The Heat is On: How Crop Growth, Development and Yield Respond to High Temperature

Tingting ZHU1,2, Cassio Flavio FONSECA DE LIMA1,2, Ive DE SMET1,2

1Ghent University, Department of Plant Biotechnology and Bioinformatics, B-9052 Ghent, Belgium
2VIB Center for Plant Systems Biology, B-9052 Ghent, Belgium

Equal contribution

Correspondence: I. De Smet, VIB-UGent Center for Plant Systems Biology, Ghent, Belgium. Email: Ive.DeSmet@psb.vib-ugent.be

ORCID IDs: Tingting ZHU (0000-0002-0904-7636), Cassio Flavio FONSECA DE LIMA (0000-0001-7787-8784), Ive DE SMET (0000-0003-4607-8893)
**Highlights:** Extreme high temperature is harmful to plants, but moderate high temperature leads to escape and avoidance mechanisms. Overall, reproductive organs are more sensitive to high temperature than vegetative, negatively impacting crop yield.
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. Increasing global temperatures negatively impact crop performance, and several physiological, biochemical, morphological and developmental responses to increased temperature have been described that allow plants to mitigate this. In this review, we assess various growth, development, and yield-related responses of crops to extreme and moderate high temperature, focusing on knowledge gained from both monocot (e.g. wheat, barley, maize, rice) and dicot crops (e.g. soybean and tomato) and incorporating information from model plants (e.g. Arabidopsis and Brachypodium). This revealed common and different responses between dicot and monocot crops, and defined different temperature thresholds depending on the species, growth stage and organ.

Keywords: High temperature, crop, monocot, dicot, wheat, tomato, maize, rice, soybean, fruit, seed, pollen, shoot, flowering
Introduction

Plants face a wide range of temperatures during their life cycle, both on a seasonal and daily level (with temperature differences of more than 15 °C during a single day and recurring spikes of extreme heat), and need to continuously adapt (Gourdji et al., 2013; Hatfield et al., 2011; Lobell and Gourdji, 2012; Ray et al., 2015) (Figure 1A-B). Furthermore, due to the global warming trend (average rate of increase in combined land and ocean temperature shifted from 0.08 °C per decade since 1880 to 0.18 °C since 1981 (NOAA - National Centers for Environmental Information, 2020)) (Figure 1C), crops are exposed to greater variation in environmental conditions – especially mean night-time temperatures are rising at a faster rate than those during the daytime (e.g. diurnal temperature variation asymmetry was >0.25 °C in over half of the land surface from 1983-2017) (Cox et al., 2020; Sadok and Jagadish, 2020) – and this has a negative impact on their performance (Lesk et al., 2016; Lobell and Gourdji, 2012; Lobell et al., 2011). The yields of staple crops (e.g. wheat, maize, rice, and soybean) and horticultural crops (e.g. tomato), have already significantly dropped due to increased temperature (Asseng et al., 2014; Pathak et al., 2018; Schaubberger et al., 2017; Zhao et al., 2017), and this jeopardizes 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 in global mean temperature, crop yield will be reduced by 6% (wheat), 10-12% (rice) or 3% (soybean), thus impacting global food security further (Asseng et al., 2014; Nelson et al., 2010; Zhao et al., 2017). In this context, nearly all the warmest years in the last 136 years have occurred since 2000 (Figure 1C) 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).

Physiological, biochemical and developmental consequences of crops to increased temperature include shorter time of growth and development, cooling responses, changes in grain number, changes in seed size, early or limited seed setting, accelerated senescence in photosynthetic organs, denaturation, aggregation and degradation of proteins, degradation of chlorophyll, increased fluidity of membrane lipids, increased membrane permeability, disruption of cell organelle function, inhibition of protein synthesis, altered photosynthesis and respiration, and cell death (Asseng et al., 2014; Atkin, 2003; Cossani and Reynolds, 2012; Draeger et al., 2020; Dusenge et al., 2019; Hatfield et al., 2011; Hedhly et al., 2009; Los and Murata, 2004; Nagar et al., 2015; Sadok and Jagadish, 2020; Scafaro et al., 2021; Wang et al., 2015; Zhao et al., 2016). Moderate high temperature is the temperature range that causes morphological, physiological and biochemical changes that together contribute to adaptive thermal acclimation to largely non-detrimental high temperature conditions (Quint et al., 2016; Vu et al., 2019). In contrast, extreme high temperature or heat stress is an increase in temperature above a critical threshold for a period that is sufficient to cause (often irreversible) damage to plant growth, development, and physiology, even death (Wang et al., 2020c).

