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Review

Genetic Improvement of Heat Stress Tolerance in Cereal Crops

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Abstract: Crop heat stress is a threat to food supply, with heatwaves expected to increase in frequency and intensity globally. In addition to yield loss, heat stress dramatically reduces fertility and seed-setting rate, grain quality and weight, and seed germination and growth. Genetic variability for heat stress tolerance can be used in breeding programs to develop tolerant genotypes. The availability of genome assemblies with high-confidence sequences for many cereal crops, including rice, maize, wheat and barley, now allows the identification of heat stress tolerance-associated genes and gene networks. This review focuses on synthesizing current advances in understanding the detrimental effects of heat stress on cereal crop production at the physiological and genetic levels. It provides an account of available genomic resources, genetic variation, candidate genes, and molecular markers for heat stress tolerance. Lastly, this review offers insight into crop genetic improvement for heat stress tolerance, including germplasm screening in glasshouse and field trials, marker-assisted selection, mapping genomic loci and identification of candidate genes, and genomic-assisted breeding.

Keywords: heat stress; breeding; wheat; barley; rice; maize; genomics; candidate gene; climate change; QTL

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1. Introduction

Human-induced changes in global climate have rapidly changed the production environments within which crops and farming practices developed over the past 10,000 years. Under all considered emissions scenarios released by the Intergovernmental Panel on Climate Change (IPCC), global surface temperatures will continue to increase and surpass 2 °C this century [1]. Since pre-industrial times, observed changes in climate extremes include an increased frequency and intensity of extreme precipitation, tropical cyclones, droughts, and heatwaves.

Climate change has already influenced the patterns of agricultural production. Crops are susceptible to changes in temperature, precipitation, and rising atmospheric CO_2 concentration. The interaction between climate variability and climate change threatens global food security: Climate variability accounts for more than 60% of the yield variability in maize, rice, wheat, and soybean in the globally most productive agricultural regions, including the Midwestern Corn Belt of the United States and the Northeastern Corn Belt of China, and wheat-growing areas in Western Europe and Australia [2].

Among the abovementioned changes, temperature increase has the most likely negative impact on crop yields [3,4]. Heat stress is a period of elevated day or night-time temperatures that cause significant and irreversible damage to plant growth. Heatwaves directly affect plant growth and development and indirectly through increased atmospheric water demand, increasing water pressure deficits. These can lead to additional water stress due to reduced soil moisture, resulting in detrimental growth and lower yields. Under the current climate scenario, high temperatures and extreme heat events will occur more

frequently, much earlier, and will last longer in the future [1], raising an urgent need to breed adapted plants with optimized temperature responses.

Heat tolerance is the ability of the plant to grow, produce yield, and sustain biomass production under high temperatures. Researchers have extensively studied the physiological, molecular and biochemical mechanisms underlying heat stress sensitivity and tolerance in plants in the past decades. Quantitative trait loci (QTLs) linked to heat tolerance were identified but rarely narrowed down to the (candidate) gene level. Novel phenotyping and genotyping platforms and computational tools, including genomic selection and cropping simulations, can further contribute to our understanding of plant heat stress tolerance in the future [5,6].

The topic of this review is to report, compare, and contrast the current understanding of heat stress effects at the physiological and molecular levels in the four major cereal crop species, namely bread wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), rice (*Oryza sativa*), and maize (*Zea mays*). We highlight the genetic and physiological basis of agronomic traits under heat stress, including traits regarding crop development and reproduction, grain quality, and senescence and biomass. We describe how heats shock stress factor genes play a significant role in controlling gene action in response to heat stress. We detail current genomic resources, genetic variation, candidate genes, and molecular markers for heat stress tolerance. This review's final part discusses methodologies and approaches for genetic improvement of heat stress tolerance, including germplasm screening, marker-assisted selection, mapping of genomic loci and identification of candidate genes, and genomic-assisted breeding that enhances heat tolerance in cereal crops.

2. Impact of Heat Stress on Cereal Crop Production

Hotspots of crop heat stress overlap with agricultural regions in Australia, China, North America, and other countries, resulting in economic penalties in the billion-dollar range (Figure 1) [7]. According to recent estimates, a 1 °C increase in global temperatures will decrease yields worldwide by 7.4% [4]. Pronounced differences in the forecasts for yield loss exist for cool-season crops wheat and barley, warm-season crops rice and maize, and differ between major crop-producing countries.

2.1. Cool-Season Cereal Crops: Wheat and Barley

Wheat and barley are cool-season cereal crops. Depending on the developmental stage, air temperatures of about 11–20 °C are considered optimal for growth and development [9]. Wheat is an essential temperate crop and the staple food crop for millions of humans and livestock. Global wheat production areas are prone to high temperatures [10]. A recent report on the effect of temperature increases on global yields used statistical regressions, global grid-based and local point-based models, and field-warming experiments, and estimated wheat yield losses of 5.5% and 6% per 1 °C increase for the United States and France, respectively, on par with the global average of 6% yield loss [4]. Two major wheat-producing countries, namely India and Russia, are more susceptible to a rise in temperature, with wheat yields reduced by 9.1% and 7.8% for each 1 °C increase. China is estimated to lose around 2.6% yield for each 1 °C increase in global mean temperature.

A wheat simulation model and local-scale climate scenarios predicted heat stress and drought impacts on winter wheat in Europe [3]. This analysis showed that an increase in frequency and magnitude of heat stress around flowering is a more severe threat than drought stress for wheat production in Europe, particularly for heat sensitive wheat cultivars grown in Northern European countries. Despite lower summer precipitation projected for the 2050s across Europe, wheat is predicted to mature earlier and thus escape severe drought, but the risk of heat stress around flowering will increase. In Australia, variations in average growing-season temperatures of 2 °C are estimated to cause a 50% grain production reduction [11].

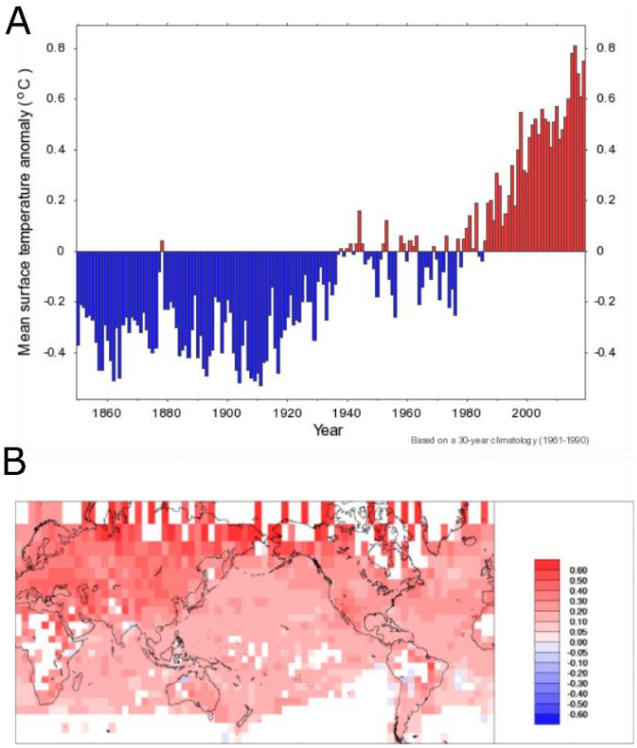

Figure 1. Global climate variability. (**A**) Time series graph of global mean surface temperature anomalies (°C) (1850 to 2019). The current international standard of a 30-year average from 1961 to 1990 was used as the long-term average. Blue bars indicate cooler-than-average years; red bars show warmer-than-average years. (**B**) Trend map in global annual temperature (°C/10 years) from 1970 to 2019. White means little to no change, while red shows places that warmed, and blue shows places that cooled. The time series and trend analyses use the Climatic Research Unit HadCRUT4 global gridded (5 × 5 degree resolution) temperature data set [8]. Source: Australian Government Bureau of Meteorology.

Barley, mainly used as animal feed, human food, and malting, is the 4th most important cereal crop grown after rice, wheat, and maize in terms of area and production [12]. Europe, Russia, Australia, Ukraine, and Canada are leading barley-producing countries. Heat also significantly limits barley yield: Even a moderate heatwave during early grain development, typical in spring to early summer in Western European countries, strongly affects grain developmental parameters and decreases barley yields by 15% [13,14].

2.2. Warm-Season Cereal Crops: Rice and Maize

Rice and maize are warm-season cereal crops. Rice is the world's most important food crop and feeds more than 50% of the global human population. More than 90% of rice is grown in Asia, principally in China, India, Indonesia, Bangladesh, Japan, and other Southeast Asian nations. Rice is also grown in North and South America, Europe, and Australia. Temperatures of about 26–30 °C (*Oryza sativa* L. subsp. indica) or 21–29 °C (*Oryza sativa* L. subsp. japonica), depending on the developmental phase, are considered optimal for growth and development [15]. Recent estimates show that a 1 °C rise in global mean temperature would, on average, reduce global yields of rice by 3.2% [4]. The Yangtze River basin contributes nearly half of China's crop production, including more than two-thirds of the total volume of rice. Latest estimates expect a temperature increase in the Yangtze River basin by up to 2 °C by 2050 relative to 1950, reducing rice yields by 41% by the end of this century [16].

Maize is planted over a wide latitude range, from ca. 60° N in Finland and northern Eurasia to 40° S in Australia, Africa and South America. The United States, China, Brazil and Argentina account for over two-thirds of global production. In Asian countries, maize

is grown mainly as a rainfed crop and is susceptible to heat and drought. Temperatures of about 26 °C (grain filling) to 31 °C (leaf initiation) are optimal for maize growth. Of all major cereal crops, the loss in yield for each 1 °C increase in global mean temperature is the largest for maize (7.4% global yield loss average) [4]. Yield reductions for major maize producers are estimated at 5.2% (India), 5.5% (Brazil), 8% (China), and 10.3% (United States) per 1 °C. Maize production is estimated to reduce by 50% in the Yangtze River basin in China [16]. For sub-Saharan Africa, an increase of 2 °C is predicted to reduce maize yields by more than 20% [17].

These reports highlight the need for genetic improvement of heat stress tolerance in wheat, barley, rice, and maize.

3. Genetic Improvement of Heat Stress Tolerance—Lessons and Insights from *Arabidopsis thaliana*

Arabidopsis thaliana is an undomesticated plant model organism for genetics that has been exposed to an array of environmental challenges throughout its evolutionary history. Research in Arabidopsis has provided essential prerequisites for fundamental breakthroughs and has been used to inform cereal crop research. For example, three out of four Arabidopsis gene families exist in other flowering plants, with often similar gene functions and roles [18,19]. However, as any single plant species cannot fully explain the characteristics of all other species, this has led only to limited success in engineering abiotic stress tolerance in crops. Currently, little knowledge exists of combining resistance to environmental stresses with growth and productivity traits, as trade-offs may exist with some of these investments.

Nevertheless, the availability of natural variation (>750 accessions) and genetic and genomic resources of Arabidopsis are a great asset to understanding the mechanisms of multiple stress tolerances and have enabled the identification and detailed characterization of abiotic stress signaling pathways. Candidate genes for Arabidopsis heat tolerance have been identified based on assessments that include seed germination, seedling survival, hypocotyl and root elongation assays, as well as H_2O_2, chlorophyll content and ion leakage measurements, chromatin immunoprecipitation (ChIP) analysis and in vitro histone acetyltransferase (HAT) assays [20,21].

Heat shock response (HSR) is a defense program in eukaryotic cells to counter the impairment of cell function caused by protein misfolding due to heat stress [22]. Distinct transcriptional regulatory networks are involved in the HSR. In the following, we focus on two extensively researched molecular processes conserved across much of the plant kingdom: the acquisition of thermotolerance through the expression of molecular chaperones (Section 3.1) and long-term adaptation to heat stress through chromatin remodeling (Section 3.2).

3.1. Acquisition of Thermotolerance: Expression of Molecular Chaperones

Sequencing of the Arabidopsis genome discovered large and complex heat stress transcription factor (HSF) families, allocated into three major classes (class A, B and C) and 14 groups (A1–9, B1–4 and C1) [23]. First cloned in yeast in 1988 [24], HSFs have a conserved modular structure and are responsible for the induction of HSR genes, including molecular chaperones such as heat shock proteins (HSPs) and reactive oxygen species (ROS)-scavenging enzymes. These proteins prevent or repair heat stress damage and thus help to confer increased heat stress tolerance [25]. HSFs recognize inverted tandem repeats of the short consensus sequence "nGAAn", known as heat shock element (HSE), common among many heat-inducible gene promoters [26].

In Arabidopsis, the biological functions of class A HSFs are relatively well understood. HSFA1s have critical roles as master regulators indispensable in activating transcriptional networks [27]. Under non-stress conditions, HSFA1a is monomeric and inactive. Heat shock induces HsfA1a trimerization and binding to cis-acting sequences of designated heat shock elements (*HSEs*) in the promoters of *HSPs*, leading to rapid *HSP* expression correlated

with enhanced thermotolerance [28]. Arabidopsis *HSFA9* is regulated by the seed-specific transcription factor ABI3 and is exclusively expressed in the late seed development stages. HSFA9 plays a specialized role in regulating heat shock protein (*HSP*) genes during seed maturation [29]. *HSFA3* is the only *HSF* among the 21 Arabidopsis *HSF* gene family members transcriptionally induced during heat stress by dehydration-responsive element-binding protein 2A (DREB2A) [30]. DREB2A belongs to 14 AP2-domain transcription factors [31], sometimes referred to as C-repeat binding factors (CBFs). HSFA3 also regulates the expression of *HSP*-encoding genes. Although many studies support the finding that HSPs are crucial in thermotolerance, there remains a lack of knowledge about the specific functions and targets of HSPs.

ROS, such as H_2O_2 and O_2^-, are generated under various environmental stress conditions and enhance heat stress-responsive pathways and cell death. Heat stress induces ROS-scavenging enzymes necessary for detoxifying excessive ROS produced under stress conditions, including ascorbate peroxidase (APX) and catalase (CAT). Arabidopsis plants deficient in cytosolic APX1 had suppressed growth, altered stomatal responses, higher oxidative stress sensitivity, and accumulated high H_2O_2 levels [32]. Arabidopsis *CATALASE* genes (*CAT1-CAT3*) are involved in many physiological processes, including abiotic stress responses. *CAT2* plays an essential role in heat tolerance and shows increased gene expression after long-term but not short-term exposure to heat stress [33].

Table 1 summarizes candidate genes and gene families for acquiring heat tolerance identified in Arabidopsis.

Table 1. Candidate genes and gene families for the acquisition of heat tolerance identified in *Arabidopsis thaliana*.

Gene Name	Gene Symbol	Function	Reference
DEHYDRATION-RESPONSIVE ELEMENT BINDING PROTEIN	*DREB2A*	Transcriptional regulators involved in plant responses to cold, drought, and salt stress	[30]
HEAT SHOCK PROTEIN	*HSP*	Molecular chaperones protecting the proteome against environmental stresses; thermomemory	[25]
HEAT SHOCK TRANSCRIPTION FACTOR	*HSF*	Part of signal transduction chains mediating the activation of genes responsive to both heat stress and other stresses	[23]
ASCORBATE PEROXIDASE	*APX*	Antioxidant system-related enzyme	[32]
CATALASE	*CAT*	Antioxidant system-related enzyme, long-term heat tolerance	[33]

3.2. Long-Term Adaptation to Heat Stress: Heat Stress Memory

Moderate heat stress primes a plant to acquire thermotolerance, allowing subsequent survival of more severe heat stress conditions [34]. After the stress has passed, the maintenance of acquired thermotolerance is termed heat stress memory (or thermomemory). Thermomemory is actively maintained over a period of time and requires sustained memory-related gene induction. The genetic basis for thermomemory is unclear, but evidence is accumulating that transcription factors, epigenetic regulators, histone modification, and small RNAs, including miRNAs, are involved.

Chromatin remodeling regulates many genes in plant response to heat stresses. Under recurring heat stress conditions, histone H3 lysine 4 (H3K4) hypermethylation was shown to function as a form of thermomemory for survival [35]. This histone modification is associated with HSFA2 binding, indicating that HSFA2 recruits histone methyltransferases to thermomemory loci. In a recent study, *FORGETTER3/HEAT SHOCK TRANSCRIPTION FACTOR A3* (*FGT3/HSFA3*) was shown to play a vital role in physiological heat stress memory and maintaining sustained memory-gene expression after the heat stress has passed [34]. Following heat stress, HSFA3 mediates thermomemory by directly activating memory-related genes, including *APX2* and *HSFA1E*. HSFA3 binds HSFA2, and in vivo, both proteins form heteromeric complexes with additional HSFs. Only complexes containing both HSFA2 and HSFA3 promote transcriptional memory by jointly recruiting histone H3K4 methylation.

Under heat stress conditions, the histone chaperone ANTI-SILENCING FUNCTION 1 (ASF1) is recruited to heat stress-inducible genes and involved in nucleosome dissociation and H3K56 acetylation [21]. Several miRNAs affect the HSR by regulating the activity of transcription factors. For example, miR398 was found to regulate ROS-scavenging enzymes during heat stress negatively [36]. The downregulation of these genes leads to ROS accumulation, which subsequently activates HSFA1.

