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REVIEW ARTICLE

Molecular breeding approaches involving physiological and reproductive traits for heat tolerance in food crops

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Abstract Heat stress is a significant threat that limits crop yield and fecundity all over the world. Prevalent strategies for heat adaptation that alter technical and management systems are inadequate to sustain yield. As such, the identification of heat-tolerant genotypes with improved yield potential is crucial. Raising tolerant and stable cultivars can be tedious as heat-stress responses are highly variable across different developmental stages. While molecular breeding has progressed in engineering heat-tolerant lines, the complexity of genetic networks and divergence of heat tolerance mechanisms is the main hindrance for plant breeders. Hence, insight into the physiological and reproductive traits associated with heat tolerance could assist in the development of strategies to screen germplasm for heat tolerance. Exploitation and use of landraces and wild relatives in breeding may enhance favorable genetic diversity in crop plants. A holistic approach to delineate molecular markers, where quantitative trait loci (QTLs) for different traits linked to heat tolerance involving physiological and reproductive traits are characterized in well-controlled field environments, may be an option for optimizing germplasm under heat stress. Here, we present an outline of the effects of heat stress and its associated tolerance mechanisms in food crops, along with some physiological, molecular and reproductive characteristics such as 'stay-green,' membrane thermostability, canopy temperature depression, metabolites, genes, QTLs, and pollen fertility. Further, we provide information on conventional and molecular breeding approaches as well as different selection strategies for heat stress tolerance.

Keywords Heat stress · Genes · QTL · HSP · Traits · Plant breeding · Thermotolerance

Introduction

Plants as immobile organisms face fluctuating environmental conditions and abiotic stress factors such as drought, salt, temperature and oxidative stress (Mittler et al. 2012). When plants are exposed to aberrant environmental constraints, several physiological and biological changes occur in cells that threaten plant survival (Jenks and Hasegawa 2008). In recent decades, global climate change and related weather conditions have become a serious challenge, with the increase in the earth's surface temperature (Usman et al. 2014). The combined earth and ocean temperature has increased by 0.72 °C from 1951 to 2012 (Team et al. 2014). Further, the fourth IPCC report projected the risk of an additional 2 °C warming and reduction in the water table by the end of the twenty-first century (IPCC 2014). In many parts of the world, the increase in temperature has been higher and more abrupt than the global averages, resulting in serious losses in crop yields (Kaushal et al. 2016). Among environmental factors, surging global temperatures will severely impact plant

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growth and productivity, especially in the arid and semiarid tropics (Hatfield and Prueger 2015). Seasonal shifts in plant phenologies have occurred in different plant species and within species due to the continual rise in temperature (Li et al. 2014a, b). Heat stress shortens crop life cycles and reduces yield; however, premature flowering can serve as an escape mechanism for terminal heat stress in crop plants (Prasad et al. 2017). Photosynthesis and the reproductive phase of plant growth are highly sensitive to high-temperature stress, which can severely affect pollen viability, anthesis and grain set (Awasthi et al. 2014). The molecular targets of heat stress involve protein denaturation, and damage to lipids, nucleic acids, and other molecules due to the high production of reactive oxygen species (ROS) (Qu et al. 2013). Plants overcome these adversities by synthesizing various protective molecules, such as antioxidants, stress chaperones (which prevent protein motifs from thermoaggregation) and scavengers to maintain cellular homeostasis (Sita et al. 2017a, b). The inherent ability of plants to survive in warmer temperatures without any yield loss is termed ‘heat tolerance’, which is a highly sophisticated phenomenon and requires synchronization of various physiological, biochemical and molecular events at the whole plant level (Hatfield and Prueger 2015).

Comparatively little progress has been made towards breeding tolerant cultivars with high heat resilience, despite the severe damage caused to different crops, even with moderate rises in temperature (Grover et al. 2013). Hence, a concerted effort is needed to raise plant cultivars that can adapt to sudden environmental disturbances using prime molecular tools and by studying the underlying thermotolerance mechanisms (Driedonks et al. 2016). Molecular biologists had limited success in the development of heat-tolerant varieties due to the complexity of gene expression during heat stress (de Souza et al. 2012). Conventional breeding approaches employing screening methods have identified few promising tolerance-related traits (Devasirvatham et al. 2016), which could be incorporated into commercial cultivars, via genetic engineering to enhance heat tolerance in crop plants (Singh and Grover et al. 2008). Relevant information regarding heat sensitivity in different plant species may assist in the development of new selection criteria that address the factors responsible for tremendous yield losses (Fahad et al. 2017). Various morpho-physiological traits have been explored as indicators of heat tolerance (Fahad et al. 2017). This review emphasizes on the adversities of heat stress as well as molecular, physiological, morphological, and yield traits associated with thermotolerance. Generally, plant adaptation to heat stress is determined by minimum photosynthetic damage and enhanced synthesis of protective molecules (Bita and Gerats 2013). A heat-resilient genotype should perform better in terms of membrane thermostability, photosynthetic efficiency, and fruit set (Nagarajan et al. 2010). Other indirect indices for selection include stomatal conductance, chlorophyll fluorescence, canopy temperature depression (CTD), stay-green trait, duration of grain filling, grain weight, and pollen fertility (Yang et al. 2002a, b; Sharma et al. 2008), which have been briefly highlighted below. An overview of conventional as well as advanced breeding techniques is provided, with a focus on the effective utilization of existing genetic resources, along with an exploration of the scope for articulating an array of surging forward and reverses breeding techniques. Furthermore, current strategies for raising transgenic plants with improved thermotolerance have been reviewed.