In this review, we assess various growth, development and yield-related high temperature responses of crops, focusing on knowledge gained from both monocots (e.g. wheat, barley, maize, rice) and dicots (e.g. soybean or tomato), and supplement this with relevant insight from model plants, such as Arabidopsis and Brachypodium. These responses include thermonasty (elongated petioles moving upwards under moderate high temperature), shoot architecture, photosynthesis during vegetative development, early reproductive phase (e.g. floral transition and pollen development) and late generative stage (seed and fruit set and development) (Figure 2). Interestingly, distinct organs and developmental stages (e.g. vegetative versus reproductive
development) respond differently to increased temperature. Among those responses, common and specific responses between dicots and monocots are described where possible. For biotic stress-related processes we refer to other reviews (Cohen and Leach, 2020; Venkatesh and Kang, 2019). We also include some molecular mechanisms underlying the physiological, biochemical, morphological and developmental changes caused by moderate or more extreme high temperature, from which biotechnological and breeding strategies can benefit (Chen et al., 2020; Shen et al., 2019).

**Strategies to avoid and escape high temperature**

Upon exposure to high temperature within a moderate range, plants undergo acclimation and ensure fitness by three main strategies: avoidance, escape and tolerance. High temperature stress tolerance is one of the most crucial agronomic traits. For example, in rice, *EXTRA GLUME 1 (EG1)* encodes a predominantly mitochondria-localized functional lipase that functions upstream of floral identity genes (*OsMADS1, OsMADS6* and *OsG1*) to promote floral developmental robustness in a high temperature-dependent manner (Zhang et al., 2016). The rice *eg1* mutant shows high plastic spikelet development under (moderate) high temperature, resulting in a negative effect on maintaining floral stable development (Zhang et al., 2016). Additionally, rapid physiological, biochemical and molecular responses induced by high temperature confer to some extent tolerance when crop plants are gradually or shortly exposed to moderate or high temperature; but, if the intensity, frequency and duration of the exposure is too high, the effects are detrimental. As there are several recent reviews on heat tolerance in crops (Higashi and Saito, 2019; Jagadish, 2020; Janni et al., 2020), we focus on avoidance and escape.
Under moderate high temperature conditions, plants can accelerate growth to promote plant thermonastic responses and architectural changes to move susceptible parts away from soil heat flow or to improve evaporative cooling (Havko et al., 2020). In Arabidopsis, moderate high ambient temperature induces a suite of morphological changes (including hypocotyl elongation, petiole elongation and leaf hyponasty), referred to as thermomorphogenesis (Figure 2) (Casal and Balasubramanian, 2019; Quint et al., 2016; Vu et al., 2019). Similarly, the leaf and coleoptile of monocot crops (wheat, barley, rice and maize) or the hypocotyl of dicot crops (soybean and tomato, or cabbage) are elongated at moderately high temperatures, and – for example – tomato displays leaf hyponasty (Bawa et al., 2020; Bellstaedt et al., 2019; Havko et al., 2020; Ohtaka et al., 2020; Vu et al., 2021) (Figure 3A). Furthermore, high temperature promotes stomatal opening in Arabidopsis (Kostaki et al., 2020), tomato (Havko et al., 2020) and barley (Kostaki et al., 2020) (Figure 2). However, while these rapid physiological and morphological changes are associated with leaf cooling in, for example, Arabidopsis thaliana and tomato (Havko et al., 2020; Park et al., 2019), this has not yet been shown in economically important cereal crops. Although hypocotyl elongation in dicotyledons (e.g. tomato and cabbage) requires temperature sensing in cotyledons (Bellstaedt et al., 2019), the molecular mechanisms regulating thermomorphogenesis in crops are largely unexplored.