The plastidial small heat shock protein HSP21 rapidly accumulates after heat stress and remains abundant during the thermomemory phase, promoting thermomemory capacity [37]. The plastid-localized metalloprotease FtsH6 regulates HSP21 abundance. The genome of Arabidopsis contains twelve *Filamentous temperature sensitive H* (*FtsH*) genes, which are either targeted to mitochondria, the chloroplast, or both. *FtsH6* is involved in high light acclimation and was found to have highly induced expression levels after heat treatment in Arabidopsis, wheat and sorghum, indicating a pivotal role of *FtsH* in response to heat stress.

Table 2 summarizes candidate gene and gene families for long-term adaptation of heat tolerance identified in Arabidopsis.

Table 2. Candidate gene and gene families for heat stress memory identified in *Arabidopsis thaliana*.

Gene Name	Gene Symbol	Function	Reference
Filamentous temperature sensitive H	*FtsH*	Metalloprotease, regulation of heat-shock transcription factor σ^{32}; thermomemory	[37]
HEAT SHOCK PROTEIN 21	*HSP21*	Molecular chaperones protecting the proteome against environmental stresses; thermomemory	[25,37]
ANTI-SILENCING FUNCTION 1	*ASF1*	Histone chaperone	[21]
FORGETTER3/ HEAT SHOCK TRANSCRIPTION FACTOR A3	*FGT3/HSFA3*	*FGT3* encodes the *HSFA3* gene; mediates heat stress memory by direct transcriptional activation of memory-related genes	[34]

4. Genetic and Physiological Basis of Agronomic Traits under Heat Stress

Wheat, barley, rice, and maize are globally important crops. Still, understanding crop biology has been hampered due to their long life cycle and technological barriers in analyzing their large and complex genomes. Heat stress tolerance is a quantitative trait controlled by many genes (G) or loci (QTLs). These often interact with each other (G × G interaction) and with the environment (E) (G × E interactions) and thus are rarely consistent and robustly identified across different growing environments. The availability of high-quality genome [38,39] and pangenome [40,41] assemblies and accurate gene model annotations, coupled with recent developments in CRISPR-Cas9 gene editing [42,43], sequenced mutant populations [44,45], speed breeding to shorten generation times [46], and high-throughput field phenotyping methods [47–49] have helped to overcome challenges associated with research conducted in major cereal crops. These advances have made cereal crops more appealing experimental systems for genetic discoveries in heat stress tolerance that directly translate to increasing crop production.

In the next sections, we will focus on reviewing recent discoveries that shed light on the genetic and physiological basis of key agronomic traits related to heat stress tolerance in the four major cereal crops: crop development and reproduction (Section 4.1), grain yield and quality (Section 4.2), and senescence and biomass (Section 4.3).

4.1. Crop Development and Reproduction

Responses to high temperatures change throughout the different phenological phases of plant development (Figure 2). The cereal crop life cycle is made up of distinct growth phases, including the vegetative growth phase (germination, tillering, stem elongation), reproductive growth phase (inflorescence development), anthesis (flowering), grain filling, and seed set/maturity. Environmental factors such as photoperiod and temperature, as well as endogenous cues, modulate the genetically regulated transition between different

phenological stages [18]. In general, high temperatures alter the relative lengths of phenological phases, speed up crop development and shorten the life cycle [50]. Heat stress damage can become critical to crop productivity when high temperatures coincide with critical crop development stages. Although vegetative growth can benefit from moderately warmer temperatures, heat stress reduces yield dramatically even when plants experience only short periods of high temperatures during the reproductive period [3].

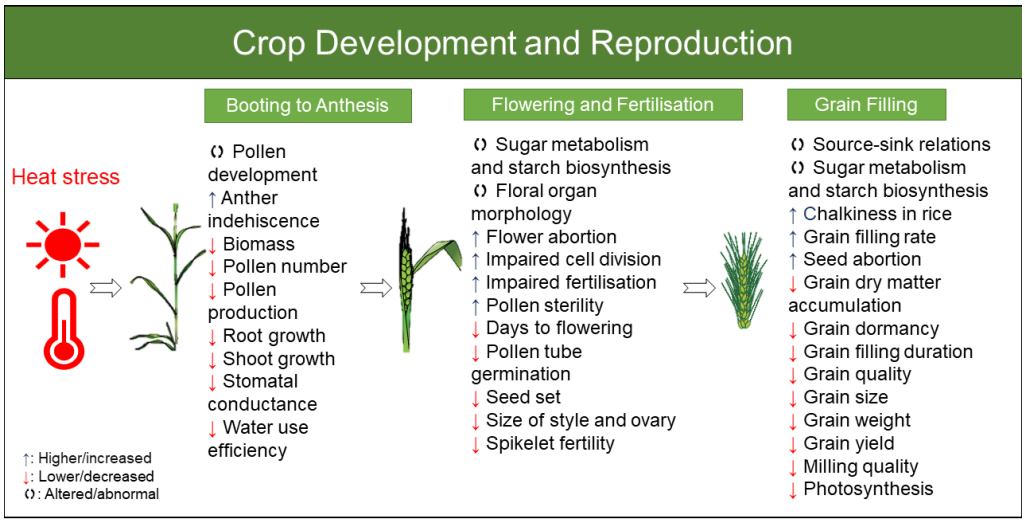

Figure 2. Adverse effects of heat stress on the different stages of the reproductive phase in cereal crop plants.

4.1.1. Wheat

Heat stress is particularly detrimental in wheat during reproductive development and grain-filling [51–53]. A key breeding goal is to optimize crop phenology to the specific environmental conditions at target growing regions, such that flowering and grain development occurs under optimal conditions. Matching maturity to the growing season can be achieved in wheat through designed combinations of major phenology genes. *Photoperiod response* (*PPD*), and *vernalization* (*VRN*) genes, which control the transition to flowering in response to environmental cues, and *Earliness per se* genes and loci (*EPS*), which regulate the transition to flowering independently of the environment, are key phenology genes [18].

As a long-day plant, wheat needs an extended day length to initiate flowering, genetically controlled by the *Photoperiod-1* (*PPD-1*) gene. Three copies of *PPD-1*, namely *PPD-A1*, *PPD-B1* and *PPD-D1*, are located on the short arm of the homoeologous group 2 chromosomes. During wheat domestication, genetic mutations in the *PPD-1* gene led to photoperiod insensitivity which allowed for rapid flowering irrespective of day length, and extended the adaptive range of wheat. In cool and humid Northern European countries, photoperiod-sensitive winter varieties dominate wheat production as these growing regions only have a relatively narrow window of flowering time [54]. In many Mediterranean growing environments, where early flowering is favorable as it avoids heat and drought stress occurring late in the season, photoperiod-insensitive varieties are favored.

Prolonged cold periods (vernalization) trigger flowering in wheat by inducing the expression of *VERNALIZATION1* gene (*VRN1*) transcription [55]. *VRN1* encodes a MADS-box transcription factor that promotes flowering by regulating the expression downstream regulatory targets *VRN2* and *VRN3*. *VRN3* is the cereal orthologue of Arabidopsis *FLOWERING LOCUS T* (*FT1*) and is expressed in leaves induced by long days and then transported to the shoot apex to accelerate inflorescence development. *EPS* genes regulate flowering independent of both vernalization and photoperiod. Its effects can be measured as the difference in time to heading that remains after being satisfied with photoperiod and vernalization requirements. A recent study showed that *EPS*-early and -late alleles determine different degrees of sensitivity to temperature [56]. The expression of *ELF3*, which is considered

the most likely candidate for *EPS-D1*, also interacts with temperature. This study also provided evidence that introgression of the *EPS*-early allele from chromosome 1DL of the wheat cultivar Spark into Rialto (which carries the *EPS*-late allele in 1DL) produced an early flowering phenotype and was mainly associated with an increase in temperature sensitivity during the late reproductive phase.

4.1.2. Barley

Barley is broadly adapted to varying climatic and regional conditions, partly attributed to the extensive natural diversity found in its flowering time genes [57–59]. Early maturity of cool-season cereals such as barley is beneficial in many grain-producing regions experiencing terminal drought and heat stress. The genomic region containing *PPD-D1* in wheat is colinear with the barley photoperiod gene *PPD-H1* on chromosome 2HS [60]. According to a recent study, the sensitive *PPD-H1* allele is more stable in heat and drought conditions [61]. Thus, it may gain more importance in barley growing regions affected by increased climate extremes, including heat stress. In a study of natural variation of promoter and intron 1 haplotypes in a barley landrace collection, different *VRN-H3* alleles (*vrn-H3a-d*) were associated with flowering time differences [62]. They were found to either shorten (6–8 days, *vrn-H3c*) or lengthen (*vrn-H3d*) the late reproductive phase in barley independently of vernalization treatment. Therefore, these different alleles can fine-tune phenology to escape terminal heat stress (*vrn-H3c*) or increase the number of grains and yield under optimum conditions (*vrn-H3d*).

As in wheat, barley *EPS* genes determine the time and duration of reproductive phases. The gene *CENTRORADIALIS* (*CEN*) is a candidate gene for the *EPS2* locus, and different *CEN* haplotypes affect the time to flowering [61,63]. *ELF3* regulates photoperiod-dependent flowering and gibberellic acid (GA) synthesis in barley [64]. Recent studies show that it may also play a role in high temperature-dependent growth and development. The recessive allele (*elf3*) causes photoperiod insensitivity and early flowering. In *elf3* loss-of-function mutants, the high temperature-dependent transcript expression of several circadian clock genes, including *GIGANTEA* (*GI*), *LUX ARRHYTHMO* (*LUX*), and *PSEUDO RESPONSE REGULATOR* (*PRR*), was disrupted, thus compromising the functioning of the circadian clock.

4.1.3. Rice

The rice flowering stage is the most sensitive period to high day or night temperatures [65]. Daily temperatures above 30 °C with daily maximum temperatures above 35 °C reduce yield by inhibiting seedling growth and tillering [66]. When high day temperature coincides with the reproductive stage (booting to anthesis), it results in lower pollen production, poor pollen development, and reduced anther dehiscence (pollen shedding), limiting the release of mature pollen, and spikelet fertility. High temperatures during seed development and maturation stage result in reduced grain weight and quality and inhibited grain-filling duration. Recent QTL mapping studies were conducted for spikelet fertility under heat stress during the booting [67] and flowering stages [68,69]. Two significant QTLs on chromosome 1 and chromosome 4 explained 12.6% (*qHTSF1.1*) and 17.6% (*qHTSF4.1*) of the variation in spikelet fertility at high temperatures, respectively. Studies also detected QTLs for anther length, longitudinal dehiscence [70], and pollen fertility [71].

RILs derived from a cross between the heat-tolerant cultivar Nagina22 and the heat-sensitive IR64 were used to map the QTLs for heat tolerance at flowering [72]. Five QTLs, identified on chromosomes 3, 5, 9 and 12 for stress susceptibility and stress tolerance indices (SSI and STI) of spikelet sterility and yield per plant, explained phenotypic variation of up to 29%. Two of the five QTLs were located in less than 400 Kbp genomic regions, comprising 65 and 54 genes. Genes mapped within these genomic regions included transporters, transcription factors including *HSF* (*HsfB4c*), *PERSISTENT TAPETAL CELL1* (*PTC1*), and *GLYCOSYLTRANSFERASE1* (*GT1*). *PTC1* encodes a PHD-finger protein that controls programmed development and degradation of the tapetum, the innermost cell

layer of the anther wall, to ensure functional pollen formation in rice. Loss of function of *PTC1* leads to uncontrolled tapetal cell proliferation and delayed pollen wall development, causing complete male sterility [73]. Glycosyltransferases catalyze the transfer of saccharide moieties to a wide range of acceptor molecules such as lipids, proteins, and oligosaccharides. GT1 of rice present is involved in pollen wall development, especially the exine and intine construction and pollen maturation.

Two heat stress tolerance QTLs affecting seed set percentage (SSP) were identified at the flowering stage in both controlled and field experiments using recombinant inbred lines (RILs) [71]. A QTL on chromosome 4 explained up to 25.8% of the total phenotypic variation in SSP and increased SSP by up to 9.3% under heat stress conditions. The QTL on chromosome 10 explained 11.5% of the SSP phenotypic variation, increasing the SSP by up to 7.2% when plants were subjected to heat stress.

Bheemanahalli et al. suggest that Early-morning flowering (EMF) can advance flower opening times to escape heat stress at flowering in growing regions experiencing high daytime temperatures [74]. Rice plants with EMF traits shed viable pollen onto a receptive stigma during the cooler hours in the morning, thus escaping spikelet sterility-inducing high temperatures at noon. An EMF trait allele identified in wild rice (*Oryza officinalis*) on chromosome 3 and introgressed into the *indica* genetic background (IR64 + qEMF3) shifted peak anthesis by two hours compared to the recurrent parent and reduced heat stress-induced spikelet sterility in the glasshouse [75]. Bheemanahalli et al. quantified EMF traits as time-of-day of flowering characteristics such as first spikelet opening time (FSOT) and peak spikelet opening time (PSOT) in *indica* cultivars originating from 33 major rice-growing regions in the field [74]. They compared it to IR64 + qEMF3 but found no cultivars with the EMF trait.

Another beneficial flower characteristic for high-temperature tolerance is cleistogamy, a method of self-fertilization within closed flowers. Cleistogamy was hypothesized to decrease the severity of temperature stress-induced sterility in rice [76,77] and other cereal crops such as barley [78]. The temperature-sensitive cleistogamous rice mutant, *superwoman1-cleistogamy* (*spw1-cls*), only shows the mutant cleistogamous phenotype under constant warm day temperatures [76]. Cleistogamous rice plants had higher spikelet fertility, higher germinated pollen grains per stigma, and lower temperatures within the closed flowering spikelets than chasmogamous (open-flowering) rice plants [77]. The benefit of cleistogamy against high temperature-induced sterility is yet to be evaluated and confirmed in field trials.

4.1.4. Maize

High-temperature stress, especially during the reproductive stages of anthesis, silking and grain filling, negatively affects maize production [79]. In contrast with other cereal crops, maize is monoecious, bearing separate male (tassel) and female (ear) flowers. Most heat stress research used temperate maize germplasm for high production areas. Therefore, limited breeding progress has been made to develop improved maize germplasm with specific tolerance to elevated temperatures. The temperature threshold for damage by heat stress is significantly lower in reproductive organs than in vegetative organs in maize. Heat stress during the reproductive phase can reduce grain yields by up to 90% [17,80] and decrease grain number and (to a lesser degree) kernel weight, ultimately reducing yield [81,82]. Maize has a relatively shorter anthesis duration (3–5 d) compared to wheat and rice (>1 week). This likely reduces relative thermotolerance, as a longer anthesis duration minimizes the likelihood of a single extreme heat event affecting all flowers [80].

The optimum temperature for maize anthesis is 30.5 °C, and temperatures above 38 °C can negatively impact maize pollen germination. A recent study conducted in a controlled glasshouse environment showed that when maize experiences high temperatures of 40 °C during flowering, grain yield, seed-set, and grain number decreased by almost 80% compared to optimum growing temperatures, with only minor effects on kernel weight [82]. Liu et al. reported that high temperatures also advance tasseling and pollen shedding

time, extend the anthesis—silking interval (ASI), reduce silking rate and pollen viability, ultimately affecting kernel formation [83]. In this study, heat stress advanced or delayed silking time in a genotype-dependent manner. For breeding high-temperature tolerant maize, both male and female reproductive organs are important when aiming to achieve high and stable yields in heat-prone environments. Heat stress further affects cell division, sugar metabolism, and starch biosynthesis, reducing subsequent dry matter accumulation within kernels during the reproductive stage [17].

Under heat stress, traits associated with reproductive success include anthesis-silking interval, tassel blast, tassel sterility, pollen viability, stigma receptivity, and seed set percentage under open-pollinated conditions [84]. Maize genotypes with heat-tolerant plant architectural traits such as compact tassel and lower cob angle show improved performance under heat stress conditions because of their ability to reduce the evaporation rate and direct sunlight exposure [85]. A recent study found a high variation for heat tolerance during the seedling stage in a set of European maize inbred lines and identified 39 heat tolerance candidate genes but with currently unknown molecular functions for heat tolerance and adaptation [86].

Table 3 summarizes the effects of heat on cereal crop development and reproduction and previously identified QTLs or candidate genes for all four cereal crops.

Table 3. Effects of high temperatures on cereal crop development and reproduction. The '+' sign indicates an increase, and the '−' sign shows a decrease in the performance of the trait of interest. n.a.: not assigned.