Effects of heat stress on plants

With rapid climatic transitions and large-scale industrialization, the severity of heat stress is increasing worldwide, which is adversely affecting plant growth and fecundity (Jha et al. 2014). High temperature-induced reductions in plant phenology, shortened life cycles, and yield losses are a major concern for plant breeders (Han et al. 2009; Fig. 1). Heat stress severely affects the vegetative stage of plant growth causing leaf chlorosis, senescence, and abscission, inhibited root and shoot growth, and reduced internode lengths (Kaushal et al. 2016). Reproductive development in higher plants is highly susceptible to unfavorable environmental conditions, especially thermal changes; a single, hot day in the warm season can prove fatal to reproductive vigor (Zinn et al. 2010). Heat stress injures the reproductive tissues that contribute to harvest index (Harsant et al. 2013). For instance, a heat wave can impair reproductive development by affecting anther dehiscence and pollen dispersal, and consequently grain set (Das et al. 2014). Such responses are highly variable depending on the duration and severity of the heat stress (Barnabás et al. 2008). Various studies have assessed the impact of heat stress on the cellular and developmental behavior of anther/pollen (Harsant et al. 2013; Sage et al. 2015) using Alexander’s triple stain as an effective method to point pollen maturation as a determinant of anther function (Harsant et al. 2013). Knowledge on anther/pollen structure as well as the exact timing of their development would be useful in determining the factors responsible for heat stress-induced male sterility or for enhancing thermotolerance (Sage et al. 2015). Heat stress also affects almost every developmental phase of the female gametophyte; for instance, reduced stigma receptivity in chickpea at 40/30 and 45/35 °C (Kumar et al. 2013), and decreased ovule viability in common bean at 30 °C (Suzuki et al. 2001). Most importantly, heat stress has an adverse impact