In contrast to plastic vegetative development under moderate high temperature, reproductive characteristics like floral identity and architecture often show low plasticity (or phenotypic robustness or stability) against environmental fluctuation (Fal et al., 2019; Gol et al., 2017; Jacott and Boden, 2020; Klingenberg, 2019). In contrast to the above-described strategies for temperature-stress avoidance associated with vegetative organs, reproductive organs show an effective heat escape mechanism (Jagadish, 2020). For example, some dryland crops (e.g. wheat and sorghum) are able to optimize their anthesis during the morning or cooler evening periods under heat stress (Aiqing et al., 2018; Chiluwal et al., 2020) and in most rice varieties an early morning flowering trait was introduced to shift their flower opening time (Jagadish, 2020). High temperature
negatively affects diverse stages of flowering (e.g. early floral transition and heading) (Chen et al., 2018; Jagadish et al., 2015; Wang et al., 2019a). Moreover, moderate high temperature can influence organ growth rate and proportionally shorten or prolong the duration of the developmental phases to protect the sensitive stages from negative effects of increasing temperature in a photoperiod-dependent or -independent way (Capovilla et al., 2014; Del Olmo et al., 2019; Heschel et al., 2007; Parent and Tardieu, 2012). In this context, moderate high temperature induces the expression of flowering-promoting genes, such as FLOWERING LOCUS T (FT), and subsequently triggers floral transition in Arabidopsis (Balasubramanian et al., 2006; Casal and Balasubramanian, 2019; Vu et al., 2019) or promotes the expression of floral activators (GmFT2a and GmFT5a) and inhibits the upstream negative regulators (E1 and E2) in soybean (No et al., 2021) under non-inductive day-length conditions. However, moderate high temperature treatments do not induce the transcript levels of the barley and wheat ortholog of FLOWERING LOCUS T1 (FT1) in short days (Dixon et al., 2018; Hemming et al., 2012; Kiss et al., 2017), and cannot compensate for photoperiod as a floral inductive signal, suggesting FT1-independent high temperature responsiveness of flowering in cereals (Jacott and Boden, 2020). For wheat, barley and Brachypodium grown under long-day 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) (Figure 4A). Furthermore, temperature shifts during the normal seasons, such as those caused by climate change, accelerate flowering time in a vernalization duration-dependent manner (Dixon et al., 2019; Zhao et al., 2020). In wheat, the VRN-A1 wild type allele plays a crucial role for completing and maintaining vernalization. A wheat variety with a higher level of the VRN-A1 SNP allele (causing an amino acid substitution, L117F) shows an extended vernalization duration requirement, in which warm temperature induces longer flowering time due to the incomplete vernalization. However, warm temperature-induced interruption of vernalization accelerates flowering in a wheat variety with a higher level of the wild type VRN-A1 allele under long-day photoperiod, resulting in the
formation of additional spikelets due to a delay in the early stages of inflorescence development (Dixon et al., 2019; Ejaz and von Korff, 2017; Greenup et al., 2011) (Figure 4B).

**The pace of plant growth: temperature versus the circadian clock**

Under controlled conditions, growth peaks at the end of the night or the beginning of the night with an added effect by high temperature in dicots, such as *Arabidopsis* (Gil and Park, 2019) and soybean (Kronenberg et al., 2020) (Figure 3B). For eudicots, the circadian clock plays a major role in dictating the pace of plant growth; however, for some monocot species, such as *Brachypodium*, maize and rice, temperature is the principal cue for leaf growth and elongation (Matos et al., 2014; Poire et al., 2010) (Figure 2 and Figure 3B). Interestingly, ELF3, one of the Evening Complex components, contains a prion-like domain (PrLD) with a high proportion of glutamine residues (polyQ region) that plays an important role in moderate high temperature sensing in *Arabidopsis* (Jung et al., 2020). However, *Brachypodium* ELF3 (BdELF3) lacks those sequences. The temperature-dependent DNA binding of AtELF3 is abolished by replacing its PrLD with the corresponding region from BdELF3 (Jung et al., 2020). This indirect evidence suggests that high temperature sensing mechanisms in monocot crops are likely to be (in part) independent of the circadian clock. However, the underlying molecular basis of (moderate) high temperature-induced leaf growth without the internal clock control in monocot crops remains unknown.
**Shoot architecture and photosynthesis are affected by high temperature**

