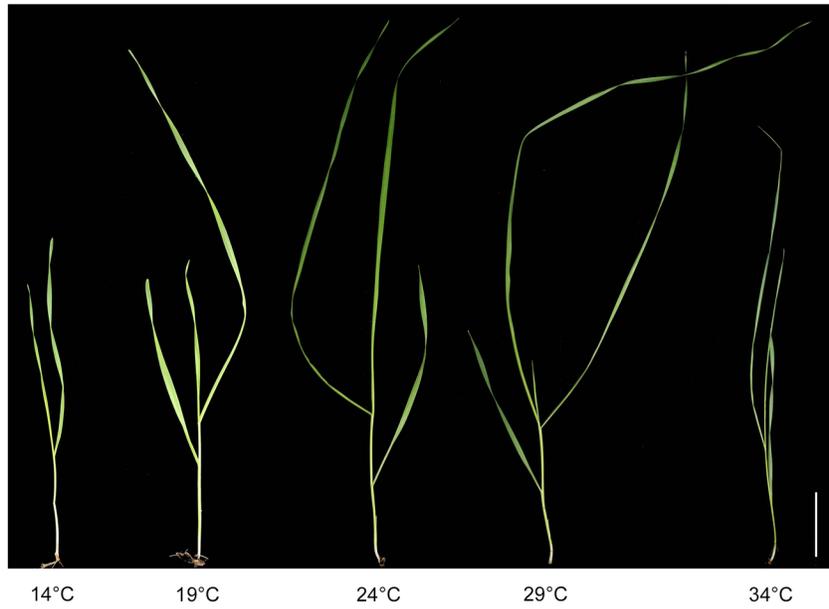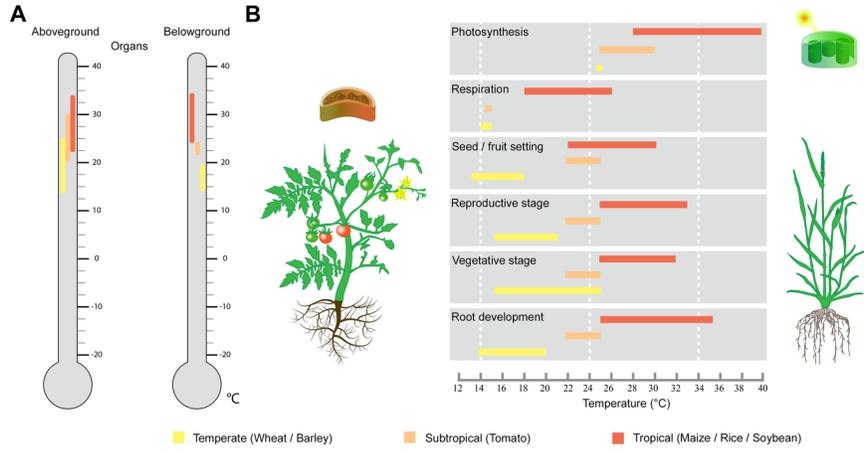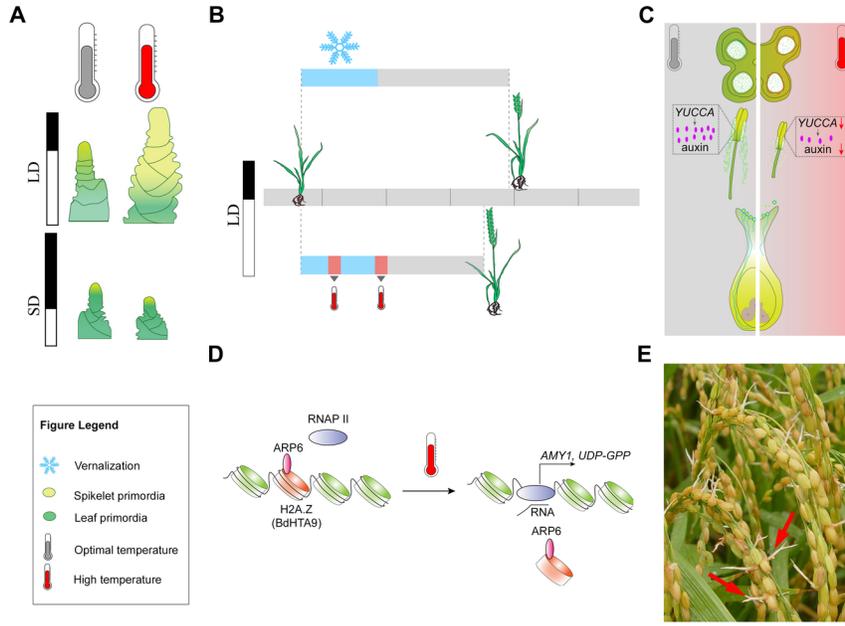
Figure Legend

❄ Vernalization

⬤ Spikelet primordia

⬤ Leaf primordia

🌡 Optimal temperature

🌡 High temperature

Thylakoids

RuBisCO (active)

CO_2

TCA cycle

O_2

Photorespiration