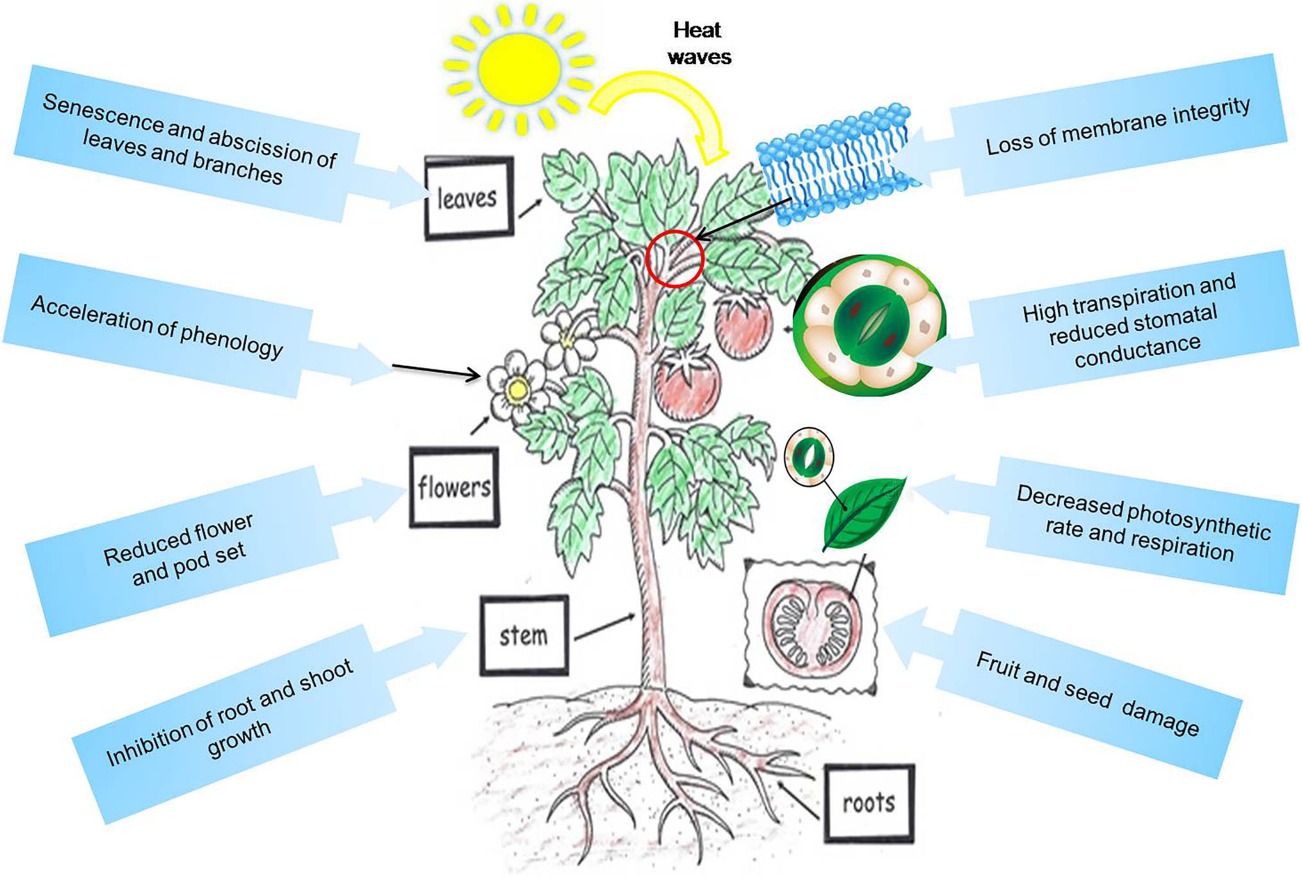

Fig. 1 Effect of heat stress on plants. The major impact of heat stress in various crop species involves inhibition of root and shoot growth, senescence and abscission of leaves, reduced flower and pod set, loss of membrane function, and reduced photosynthetic and respiration rate

on flowering including reduced flower numbers, small-sized flowers, and mutilated floral structures (Morrison and Stewart 2002), which reduces crop yield and productivity, as reported in faba bean (Bishop et al. 2016), mungbean (Kaur et al. 2015), chickpea (Kausal et al. 2013: Shukla 2013), lentil (Sita et al. 2017a, b) and kidney bean (Prasad et al. 2002). Heat stress limits the yield potential of field crops by accelerating phenology and reducing the seed filling duration (Boote et al. 2005). The detrimental effects of heat stress on staple food crops like wheat (Talukdar et al. 2014a, b; Vignjevic et al. 2015), maize (Debnath et al. 2016; Shi et al. 2017) and rice (Jagadish et al. 2014; Shi et al. 2015) were also studied in detail by various plant scientists (Barnabas et al. 2008; Bita and Gerats 2013; Jha et al. 2014; Kaushal et al. 2016).

High temperatures beyond the optimum range disrupt various physiological processes, including photosynthesis, respiration, nitrogen fixation and water relations (Milter 2006; Fig. 1), causing flower and pod abortion, and ultimately yield losses (Gaur et al. 2013). Several pieces of evidence advocate that the composition of membranes, especially lipids, may alter during high temperature (Hofmann and Todgham 2010) and hasten the kinetic energy of molecules across membranes (Savchenko et al. 2002). Such structural alterations, including phase transition of membrane components, are related to characteristic functional disruption of differential permeability and membrane transport (Wahid and Shabbir 2005). Membrane and protein destruction consequently enhance ROS production, which causes oxidative damage in plants (Jha et al. 2014). Relevant data show that heat stress negatively influences plant growth and N_2 fixation, particularly at temperatures > 25 °C (Erice et al. 2006). Warmer temperatures also alter enzyme functioning that can imbalance metabolic pathways and terminate cellular activities completely (Peverelli and Rogers 2013). It is clear that there is an immediate need to understand the mechanisms that control heat tolerance at molecular, physiological and morphological levels in the current era of global warming for future successful development of heat-tolerant crop cultivars (Jha et al. 2017). Molecular and genetic approaches for understanding heat-induced detrimental effects may play a critical role in sustaining plant growth under such conditions.