High temperature-mediated changes in crop canopy architecture affect light capture and photosynthesis (Allen et al., 2018; Li et al., 2020). The impact of high temperature on shoot architecture depends on the crop species (e.g. monocot versus dicot) and on when high temperature occurs during plant growth and development (e.g. vernalization). In wheat and barley, moderate high temperature decreases the number of leaves and tillers, as well as final stem height (Dixon et al., 2019; Hemming et al., 2012) (Figure 2 and Figure 3C). In soybean, high temperature increases the number of nodes and leaves, but decreases the length of individual internodes and final plant height, which—as a whole—reduces light capture by the photosynthetic leaves (Allen et al., 2018) (Figure 3C). In addition, high temperature-mediated changes in wheat leaf angle (including a big leaf angle at the top versus a small leaf angle at the bottom of the plant) impact light capture (Li et al., 2020) (Figure 3C). Apart from these developmental changes, high temperature impacts photosynthesis itself through reducing chlorophyll content (Mishra et al., 2020; Sattar et al., 2020), affecting the repair system photosystem II (Chen et al., 2020), and reducing rubisco activase (Rca) abundance or activity (Degen et al., 2020a; Degen et al., 2020b; Scafaro et al., 2018; Yamori et al., 2012). For more details on this, we refer to a recent review on the effect of increasing temperature on crop photosynthesis (Hu et al., 2020; Moore et al., 2021). Interestingly, maintaining the capability of PSII repair under heat stress and controlling the thermostability of Rca are promising ways to improve photosynthesis and thermotolerance for crops exposed to warmer temperature or severe heat stress (Chen et al., 2020; Scafaro et al., 2018; Scafaro et al., 2019).
High temperature affects male fertility

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 temperature than vegetative stages (Draeger and Moore, 2017) (Table 1). Noteworthy, all the causes of reproductive organ sterility are differentially affected by short-term or long-term high temperature exposure (Karapanos et al., 2010; Zhang et al., 2018). Obviously, temperature extremes or heat waves are more immediate and harmful to reproductive tissues than moderate high ambient temperature (Draeger and Moore, 2017; Jagadish et al., 2010; Wang et al., 2019a). High temperature affects both male and female reproductive organs (Begcy et al., 2019; Djanaguiraman et al., 2013; Draeger and Moore, 2017; Gonzalo et al., 2020; Hedhly, 2011; Hedhly et al., 2009; Herrero, 2003; Jagadish et al., 2010; Sakata et al., 2010; Shi et al., 2018; Wang et al., 2019a; Wang et al., 2021; Yu et al., 2017; Zhang et al., 2018); but, here we focus on the highly complex male gametophyte life cycle that is very responsive to changes in the environment (Zinn et al., 2010) (Figure 4C).

Heat sensitivity during different stages of pollen development is variable, peaking at the interval between meiosis and mitosis I, and upon heat stress, might lead to pollen abortion and failure at later stages (Rieu et al., 2017). Under increased temperature aberrations in tapetum development, morphology and degeneration occur (Rieu et al., 2017). In this context, the rice 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 moderate high temperature (Yu et al., 2017). Moderate high temperature is already enough to lead to male sterility in tms10 mutant plants, but the mutant is still fertile at control temperature (Yu et al., 2017). Similarly, the rice tms5 line is also male-sterile at moderate high temperature and male-
fertile at optimal temperature (Wen et al., 2019; Zhou et al., 2014). TMS5 encodes a conserved ribonuclease Z protein (RNase Z$^5$), which cleaves the microspore mother cells-expressed ubiquitin fusion ribosomal protein L40 (Ub$_{L40}$) mRNA to maintain microspore development and male fertility (Wen et al., 2019; Zhou et al., 2014). In brief, moderate high temperature induces an overaccumulation of unprocessed Ub$_{L40}$ mRNAs resulting from the failure of RNase Z$^5$ generation in tms5 mutants, leading to the production of defective pollen and male sterility (Wen et al., 2019; Zhou et al., 2014). Interestingly, in barley, overexpressing an anther tapetum-specific MALE STERILITY1 (MS1) transcription factor (HvMS1) causes complete male sterility due to incomplete tapetum degeneration under standard growth condition. This male sterility, however, is restored by exposing or transferring barley plants during flowering prior to pollen mitosis I stage to moderate high temperature (Fernandez-Gomez et al., 2020). But the mechanism of the environmentally restorable male sterility in barley remains to be decoded, and this is of value in hybrid crop breeding.