Trait	Impact	QTL, Locus or Marker	Candidate Gene	Chromosome	Crop Species	Reference
Grain filling period duration	−	*QHgfd.iiwbr-1B, QHgfd.iiwbr-5A*	n.a.	1B, 2B, 3B, 5A, 6B	bread wheat	[53]
Grain filling period duration	−	*QHgfd.tam-1D (gwm337), QHgfd.tam-2A (wmc407), QHgfd.tam-6D (gwm325), QGfd.tam-1Bc (barc137), QGfd.tam-2A (wmc407), QGfd.tam-2D (cfd43)*	n.a.	1B, 1D, 2A, 2D 6D,	bread wheat	[52]
Grain filling period duration	−	*Xgwm11, Xgwm293*	n.a.	1B, 5A	bread wheat	[51]
Temperature sensitivity (late reproductive phase)	+	*Eps*	*ELF3*	1D	bread wheat	[56]
Early inflorescence development	+	n.a.	*Ppd-1*	2H	bread wheat	[50]
Life cycle duration/temperature sensitivity	−/+	*Mat.a8, eam8*	*ELF3*	1HL	barley	[64]
Reproductive phase duration	+	n.a.	*ODDSOC2*	3H	barley	[87]
Flower opening time	−	*qEMF3*	n.a.	3	rice	[75]
Cleistogamy	+	*spw1-cls*	*SPW1*	6	rice	[76,77]
Spikelet fertility at flowering	−	*qHTSF1.1, qHTSF4.1*	n.a.	1, 4	rice	[68]
Spikelet fertility at flowering	−	*109 QTLs*	n.a.	1–12	rice	[88]
Pollen fertility	−	*qPF4 (RM5687—RM471), qPF6 (RM190—RM225)*	n.a.	4, 6	rice	[71]

4.2. Grain Yield and Quality

High day and night-time temperatures accelerate the rate of grain-filling and shorten the grain-filling duration in cereal crops [89,90]. Heat stress during the grain-filling period

also impairs several physiological and metabolic processes linked to grain size and quality (Figure 2). Examples include markedly decreased starch and sugar levels such as fructose, sugar nucleotides, and hexose phosphate, resulting in reduced yield and low grain and milling quality [91]. The majority of heat stress studies lack information on the impact of heat stress on the quality of the produced grains. As grains are the main nutritional source for human food, animal feed, and beverage industries, it is vital to assess grain quality in addition to quantity (i.e., grain yield).

4.2.1. Wheat

Heat stress affects grain quality due to the limitation of assimilate supply and lower remobilization of nutrients, and increases grain protein concentration in wheat [92,93]. During grain filling, heat stress affects starch deposition and sugar supply to the developing grain, leading to reduced grain size and yield in wheat [94,95]. Heat stress during grain filling also reduces photosynthesis, increases the mobilization of stem reserves (water-soluble carbohydrates, WSC) and accelerates senescence.

Precocious germination before harvest, also known as Pre-Harvest Sprouting (PHS), triggers the premature production of α-amylases and proteases, which break down starch and gluten reserves in the endosperm [96]. Late-maturity α-amylase (LMA) occurs when α-amylases, encoded by *α-Amylase1* (*α-Amy1*) genes on chromosomes 6A, 6B, and 6D, are produced in the aleurone during grain filling and maturation in the absence of PHS. The enzyme activity is retained in the mature grain, resulting in an unacceptably low Falling Number (FN), failure to meet receival standards, and consequent grain downgrading. A recent study showed that heat stress during mid to late grain filling reduces grain size and dormancy and can trigger LMA within a wide range of winter and spring varieties [97].

Heat stress leads to the inactivation of many heat-labile proteins. Soluble starch synthase is an amyloplastic enzyme in the wheat endosperm and the rate-limiting component of the starch synthesis pathway of the developing wheat grain. This enzyme is sensitive to temperatures above 25 °C, and a 3 h exposure of 30 °C during grain filling can reduce soluble starch synthase activity by 30% [94]. Several heat protection proteins exist in wheat, such as HSPs, APX, and galactinol synthase (GOLS). A study of heat-induced expression profiles of *HSFs* and *HSPs* in different wheat tissues has shown that expression of A2 and A6 members of the *HSF* family within class A increased strongly during heat stress [98]. *HSFC2a* is a member of the monocot-specific *HSFC2* subclass and regulates heat protection genes. A recent study found that three *HSFC2a* genes were highly expressed in wheat grains during grain filling and strongly up-regulated by drought and abscisic acid (ABA) treatment [99]. *HSFC2a-B* is a transcriptional activator of heat protection genes via the ABA-mediated regulatory pathway. Transgenic wheat constitutively overexpressing *HSFC2a-B* strongly improved thermotolerance but not dehydration tolerance.

Grain number is directly associated with grain yield. Heat stress reduces grain number and lowers the harvest index in wheat. When heat stress coincides with the young microspore and dehiscence stage at anthesis, failure to release pollen from the anther locules inhibits pollination, leading to sterility and reduced grain numbers. Previous studies focused on understanding the genetic basis of grain quality and yield reduction in response to heat stress in wheat have detected QTLs for grain number on chromosomes 2A and 6D [100], as well as on 1B, 3B, 4A, 4B, 4D, 5B, and 6B [101]. Other studies detected QTLs for grain size [95], grain fill duration [100–103], and grain yield [100,101,103,104] in wheat in response to heat stress.

A study defined a QTL on chromosome 3BL previously associated with grain yield, thousand-grain weight and early vigor under combined drought and heat stress in the field [104]. To further narrow down the genetic region from initially 20 cm to around 5 cm, RILs with alternative alleles were trialed and phenotyped in environments varying in drought and heat stress levels. Depending on the environment, different alleles either had a positive or a negative effect on yield, believed to be due to crop management factors present at the various field sites. For example, sowing density, soil composition, and biotic

or abiotic stresses would favor different root systems over others. Parent et al. found the allele effect at *qYDH.3BL* depends on environmental conditions, including growth temperatures [105]. The QTL was fine-mapped, and sequence variants and differential expression analyses identified a sequence variant in the promoter region of the *Seven in absentia* (*SINA*) gene consistent with increased biomass, grain number, and grain weight following heat stress [106]. This allele has been selected only in breeding programs in Mexico and Australia. It could be beneficial in other regions with the increasing occurrence of heat stress events in the future.

4.2.2. Barley

In barley, heat stress during the grain filling stage reduces grain yield and malt quality, attributed to high protein concentrations and low accumulation of carbohydrates [107]. When subjected to heat stress at heading, malting trait profiles show varietal-specific changes in β-glucan levels, diastatic power, and α-amylase activity [108]. When heat-stressed at meiosis, most pollen grains lack starch, causing high floret sterility and consequently low levels of seed-set in barley [109].

A recent study assessed 157 barley varieties of contrasting genetic backgrounds for developmental, agro-morphological, and physiological traits and examined the effects of heat stress on physical grain quality [110]. Heat stress in the field due to delayed sowing (to ensure heat stress coincided with grain-filling reduced duration of developmental phases) decreased grain number, grain plumpness, and harvest index, but increased screenings, grain-filling rate, water-soluble carbohydrates, and grain protein content. Heat tolerant genotypes had heavier and plumper grains, higher grain-filling rate, longer grain-filling duration, and flowered comparatively early. Grain-filling rate was most highly and consistently associated with physical grain quality stability and barley heat tolerance. Selecting high grain plumpness under low-stress conditions and high grain-filling rate may enhance the breeding for heat stress tolerance.

There is currently limited knowledge on specific genes controlling grain size and based primarily on sequenced-based co-linearity between crop species. The gene *DENSE AND ERECT PANICLE 1* (*DEP1*) is a candidate gene underlying a major quantitative trait locus for grain length [111]. In rice, the *DEP1* locus is pleiotropic for erect panicle, grain number per panicle, nitrogen uptake and metabolism, ABA response and drought tolerance. *DEP1* is located on chromosome 5H and encodes a plasma-membrane-associated G-protein γ-subunit in barley. Watt et al. observed an increase in grain length and a reduction in grain width and thickness in response to high field temperatures during grain-filling in barley [112,113]. A novel polymorphism in the promoter region of *DEP1* significantly reduced *DEP1* gene expression in developing inflorescences. It was associated with reduced grain length and thousand-kernel weight in barley cultivars carrying the allele.

4.2.3. Rice

The grain filling stage is sensitive to environmental stress and critical for rice yield and grain quality. Starch is a glucose polymer and consists of amylose, composed of largely unbranched glucose molecules, and highly branched amylopectin. The proportion of short and long amylopectin chains determines the texture of cooked rice. Starch synthases (SSs) have a central role in starch biosynthesis in rice [114]. ADP-glucose pyrophosphorylase (AGPase) catalyzes the first step in starch biosynthesis, converting glucose (Glc)-1-phosphate and ATP to ADP-glucose and pyrophosphate. Starch synthase IIA (SSIIa) and granule-bound starch synthase I (GBSSI) genes primarily synthesize amylose and are located closely on chromosome 6.

High day or night temperatures accelerate grain filling rate, shorten grain filling duration, lower grain weight, reduce milling quality, and increase chalk formation in rice [115,116]. The grain-filling stage is subject to the activity of various enzymes, primarily temperature-sensitive GBSS and SSIIa. GBSS and SSIIa are the highly expressed isoforms in the rice endosperm during grain filling stages, and mutations in these genes affect grain

chalkiness [117]. Chalking occurs when air spaces form among the irregular packed starch granules (amyloplasts) in the rice endosperm, resulting in opaque (or chalky) white regions of the kernel. Chalky kernels are more prone to breakage during milling than translucent kernels, degrading the overall appearance of milled rice.

Gene expression profiling of chalky and translucent grains in Japanese rice showed genotypic and heat-induced changes in the starch genes. Specifically, starch synthesis gene expression increased in the conditional chalky grain mutant *flo11-2*, which developed highly chalky grains only under heat stress conditions. *flo11-2* has a single amino acid substitution at the conserved ATPase domain of *HSP70-2*, essential for translocation of GBSSI and other amyloplast-localized proteins [118]. In addition, the *flo11-2* mutant was highly susceptible to preharvest sprouting.

Gene expression analyses of developing rice caryopses of the high chalky cultivar 'Nipponbare' exposed to high or controlled temperature during the milky stage elucidated the effect of high temperature on grain-filling metabolism [119]. Starch synthesis gene expression was suppressed in heat, whereas *HSP26*, *HSP22a*, and *HSF* gene expression increased. A recent study performed gene expression analysis on six rice genotypes with different chalkiness levels [117]. They found that the expression patterns of AGPL, which encodes a unique subunit of the cytosolic AGPase, as well as GBSSI and SSIIA, are genotype-dependent and heat sensitive. The disruption in the expression pattern of these starch biosynthesis genes by heat appears to be associated with environment-induced chalkiness, highlighting the importance of coordinated starch biosynthesis during the critical stages of grain filling to produce non-chalky rice grains. In the chalky genotypes, peak expression of AGPase occurred in the stages before grain filling commenced, creating a gap between the upregulation of GBSSI and SSIIA. Whereas, in low-chalk genotypes, peak expression of AGPase occurred later, following the expression patterns of GBSSI and SSIIA. High temperatures altered the expression of starch synthase genes, changed grain morphology and increased chalkiness. AGPase subunit gene expression was suppressed during early grain-filling stages in the chalky genotypes or upon heat treatment. This resulted in a limited pool of ADP-glucose for synthesizing amylose and amylopectin, which negatively impacted the starch biosynthesis process and increased chalkiness.

4.2.4. Maize

As a C_4 plant species, maize has a higher temperature optimum for photosynthesis than C_3 plants wheat, barley and rice. In C_3 plants, an increase in Rubisco oxygenase/Rubisco carboxylase ratio inhibits net photosynthesis at moderate heat stress [120]. The ratio of dissolved O_2/CO_2 and the specificity of Rubisco for O_2 increases with rising temperatures, thus favoring oxygenase activity and resulting in net photosynthesis inhibition. Consequently, when C_3 plants are exposed to conditions that reduce oxygenase activity (high CO_2 or low O_2), the temperature optimum for net photosynthesis increases. In C_4 plants, CO_2 concentrates around Rubisco in bundle sheath chloroplasts, inhibiting Rubisco oxygenase activity and photorespiration at elevated temperatures. C_4 photosynthesis may also be limited through the inactivation of Rubisco or by rates of other C_4 bundle sheath enzymes, which show species-specific temperature responses. When high temperatures coincide with the early stages of kernel development, the number and size of endosperm cells reduce, leading to lower final kernel mass and size. Heat stress shortens grain filling duration, but the more considerable reduction in grain filling rate is responsible for the heat-related reduction in seed mass [121].

The starch of waxy maize comprises 100% amylopectin. Heat stress at the early development stage (stage of division and differentiation of endosperm cells) increased starch content, starch granule size, and crystallinity in waxy maize varieties [122]. Still, it decreased protein and soluble sugar content, thus negatively impacting kernel quality. When heat stress occurred at the later grain filling stages, the soluble sugar content was unaffected, protein levels increased, but starch content and crystallinity reduced [91,122,123]. Sucrose is the primary transport substrate for starch synthesis in cereal endosperms. A reduction

in the activity of enzymes involved in sucrose and starch synthesis, including sucrose synthase (SuSy), AGPase, soluble starch synthase (SSS) and starch branching enzyme (SBE), suppressed starch deposition in response to heat stress [91].

A genome-wide expression profiling study of temperate European Flint and Dent maize inbred lines grown under heat stress identified 607 heat-responsive and 39 heat-tolerance genes, including heat shock genes and genes involved in protein folding and biosynthesis, cell wall modification, and calcium signaling [86]. Genome-wide association mapping in tropical maize inbred lines identified 150 significant SNP associations for grain yield within 89 genes on chromosomes 1, 2, 4, 5, 8 and 10 under combined drought and heat stress [124]. A recent mapping study used a sub-tropical DH maize panel to identify 12 significant SNP associations for grain yield under heat stress. These SNPs were located on chromosomes 1, 3, 6, 7 and 10, accounting for 18.7% of the phenotypic variation [125]. Identified candidate genes regulating plant development and protein translocation included *U-box domain-containing protein*, *GRAS family transcription factor*, and *protein kinase family protein*. A recent study identified genomic regions associated with heat stress tolerance in tropical maize trialed at nine locations in South Asia [126]. The association mapping panel included 543 tropical maize inbred lines from diverse genetic backgrounds and was trialed across nine locations in South Asia under natural heat stress. A total of 269 SNPs within 140 candidate genes, including *basic-Helix-Loop-Helix* (*bHLH*), *basic leucine zipper* (*bZIP*), and *Ethylene Responsive Element Binding-like* (*EREB*) *transcription factor* genes, were detected for grain yield under heat stress.

Table 4 summarizes the effects of heat on cereal crop grain quality and previously identified QTLs or candidate genes for all four cereal crops.

Table 4. Effects of heat on cereal crop grain yield and quality. The '+' sign indicates an increase, and the '−'sign indicates a decrease in the performance of the trait of interest. n.a.: not assigned.

Trait	Impact	QTL, Locus or Marker	Candidate Gene	Chromosome	Crop Species	Reference
Grain number	−	*QHknm.tam-1A (cfa2129)*, *QHknm.tam-2B (barc200.2)*, *QHknm.tam-3Bc (barc147)*, *QHknm.tam-4A (wmc89)*, *QHknm.tam-5B* (gwm213)	n.a.	1A, 2B, 3B, 4A, 5B	bread wheat	[52]
Grain weight	−	*QHkwm.tam-1B* (gwm268), *QHkwm.tam-2B* (gwm111.2), *QHkwm.tam-3B* (wmc527), *QHkwm.tam-5A* (gwm291), *QHkwm.tam-6D* (gwm325)	n.a.	1B, 2B, 3B, 5A, 6D	bread wheat	[52]
Grain weight	−	*QTL11*, *QTL27*	n.a.	3B, 6B	bread wheat	[95,127]
Grain yield	−	*Q.Yld.aww-3B-2*, *Q.Yld.aww-3B-1*, *Q.Yld.aww-3D*, *Q.Yld.aww-4D*, *Q.Yld.aww-5B*, *Q.Yld.aww-7A-1*, *Q.Yld.aww-7A-2*	n.a.	3A, 3D, 4D 5B, 7A	bread wheat	[127]
Grain yield, grain number, grain weight	−	*qYDH.3BL*	*SINA*	3B	bread wheat	[104,106]
Grain size, thousand-kernel weight	−	*qGL5H*	*DEP1*	5H	barley	[112,113]
Chalkiness	+	*flo11-2*	*cpHSP70-2*	12	rice	[118,128]
Grain yield	−	*qSSPF10*, *qHT6* (*RM190-RM587-RM510-RM225-RM217-RM50*)	n.a.	6	rice	[128,129]

Table 4. *Cont.*

Trait	Impact	QTL, Locus or Marker	Candidate Gene	Chromosome	Crop Species	Reference
Grain yield	–	1549 SNPs	673 candidate genes including *U-box domain-containing protein*, *GRAS family transcription factor*, and *protein kinase family protein*	1, 2, 4, 5, 8, 10	maize	[124]
Grain yield	–	269 SNPs	140 candidate gene models, including *bHLH* (*basic-Helix-Loop-Helix*) *transcription factors*	1–10	maize	[126]
Grain yield	–	12 SNPs	9 candidate gene models	1, 3, 6, 7, 10	maize	[125]

4.3. Senescence and Biomass

Apart from causing a shortened grain filling duration, post-anthesis heat stress can induce premature leaf senescence, significantly limiting grain yield, crop biomass, and grain quality. Accelerated plant senescence is part of a 'heat escape' strategy that facilitates the next generation's survival under stress [130]. During senescence, plants recycle nutrients, modify source-sink balances, and alter organ morphology and chemical composition, including redox status and hormone levels. Heat-stress induced membrane and protein damage can result in elevated ROS that causes oxidative stress and induce programmed cell death. High temperatures can also indirectly affect photosynthetic activity by compromising plant water status due to increased evaporative demand. Complex genetic networks control these changes by regulating physiological, biochemical, and molecular mechanisms (Figure 3).