Traits associated with heat–stress tolerance in plants

Leaf traits

Stay-green trait

Stay-green (SGR) or delayed leaf senescence is one of the most dominant traits that enable plants to retain their photosynthetic activity during stress conditions (de Luche et al. 2015). Exploring the SGR trait could enhance plant productivity and yield (Thomas and Oughum 2014). In the current era of global climate change, the introduction of SGR trait would be vital for developing heat-resistant cultivars (Kumar et al. 2013). The term SGR refers to a variant that shows delayed leaf senescence when compared to a standard reference type (Joshi et al. 2007). The onset of senescence during early growth adversely affects grain filling as well as assimilation; hence, any protective mechanism that keeps leaves in the active photosynthetic state by delaying senescence is likely to enhance the yield potential of crops (de Luche et al. 2015). During grain filling, the SGR character establishes a senescence pattern for plant survival whereby the stems and leaves retain their photosynthetic ability, thus increasing sugar production from photosynthesis (Pinto et al. 2016) Recently, this trait was characterized as an essential component in the genetic recovery of various crops to improve heat resilience and yield gain (Kusaba et al. 2013). It has been suggested that the stay-green character may enhance yield potential (Thomas and Oughum 2014), making it a significant genetic tool for breeding heat tolerance (Parry et al. 2010). Recently, more heat tolerance was observed in SGR wheat genotypes due to increased stability of photosynthetic structures and less accumulation of reactive oxygen species (Tian et al. 2012).

The practicality of the stay-green character is related to reduction of canopy temperatures and retention of photosynthesis even during warmer temperatures (> 30 °C); hence, this feature can serve as a useful trait for engineering heat-tolerant wheat cultivars (Kumari et al. 2013). A significant co-relation was detected between heat resilience and the stay-green trait in 936 elite wheat genotypes (Kumari et al. 2007), suggesting that delayed senescence is an essential selection criterion for heat adaptability. Further, photosynthetic activity declined less in plants with the stay-green trait during grain filling (Ahlawat et al. 2008). Likewise, the wheat cultivar “Mairaj-2008”, possessing stay-green traits, had greater yield gains under heat stress than heat-susceptible cultivars lacking the stay-green ability (Nawaz et al. 2013). A recent study, based on computational re-modeling for the climatic change scenario in 2050, revealed that delaying senescence and shifting the grain-filling duration increased wheat productivity in warmer environments (Stratonovitch and Semenov 2015). Panigrahy et al. (2011) revealed that four heat-tolerant rice mutants with stay-green characteristics had higher chlorophyll and carotenoids’ contents and lower reactive oxygen species (ROS) levels than wild plants when exposed to prolonged heat. A field assay of 15 spring wheat genotypes showed that the “Vee/Nac” and “Dena” genotypes with SGR traits (flag leaf area and chlorophyll content) were highly tolerant to both heat and drought stress during flowering (Zarei et al. 2013). Moreover, a strong positive link between stay-green traits, grain filling, and total seed weight was observed and attributed to better photosynthetic activity (Pinto et al. 2016). Similarly, the introduction of the stay-green character in some superior wheat lines resulted in higher grain yields and stability during high-temperature conditions and may serve as a promising technique for raising more tolerant and productive wheat lines (de Luche et al. 2015). A constant supply of assimilates to the ovaries and anthers is necessary to fulfill energy demands and to maintain pollen and ovule viability under heat stress; this can be achieved by incorporating functional SGR traits that enhance photosynthetic efficiency (Jagadish et al. 2014). The advantages of the SGR trait for increased yield production during heat stress have also been described in other crop plants including barley (*Hordeum vulgare*; Gous et al. 2016), sorghum (*Sorghum bicolor;* Borrell et al. 2014) maize (*Zea mays;* Almeida et al. 2014), rice (*Oryza sativa;* Jiang et al. 2007) and cowpea (*Vigna unguiculata*; Muchero et al. 2013).

While the cumulative effect of the SGR character in providing thermotolerance and improving yield potential in all crops has been described here, detailed knowledge of the physiology of senescence in different crops may serve as a key tool for improving productivity under heat stress. Though, SGR is identified as a potential tool for heat stress tolerance, the optimal pattern of pigment loss/senescence in terms of improving grain yield is difficult to determine. Furthermore, chlorosis is an elemental part of programmed senescence; maintenance of photosynthetic efficiency and remobilization of nutrients to the maturing grain is tedious task (Vijayalakshmi et al. 2010).