In addition, sterility is caused by cessation of pollen tube elongation due to heat-induced reduction of endogenous auxin in pollinated pistils in rice, barley, and Arabidopsis (Sakata et al., 2010; Zhang et al., 2018). In barley and Arabidopsis, this sharp decrease in endogenous auxin is caused by high temperature-induced downregulation of YUCCA auxin biosynthesis genes, and application of auxin indeed completely reverses male sterility (Sakata et al., 2010; Zhang et al., 2018) (Figure 4C). This is in sharp contrast with, for example, the Arabidopsis shoot where moderate high temperature promotes auxin biosynthesis to control growth (Bellstaedt et al., 2019). This further strengthens the notion that there is an organ-specific response to similar moderate high temperature triggers, but it remains to be investigated how this is regulated.
High temperature affects seed and fruit set and development

Compared to other reproductive phases, the early seed and fruit-setting stages are more sensitive to temperature changes (Table 1). At a cellular level, high temperature directly and negatively affects endosperm cellularization during early seed development, which impairs the sink capacity (Begcy et al., 2018; Chen et al., 2016). Subsequently, biosynthesis, transport or catabolism of storage materials are sensitive to high temperature, which causes incomplete seed or fruit filling. For example, normal maize endosperm starch biosynthesis requires PGD3, a plastidic 6-phosphogluconate dehydrogenase (6PGDH), and the activity of PGD3 is reduced by high temperature (Ribeiro et al., 2020). Furthermore, targeting heat-stable cytosolic PGD1 and PGD2 isozymes to the amyloplast complements the heat-sensitive and amyloplast-localized PGD3 seed filling defect and increases maize seed yield upon high nighttime-temperature stress (Ribeiro et al., 2020). In addition, chromatin remodeling plays a role during moderate high temperature-controlled gene expression and seed setting (Boden et al., 2013). In Brachypodium, the H2A.Z transcript level is stable with temperature, but at moderate 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 mild high temperature, where ARP6 is required for proper H2A.Z deposition. Indeed, also in Arabidopsis H2A.Z is involved in temperature-dependent flowering (Kumar and Wigge, 2010), making this a more general regulatory mechanism at moderate high temperature. Finally, both moderate high temperature or more extreme high temperature accelerate senescence of terminal leaves, in which the majority of assimilates and metabolites that
are translocated to the seeds or fruit are fixed, which leads to loss of photosynthetic and respiratory ability (Wang et al., 2019b; Xu et al., 2020). On the other hand, the expansion of tomato fruits is positively regulated by increasing temperature (10-30°C) and less related to assimilate supply. However, several regulators of tomato fruit ripening (e.g. FUL1, TAGL1 and ARF2a) are transcriptionally repressed by moderate high temperature, resulting in a reduction of final mean weight in tomato fruits (Almeida et al., 2020; Li et al., 2015).

With respect to developmental time, a shortened seed or fruit-setting duration due to moderate high temperature, also results in a significant reduction in final weight (Boden et al., 2013; Boehlein et al., 2019; Shi et al., 2017), which is one of the strategies to reduce overall high temperature-caused seed yield reduction. In addition to yield, seed, or fruit quality impact the economic value. The faster pace at which night-time temperatures are rising – in contrast to daytime temperatures – results in challenges for grain production in winter wheat, since physiological traits, grain yield and yield components are significantly reduced at increasingly high night temperatures over 15°C (Impa et al., 2020). Moreover, when seeds are not matured under optimal temperature conditions, proper dormancy might not be established and seeds may exhibit unwanted agricultural traits, such as pre-germination or even germination while still attached to the mother plant, known as preharvest sprouting (Figure 4E). (Fang and Chu, 2008; Liu et al., 2015; Rodríguez et al., 2015; Soppe and Bentsink, 2016). Preharvest sprouting is a serious quality defect in grain production and is the cause of losses in yield and end-use quality worldwide in wheat and barley (Nakamura, 2018; Wang et al., 2020b). The shallow level of dormancy in wheat grains matured under high temperature is partially attributed to a 4-fold transcript enrichment of TaGAMYB, a gibberellic acid signaling gene and not to differences in embryonic ABA levels (Tuan et al., 2020).
High temperature threshold varies according to crop species, developmental stage, and organ