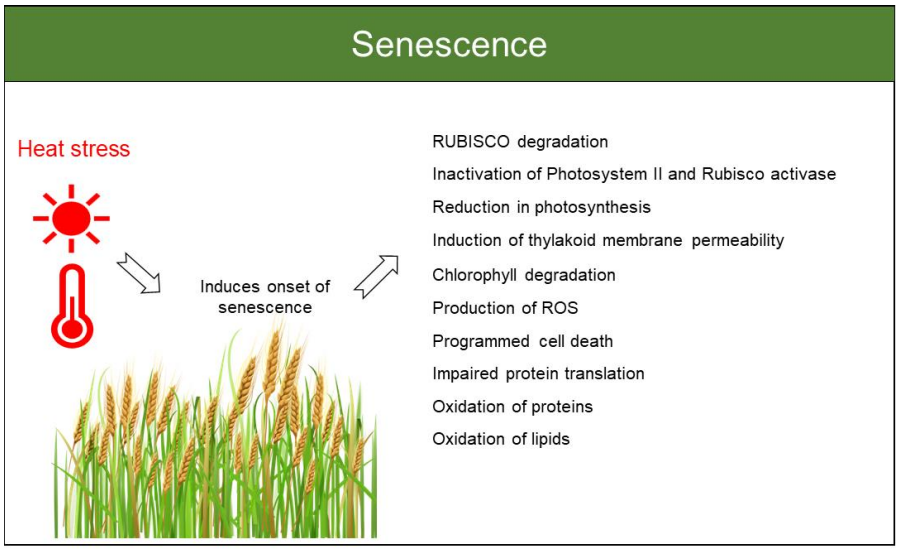

Figure 3. Adverse effects of induced senescence mediated by heat stress in plants.

Many processes of photosynthetic metabolism are very temperature-sensitive [131]. Enzymes are often heat sensitive and lose their activity or denature with rising temperatures. A significant cause of photosynthetic inhibition of cereal crops is the thermal lability of enzymes directly involved in net photosynthetic carbon assimilation, which is primarily determined by Rubisco efficiency and activation and ribulose bisphosphate (RuBP) regeneration. Enzyme degradation at high temperatures can impede the function of Photosystem II (PSII) and Rubisco activase (Rca), decrease electron transport rates, and reduce chlorophyll

content. High temperature can also induce membrane permeability, directly damaging the chloroplast thylakoid membranes, inhibiting light harvesting, electron transport rates, and ATP generation.

Key regulatory molecules and signaling pathways are involved in gene expression changes during leaf senescence. They include chromatin-modifying factors, transcription factors, as well as post-transcriptional, post-translational, and metabolic regulators [132]. Almost one-fourth of Arabidopsis genes are associated with senescence, including transcription factors such as *DREB2A*, a key regulator in drought and heat stress responses, and *HSP*-encoding genes [133,134]. The leaf senescence database provides information concerning senescence-associated genes and their corresponding mutants [135]. Currently, it contains 5,853 genes and 617 mutants from 68 species, including three wheat, one barley, 78 rice, and two maize mutants with altered leaf senescence phenotypes.

4.3.1. Wheat

A modelling study of key wheat-growing regions of Australia demonstrated that variations in average growing-season temperatures of 2 °C could cause reductions in grain production of up to 50%, primarily due to increased leaf senescence in response to high temperatures [11]. Heat can accelerate senescence in photosynthetic organs, limits the availability of assimilates for reproduction, inhibits chlorophyll biosynthesis, and accelerates the breakdown of thylakoid components causing reductions in chlorophyll content and functionality [136]. Heritable plant chlorophyll retention, a trait also known as 'Staygreen', delays foliar senescence and allows plants to maintain photosynthetically active leaves under environmental stress conditions. *STAY GREEN* (*SGR*) genes play significant roles in regulating chlorophyll breakdown under age-induced and environmental stress-induced senescence in Arabidopsis [137]. In wheat, Staygreen contributes to a long grain-filling period and stable yield under heat stress conditions by maintaining chlorophyll content and functionality and thus maintaining sugar supply during grain filling. The ability to maintain grain weight under heat stress conditions in the field correlated with Staygreen in wheat [138–140]. Genetic variability for Staygreen has been identified and exploited in maize, rice, wheat, and other plant species.

Previous studies on the genetic basis of grain quality and yield reduction in response to heat stress in wheat have found numerous QTLs for leaf senescence and Staygreen [103,141]. Mapping analyses identified 44 QTLs on chromosomes 1B, 2A, 2B, 4A, 4B and 7D associated with Staygreen, some of which were also co-locating with yield and yield-related traits [103]. A recent study showed that certain RILs maintained Staygreen traits under combined heat and drought stress at the anthesis stage. These RILs up-regulated known chlorophyll biosynthesis gene expression (including *CHLD*, a key enzyme for chlorophyll synthesis and chloroplast development), as well as down-regulated chlorophyll degradation gene expression (including *pheide a oxidase* (*PaO*), *pheophytin pheophorbide hydrolyase* (*PPH*) and *Stay Green 1* (*SGR1*)) [141].

Among other developmental and environmental signals, plant hormones control senescence in response to environmental stress. The gaseous phytohormone ethylene plays multifunctional roles in plant growth, development, and stress responses. Ethylene inhibits vegetative growth by restricting cell elongation, mainly through cross-talk with auxins, accelerates senescence, and modulates responses to environmental stress. In mature wheat plants, increased ethylene accelerates maturity, shortens the grain-filling period, decreases thousand-grain weight, and induces premature senescence [142]. Heat stress-induced ethylene production in wheat regulates kernel abortion and grain maturation suppression. Exposure to a heat stress of 38 °C during early kernel development resulted in a significant increase in ethylene production in developing kernels and flag leaves of a heat susceptible wheat cultivar 'Karl 92', but not in the heat-tolerant wheat cultivar 'Halberd'. Treatment of 'Karl 92' plants with ethylene receptor inhibitor 1-methyl cyclopropane before heat stress blocked heat stress-induced kernel abortion and reduced kernel weight. Ethylene

was hypothesized to regulate susceptibility to heat stress by triggering the transition to developmental arrest and senescence in wheat.

4.3.2. Barley

Heat stress accelerates the rate of senescence and leaf chlorophyll loss, leading to reduced photosynthetic capacity and assimilate supply to the developing grains. In barley, direct selection for yield may have led to indirect selection for Staygreen [143]. Yield under heat stress is a complex trait, often confounded by many low heritability factors. Targeting heritable traits that likely underpin heat stress-adaptation, such as Staygreen, using molecular markers and marker-assisted selection (MAS) can offer higher rates of genetic gain for heat stress tolerance in breeding programs. A QTL study evaluated Staygreen by Soil Plant Analysis Development (SPAD) chlorophyll meter readings or visual assessment of an ND24260 × Flagship DH population and detected six QTLs for Staygreen associated with terminal heat-stress on chromosomes 3H, 4H, 5H and 6H. Transgressive segregation indicated that multiple genes likely control Staygreen. The most significant QTLs detected in the heat-stress experiment was *HSPFLQ1*, positioned at Diversity Arrays Technology (DArT) marker bPb-5529 on chromosome 5H, explaining 17.4% of the phenotypic variance. This marker is associated with *Long basal rachis internode 1* (*lbi1*) gene expression. The QTLs identified for Staygreen under terminal heat and drought stress were located at different positions on the chromosomes. In the heat treatment, the Staygreen traits examined were correlated, but not with biomass, thousand-kernel weight, or tiller and spike number. Staygreen expression was also independent of anthesis date and maturity.

4.3.3. Rice

Crop biomass comprises vegetative plant material above (shoot biomass) and below (root biomass) the ground surface area. A recent study used genotyping-by-sequencing to generate single nucleotide polymorphic (SNP) markers for 150 RILs from heat tolerant N22 × heat susceptible IR64 to determine seedling stage tolerance to heat stress [144]. One QTL was identified for root length, and three QTLs were identified for coleoptile length under heat stress, explaining 20.4% and up to 10.2% of the phenotypic variation, respectively. Candidate genes underlying the significantly associated SNPs include genes encoding transcription factors, heat shock proteins, proteases, protein kinases, and phospholipases.

Li et al. assessed seedling survival under heat stress of chromosome segment substitution lines (CSSLs) with a heat susceptible Asian rice variety as the donor parent and heat stress tolerant African rice (*O. glaberrima* accession CG14) as the recurrent parent [145]. The Asian rice variety contained five QTLs contributing to thermotolerance, including a major QTL on chromosome 3 termed *Thermo-tolerance 1* (*TT1*). The candidate gene underlying *TT1* was identified as *Os03g0387100*, also known as *Proteasome alpha 2 subunit 1* (*PAB1*). *PAB1* encodes the α2 subunit of the 26S proteasome, which is a multi-catalytic protease complex responsible for the selective, ATP-dependent degradation of ubiquitylated proteins. Overexpression of *PAB1*led to higher, and *PAB1* gene knockout led to lower heat tolerance in transgenic lines than control plants, providing evidence that *PAB1* is the underlying causal gene for the *TT1* locus. The authors hypothesized that *TT1* enhances the elimination and recycling of ubiquitinated proteins denatured due to heat stress.

Ribosomal RNA homeostasis is crucial to normal growth and development and is impacted by temperature stress [146]. The nucleolar-located RNA helicase Thermotolerant Growth Required 1 (TOGR1) is a crucial chaperone for rRNA homeostasis and regulates thermotolerant growth in rice [147]. TOGR1 is controlled by temperature and the circadian clock and is associated with the small subunit (SSU) pre-rRNA processome, a prerequisite to maintaining normal rRNA homeostasis at high temperatures. Transcriptome analysis revealed that TOGR1 is essential in coordinating primary metabolisms to support thermotolerant growth. Natural variation in its transcript level is positively correlated with plant height, and the enhanced expression of *TOGR1* significantly increased rice biomass under hot conditions. Ascorbate peroxidase 2 (APX2) and galactinol synthase 2 (GolS2) both

protect plants from heat stress by scavenging ROS (reactive oxygen species) and producing osmoprotectants, respectively. Transcript level measurements of homologues of *APX2* and *GolS2* in wild type rice and *togr1-1* mutant seedlings showed that these genes were more highly expressed in the mutant than the wild type in response to heat stress.

He et al. identified a rice mutant highly susceptible to heat, with higher hydrogen peroxide (H_2O_2) content and increased cell death under heat than the wild-type [148]. Using map-based re-sequencing (IMBR), they identified the causal gene *PREMATURE SENESCENCE LEAF 50* (*PSL50*). *PSL50* negatively regulates heat-induced premature leaf senescence in rice, probably by acting as a modulator of H_2O_2 signaling in response to heat stress.

4.3.4. Maize

Plant leaves are specialized organs that capture light energy by photosynthesis and allow photo assimilation for grain development. Heat stress during grain filling accelerates leaf senescence and also decreases plant height, leaf area, and biomass at maturity in maize [149]. Leaf senescence is an oxidative process that involves the degradation of cellular and sub-cellular structures, hydrolysis of macromolecules such as proteins and lipids, and mobilization of nutrients from senescing leaves to growing or sink organs [150]. It is associated with higher oxidative stress and a decline in antioxidant activity and levels of membrane lipids, including phospholipids and galactolipids [151]. ROS play a role in lipid peroxidation, protein oxidation, chlorophyll degradation, membrane damage, activation of programmed cell death (PCD) pathway, and ultimately leading to leaf senescence.

In response to heat stress, induction of the HSR leads to the rapid and robust expression of molecular chaperones, including *HSF* and *HSP* and other genes of cell-protective pathways. Molecular chaperones help protect protein synthesis and folding, prevent misfolding, and promote recovery from stress-induced leaf senescence processes. Maize contains twenty-five *HSF* homologues which are more closely related to rice *HSFs* than Arabidopsis *HSFs* [152]. Six *HSF* genes (*ZmHSF01*, *ZmHSF03*, *ZmHSF04*, *ZmHSF23*, *ZmHSF24* and *ZmHSF25*) were significantly up-regulated, and five (*ZmHSF06*, *ZmHSF10*, *ZmHSF14*, *ZmHSF20* and *ZmHSF21*) were strongly down-regulated in response to heat shock treatment. Arabidopsis plants overexpressing *ZmHSF06* have an enhanced seed germination rate, heat and drought tolerance, longer roots, higher levels of leaf chlorophyll, superoxide dismutase (SOD), peroxidase (POD) and CAT after heat stress treatment compared with the wild type [153]. Expression of *ZmHSF04* was up-regulated in response to ABA treatment and heat stress, displaying the highest peak one hour after the onset of heat stress [154]. Arabidopsis plants overexpressing *ZmHSF04* have enhanced heat and salt tolerance and higher expression levels of heat-specific *HSP* genes (*AtHSP25.3-P*, *AtHSP18.2-CI*, *AtHSP70B*, *AtHSP101*) and stress-related genes (*AtAPX2*, and *AtGOLS1*) compared to the wild type.

Delaying leaf senescence can extend the photosynthetic period and increase crop biomass, whereas premature senescence can lead to substantial biomass losses. The natural recessive *EARLY LEAF SENESCENCE 5* mutant (*ZmELS5*) was used to identify senescence-associated genes between *ZmELS5* and wild type NIL [132]. Comparative transcriptome analyses identified about 9000 differentially expressed genes (DEG), of which ~4000 were up-regulated and ~5000 were down-regulated. Among these genes were *bHLH*, *WRKY*, *APETALA2* and *Ethylene-Responsive Element Binding Protein* (*AP2/EREBP*) family transcription factors that regulate leaf senescence through ethylene or jasmonate signaling-dependent pathways. These changes cause stress responses and reductions in the chlorophyll a/b-binding protein activity levels, decrease ATP synthase activity, and increase photosystem II photo-damage, thus hastening leaf senescence.

Table 5 summarizes the effects of heat on cereal crop senescence and biomass and identifies QTLs or candidate genes for all four cereal crops.

Table 5. Effects of heat on cereal crop senescence and biomass. The '+' sign indicates an increase, and the '−' sign shows a decrease in the performance of the trait of interest. n.a.: not assigned.

Trait	Impact	QTL, Locus or Marker	Candidate Gene	Chromosome	Crop Species	Reference
Chlorophyll content	−	*Q.Spad.aww-4D*, *Q.Spad.aww-6D*	n.a.	4D, 6D	bread wheat	[127]
Various senescence traits (incl. chlorophyll content)	−	*QTL2*, *QTL13*, *QTL15*, *QTL18*, *QTL21*, *QTL29*	n.a.	1A, 4A, 4B, 5A, 7B	bread wheat	[95,155]
Staygreen	−	44 QTLs	n.a.	*2A*, *4B*, *4D*, *6A*, *7D*	bread wheat	[103]
Staygreen	−	6 QTLs, including *HSPFLQ1* (bPb-5529)	*lbi1*	3H, 4H, 5H, 6H	barley	[143]
Seedling survival	−	*TT1*	*Os03g0387100* (*PAB1*)	3	rice	[145]
Biomass	−	*togr1-1*	*Os03g46610* (*TOGR1*)	3	rice	[147]
Leaf senescence	+	*psl50*	*Os01g50770* (*PSL50*)	1	rice	[148]
Seed germination rate, chlorophyll content	−	n.a.	*ZmHsf06*	1	maize	[152]
Seedling survival	−	n.a.	*ZmHsf04*	1	maize	[154]
Leaf senescence	+	*ZmELS5*	n.a.	n.a.	maize	[132]

5. Effective Methodology and Approaches for Genetic Improvement of Heat Stress Tolerance

5.1. Germplasm Screening in the Glasshouse and Field Trials

Abiotic stress tolerance trait screening based on glasshouse and laboratory-based experiments rarely translate into the field, as screening conditions can vary significantly between target environments and controlled experiments [156]. The great advantage of glasshouse and laboratory-based experiments is that heat treatment can be applied precisely to select plants that otherwise experience the same growing conditions as untreated control plants. The control experiment can be used as a benchmark or a reference point against which the stress-treated results can be compared. Screening for heat stress tolerance under field conditions is arduous due to variability in severity, timing and duration of the stress and significant differences in climatic variables (e.g., precipitation, temperature, solar radiation) between growing seasons.

Optimal temperatures for growth and development vary greatly for different phenological phases of plant development. Heat damage can become critical to crop productivity and survival when high temperatures coincide with critical crop development stages. Small changes in phenology can lead to significant changes in the environmental impacts the crops are exposed to at critical developmental stages. The major phenology traits in crops are highly heritable, and in some cases, the genes underlying these loci have been cloned [18]. On the other hand, significant G × E and epistatic interactions lead to low heritability for many agronomically relevant traits, such as grain yield and quality, making direct selection challenging. Differences in plant maturity have long been known also to influence agronomic characteristics. Hill et al. [157,158] discussed the confounding effects of phenology on field-based QTL mapping studies in wheat and found four of five phenology-related loci affect agronomic trait variation. Flowering time may mask the critical variation and, therefore, the QTL identification. Variability within populations for flowering time further confounds results, a particular problem in mapping populations such as the Excalibur × Kukri DH population, extensively used in many drought and heat-stress QTL studies. For example, when the wheat Excalibur × Kukri DH population was developed, markers for major phenology genes were not available. However, despite showing similar maturity in the field, the parental lines differed at phenology-related loci.

This led to phenologically different offspring in the population, which were segregated for phenology-related loci. Using progeny from crosses with a narrow range of phenology [159] or treatment of individual plants according to their flowering time [160] has been shown to have low variation for flowering time and improved QTL detection.