Canopy temperature depression

Canopy temperature depression (CTD) is an indirect measurement of the yield potential of crop plants and represents their metabolic fitness under specific environmental conditions (Kumari et al. 2012). Canopy temperature depression may serve as a desirable criterion for selecting heat-tolerant genotypes on the basis of phenotypic variation (Mason and Singh 2014). Previous data have shown a strong correlation between CTD and yield performance in both warm and temperate conditions (Reynolds et al. 1998). CTD is easy to measure, and even a single reading can articulate the temperature of scores of leaves, thus decreasing experimental error (Balota et al. 2008). As such, the integrated CTD value can be assessed rapidly in a small breeding field; a successful attempt has been made to interpret its potential as a dominant physiological trait for genetic improvement in yield (Chandra et al. 2017). Cornish et al. (1991) showed the crucial involvement of CTD in imparting heat tolerance to cotton plants. Likewise, CTD was authenticated as an effective physiological trait against heat stress in wheat (Amani et al. 1996; Fischer et al. 1998) and lower canopy temperatures reportedly enhanced yield potential in wheat exposed to warmer temperatures (Mason et al. 2013). Moreover, a significant level of phenotypic variation has been observed in wheat (Sant Pierre et al. 2010), indicating a correlation between the CTD value and heat resilience (Pradhan et al. 2012). Reynolds et al. (1994) revealed that in wheat, CTD along with flag leaf photosynthesis and stomatal conductance were positively associated with grain yield under heat stress. In another study, Indian and CIMMYT wheat germplasm was screened for the SGR trait and CTD (Kumari et al. 2013). In all of the lines, higher CTD values occurred in the SGR genotypes, due to transpirational cooling and lower canopy temperatures (Kumari et al. 2013). Similarly, four heat-tolerant (Gourab, Sourav, Kanchan, and Shatabdi) and two heat-sensitive (Sonora and Kalyansona) wheat genotypes were tested under normal as well as late-sown conditions for post-anthesis heat sensitivity (Sikder and Paul 2010). The heat-tolerant lines exhibited higher CTD than the heat-sensitive lines in both growing seasons, suggesting that heat-tolerant cultivars retained cooler canopies than heat-sensitive cultivars (Sikder and Paul 2010). Similarly, 40 wheat varieties were tested for heat sensitivity in two growing seasons (Saxena et al. 2014). All of the tolerant lines had high CTD scores during the vegetative stage, which reduced transpirational loss and helped to retain the stay-green trait for longer, further enhancing yield potential (Saxena et al. 2014). Ray and Ahmed (2015) demonstrated that, during the post-anthesis heat period, wheat genotypes maintaining high CTD performed better in terms of yield and grain growth, and may serve as a promising selection criterion for heat tolerance (Ray and Ahmed 2015).

From above it is clear that, CTD is highly useful trait for genetic improvement in the early breeding generations where yield tests are not performed, however further considerations are required for experimental design that utilizes a repeated yield tests for cultivars to regulate spatial variation. Further, high throughput tools for measuring CTD are also necessary for breeders to the enhance accuracy and speed of genetic gain from CTD.

Stomatal conductance

One possible mechanism for heat adaptation in plants is stomatal control of transpirational activities, which will determine the extent to which leaf temperatures can be lowered by evaporation (Condon et al. 2007). As leaves open their stomata, differences in the rate of gaseous exchange may create differences in stomatal behavior under stressed conditions, which can be observed with a leaf porometer (Chandra et al. 2017). Fully opened stomata in high-yielding varieties will increase their transpiration rate, and photosynthetic efficiency may also improve due to enhanced diffusion of CO_2 and water vapor (Condon et al. 2007). An advanced breeding and selection program in the USDA-ARS developed the cotton cultivar Pima S-6, but the basis for its heat adaptation was unknown (Cornish et al. 1991). A heat-tolerant advanced cotton line (Pima S-6) showed significant increases in stomatal conductance (gS) and photosynthetic rate (P_N) under heat stress, possibly due to the cooling ability of plants through transpiration and high gaseous exchange (Cornish et al. 1991). Likewise, heat-tolerant wheat genotypes had high gS under heat stress (Chauhan et al. 2009). Similarly, heat-tolerant chickpea lines increased gS under heat stress to improve water status (Kaushal et al. 2013). Sharma et al. (2015) identified a heat-tolerant wheat cultivar with high gS and photosynthetic efficiency under severe heat stress as a valuable genetic resource for developing heat tolerance. Likewise, gS in heat-tolerant lentil genotypes increased with increasing temperatures up to 38/28 °C (Sita et al. 2017). In mungbean, a heat-tolerant genotype had higher gS than a heat-sensitive genotype under both normal and late-sown conditions (Kaur et al. 2015). Since high temperature is strongly correlated with gS and grain yield (Rekika et al. 2000), it could be a valuable physiological trait for enhancing yield under stressed conditions and may provide a robust understanding of plant thermostability in future breeding programs. Although heritability of this trait is moderately high; the gain yield and retrospective gains from selection are small and require future investigation.