As illustrated above, different plant species respond differently to the wide range of temperatures they are exposed to throughout their life cycle. Each species, including crops, shows an optimum temperature range (or a temperature threshold) that regulates growth and that is specific for a particular developmental stage (Hatfield et al., 2011) (Figure 5 and Table 1). Warm season crops (e.g. maize, rice, tomato and soybean) generally have higher temperature thresholds during their life cycle than those crops from temperate zones (e.g. wheat and barley), reproductive tissues and organs are developmentally more responsive to moderate or extreme high temperature than vegetative parts (Ayenan et al., 2019; Draeger et al., 2020; Wiebbecke et al., 2012) (Figure 5 and Table 1) and the temperature threshold 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 et al., 2002; Sehgal et al., 2018) (Figure 5 and Table 1). Importantly, plants adjust their growth to avoid negative effects by high temperature, with each species having its own growth-promoting temperature range (Parent and Tardieu, 2012). First, high temperature shortens or prolongs the duration of the developmental phases to protect the sensitive stages from temperature (Heschel et al., 2007; Parent and Tardieu, 2012). Second, high temperature accelerates growth to promote plant thermonastic responses and architectural changes to move susceptible parts away from soil heat flow or improve evaporative cooling (Havko et al., 2020). Finally, several biochemical processes that are key during the whole life cycle of the plant also have relevant temperature thresholds: photosynthesis mainly depends on day-time temperature, while night-time temperature mainly affects respiration (Ahammed et al., 2018;
Bianchetti et al., 2020; Crafts-Brandner and Salvucci, 2002; Dusenge et al., 2019; Impa et al., 2021). Acclimation of photosynthetic and respiratory reactions to high temperature is important when the temperature rises gradually, which, however, is less likely during sudden heat waves or intense heat stress (Atkin, 2003; Impa et al., 2019; Kaur et al., 2019; Posch et al., 2019). Interestingly, organelles also display an organ-specific high temperature threshold. For example, pea seed mitochondria can retain activity even under temperatures as high as 40°C; whereas mitochondria from the etiolated epicotyl collapse at 30°C (Stupnikova et al., 2006). Taken together, the temperature threshold varies according to crop species, developmental stage, and organ. It will thus require very specific analyses to identify all the underlying molecular mechanisms and unravel how each mechanism contributes to the overall performance of a crop exposed to high temperature.

Conclusions and outlook

With global climate change, increasing temperature has an enormous impact on crop productivity from seedling to mature stages (Allen et al., 2018; Boden et al., 2013; Dixon et al., 2018; Draeger and Moore, 2017; Havko et al., 2020). Climate-smart crops will benefit from a better understanding of high temperature-associated processes (Zhang et al., 2016). 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 (Crawford et al., 2012; Havko et al., 2020) can be assigned to monocot crop plants. Additionally, the underlying molecular mechanisms of leaf growth induced by moderate high temperature, with limited control by the internal clock in monocot crops
is likely to be different (Figure 2 and 3B) (Matos et al., 2014; Poire et al., 2010). Furthermore, comprehensively identifying and characterizing the temperature sensing mechanism(s) in monocot crops is an important next step. This requires exploring high temperature-related mechanisms directly in the relevant crop and requires identifying common and different (organ-specific) responses in dicot and monocot crops (Figure 2).

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 (Figure 2). 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 et al., 2020). In addition, developing higher ratios of VRN-A1 wild type allele relative to the VRN-A1 mutant allele in wheat could improve flexibility of winter crops respond to temperature shifts (Dixon et al., 2019). For crops, the domestication process already resulted in selection of cultivars with less dormant seeds than the ones found in nature (Benech-Arnold et al., 2013). Therefore, understanding the effects of high temperature in context of seed maturation and germination in crops will contribute to food security.