5.2. Genetic Mapping of Heat Stress Tolerance Genes

Genetic diversity, ranging from a single base pair to duplications, inversions and translocations of entire chromosomal regions, can be traced using molecular markers in plant populations. Genotyping is used to accurately determine the chromosomal position of genes and QTLs responsible for heat stress in different crops and in marker-assisted selection (MAS) to expedite the development of lines with desired traits. Based on the stability of QTL effects across environments, QTLs can be classified as "constitutive" if consistently detected across different environments or as "adaptive" if detected only under specific environmental conditions. An essential prerequisite for a successful MAS program to improve heat tolerance is identifying environmentally stable (constitutive) QTLs, or QTLs confirmed using different mapping populations, as detected for heat stress tolerance in wheat [102,161], and rice [69,75].

Next-generation sequencing (NGS) genotyping technologies have greatly enhanced the discovery rate of polymorphisms and enabled the cost-effective genotyping of hundreds or thousands of mapping populations. They include whole-genome re-sequencing, SNP arrays, and reduced representation sequencing, which are widely applied in crops [57–59]. Linkage mapping studies using bi-parental mapping populations derived from crossing two inbred lines have successfully identified heat tolerance QTLs. However, this standard design for genetic mapping in crops requires a lot of resources and time to develop mapping populations. In addition, only alleles differing in the parents are considered with this approach, which relies on a single recombination event resulting in low mapping resolution and low genetic diversity.

Germplasm collections generally contain a broader gene pool with higher genetic diversity than segregating progenies from bi-parental mapping populations. GWAS exploits the linkage disequilibrium (LD) due to past recombination events present in a diverse population of distantly related or unrelated individuals, resulting in high mapping resolution compared with linkage mapping. Since LD is lower in a GWAS population than in a bi-parental population, GWAS requires a higher marker density than traditional QTL mapping. Genes controlling heat tolerance-related traits were discovered using GWAS approaches in wheat [162], barley [163], rice [164,165], and maize [125,126].

5.3. Targeted Manipulation of Heat Stress Tolerance Genes

An alternative strategy for improving heat tolerance is transgenesis or transgenetic breeding. Transgenetic breeding enables the transfer of beneficial alleles from another plant species to elite crop cultivars without linkage drag. This allows the exploitation of genes and the introduction of new traits not accessible through hybridization-based breeding. Five hundred forty different transgenic events in 32 crops have been approved for cultivation in 51 countries, including wheat, rice, and maize [166]. Recent examples include the expression of a rice soluble starch synthase gene in transgenic wheat which improves thousand kernel weight by up to 34% under heat stress conditions [167], and the over-expression of a rive MYB transcription factor in maize which reduced plant growth and performance under heat and drought stress conditions [168].

While transgenic crops are now grown commercially on several million hectares globally, public concerns exist about their health and safety. Alternative technologies such as genome editing may address many public concerns as their application can result in modifications identical to those from conventional breeding, naturally occurring, or induced mutations. Targeted gene editing using Clustered Regularly Interspaced Short Palindromic Repeat/CRISPR associated proteins (CRISPR/Cas) technology is a relatively new transgene-free approach to engineering novel stress tolerance in crops using site-directed

nuclease (SDN) technologies [169]. Only a few studies regarding CRISPR/Cas9 technology managing heat stress in crop plants have been published: A heat-shock inducible CRISPR/Cas9 system was developed in rice by expressing Cas9 governed by soybean heat shock promoter (*HsCas9*) and sgRNA under the rice ubiquitin 3 promoter [170]. Rice plants expressing *HsCas9* showed higher mutagenesis and a lower rate of off-target mutations after heat shock treatment than those constitutively expressing Cas9, and these mutations were also heritable. Heat stress also has a direct correlation with chloroplast biogenesis in plants. *Heat-sensitive albino1* (*hsa1*) encodes a putative fructokinase-like protein 2 (OsFLN2) essential for chloroplast development. CRISPR/Cas9-mediated deletion of *HSA1* disturbs plastid-encoded RNA polymerase (PEP)-dependent plastid gene expression, enhances heat sensitivity and greening recovery compared to the wild-type *hsa1* allele in rice [171].

6. Prospects and Challenges

The Green revolution during the 1960s introduced modern semi-dwarf, high-yielding and fertilizer-responsive cereal crop varieties into developing countries. Subsequently, several-fold increases in productivity have been achieved through modern plant breeding. However, current yields stagnate in many parts of the world [172,173]. For example, a remarkable increase in the global average yield of wheat was achieved between 1980 and 2020, which almost doubled from 1.9 t ha^{-1} to 3.5 t ha^{-1} [12]. However, average wheat yields in Australia and New Zealand only increased from about 1 t ha^{-1} to 1.5 t ha^{-1} in the same period.

Climate change affects the production of cereal crops in many parts of the world due to increases in the frequency, intensity, and impacts of extreme weather events. This has shifted the focus of breeders from primarily increasing yield to combining yield with abiotic stress tolerance to maintain yields under adverse climate events. Consequently, major discoveries have been made in recent years for wheat, barley, rice, and maize, some of which were reported and discussed in this review. However, further developments are needed to translate these findings into farmer-ready cultivars to improve yield in the field under heat stress, particularly in the following areas:

1. Heat tolerance in crops is a polygenic trait that is difficult to quantify, and thus different definitions of heat tolerance are currently used for field-based and laboratory evaluations. Until now, no direct method is available to select heat-tolerant plants, but some traits such as canopy temperature depression, membrane thermo-stability and chlorophyll fluorescence may be effective indicators of plant heat tolerance.
2. Crops often experience several environmental stresses, such as drought, nutrient stress, and heat stress, simultaneously in the field. Therefore, many studies screen (deliberately or unintentionally) for the combined effect of different environmental stresses, and the interaction between stress responses, on the target traits. Past studies have used late sowing times [100,110] or in-field heat tents [174] to control the timing and incidence of heat stress. It remains unclear how comparable results obtained from these experiments are to heat events experienced in more typical production environments.
3. Uncertainties in the knowledge of molecular crop responses to heat are limiting current research and breeding efforts. Despite considerable research to map QTLs and quantify their effects and interactions, most quantitative trait variation's biological and molecular basis remains poorly understood. The information from QTL studies alone is often not sufficient to determine whether a genetic locus and a phenotype are connected directly, for example, via a specific gene or through multiple steps and pathways, such as transcription factors or other regulatory sequences. High-resolution mapping of specific genomic regions would help clarify whether coincident QTLs are due to linkage or pleiotropy.
4. MAS and association genetics require long selection cycles and cannot capture significant marker–QTL associations with minor gene effects. Genomic selection is a technique that employs genome-wide markers to predict the phenotype of lines based

on the genotype [175]. The marker effects are estimated in a fully genotyped and phenotyped training population and then used to obtain genomic estimated breeding values (GEBV) of the test population that has only been genotyped. The prediction's reliability relies on the genetic diversity and size of the training population used to calibrate the prediction models, and the density of the molecular markers used to genotype lines. Genomic selection enables indirect selection for quantitative traits before phenotyping and has long been applied to animal breeding but has only a recent history in crop breeding. When used to enhance wheat's heat and drought tolerance, genomic selection has shown that canopy temperature and normalized difference vegetation index (NDVI) measurements can increase genomic prediction model accuracies for grain yield [176]. A prediction accuracy of 0.62 using an item-based collaborative filtering approach was reported for grain yield in heat-stressed environments from NDVI measurements [5]. These results suggest a great potential for incorporating high-throughput phenotyping in genomic selection studies to improve the heat-stress tolerance of crops.

5. Recently, regulatory connections between heat stress response pathways and the plant circadian clock have been revealed [177,178], opening new avenues for crop improvement if better understood. Adjustments in clock function may allow crops to re-adjust the balance between crop growth and stress tolerance in response to changes in the environment and ensure a sustained increase in heat stress tolerance when needed [179].
6. Heatwave events have extremely high economic costs, but even with adjustments in sowing date, high temperatures are largely unavoidable during the reproductive phase of cereal crops in many parts of the world. Biotechnology, particularly genetic modifications and molecular markers, is key to speeding up plant breeding programs to deliver improved and better-adapted varieties sooner. Despite this, only small efforts have been made to identify genetic markers associated with heat tolerance that can be deployed in cereal crop breeding programs. There remains an urgent need to identify diagnostic markers for MAS breeding to maintain and improve the grain yield of cereal crops under heat-stressed environments.
7. Regulatory hurdles hinder the development and adoption of new genetic variations with DNA technologies, mutational breeding, or genome editing. Added value contributed by the transgenes to enhancing stress tolerance must be demonstrated first before acceptance in breeding programs. This can only be achieved through costly large-scale extensive field evaluations of transgenic germplasm—a task difficult to accomplish in the current regulatory environment in many parts of the world. Given the regulatory complications and costs, the yield benefit under heat stress needs to be substantial without negative impacts in normal production environments. Argentina, one of the first countries with a regulatory framework for genetically modified crops, has recently approved the transgenic HB4 drought-tolerant wheat for growth and consumption [180]. Based on field trials conducted over ten years, transgenic HB4 wheat shows a 20% increased yield in seasons affected by drought with no yield penalty under normal growth conditions. HB4 technology is based on *HaHB4*, a sunflower transcription factor belonging to the homeodomain-leucine zipper I family whose ectopic expression in several plant species triggered drought tolerance. Given the recent advancements, it may only be a matter of time before the first heat-stress tolerant cereal crops will be commercially released.

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References

1. Zhongming, Z.; Linong, L.; Xiaona, Y.; Wangqiang, Z.; Wei, L.; IPCC. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. In *Climate Change 2021: The Physical Science Basis*; Masson-Delmotte, V., Zhai, P.A., Pirani, S.L., Connors, C., Péan, S., Berger, N., Caud, Y., Chen, L., Goldfarb, M.I., Gomis, M., et al., Eds.; Cambridge University Press: Cambridge, UK, 2021; *in press*.
2. Ray, D.K.; Gerber, J.S.; MacDonald, G.K.; West, P.C. Climate Variation Explains a Third of Global Crop Yield Variability. *Nat. Commun.* **2015**, *6*, 5989. [CrossRef] [PubMed]
3. Semenov, M.A.; Shewry, P.R. Modelling Predicts That Heat Stress, Not Drought, Will Increase Vulnerability of Wheat in Europe. *Sci. Rep.* **2011**, *1*, 66. [CrossRef] [PubMed]
4. Zhao, C.; Liu, B.; Piao, S.; Wang, X.; Lobell, D.B.; Huang, Y.; Huang, M.; Yao, Y.; Bassu, S.; Ciais, P.; et al. Temperature Increase Reduces Global Yields of Major Crops in Four Independent Estimates. *Proc. Natl. Acad. Sci. USA* **2017**, *114*, 9326–9331. [CrossRef]
5. Juliana, P.; Montesinos-López, O.A.; Crossa, J.; Mondal, S.; González Pérez, L.; Poland, J.; Huerta-Espino, J.; Crespo-Herrera, L.; Govindan, V.; Dreisigacker, S.; et al. Integrating Genomic-Enabled Prediction and High-Throughput Phenotyping in Breeding for Climate-Resilient Bread Wheat. *Theor. Appl. Genet.* **2019**, *132*, 177–194. [CrossRef] [PubMed]
6. Gao, G.; Tester, M.A.; Julkowska, M.M. The Use of High-Throughput Phenotyping for Assessment of Heat Stress-Induced Changes in Arabidopsis. *Plant Phenomics* **2020**, *2020*, 3723916. [CrossRef] [PubMed]
7. Teixeira, E.I.; Fischer, G.; van Velthuizen, H.; Walter, C.; Ewert, F. Global Hot-Spots of Heat Stress on Agricultural Crops Due to Climate Change. *Agric. For. Meteorol.* **2013**, *170*, 206–215. [CrossRef]
8. Morice, C.P.; Kennedy, J.J.; Rayner, N.A.; Jones, P.D. Quantifying Uncertainties in Global and Regional Temperature Change Using an Ensemble of Observational Estimates: The HadCRUT4 Data Set. *J. Geophys. Res.* **2012**, *117*, D08101. [CrossRef]
9. Jacott, C.N.; Boden, S.A. Feeling the Heat: Developmental and Molecular Responses of Wheat and Barley to High Ambient Temperatures. *J. Exp. Bot.* **2020**, *71*, 5740–5751. [CrossRef]
10. Langridge, P.; Reynolds, M. Breeding for Drought and Heat Tolerance in Wheat. *Theor. Appl. Genet.* **2021**, *134*, 1753–1769. [CrossRef]
11. Asseng, S.; Foster, I.; Turner, N.C. The Impact of Temperature Variability on Wheat Yields: Impact Of Temperature Variability On Wheat Yields. *Glob. Chang. Biol.* **2011**, *17*, 997–1012. [CrossRef]
12. FAOSTAT. Available online: https://www.fao.org/faostat/ (accessed on 23 March 2022).
13. Weichert, H.; Högy, P.; Mora-Ramirez, I.; Fuchs, J.; Eggert, K.; Koehler, P.; Weschke, W.; Fangmeier, A.; Weber, H. Grain Yield and Quality Responses of Wheat Expressing a Barley Sucrose Transporter to Combined Climate Change Factors. *J. Exp. Bot.* **2017**, *68*, 5511–5525. [CrossRef] [PubMed]
14. Verma, S.; Yashveer, S.; Rehman, S.; Gyawali, S.; Kumar, Y.; Chao, S.; Sarker, A.; Verma, R.P.S. Genetic and Agro-Morphological Diversity in Global Barley (*Hordeum vulgare* L.) Collection at ICARDA. *Genet. Resour. Crop. Evol.* **2021**, *68*, 1315–1330. [CrossRef]
15. Sánchez, B.; Rasmussen, A.; Porter, J.R. Temperatures and the Growth and Development of Maize and Rice: A Review. *Glob. Chang. Biol.* **2014**, *20*, 408–417. [CrossRef]
16. Ceccarelli, S.; Grando, S.; Maatougui, M.; Michael, M.; Slash, M.; Haghparast, R.; Rahmanian, M.; Taheri, A.; Al-Yassin, A.; Benbelkacem, A.; et al. Plant Breeding and Climate Changes. *J. Agric. Sci.* **2010**, *148*, 627–637. [CrossRef]
17. Lobell, D.B.; Burke, M.B. On the Use of Statistical Models to Predict Crop Yield Responses to Climate Change. *Agric. For. Meteorol.* **2010**, *150*, 1443–1452. [CrossRef]
18. Hill, C.B.; Li, C. Genetic Architecture of Flowering Phenology in Cereals and Opportunities for Crop Improvement. *Front. Plant Sci.* **2016**, *7*, 1906. [CrossRef]
19. Woodward, A.W.; Bartel, B. Biology in Bloom: A Primer on the *Arabidopsis Thaliana* Model System. *Genetics* **2018**, *208*, 1337–1349. [CrossRef]
20. Silva-Correia, J.; Freitas, S.; Tavares, R.M.; Lino-Neto, T.; Azevedo, H. Phenotypic Analysis of the Arabidopsis Heat Stress Response during Germination and Early Seedling Development. *Plant Methods* **2014**, *10*, 7. [CrossRef]
21. Weng, M.; Yang, Y.; Feng, H.; Pan, Z.; Shen, W.-H.; Zhu, Y.; Dong, A. Histone Chaperone ASF1 Is Involved in Gene Transcription Activation in Response to Heat Stress in *Arabidopsis Thaliana*: AtASF1 in Heat Stress Response. *Plant Cell. Environ.* **2014**, *37*, 2128–2138. [CrossRef]
22. Ohama, N.; Sato, H.; Shinozaki, K.; Yamaguchi-Shinozaki, K. Transcriptional Regulatory Network of Plant Heat Stress Response. *Trends Plant Sci.* **2017**, *22*, 53–65. [CrossRef]
23. Nover, L.; Bharti, K.; Döring, P.; Mishra, S.K.; Ganguli, A.; Scharf, K.-D. Arabidopsis and the Heat Stress Transcription Factor World: How Many Heat Stress Transcription Factors Do We Need? *Cell Stress Chaper.* **2001**, *6*, 177. [CrossRef]
24. Wiederrecht, G.; Seto, D.; Parker, C.S. Isolation of the Gene Encoding the S. Cerevisiae Heat Shock Transcription Factor. *Cell* **1988**, *54*, 841–853. [CrossRef]