Chlorophyll fluorescence

A recent emphasis and evaluation of chlorophyll fluorescence (ChlF; F_v/F_m ratio) under changing environments have indicated that this imaging technique, which is used for indirect measurement of photosynthetic efficiency, may be effective in screening crop plants for stress tolerance (Guanter et al. 2014; Malaspina et al. 2014). More importantly, ChlF is advancing as an effective physiological trait against heat stress in agricultural, ecological and environmental studies (Gottardini et al. 2014). As ChlF allows scientists to non-destructively score photosynthetic efficiency, it may act as a powerful component of plant heat-stress analysis (Kalaji et al. 2016). ChlF indicates photosystem II (PSII) quantum efficiency and is widely implicated in determining initial stress in plants (Sharma et al. 2014). Photosynthetic processes are highly susceptible to high-temperature stress with adverse effects on quantum efficiency (Mathur et al. 2014). For instance, heat stress markedly reduced the ratio of reduced electron acceptors (plastoquinone) to electron donors in apple *Malus* × *domestica* Borkh (Chen et al. 2009), increased the minimal fluorescence value, and decreased the maximal quantum yield of PSII (Chen et al. 2009; Brestic et al. 2013). ChlF is also a fast and useful technique to measure PSII thermolability under heat stress; plants with high F_v/F_m values could be used in breeding for heat tolerance (Kalaji et al. 2016). In a field experiment, 30 wheat (*Triticum aestivum* L.) genotypes were evaluated for PSII thermostability during heat stress by using fast ChlF kinetics (Brestic et al. 2013). The basal ChlF (common criterion for PSII thermostability) increased above 44 °C in all genotypes, indicating PSII damage due to the rise in temperature (Brestic et al. 2013). High temperature adversely affects the growth and productivity of upland cotton (*Gossypium hirsutum* L.) (Wu et al. 2014). A ChlF assay was used to screen *G. hirsutum* landraces to determine heat-tolerance in terms of photosynthetic ability, independent of agronomic yield and productivity; three genotypes (TX 2287, TX 2285 and TX 761) maintained high photosynthetic efficiency (high F_v/F_m values) and could be used as potential heat-tolerant genetic resources to improve upland cotton yield under heat stress (Wu et al. 2014). Similarly, in a field trial, a positive correlation between cotton yield and ChlF was observed in 15 upland cotton cultivars (Karademir et al. 2012). Another study tested the heat resilience of nine common bean (*Phaseolus vulgaris* L.) lines with regard to changes in ChlF; the heat-tolerant line RRR46 with a high ChlF value performed better under heat stress (measured by JIP test) and could be used in future breeding programs (Stefanov et al. 2011). Sharma et al. (2014) tested some previously selected wheat cultivars (categorized in two groups with high or low F_v/F_m values) for heat sensitivity in terms of growth and photosynthesis. The cultivars with high F_v/F_m values had a high photosynthetic rate (P_N) and chlorophyll content, accompanied by high (gS), transpiration rate (E) and evaporative cooling of the leaf (ΔT) (Sharma et al. 2014). Similarly, ChlF was more efficient for screening durum wheat genotypes than conventional methods (e.g., harvest index, grain filling, etc.) (Gautum et al. 2014). In mungbean, heat-tolerant genotypes had higher photosynthetic efficiencies (measured as F_v/F_m ratio) than heat-sensitive genotypes under both normal and late-sown conditions (Sharma et al. 2016). Similar results were obtained in lentil, where a heat-tolerant genotype (IG3263) maintained high photosynthetic efficiency under heat stress (Sita et al. 2017) and could be used in future breeding programs.

It is highly apparent that ChlF is a highly sensitive probe for physiological status of leaves that can assess plant performance rapidly in a wide range of conditions. The successful implementation of ChlF in crop breeding programmes requires careful selection of suitable fluorescence parameters to determine plant performance (Malaspina et al. 2014). Altogether, technical advancements in fluorescence imaging technique with automated sampling systems are necessary to improve the accuracy as well as rate of many different plant screening programmes.

Membrane thermostability

Membrane thermal-stability is an important selection criterion for heat tolerance and is measured by the electrical conductivity of heat-exposed leaf tissues (Asthir et al. 2015). Membrane stability tends to decline during the late developmental phase of the plant (Ahmad and Prasad 2011); the significant genetic variation in membrane thermostability among genotypes could be used for breeding purposes. Further, biochemical and physiological screening could enhance selection in addition to conventional breeding methods (Hemantaranjan et al. 2014). Enhanced ion leakage is an indirect indication of heat-stress tolerance in many crop species, including soybean (Martineau et al. 1979), wheat (Blum et al. 2001), sorghum (Marcum 1998), cowpea (Ismail and Hall 1999), and barley (Wahid and Shabbir 2005). Membrane damage as an indicator of stress injury has been observed in chickpea at 40/30 °C, which was further enhanced at 45/35 °C (Kumar et al. 2013). Similarly, reduced cellular thermostability has been observed in rice, and was closely related to yield potential of the crop (Maavimani and Saraswathi 2014). Wheat lines with high membrane stability during grain filling performed better than those with less membrane stability under hot environments (Gupta et al. 2013). Another study measured the membrane thermostability index in wheat genotypes at different developmental stages; the heat-tolerant wheat genotypes had higher membrane thermostability (56.83%) than the heat-sensitive genotypes (31.43%) at grain filling (Ramani et al. 2017). Genetic variation for membrane stability has been observed in other crops facing severe heat stress, including cotton (Cottee et al. 2010), lentil (Sita et al. 2017a, b), chickpea (Kaushal et al. 2015), and mung bean (Sharma et al. 2016). Further, Abro et al. (2015) identified several heat-tolerant cotton genotypes with high membrane thermostability at temperatures > 50 °C, which could be used to develop heat-tolerant germplasm. In a recent investigation, maize genotypes were assessed for genetic responses in cell membrane thermostability and leaf temperature for heat tolerance and to determine the inheritance pattern (Naveed et al. 2016). Their findings validated that cell membrane thermostability at the reproductive stage is beneficial for identifying heat-tolerant maize lines (Naveed et al. 2016). Similarly, heat tolerance has been observed on the basis of cellular membrane stability in wheat genotypes (BAW-1143, BARI Gom-25, BARI Gom-26 and Prodip) (Bala and Sikder 2017). Based on the above findings, cell membrane thermostability has potential as an effective trait for identifying stable and heat-tolerant genotypes suitable for heat-prone areas. However, detailed research is required to explain genetic variation in membrane thermostability and its relation with unsaturation/saturation of fatty acids to provide heat stress tolerance in plants.