Predicting crop yield in function of global warming remains complex and differs for each of the major crops. For that, the foreseen warming might not be detrimental to every crop, and this should thus be analyzed locally. For example, rice is mainly produced in the tropics where the current models point to a smaller increase in the warming trend compared to global mean temperatures (Deser et al., 2012; Iizumi et al., 2017). Moreover, rice shows a higher optimum temperature than other major crops and rice yield might therefore be maintained under the warming trend. In contrast, wheat is grown world-wide, but cooler wheat-producing regions (e.g. Canada and Northern Europe) would benefit from the increased temperature (Iizumi et al., 2017;
Qian et al., 2019). Moreover, crop yield and quality are affected by increased respiration caused by warmer night temperature (Impa et al., 2021), which is likely to occur in the near future. Molecular responses could strengthen the metabolite-based markers from high night temperature-tolerant genotypes with significant alterations in metabolites to support crop breeding programs (Impa et al., 2019). Understanding the molecular mechanisms underlying organ sterility at high temperature is an essential countermeasure for global warming (Figure 2). In addition, thermosensitive genic male sterility lines have potential applications in hybrid crop breeding, which benefits from the climate change-induced temperature increase (Wen et al., 2019; Zhou et al., 2014). 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.

Taken together, our increasing knowledge on the molecular mechanisms associated with high temperature sensing, signaling and response can be readily applied to improve crop tolerance to a changing environment. However, exploring all the above-mentioned aspects sooner than later is important, because –‘the heat is on’!
Acknowledgements

This work was supported by the Research Foundation – Flanders (FWO.OPR.2019.0009.01). T.Z. is recipient of a PhD grant from the Chinese Scholarship Council.

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 varies on a seasonal and daily level and rises year-by-year. (A) Seasonal temperature fluctuation in Sydney (Australia), Shanghai (China), Uccle (Belgium), New York (USA) and Rio de Janeiro (Brazil). Data plotted from mean of monthly recorded temperature in local meteorological stations. Thermal amplitude for Sydney, Shanghai, Uccle, New York, and Rio de Janeiro is 10.6, 24.1, 15.4, 24.1 and 6.4 °C, respectively. Depending on location, thermal amplitude along a year is less or more pronounced and affects plant production. Recorded time intervals are indicated. Data retrieved from https://data.giss.nasa.gov/gistemp/station_data_v4_globe. (B) Daily fluctuation in recorded temperatures in Melle (near Ghent, Belgium). Recorded interval from 6th to 7th May 2020. Data retrieved from www.meteo.be/nl/weer/waarnemingen/belgie. Within a single day plants experience a large thermal amplitude (indicated in red). (C) Long term global (land and ocean) temperature anomalies. Data plotted from annual average and transformed for its 10-year moving average. Recorded interval of 1850-2020 (data retrieved from www.eea.europa.eu/data-and-maps/data/external/noaa-ncdc-mlost). Red arrow in C represents shift (in 1981) in average rate of increase per decade in combined land and ocean temperature from 0.08 °C to 0.18 °C.
Figure 2. Moderate or extreme high temperature affects crop growth, development and yield. Different processes (as described in the main text) are illustrated for monocot and dicot plants. The grey and red thermometers represent optimal and high temperature, respectively. For photoperiod bar, black and white represents night and day condition, respectively. The size of the circadian clock or photoperiod icons illustrates the degree of dependency during moderate high temperature-induced growth in monocot and dicot plants. The numbers point to some outstanding questions: (1) What are the mechanisms regulating different internal clock dependency of moderate high temperature-mediated growth between monocot and dicot crops?, (2) What are the cooling and temperature sensing mechanisms in monocot plants?, (3) What are the mechanisms associated with photoperiod dependency of moderate high temperature-promoted early flowering in monocot and dicot crops?, (4) What are the mechanisms associated with unseasonal warm weather affecting vernalization and crop flowering and architecture?, and (5) What are the mechanisms associated with (tolerance to) high temperature-mediated male sterility?

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Table 1 | Optimal temperatures for indicated developmental stages and biochemical processes. The phases for monocot (wheat, barley and rice) are mainly for the main shoot. As the early reproductive stage in the main shoot happens, tillers are starting to generate. A temperature above the optimum will affect the listed processes in a moderate or extreme way, depending on the extent.