25. Charng, Y.; Liu, H.; Liu, N.; Chi, W.; Wang, C.; Chang, S.; Wang, T. A Heat-Inducible Transcription Factor, HsfA2, Is Required for Extension of Acquired Thermotolerance in Arabidopsis. *Plant Physiol.* **2007**, *143*, 251–262. [CrossRef] [PubMed]
26. Guo, L.; Chen, S.; Liu, K.; Liu, Y.; Ni, L.; Zhang, K.; Zhang, L. Isolation of Heat Shock Factor HsfA1a-Binding Sites in Vivo Revealed Variations of Heat Shock Elements in Arabidopsis Thaliana. *Plant Cell Physiol.* **2008**, *49*, 1306–1315. [CrossRef] [PubMed]
27. Liu, H.-C.; Liao, H.-T.; Charng, Y.-Y. The Role of Class A1 Heat Shock Factors (HSFA1s) in Response to Heat and Other Stresses in Arabidopsis: Master Heat Shock Factors in Arabidopsis. *Plant Cell. Environ.* **2011**, *34*, 738–751. [CrossRef]
28. Wunderlich, M.; Werr, W.; Schoffl, F. Generation of Dominant-Negative Effects on the Heat Shock Response in Arabidopsis Thaliana by Transgenic Expression of a Chimaeric HSF1 Protein Fusion Construct. *Plant J.* **2003**, *35*, 442–451. [CrossRef]
29. Kotak, S.; Larkindale, J.; Lee, U.; von Koskull-Döring, P.; Vierling, E.; Scharf, K.-D. Complexity of the Heat Stress Response in Plants. *Curr. Opin. Plant Biol.* **2007**, *10*, 310–316. [CrossRef]
30. Schramm, F.; Larkindale, J.; Kiehlmann, E.; Ganguli, A.; Englich, G.; Vierling, E.; Von Koskull-Döring, P. A Cascade of Transcription Factor DREB2A and Heat Stress Transcription Factor HsfA3 Regulates the Heat Stress Response of Arabidopsis: Role of Arabidopsis HsfA3. *Plant J.* **2007**, *53*, 264–274. [CrossRef]
31. Sakuma, Y.; Maruyama, K.; Osakabe, Y.; Qin, F.; Seki, M.; Shinozaki, K.; Yamaguchi-Shinozaki, K. Functional Analysis of an Arabidopsis Transcription Factor, DREB2A, Involved in Drought-Responsive Gene Expression. *Plant Cell* **2006**, *18*, 1292–1309. [CrossRef]
32. Davletova, S.; Rizhsky, L.; Liang, H.; Shengqiang, Z.; Oliver, D.J.; Coutu, J.; Shulaev, V.; Schlauch, K.; Mittler, R. Cytosolic Ascorbate Peroxidase 1 Is a Central Component of the Reactive Oxygen Gene Network of Arabidopsis. *Plant Cell* **2005**, *17*, 268–281. [CrossRef]
33. Ono, M.; Isono, K.; Sakata, Y.; Taji, T. Catalase2 Plays a Crucial Role in Long-Term Heat Tolerance of Arabidopsis Thaliana. Biochem. *Biophys. Res. Commun.* **2021**, *534*, 747–751. [CrossRef] [PubMed]
34. Friedrich, T.; Oberkofler, V.; Trindade, I.; Altmann, S.; Brzezinka, K.; Lämke, J.; Gorka, M.; Kappel, C.; Sokolowska, E.; Skirycz, A.; et al. Heteromeric HSFA2/HSFA3 Complexes Drive Transcriptional Memory after Heat Stress in Arabidopsis. *Nat. Commun.* **2021**, *12*, 3426. [CrossRef] [PubMed]
35. Lämke, J.; Brzezinka, K.; Altmann, S.; Bäurle, I. A Hit-and-run Heat Shock Factor Governs Sustained Histone Methylation and Transcriptional Stress Memory. *EMBO J.* **2016**, *35*, 162–175. [CrossRef] [PubMed]
36. Guan, Q.; Lu, X.; Zeng, H.; Zhang, Y.; Zhu, J. Heat Stress Induction of MiR398 Triggers a Regulatory Loop That Is Critical for Thermotolerance in Arabidopsis. *Plant J.* **2013**, *74*, 840–851. [CrossRef]
37. Sedaghatmehr, M.; Mueller-Roeber, B.; Balazadeh, S. The Plastid Metalloprotease FtsH6 and Small Heat Shock Protein HSP21 Jointly Regulate Thermomemory in Arabidopsis. *Nat. Commun.* **2016**, *7*, 12439. [CrossRef]
38. Mascher, M.; Gundlach, H.; Himmelbach, A.; Beier, S.; Twardziok, S.O.; Wicker, T.; Radchuk, V.; Dockter, C.; Hedley, P.E.; Russell, J.; et al. A Chromosome Conformation Capture Ordered Sequence of the Barley Genome. *Nature* **2017**, *544*, 427–433. [CrossRef]
39. The International Wheat Genome Sequencing Consortium (IWGSC); Appels, R.; Eversole, K.; Stein, N.; Feuillet, C.; Keller, B.; Rogers, J.; Pozniak, C.J.; Choulet, F.; Distelfeld, A.; et al. Shifting the Limits in Wheat Research and Breeding Using a Fully Annotated Reference Genome. *Science* **2018**, *361*, eaar7191. [CrossRef]
40. Jayakodi, M.; Padmarasu, S.; Haberer, G.; Bonthala, V.S.; Gundlach, H.; Monat, C.; Lux, T.; Kamal, N.; Lang, D.; Himmelbach, A.; et al. The Barley Pan-Genome Reveals the Hidden Legacy of Mutation Breeding. *Nature* **2020**, *588*, 284–289. [CrossRef]
41. Walkowiak, S.; Gao, L.; Monat, C.; Haberer, G.; Kassa, M.T.; Brinton, J.; Ramirez-Gonzalez, R.H.; Kolodziej, M.C.; Delorean, E.; Thambugala, D.; et al. Multiple Wheat Genomes Reveal Global Variation in Modern Breeding. *Nature* **2020**, *588*, 277–283. [CrossRef]
42. Han, Y.; Broughton, S.; Liu, L.; Zhang, X.-Q.; Zeng, J.; He, X.; Li, C. Highly Efficient and Genotype-Independent Barley Gene Editing Based on Anther Culture. *Plant Commun.* **2021**, *2*, 100082. [CrossRef]
43. Nishizawa-Yokoi, A.; Toki, S. A PiggyBac -mediated Transgenesis System for the Temporary Expression of CRISPR/Cas9 in Rice. *Plant Biotechnol. J.* **2021**, *19*, 1386–1395. [CrossRef] [PubMed]
44. Lu, X.; Liu, J.; Ren, W.; Yang, Q.; Chai, Z.; Chen, R.; Wang, L.; Zhao, J.; Lang, Z.; Wang, H.; et al. Gene-Indexed Mutations in Maize. *Mol. Plant* **2018**, *11*, 496–504. [CrossRef]
45. Schreiber, M.; Barakate, A.; Uzrek, N.; Macaulay, M.; Sourdille, A.; Morris, J.; Hedley, P.E.; Ramsay, L.; Waugh, R. A Highly Mutagenised Barley (Cv. Golden Promise) TILLING Population Coupled with Strategies for Screening-by-Sequencing. *Plant Methods* **2019**, *15*, 99. [CrossRef] [PubMed]
46. Watson, A.; Ghosh, S.; Williams, M.J.; Cuddy, W.S.; Simmonds, J.; Rey, M.-D.; Asyraf Md Hatta, M.; Hinchliffe, A.; Steed, A.; Reynolds, D.; et al. Speed Breeding Is a Powerful Tool to Accelerate Crop Research and Breeding. *Nat. Plants* **2018**, *4*, 23–29. [CrossRef] [PubMed]
47. Barmeier, G.; Schmidhalter, U. High-Throughput Field Phenotyping of Leaves, Leaf Sheaths, Culms and Ears of Spring Barley Cultivars at Anthesis and Dough Ripeness. *Front. Plant Sci.* **2017**, *8*, 1920. [CrossRef] [PubMed]
48. Madec, S.; Baret, F.; de Solan, B.; Thomas, S.; Dutartre, D.; Jezequel, S.; Hemmerlé, M.; Colombeau, G.; Comar, A. High-Throughput Phenotyping of Plant Height: Comparing Unmanned Aerial Vehicles and Ground LiDAR Estimates. *Front. Plant Sci.* **2017**, *8*, 2002. [CrossRef]

49. Khan, Z.; Rahimi-Eichi, V.; Haefele, S.; Garnett, T.; Miklavcic, S.J. Estimation of Vegetation Indices for High-Throughput Phenotyping of Wheat Using Aerial Imaging. *Plant Methods* **2018**, *14*, 20. [CrossRef]
50. Rawson, H.M.; Richards, R.A. Effects of High Temperature and Photoperiod on Floral Development in Wheat Isolines Differing in Vernalisation and Photoperiod Genes. *Field Crop. Res.* **1993**, *32*, 181–192. [CrossRef]
51. Yang, J.; Sears, R.G.; Gill, B.S.; Paulsen, G.M. Quantitative and molecular characterization of heat tolerance in hexaploid wheat. *Euphytica* **2002**, *126*, 275–282. [CrossRef]
52. Mason, R.E.; Mondal, S.; Beecher, F.W.; Pacheco, A.; Jampala, B.; Ibrahim, A.M.H.; Hays, D.B. QTL Associated with Heat Susceptibility Index in Wheat (*Triticum aestivum* L.) under Short-Term Reproductive Stage Heat Stress. *Euphytica* **2010**, *174*, 423–436. [CrossRef]
53. Sharma, D.; Singh, R.; Rane, J.; Gupta, V.K.; Mamrutha, H.M.; Tiwari, R. Mapping Quantitative Trait Loci Associated with Grain Filling Duration and Grain Number under Terminal Heat Stress in Bread Wheat (*Triticum aestivum* L.). *Plant Breed.* **2016**, *135*, 538–545. [CrossRef]
54. Worland, A.J. The Influence of Flowering Time Genes on Environmental Adaptability in European Wheats. *Euphytica* **1996**, *89*, 49–57. [CrossRef]
55. Deng, W.; Casao, M.C.; Wang, P.; Sato, K.; Hayes, P.M.; Finnegan, E.J.; Trevaskis, B. Direct Links between the Vernalization Response and Other Key Traits of Cereal Crops. *Nat. Commun.* **2015**, *6*, 5882. [CrossRef] [PubMed]
56. Ochagavía, H.; Prieto, P.; Zikhali, M.; Griffiths, S.; Slafer, G.A. Earliness Per Se by Temperature Interaction on Wheat Development. *Sci. Rep.* **2019**, *9*, 2584. [CrossRef] [PubMed]
57. Hill, C.B.; Wong, D.; Tibbits, J.; Forrest, K.; Hayden, M.; Zhang, X.-Q.; Westcott, S.; Angessa, T.T.; Li, C. Targeted Enrichment by Solution-Based Hybrid Capture to Identify Genetic Sequence Variants in Barley. *Sci. Data* **2019**, *6*, 12. [CrossRef] [PubMed]
58. Hill, C.B.; Angessa, T.T.; McFawn, L.; Wong, D.; Tibbits, J.; Zhang, X.; Forrest, K.; Moody, D.; Telfer, P.; Westcott, S.; et al. Hybridisation-based Target Enrichment of Phenology Genes to Dissect the Genetic Basis of Yield and Adaptation in Barley. *Plant Biotechnol. J.* **2019**, *17*, 932–944. [CrossRef] [PubMed]
59. Hill, C.B.; Angessa, T.T.; Zhang, X.; Chen, K.; Zhou, G.; Tan, C.; Wang, P.; Westcott, S.; Li, C. A Global Barley Panel Revealing Genomic Signatures of Breeding in Modern Australian Cultivars. *Plant J.* **2021**, *106*, 419–434. [CrossRef]
60. Laurie, D.A. Comparative Genetics of Flowering Time. *Plant Mol. Biol.* **1997**, *35*, 167–177. [CrossRef]
61. Fernández-Calleja, M.; Casas, A.M.; Igartua, E. Major Flowering Time Genes of Barley: Allelic Diversity, Effects, and Comparison with Wheat. Theor. *Appl. Genet.* **2021**, *134*, 1867–1897. [CrossRef]
62. Comadran, J.; Kilian, B.; Russell, J.; Ramsay, L.; Stein, N.; Ganal, M.; Shaw, P.; Bayer, M.; Thomas, W.; Marshall, D.; et al. Natural Variation in a Homolog of Antirrhinum Centroradialis Contributed to Spring Growth Habit and Environmental Adaptation in Cultivated Barley. *Nat. Genet.* **2012**, *44*, 1388–1392. [CrossRef]
63. Casas, A.M.; Djemel, A.; Ciudad, F.J.; Yahiaoui, S.; Ponce, L.J.; Contreras-Moreira, B.; Gracia, M.P.; Lasa, J.M.; Igartua, E. HvFT1 (VrnH3) Drives Latitudinal Adaptation in Spanish Barleys. Theor. *Appl. Genet.* **2011**, *122*, 1293–1304. [CrossRef] [PubMed]
64. Ford, B.; Deng, W.; Clausen, J.; Oliver, S.; Boden, S.; Hemming, M.; Trevaskis, B. Barley (*Hordeum vulgare* L.) Circadian Clock Genes Can Respond Rapidly to Temperature in an EARLY FLOWERING 3 -Dependent Manner. *J. Exp. Bot.* **2016**, *67*, 5517–5528. [CrossRef]
65. Coast, O.; Šebela, D.; Quiñones, C.; Jagadish, S.V.K. Systematic Determination of the Reproductive Growth Stage Most Sensitive to High Night Temperature Stress in Rice (*Oryza sativa*). *Crop Sci.* **2020**, *60*, 391–403. [CrossRef]
66. Ye, C.; Li, X.; Redoña, E.; Ishimaru, T.; Jagadish, K. Genetics and Breeding of Heat Tolerance in Rice. In *Rice Improvement: Physiological, Molecular Breeding and Genetic Perspectives*; Ali, J., Wani, S.H., Eds.; Springer International Publishing: Cham, Switzerland, 2021; pp. 203–220, ISBN 9783030665302.
67. Zhao, Z.; Jiang, L.; Xiao, Y.; Zhang, W.; Zhai, H.; Wan, J. Identification of QTLs for heat tolerance at the booting stage in rice (*Oryza sativa* L.). *Acta Agron. Sin.* **2006**, *32*, 640–644.
68. Ye, C.; Argayoso, M.A.; Redoña, E.D.; Sierra, S.N.; Laza, M.A.; Dilla, C.J.; Mo, Y.; Thomson, M.J.; Chin, J.; Delaviña, C.B.; et al. Mapping QTL for Heat Tolerance at Flowering Stage in Rice Using SNP Markers: Mapping QTL for Heat Tolerance at Flowering Stage in Rice. *Plant Breed.* **2012**, *131*, 33–41. [CrossRef]
69. Ye, C.; Tenorio, F.A.; Argayoso, M.A.; Laza, M.A.; Koh, H.-J.; Redoña, E.D.; Jagadish, K.S.; Gregorio, G.B. Identifying and Confirming Quantitative Trait Loci Associated with Heat Tolerance at Flowering Stage in Different Rice Populations. *BMC Genet.* **2015**, *16*, 41. [CrossRef]
70. Tazib, T.; Kobayashi, Y.; Koyama, H.; Matsui, T. QTL Analyses for Anther Length and Dehiscence at Flowering as Traits for the Tolerance of Extreme Temperatures in Rice (*Oryza sativa* L.). *Euphytica* **2015**, *203*, 629–642. [CrossRef]
71. Xiao, Y.; Pan, Y.; Luo, L.; Zhang, G.; Deng, H.; Dai, L.; Liu, X.; Tang, W.; Chen, L.; Wang, G.-L. Quantitative Trait Loci Associated with Seed Set under High Temperature Stress at the Flowering Stage in Rice (*Oryza sativa* L.). *Euphytica* **2011**, *178*, 331–338. [CrossRef]
72. Shanmugavadivel, P.S.; Sv, A.M.; Prakash, C.; Mk, R.; Tiwari, R.; Mohapatra, T.; Singh, N.K. High Resolution Mapping of QTLs for Heat Tolerance in Rice Using a 5K SNP Array. *Rice* **2017**, *10*, 28. [CrossRef]
73. Li, H.; Yuan, Z.; Vizcay-Barrena, G.; Yang, C.; Liang, W.; Zong, J.; Wilson, Z.A.; Zhang, D. PERSISTENT TAPETAL CELL1 Encodes a PHD-Finger Protein That Is Required for Tapetal Cell Death and Pollen Development in Rice. *Plant Physiol.* **2011**, *156*, 615–630. [CrossRef]