Photosynthetic efficiency

High temperature disrupts photosynthetic ability in all plants by modulating the structural integrity of cellular organelles and the concentrations of numerous pigments, metabolites and the associated enzymes (Ashraf and Harris 2013). Inhibition of photosynthesis during mildly high and extreme temperatures is generally attributed to the disruption of mesophyll activity and stomatal closure (Dias and Bruggemann 2010). Prolonged exposure to heat stress also results in premature leaf senescence and reduced leaf area, which adversely affect the total photosynthetic efficiency of plants (Yuan et al. 2017). As photosynthesis contributes to most of the plant biomass, improvements in photosynthesis efficiency are essential for increasing crop productivity and could be a suitable approach for yield gain under heat stress (Mathur et al. 2014). For instance, high temperatures strongly inhibited photochemical efficiency and chlorophyll content in chickpea (Kumar et al. 2013). Prolonged high temperatures for 45 days (40/30 °C day/night) markedly reduced the F_v/F_m ratio, photosynthetic rate, and antioxidant activities in sorghum leaves (Djanaguiraman et al. 2011). Tan et al. (2011) reported that heat stress (43 °C for 2 h) reduced photosynthetic efficiency (38%) in tobacco (*Nicotiana tabacum* L.) leaves. In maize, the photosynthetic rate was not affected by heat stress (Suwa et al. 2010); however, in tomato, increased temperature (32 °C) at both pre-anthesis and anthesis stages inhibited photosynthesis (Camejo et al. 2005). Average photosynthetic rates declined in grape (*Vitis vinifera* L.) leaves when the temperature increased from 25 to 45 °C, due to 15–30% closure of stomata (Greer and Weedon 2012).

Heat-tolerance was found to be strongly associated with maintenance of high photosynthetic efficiency. For instance, in cotton, a heat-tolerant Australian cotton cultivar (Sicot 53) exhibited high gaseous exchange, ChlF and Rubisco activity under high-temperature stress (Cotte et al. 2012). Investigation of photosynthetic efficiency of flag leaves during grain filling identified a heat-tolerant cultivar 'Jimai22' with 6% yield gain under heat stress (Feng et al. 2014). Moreover, this cultivar exhibited PSII stability and high carboxylation activity under heat stress (Feng et al. 2014). Paul et al. (2017) reported heat-induced damage to the PSII antenna complex and photosynthetic efficiency in potato (*Solanum tuberosum* L.). Based on the above findings, the heat-tolerance ability of plants is generally related to adaptation of photosynthetic metabolism, which should be evaluated thoroughly to assess crop tolerance to various environmental conditions. As yield enhancement mostly depends upon photosynthetic efficiency and assimilate partitioning, genetic gains in assimilation requires significant investigation. Further, photosynthesis and Rubisco regulation is difficult to maintain and is promising targets with high payoffs.