<table>
<thead>
<tr>
<th>Zones</th>
<th>Species</th>
<th>Stage &amp; process</th>
<th>Developmental phases &amp; process</th>
<th>Optimum (°C)</th>
<th>Ref.</th>
</tr>
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<tbody>
<tr>
<td>Temperate</td>
<td>Wheat</td>
<td>Vegetative stage</td>
<td>Emergence to Tillering</td>
<td>20-25°C</td>
<td>(Ali Tahir et al., 2015; Chavan et al., 2019)</td>
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<td></td>
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<td>Reproductive stage</td>
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<td>17-20°C</td>
<td>(Dixon et al., 2019; Draeger et al., 2020; Draeger and Moore, 2017)</td>
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<td></td>
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<td></td>
<td>Heading to Anthesis</td>
<td>18-21°C</td>
<td>(Alghabari et al., 2014)</td>
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<tr>
<td></td>
<td></td>
<td>Grain development stage</td>
<td>Seed setting</td>
<td>13-18°C</td>
<td>(Abdelrahman et al., 2020; Kino et al., 2020; Koga et al., 2016)</td>
</tr>
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<td></td>
<td></td>
<td>Biochemical process</td>
<td>Photosynthesis / Respiration</td>
<td>25°C/14-15°C</td>
<td>(Djanaguiraman et al., 2018; Impa et al., 2019; Posch et al., 2019)</td>
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<tr>
<td>Barley</td>
<td></td>
<td>Vegetative stage</td>
<td>Emergence to Tillering</td>
<td>15-21°C</td>
<td>(Ford et al., 2016; Garmash, 2005; Hemming et al., 2012)</td>
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<td>Reproductive stage</td>
<td>Double ridge to Booting</td>
<td>15-20°C</td>
<td>(Ejaz and von Korff, 2017; Ford et al., 2016; Hemming et al., 2012; Oshino et al., 2007; Oshino et al., 2011)</td>
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<td>Seed setting</td>
<td>13-18°C</td>
<td>(Cochrane et al., 2000; Howard et al., 2012)</td>
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<td>25°C/15°C</td>
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<td>Subtropical</td>
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<td>Vegetative stage</td>
<td>Leaves and Stem development</td>
<td>25-28°C</td>
<td>(Havko et al., 2020; Lu et al., 2017; Tsai et al., 2019)</td>
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<td></td>
<td>Reproductive stage</td>
<td>Inflorescence formation to flower development</td>
<td>21-25°C</td>
<td>(Ayenan et al., 2019; Paupière et al., 2017; Xu et al., 2017)</td>
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<td></td>
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<td>Post-anthesis stage</td>
<td>Fruit setting</td>
<td></td>
<td></td>
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<td>Biochemical process</td>
<td>Photosynthesis / Respiration</td>
<td>25-30°C/15°C</td>
<td>(Lu et al., 2017; Wiebbecke et al., 2012)</td>
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<td>Tropical</td>
<td>Maize</td>
<td>Vegetative stage</td>
<td>Emergence to Leaves</td>
<td>30-32°C</td>
<td>(Sanchez et al., 2014; Singh et al., 2014)</td>
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<td>Stage</td>
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<td>References</td>
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<td>(Begcy et al., 2019; Sanchez et al., 2014)</td>
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<td>Flowering (ear silking)</td>
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<td>(Commuri and Jones, 2001; Sanchez et al., 2014)</td>
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<td>Rice</td>
<td>Vegetative stage</td>
<td>Emergence to Tillering</td>
<td>25-31°C</td>
<td>(Krishnan et al., 2011)</td>
<td></td>
</tr>
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<td>Reproductive stage</td>
<td>Panicle initiation and Booting</td>
<td>26-30°C</td>
<td>(Martínez-Eixarch and Ellis, 2015; Sanchez et al., 2014)</td>
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<td>Heading to Flowering</td>
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<td>Soybean</td>
<td>Vegetative stage</td>
<td>Leaves and Stem development</td>
<td>28-30°C</td>
<td>(Alsajri et al., 2019; Jumrani and Bhatia, 2018; Lyu et al., 2020)</td>
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<td>Reproductive stage</td>
<td>Flower initiation to Anthesis</td>
<td>26-30°C</td>
<td>(Djanaguiraman et al., 2011; Wiebbecke et al., 2012)</td>
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<td>22-30°C</td>
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