74. Bheemanahalli, R.; Sathishraj, R.; Manoharan, M.; Sumanth, H.N.; Muthurajan, R.; Ishimaru, T.; Krishna, J.S.V. Is Early Morning Flowering an Effective Trait to Minimize Heat Stress Damage during Flowering in Rice? *Field Crops Res.* **2017**, *203*, 238–242. [CrossRef] [PubMed]
75. Hirabayashi, H.; Sasaki, K.; Kambe, T.; Gannaban, R.B.; Miras, M.A.; Mendioro, M.S.; Simon, E.V.; Lumanglas, P.D.; Fujita, D.; Takemoto-Kuno, Y.; et al. QEMF3, a Novel QTL for the Early-Morning Flowering Trait from Wild Rice, Oryza Officinalis, to Mitigate Heat Stress Damage at Flowering in Rice, O. *Sativa. J. Exp. Bot.* **2015**, *66*, 1227–1236. [CrossRef] [PubMed]
76. Ohmori, S.; Tabuchi, H.; Yatou, O.; Yoshida, H. Agronomic Traits and Gene Containment Capability of Cleistogamous Rice Lines with the Superwoman1-Cleistogamy Mutation. *Breed. Sci.* **2012**, *62*, 124–132. [CrossRef] [PubMed]
77. Koike, S.; Yamaguchi, T.; Ohmori, S.; Hayashi, T.; Yatou, O.; Yoshida, H. Cleistogamy Decreases the Effect of High Temperature Stress at Flowering in Rice. *Plant Prod. Sci.* **2015**, *18*, 111–117. [CrossRef]
78. Zou, M.; Zhou, G.; Angessa, T.T.; Zhang, X.-Q.; Li, C. Polymorphism of Floral Type Gene Cly1 and Its Association with Thermal Stress in Barley. *PLoS ONE* **2018**, *13*, e0193390. [CrossRef]
79. Tiwari, Y.K.; Yadav, S.K. High Temperature Stress Tolerance in Maize (*Zea mays* L.): Physiological and Molecular Mechanisms. *J. Plant Biol.* **2019**, *62*, 93–102. [CrossRef]
80. Hatfield, J.L.; Prueger, J.H. Temperature Extremes: Effect on Plant Growth and Development. *Weather Clim. Extrem.* **2015**, *10*, 4–10. [CrossRef]
81. Lizaso, J.I.; Ruiz-Ramos, M.; Rodríguez, L.; Gabaldon-Leal, C.; Oliveira, J.A.; Lorite, I.J.; Sánchez, D.; García, E.; Rodríguez, A. Impact of High Temperatures in Maize: Phenology and Yield Components. *Field Crop. Res.* **2018**, *216*, 129–140. [CrossRef]
82. Wang, Y.; Tao, H.; Tian, B.; Sheng, D.; Xu, C.; Zhou, H.; Huang, S.; Wang, P. Flowering Dynamics, Pollen, and Pistil Contribution to Grain Yield in Response to High Temperature during Maize Flowering. *Environ. Exp. Bot.* **2019**, *158*, 80–88. [CrossRef]
83. Liu, M.; Sheng, D.; Liu, X.; Wang, Y.; Hou, X.; Wang, Y.; Wang, P.; Guan, L.; Dong, X.; Huang, S. Dissecting heat tolerance and yield stability in maize from greenhouse and field experiments. *J. Agron. Crop Sci.* **2022**, *208*, 348–361. [CrossRef]
84. Alam, M.A.; Seetharam, K.; Zaidi, P.H.; Dinesh, A.; Vinayan, M.T.; Nath, U.K. Dissecting Heat Stress Tolerance in Tropical Maize (*Zea mays* L.). *Field Crop. Res.* **2017**, *204*, 110–119. [CrossRef]
85. Shah, F.; Huang, J.; Cui, K.; Nie, L.; Shah, T.; Chen, C.; Wang, K. Impact of High-Temperature Stress on Rice Plant and Its Traits Related to Tolerance. *J. Agric. Sci.* **2011**, *149*, 545–556. [CrossRef]
86. Frey, F.P.; Urbany, C.; Hüttel, B.; Reinhardt, R.; Stich, B. Genome-Wide Expression Profiling and Phenotypic Evaluation of European Maize Inbreds at Seedling Stage in Response to Heat Stress. *BMC Genom.* **2015**, *16*, 123. [CrossRef] [PubMed]
87. Hemming, M.N.; Walford, S.A.; Fieg, S.; Dennis, E.S.; Trevaskis, B. Identification of High-Temperature-Responsive Genes in Cereals. *Plant Physiol.* **2012**, *158*, 1439–1450. [CrossRef] [PubMed]
88. Ravikiran, K.T.; Gopala Krishnan, S.; Vinod, K.K.; Dhawan, G.; Dwivedi, P.; Kumar, P.; Bansal, V.P.; Nagarajan, M.; Bhowmick, P.K.; Ellur, R.K.; et al. A Trait Specific QTL Survey Identifies NL44, a NERICA Cultivar as a Novel Source for Reproductive Stage Heat Stress Tolerance in Rice. *Plant Physiol. Rep.* **2020**, *25*, 664–676. [CrossRef]
89. Prasad, P.V.V.; Pisipati, S.R.; Ristic, Z.; Bukovnik, U.; Fritz, A.K. Impact of Nighttime Temperature on Physiology and Growth of Spring Wheat. *Crop Sci.* **2008**, *48*, 2372–2380. [CrossRef]
90. Yin, X.; Guo, W.; Spiertz, J.H. A Quantitative Approach to Characterize Sink–Source Relationships during Grain Filling in Contrasting Wheat Genotypes. *Field Crop. Res.* **2009**, *114*, 119–126. [CrossRef]
91. Yang, H.; Gu, X.; Ding, M.; Lu, W.; Lu, D. Heat Stress during Grain Filling Affects Activities of Enzymes Involved in Grain Protein and Starch Synthesis in Waxy Maize. *Sci. Rep.* **2018**, *8*, 15665. [CrossRef]
92. Spiertz, J.H.J.; Hamer, R.J.; Xu, H.; Primo-Martin, C.; Don, C.; van der Putten, P.E.L. Heat Stress in Wheat (*Triticum aestivum* L.): Effects on Grain Growth and Quality Traits. *Eur. J. Agron.* **2006**, *25*, 89–95. [CrossRef]
93. Castro, M.; Peterson, C.J.; Rizza, M.D.; Dellavalle, P.D.; Vázquez, D.; IbáÑez, V.; Ross, A. Influence of Heat Stress on Wheat Grain Characteristics and Protein Molecular Weight Distribution. In *Wheat Production in Stressed Environments*; Buck, H.T., Nisi, J.E., Salomón, N., Eds.; Springer: Dordrecht, The Netherlands, 2007; Volume 12, pp. 365–371, ISBN 9781402054969.
94. Keeling, P.L.; Bacon, P.J.; Holt, D.C. Elevated Temperature Reduces Starch Deposition in Wheat Endosperm by Reducing the Activity of Soluble Starch Synthase. *Planta* **1993**, *191*, 342–348. [CrossRef]
95. Shirdelmoghanloo, H.; Taylor, J.D.; Lohraseb, I.; Rabie, H.; Brien, C.; Timmins, A.; Martin, P.; Mather, D.E.; Emebiri, L.; Collins, N.C. A QTL on the Short Arm of Wheat (*Triticum aestivum* L.) Chromosome 3B Affects the Stability of Grain Weight in Plants Exposed to a Brief Heat Shock Early in Grain Filling. *BMC Plant Biol.* **2016**, *16*, 100. [CrossRef] [PubMed]
96. Vetch, J.M.; Stougaard, R.N.; Martin, J.M.; Giroux, M.J. Review: Revealing the Genetic Mechanisms of Pre-Harvest Sprouting in Hexaploid Wheat (*Triticum aestivum* L.). *Plant Sci.* **2019**, *281*, 180–185. [CrossRef] [PubMed]
97. Barrero, J.M.; Porfirio, L.; Hughes, T.; Chen, J.; Dillon, S.; Gubler, F.; Ral, J.-P.F. Evaluation of the Impact of Heat on Wheat Dormancy, Late Maturity α-Amylase and Grain Size under Controlled Conditions in Diverse Germplasm. *Sci. Rep.* **2020**, *10*, 17800. [CrossRef] [PubMed]
98. Xue, G.-P.; Sadat, S.; Drenth, J.; McIntyre, C.L. The Heat Shock Factor Family from Triticum Aestivum in Response to Heat and Other Major Abiotic Stresses and Their Role in Regulation of Heat Shock Protein Genes. *J. Exp. Bot.* **2014**, *65*, 539–557. [CrossRef]
99. Hu, X.-J.; Chen, D.; Lynne Mclntyre, C.; Fernanda Dreccer, M.; Zhang, Z.-B.; Drenth, J.; Kalaipandian, S.; Chang, H.; Xue, G.-P. Heat Shock Factor C2a Serves as a Proactive Mechanism for Heat Protection in Developing Grains in Wheat via an ABA-Mediated Regulatory Pathway: TaHsfC2a Plays a Proactive Heat Protection Role. *Plant Cell Environ.* **2018**, *41*, 79–98. [CrossRef]

100. Bhusal, N.; Sarial, A.K.; Sharma, P.; Sareen, S. Mapping QTLs for Grain Yield Components in Wheat under Heat Stress. *PLoS ONE* **2017**, *12*, e0189594. [CrossRef]
101. Pinto, R.S.; Reynolds, M.P.; Mathews, K.L.; McIntyre, C.L.; Olivares-Villegas, J.-J.; Chapman, S.C. Heat and Drought Adaptive QTL in a Wheat Population Designed to Minimize Confounding Agronomic Effects. *Theor. Appl. Genet.* **2010**, *121*, 1001–1021. [CrossRef]
102. Paliwal, R.; Röder, M.S.; Kumar, U.; Srivastava, J.P.; Joshi, A.K. QTL Mapping of Terminal Heat Tolerance in Hexaploid Wheat (*T. aestivum* L.). *Theor. Appl. Genet.* **2012**, *125*, 561–575. [CrossRef]
103. Pinto, R.S.; Lopes, M.S.; Collins, N.C.; Reynolds, M.P. Modelling and Genetic Dissection of Staygreen under Heat Stress. *Theor. Appl. Genet.* **2016**, *129*, 2055–2074. [CrossRef]
104. Bonneau, J.; Taylor, J.; Parent, B.; Bennett, D.; Reynolds, M.; Feuillet, C.; Langridge, P.; Mather, D. Multi-Environment Analysis and Improved Mapping of a Yield-Related QTL on Chromosome 3B of Wheat. *Theor. Appl. Genet.* **2013**, *126*, 747–761. [CrossRef]
105. Parent, B.; Bonneau, J.; Maphosa, L.; Kovalchuk, A.; Langridge, P.; Fleury, D. Quantifying Wheat Sensitivities to Environmental Constraints to Dissect Genotype × Environment Interactions in the Field. *Plant Physiol.* **2017**, *174*, 1669–1682. [CrossRef] [PubMed]
106. Thomelin, P.; Bonneau, J.; Brien, C.; Suchecki, R.; Baumann, U.; Kalambettu, P.; Langridge, P.; Tricker, P.; Fleury, D. The Wheat Seven in Absentia Gene Is Associated with Increases in Biomass and Yield in Hot Climates. *J. Exp. Bot.* **2021**, *72*, 3774–3791. [CrossRef] [PubMed]
107. Mangelsen, E.; Kilian, J.; Harter, K.; Jansson, C.; Wanke, D.; Sundberg, E. Transcriptome Analysis of High-Temperature Stress in Developing Barley Caryopses: Early Stress Responses and Effects on Storage Compound Biosynthesis. *Mol. Plant* **2011**, *4*, 97–115. [CrossRef]
108. Mahalingam, R.; Bregitzer, P. Impact on Physiology and Malting Quality of Barley Exposed to Heat, Drought and Their Combination during Different Growth Stages under Controlled Environment. Physiol. *Plantarum* **2019**, *165*, 277–289. [CrossRef] [PubMed]
109. Sakata, T.; Takahashi, H.; Nishiyama, I.; Higashitani, A. Effects of High Temperature on the Development of Pollen Mother Cells and Microspores in Barley *Hordeum vulgare* L. *J. Plant Res.* **2000**, *113*, 395–402. [CrossRef]
110. Shirdelmoghanloo, H.; Chen, K.; Paynter, B.; Angessa, T.T.; Westcott, S.; Khan, H.A.; Hill, C.B.; Li, C. Grain-filling rate improves physical grain quality in barley under heat stress conditions during the grain-filling period. *Front. Plant Sci.* **2022**, *13*, 858652. [CrossRef]
111. Zhang, D.-P.; Zhou, Y.; Yin, J.-F.; Yan, X.-J.; Lin, S.; Xu, W.-F.; Baluška, F.; Wang, Y.-P.; Xia, Y.-J.; Liang, G.; et al. Rice G-Protein Subunits QPE9-1 and RGB1 Play Distinct Roles in Abscisic Acid Responses and Drought Adaptation. *J. Exp. Bot.* **2015**, *66*, 6371–6384. [CrossRef]
112. Watt, C.; Zhou, G.; McFawn, L.-A.; Chalmers, K.J.; Li, C. Fine Mapping of QGL5H, a Major Grain Length Locus in Barley (*Hordeum vulgare* L.). *Theor. Appl. Genet.* **2019**, *132*, 883–893. [CrossRef]
113. Watt, C.; Zhou, G.; Angessa, T.T.; Moody, D.; Li, C. A Novel Polymorphism in the 5′ UTR of HvDEP1 Is Associated with Grain Length and 1000-Grain Weight in Barley (*Hordeum vulgare* L.). *Crop Pasture Sci.* **2020**, *71*, 752. [CrossRef]
114. Miura, S.; Crofts, N.; Saito, Y.; Hosaka, Y.; Oitome, N.F.; Watanabe, T.; Kumamaru, T.; Fujita, N. Starch Synthase IIa-Deficient Mutant Rice Line Produces Endosperm Starch With Lower Gelatinization Temperature Than Japonica Rice Cultivars. *Front. Plant Sci.* **2018**, *9*, 645. [CrossRef]
115. Liu, X.; Guo, T.; Wan, X.; Wang, H.; Zhu, M.; Li, A.; Su, N.; Shen, Y.; Mao, B.; Zhai, H.; et al. Transcriptome Analysis of Grain-Filling Caryopses Reveals Involvement of Multiple Regulatory Pathways in Chalky Grain Formation in Rice. *BMC Genom.* **2010**, *11*, 730. [CrossRef] [PubMed]
116. Ambardekar, A.A.; Siebenmorgen, T.J.; Counce, P.A.; Lanning, S.B.; Mauromoustakos, A. Impact of Field-Scale Nighttime Air Temperatures during Kernel Development on Rice Milling Quality. *Field Crop. Res.* **2011**, *122*, 179–185. [CrossRef]
117. Gann, P.J.; Esguerra, M.; Counce, P.A.; Srivastava, V. Genotype-dependent and Heat-induced Grain Chalkiness in Rice Correlates with the Expression Patterns of Starch Biosynthesis Genes. *Plant-Environ. Interact.* **2021**, *2*, 165–176. [CrossRef]
118. Tabassum, R.; Dosaka, T.; Ichida, H.; Morita, R.; Ding, Y.; Abe, T.; Katsube-Tanaka, T. FLOURY ENDOSPERM11-2 Encodes Plastid HSP70-2 Involved with the Temperature-dependent Chalkiness of Rice (*Oryza sativa* L.). *Grains. Plant J.* **2020**, *103*, 604–616. [CrossRef]
119. Yamakawa, H.; Hirose, T.; Kuroda, M.; Yamaguchi, T. Comprehensive Expression Profiling of Rice Grain Filling-Related Genes under High Temperature Using DNA Microarray. *Plant Physiol.* **2007**, *144*, 258–277. [CrossRef]
120. Crafts-Brandner, S.J.; Salvucci, M.E. Sensitivity of Photosynthesis in a C4 Plant, Maize, to Heat Stress. *Plant Physiol.* **2002**, *129*, 1773–1780. [CrossRef]
121. Wilhelm, E.P.; Mullen, R.E.; Keeling, P.L.; Singletary, G.W. Heat Stress during Grain Filling in Maize: Effects on Kernel Growth and Metabolism. *Crop Sci.* **1999**, *39*, 1733–1741. [CrossRef]
122. Yang, H.; Lu, D.; Shen, X.; Cai, X.; Lu, W. Heat Stress at Different Grain Filling Stages Affects Fresh Waxy Maize Grain Yield and Quality. *Cereal Chem. J.* **2015**, *92*, 258–264. [CrossRef]
123. Lu, D.; Lu, W. Effects of Heat Stress During Grain Filling on the Functional Properties of Flour from Fresh Waxy Maize. *Cereal Chem. J.* **2013**, *90*, 65–69. [CrossRef]

124. Yuan, Y.; Cairns, J.E.; Babu, R.; Gowda, M.; Makumbi, D.; Magorokosho, C.; Zhang, A.; Liu, Y.; Wang, N.; Hao, Z.; et al. Genome-Wide Association Mapping and Genomic Prediction Analyses Reveal the Genetic Architecture of Grain Yield and Flowering Time Under Drought and Heat Stress Conditions in Maize. *Front. Plant Sci.* **2019**, *9*, 1919. [CrossRef]
125. Longmei, N.; Gill, G.K.; Zaidi, P.H.; Kumar, R.; Nair, S.K.; Hindu, V.; Vinayan, M.T.; Vikal, Y. Genome Wide Association Mapping for Heat Tolerance in Sub-Tropical Maize. *BMC Genom.* **2021**, *22*, 154. [CrossRef] [PubMed]
126. Seetharam, K.; Kuchanur, P.H.; Koirala, K.B.; Tripathi, M.P.; Patil, A.; Sudarsanam, V.; Das, R.R.; Chaurasia, R.; Pandey, K.; Vemuri, H.; et al. Genomic Regions Associated with Heat Stress Tolerance in Tropical Maize (*Zea mays* L.). *Sci. Rep.* **2021**, *11*, 13730. [CrossRef] [PubMed]
127. Bennett, D.; Reynolds, M.; Mullan, D.; Izanloo, A.; Kuchel, H.; Langridge, P.; Schnurbusch, T. Detection of Two Major Grain Yield QTL in Bread Wheat (*Triticum aestivum* L.) under Heat, Drought and High Yield Potential Environments. *Theor. Appl. Genet.* **2012**, *125*, 1473–1485. [CrossRef] [PubMed]
128. Liu, Q.; Yang, T.; Yu, T.; Zhang, S.; Mao, X.; Zhao, J.; Wang, X.; Dong, J.; Liu, B. Integrating Small RNA Sequencing with QTL Mapping for Identification of MiRNAs and Their Target Genes Associated with Heat Tolerance at the Flowering Stage in Rice. *Front. Plant Sci.* **2017**, *8*, 43. [CrossRef] [PubMed]
129. Withanawasam, D.M.; Kommana, M.; Pulindala, S.; Eragam, A.; Moode, V.N.; Kolimigundla, A.; Puram, R.V.; Palagiri, S.; Balam, R.; Vemireddy, L.R. Improvement of Grain Yield under Moisture and Heat Stress Conditions through Marker-Assisted Pedigree Breeding in Rice. *Crop Pasture Sci.* **2022**, *73*, 356–369. [CrossRef]
130. Sade, N.; del Mar Rubio-Wilhelmi, M.; Umnajkitikorn, K.; Blumwald, E. Stress-Induced Senescence and Plant Tolerance to Abiotic Stress. *J. Exp. Bot.* **2018**, *69*, 845–853. [CrossRef]
131. Moore, C.E.; Meacham-Hensold, K.; Lemonnier, P.; Slattery, R.A.; Benjamin, C.; Bernacchi, C.J.; Lawson, T.; Cavanagh, A.P. The Effect of Increasing Temperature on Crop Photosynthesis: From Enzymes to Ecosystems. *J. Exp. Bot.* **2021**, *72*, 2822–2844. [CrossRef]
132. Chai, M.; Guo, Z.; Shi, X.; Li, Y.; Tang, J.; Zhang, Z. Dissecting the Regulatory Network of Leaf Premature Senescence in Maize (*Zea mays* L.) Using Transcriptome Analysis of ZmELS5 Mutant. *Genes* **2019**, *10*, 944. [CrossRef]
133. Breeze, E.; Harrison, E.; McHattie, S.; Hughes, L.; Hickman, R.; Hill, C.; Kiddle, S.; Kim, Y.; Penfold, C.A.; Jenkins, D.; et al. High-Resolution Temporal Profiling of Transcripts during Arabidopsis Leaf Senescence Reveals a Distinct Chronology of Processes and Regulation. *Plant Cell* **2011**, *23*, 873–894. [CrossRef]
134. Zentgraf, U.; Doll, J.; Riester, L. Live and Let Die: The Core Circadian Oscillator Coordinates Plant Life History and Pilots Leaf Senescence. *Mol. Plant* **2018**, *11*, 351–353. [CrossRef]
135. Li, Z.; Zhang, Y.; Zou, D.; Zhao, Y.; Wang, H.-L.; Zhang, Y.; Xia, X.; Luo, J.; Guo, H.; Zhang, Z. LSD 3.0: A Comprehensive Resource for the Leaf Senescence Research Community. *Nucleic Acids Res.* **2020**, *48*, D1069–D1075. [CrossRef]
136. Farooq, M.; Bramley, H.; Palta, J.A.; Siddique, K.H.M. Heat Stress in Wheat during Reproductive and Grain-Filling Phases. *Crit. Rev. Plant Sci.* **2011**, *30*, 491–507. [CrossRef]
137. Sakuraba, Y.; Park, S.-Y.; Kim, Y.-S.; Wang, S.-H.; Yoo, S.-C.; Hörtensteiner, S.; Paek, N.-C. Arabidopsis STAY-GREEN2 Is a Negative Regulator of Chlorophyll Degradation during Leaf Senescence. *Mol. Plant* **2014**, *7*, 1288–1302. [CrossRef] [PubMed]
138. Kumari, M.; Pudake, R.N.; Singh, V.P.; Joshi, A.K. Association of Staygreen Trait with Canopy Temperature Depression and Yield Traits under Terminal Heat Stress in Wheat (*Triticum aestivum* L.). *Euphytica* **2013**, *190*, 87–97. [CrossRef]
139. Lopes, M.S.; Reynolds, M.P. Stay-Green in Spring Wheat Can Be Determined by Spectral Reflectance Measurements (Normalized Difference Vegetation Index) Independently from Phenology. *J. Exp. Bot.* **2012**, *63*, 3789–3798. [CrossRef] [PubMed]
140. Talukder, S.K.; Babar, M.A.; Vijayalakshmi, K.; Poland, J.; Prasad, P.V.V.; Bowden, R.; Fritz, A. Mapping QTL for the Traits Associated with Heat Tolerance in Wheat (*Triticum aestivum* L.). *BMC Genet.* **2014**, *15*, 97. [CrossRef]
141. Kumar, R.; Harikrishna; Barman, D.; Ghimire, O.P.; Gurumurthy, S.; Singh, P.K.; Chinnusamy, V.; Padaria, J.C.; Arora, A. Stay-Green Trait Serves as Yield Stability Attribute under Combined Heat and Drought Stress in Wheat (*Triticum aestivum* L.). *Plant Growth Regul.* **2022**, *96*, 67–78. [CrossRef]
142. Hays, D.B.; Do, J.H.; Mason, R.E.; Morgan, G.; Finlayson, S.A. Heat Stress Induced Ethylene Production in Developing Wheat Grains Induces Kernel Abortion and Increased Maturation in a Susceptible Cultivar. *Plant Sci.* **2007**, *172*, 1113–1123. [CrossRef]
143. Gous, P.W.; Hickey, L.; Christopher, J.T.; Franckowiak, J.; Fox, G.P. Discovery of QTL for Stay-Green and Heat-Stress in Barley (*Hordeum vulgare* L.) Grown under Simulated Abiotic Stress Conditions. *Euphytica* **2016**, *207*, 305–317. [CrossRef]
144. Kilasi, N.L.; Singh, J.; Vallejos, C.E.; Ye, C.; Jagadish, S.V.K.; Kusolwa, P.; Rathinasabapathi, B. Heat Stress Tolerance in Rice (*Oryza sativa* L.): Identification of Quantitative Trait Loci and Candidate Genes for Seedling Growth Under Heat Stress. *Front. Plant Sci.* **2018**, *9*, 1578. [CrossRef]
145. Li, X.-M.; Chao, D.-Y.; Wu, Y.; Huang, X.; Chen, K.; Cui, L.-G.; Su, L.; Ye, W.-W.; Chen, H.; Chen, H.-C.; et al. Natural Alleles of a Proteasome A2 Subunit Gene Contribute to Thermotolerance and Adaptation of African Rice. *Nat. Genet.* **2015**, *47*, 827–833. [CrossRef] [PubMed]
146. Owttrim, G.W. RNA Helicases and Abiotic Stress. *Nucleic Acids Res.* **2006**, *34*, 3220–3230. [CrossRef] [PubMed]
147. Wang, D.; Qin, B.; Li, X.; Tang, D.; Zhang, Y.; Cheng, Z.; Xue, Y. Nucleolar DEAD-Box RNA Helicase TOGR1 Regulates Thermotolerant Growth as a Pre-RRNA Chaperone in Rice. *PLoS Genet.* **2016**, *12*, e1005844. [CrossRef] [PubMed]
148. He, Y.; Zhang, X.; Shi, Y.; Xu, X.; Li, L.; Wu, J.-L. Premature Senescence Leaf 50 Promotes Heat Stress Tolerance in Rice (*Oryza sativa* L.). *Rice* **2021**, *14*, 63, Erratum in *Rice* **2021**, *14*, 53. [CrossRef] [PubMed]

149. Yang, H.; Huang, T.; Ding, M.; Lu, D.; Lu, W. High Temperature during Grain Filling Impacts on Leaf Senescence in Waxy Maize. *Agron. J.* **2017**, *109*, 906–916. [CrossRef]
150. Diaz-Mendoza, M.; Velasco-Arroyo, B.; Santamaria, M.E.; González-Melendi, P.; Martinez, M.; Diaz, I. Plant Senescence and Proteolysis: Two Processes with One Destiny. *Genet. Mol. Biol.* **2016**, *39*, 329–338. [CrossRef]
151. Prochazkova, D.; Sairam, R.K.; Srivastava, G.C.; Singh, D.V. Oxidative Stress and Antioxidant Activity as the Basis of Senescence in Maize Leaves. *Plant Sci.* **2001**, *161*, 765–771. [CrossRef]
152. Li, H.; Zhang, H.; Li, G.; Liu, Z.; Zhang, Y.; Zhang, H.; Guo, X. Expression of Maize Heat Shock Transcription Factor Gene ZmHsf06 Enhances the Thermotolerance and Drought-Stress Tolerance of Transgenic Arabidopsis. *Funct. Plant Biol.* **2015**, *42*, 1080. [CrossRef]
153. Li, H.; Li, G.; Guo, X. Cloning, expression characteristics and subcellular location of heat shock transcription factor gene (ZmHsf06) in Zea mays. *J. Agric. Biotech.* **2015**, *23*, 41–51.
154. Jiang, Y.; Zheng, Q.; Chen, L.; Liang, Y.; Wu, J. Ectopic Overexpression of Maize Heat Shock Transcription Factor Gene ZmHsf04 Confers Increased Thermo and Salt-Stress Tolerance in Transgenic Arabidopsis. *Acta Physiol. Plant.* **2018**, *40*, 9. [CrossRef]
155. Shirdelmoghanloo, H.; Cozzolino, D.; Lohraseb, I.; Collins, N.C. Truncation of Grain Filling in Wheat (*Triticum aestivum* L.) Triggered by Brief Heat Stress during Early Grain Filling: Association with Senescence Responses and Reductions in Stem Reserves. *Funct. Plant Biol.* **2016**, *43*, 919. [CrossRef]
156. Gaudin, A.C.M.; Henry, A.; Sparks, A.H.; Slamet-Loedin, I.H. Taking Transgenic Rice Drought Screening to the Field. *J. Exp. Bot.* **2013**, *64*, 109–117. [CrossRef]
157. Hill, C.B.; Taylor, J.D.; Edwards, J.; Mather, D.; Bacic, A.; Langridge, P.; Roessner, U. Whole-Genome Mapping of Agronomic and Metabolic Traits to Identify Novel Quantitative Trait Loci in Bread Wheat Grown in a Water-Limited Environment. *Plant Physiol.* **2013**, *162*, 1266–1281. [CrossRef] [PubMed]
158. Hill, C.B.; Taylor, J.D.; Edwards, J.; Mather, D.; Langridge, P.; Bacic, A.; Roessner, U. Detection of QTL for Metabolic and Agronomic Traits in Wheat with Adjustments for Variation at Genetic Loci That Affect Plant Phenology. *Plant Sci.* **2015**, *233*, 143–154. [CrossRef] [PubMed]
159. Liu, C.; Sukumaran, S.; Claverie, E.; Sansaloni, C.; Dreisigacker, S.; Reynolds, M. Genetic Dissection of Heat and Drought Stress QTLs in Phenology-Controlled Synthetic-Derived Recombinant Inbred Lines in Spring Wheat. *Mol. Breed.* **2019**, *39*, 34. [CrossRef]
160. Schmidt, J.; Tricker, P.J.; Eckermann, P.; Kalambettu, P.; Garcia, M.; Fleury, D. Novel Alleles for Combined Drought and Heat Stress Tolerance in Wheat. *Front. Plant Sci.* **2020**, *10*, 1800. [CrossRef] [PubMed]
161. Guan, P.; Lu, L.; Jia, L.; Kabir, M.R.; Zhang, J.; Lan, T.; Zhao, Y.; Xin, M.; Hu, Z.; Yao, Y.; et al. Global QTL Analysis Identifies Genomic Regions on Chromosomes 4A and 4B Harboring Stable Loci for Yield-Related Traits Across Different Environments in Wheat (*Triticum aestivum* L.). *Front. Plant Sci.* **2018**, *9*, 529. [CrossRef]
162. Maulana, F.; Ayalew, H.; Anderson, J.D.; Kumssa, T.T.; Huang, W.; Ma, X.-F. Genome-Wide Association Mapping of Seedling Heat Tolerance in Winter Wheat. Front. *Plant Sci.* **2018**, *9*, 1272. [CrossRef]
163. Templer, S.E.; Ammon, A.; Pscheidt, D.; Ciobotea, O.; Schuy, C.; McCollum, C.; Sonnewald, U.; Hanemann, A.; Förster, J.; Ordon, F.; et al. Metabolite Profiling of Barley Flag Leaves under Drought and Combined Heat and Drought Stress Reveals Metabolic QTLs for Metabolites Associated with Antioxidant Defense. *J. Exp. Bot.* **2017**, *68*, 1697–1713. [CrossRef]
164. Wei, Z.; Yuan, Q.; Lin, H.; Li, X.; Zhang, C.; Gao, H.; Zhang, B.; He, H.; Liu, T.; Jie, Z.; et al. Linkage Analysis, GWAS, Transcriptome Analysis to Identify Candidate Genes for Rice Seedlings in Response to High Temperature Stress. *BMC Plant Biol.* **2021**, *21*, 85. [CrossRef]
165. Wu, N.; Yao, Y.; Xiang, D.; Du, H.; Geng, Z.; Yang, W.; Li, X.; Xie, T.; Dong, F.; Xiong, L. A MITE Variation-associated Heat-inducible Isoform of a Heat-shock Factor Confers Heat Tolerance through Regulation of Jasmonate Zim-Domain Genes in Rice. *New Phytol.* **2022**, *234*, 1315–1331. [CrossRef] [PubMed]
166. GM Approval Database. Available online: https://www.isaaa.org/gmapprovaldatabase/ (accessed on 23 March 2022).
167. Tian, B.; Talukder, S.K.; Fu, J.; Fritz, A.K.; Trick, H.N. Expression of a Rice Soluble Starch Synthase Gene in Transgenic Wheat Improves the Grain Yield under Heat Stress Conditions. *In Vitro Cell. Dev. Biol.-Plant* **2018**, *54*, 216–227. [CrossRef] [PubMed]
168. Casaretto, J.A.; El-kereamy, A.; Zeng, B.; Stiegelmeyer, S.M.; Chen, X.; Bi, Y.-M.; Rothstein, S.J. Expression of OsMYB55 in Maize Activates Stress-Responsive Genes and Enhances Heat and Drought Tolerance. *BMC Genom.* **2016**, *17*, 312. [CrossRef]
169. Kumar, R.; Kaur, A.; Pandey, A.; Mamrutha, H.M.; Singh, G.P. CRISPR-Based Genome Editing in Wheat: A Comprehensive Review and Future Prospects. *Mol. Biol. Rep.* **2019**, *46*, 3557–3569. [CrossRef] [PubMed]
170. Nandy, S.; Pathak, B.; Zhao, S.; Srivastava, V. Heat-shock-inducible CRISPR/Cas9 System Generates Heritable Mutations in Rice. *Plant Direct* **2019**, *3*, e00145. [CrossRef]
171. Qiu, Z.; Kang, S.; He, L.; Zhao, J.; Zhang, S.; Hu, J.; Zeng, D.; Zhang, G.; Dong, G.; Gao, Z.; et al. The Newly Identified Heat-Stress Sensitive Albino 1 Gene Affects Chloroplast Development in Rice. *Plant Sci.* **2018**, *267*, 168–179. [CrossRef]
172. Suh, S.; Johnson, J.A.; Tambjerg, L.; Sim, S.; Broeckx-Smith, S.; Reyes, W.; Chaplin-Kramer, R. Closing Yield Gap Is Crucial to Avoid Potential Surge in Global Carbon Emissions. *Glob. Environ. Chang.* **2020**, *63*, 102100. [CrossRef]
173. Tian, X.; Engel, B.A.; Qian, H.; Hua, E.; Sun, S.; Wang, Y. Will Reaching the Maximum Achievable Yield Potential Meet Future Global Food Demand? *J. Clean. Prod.* **2021**, *294*, 126285. [CrossRef]
174. Bergkamp, B.; Impa, S.M.; Asebedo, A.R.; Fritz, A.K.; Jagadish, S.V.K. Prominent Winter Wheat Varieties Response to Post-Flowering Heat Stress under Controlled Chambers and Field Based Heat Tents. *Field Crop. Res.* **2018**, *222*, 143–152. [CrossRef]

175. Meuwissen, T.H.E.; Hayes, B.J.; Goddard, M.E. Prediction of Total Genetic Value Using Genome-Wide Dense Marker Maps. *Genetics* **2001**, *157*, 1819–1829. [CrossRef]
176. Rutkoski, J.; Poland, J.; Mondal, S.; Autrique, E.; Pérez, L.G.; Crossa, J.; Reynolds, M.; Singh, R. Canopy Temperature and Vegetation Indices from High-Throughput Phenotyping Improve Accuracy of Pedigree and Genomic Selection for Grain Yield in Wheat. *G3 Genes Genomes Genet.* **2016**, *6*, 2799–2808. [CrossRef] [PubMed]
177. Gil, K.; Park, C. Thermal Adaptation and Plasticity of the Plant Circadian Clock. *New Phytol.* **2019**, *221*, 1215–1229. [CrossRef] [PubMed]
178. Mody, T.; Bonnot, T.; Nagel, D.H. Interaction between the Circadian Clock and Regulators of Heat Stress Responses in Plants. *Genes* **2020**, *11*, 156. [CrossRef] [PubMed]
179. Bonnot, T.; Gillard, M.B.; Nagel, D.H. CAST-R: An Application to Visualize Circadian and Heat Stress-Responsive Genes in Plants. *Plant Physiol.* **2022**, kiac121. [CrossRef] [PubMed]
180. Sheridan, C. Argentina First to Market with Drought-Resistant GM Wheat. *Nat. Biotechnol.* **2021**, *39*, 652. [CrossRef]