Metabolites

The emergence of metabolomics in heat-stress responses has allowed greater understanding of survival mechanism at the metabolic level (Obata and Fernie 2012). Metabolomics has had limited application in governing the heat resilience pathways/adaptation in plants (Arbona et al. 2013). Given the high susceptibility of seed germination and emergence to heat stress, metabolite profiling in soybean revealed that antioxidants such as flavonoids, tocopherols, ascorbate, and phenylpropanoids confer heat tolerance in tolerant genotypes (Chebrolu et al. 2016). Likewise, accumulation of soluble sugars (maltose, sucrose, and trehalose), amino acids (α-alanine) and sugar alcohols (glycerol) are also involved in heat-stress resilience in plants (Rodziewicz et al. 2014). Recently, the responses of rice floral organs to heat and drought stress and the integrative examination of transcriptomic and metabolomics of floral organs affirmed that sugar deprivation is the main cause of reproductive failure under heat and drought stress (Li et al. 2015). The anthers of a heat-tolerant rice genotype (N22) had low levels of fructose-6-P and glucose-6-P, while those of heat-sensitive (Moroberekan) had low levels of myo-inositol and sucrose and high levels of raffinose and galactinol (Li et al. 2015). Metabolomic changes in Moroberekan rice anthers upregulated the expression of the carbon starved anthers (CSA) gene (an intercellular sugar transport regulation gene) (Zhang et al. 2010). However, the expression of INV4 (a cell wall invertase gene) and MST8 (a sugar transporter gene) increased in N22 rice (Li et al. 2015; Zhang et al. 2010). In *Arabidopsis*, darkness and high-temperature stress responses in leaves were determined using GC–MS profiling along with transcriptomic analysis. As protein degradation occurs rapidly during heat stress, the supply of cellular energy occurs via breakdown of amino acids in the absence of photosynthesis, as evidenced by the strong relationship between the Krebs cycle and amino acid metabolism (Guy et al. 2008).

Limited insight of stress-related metabolism in plants is a major flaw in the perception of stress signals (Roychoudhary et al. 2011). Hence, complete profiling of stress-related metabolites is necessary for successful engineering of stress-resilient crop species (Jha et al. 2017).

Reproductive traits

Pollen fertility

Plants have an inherent ability to thrive under a wide range of temperatures during vegetative growth; however, plants are more temperature sensitive during the reproductive phase of growth, even with moderate rises in temperature (Mesihovic et al. 2016). Breeding for pollen thermotolerance and the heat-stress response is important for molecular biologists and agronomists to improve heat tolerance in core germplasm (Mittler et al. 2012). While considerable information is available on standard methods for screening thermotolerance in plants (Li et al. 2011), there is currently no realistic approach for assessing pollen thermotolerance that offers consistent results.

Jagadish et al. (2008) revealed that, during heat stress, rice genotype CG14 (*Oryza glaberrima*) reaches peak anthesis stage earlier than *Oryza sativa*. Further, they reported that rice cultivar N22 exhibited significant heat tolerance (Jagadish et al. 2010; Madan et al. 2012) with more spikelet fertility (64–86%) at high temperature (38 °C) than sensitive cultivars (Azucena and Moroberekan), which had reduced fertility (8%) (Jagadish et al. 2008). Similarly, two rice cultivars (Todorokiwase and Dular) had high thermotolerance at 39 °C during booting, while Milyang 23 was thermotolerant to 38 °C at flowering, and Giza 178 was highly thermotolerant at both stages (Tonorio et al. 2013). Further, two rice cultivars (N22 and NH219) increased spike fertility and pollen viability under heat stress (Poli et al. 2013). Recent breeding programs in rice facilitated the transfer of heat tolerance from N22 to Xieqingzao B by producing BC1F8 lines (Liao et al. 2011). Moreover, an advanced variety from N22 × Gayabyeo exhibited enhanced thermotolerance and increased yield (Norvie et al. 2014). Considering the significance of anther dehiscence in dispensing heat tolerance, rice plants were analyzed for anther characteristics, particularly locule closure during heat stress (Matsui and Omasa 2002); two japonica rice cultivars (Nipponbare and Akitakomachi) showed high fertility at 37.5 °C/26 °C at flowering (Matsui and Omasa 2002). Various heat-tolerant lines of various crop species have been developed from pollen-based screening; for instance, AZ100 in maize (Petolino et al. 1992), DG 5630RR in soybean (Salem et al. 2007) and ICC15614 and ICC1205 in chickpea (Devasirvatham et al. 2012, 2013). Recently, two heat- and drought-tolerant lines in maize (La Posta Sequia C7-F64-2-6-2-2 and DTPYC9-F46-1-2-1-2) were identified on the basis of pollen traits (Cairns et al. 2013). In a similar way, a chickpea breeding line (ICCV 92944) with high heat-tolerance has been released in two countries (JG 14 in India and Yezin 6 in Myanmar), which is performing better under heat stress (Gaur et al. 2013). In a recent study, heat-tolerant tomato genotypes (LA2854, LA1478, and LA0417) were identified on the basis of pollen fertility (Paupière et al. 2017) with a high fraction of viable pollen grains. Similarly, two tomato (*Solanum lycopersicum*) varieties (Nagcarlang and Saladette) from Radboud University, Nijmegen, were identified in the database of TGRC as heat-stress tolerant based upon pollen traits (Paupière et al. 2017). In a field trial, Sharma et al. (2016) identified five heat-tolerant mungbean genotypes (EC693357, EC693358, EC693369, Harsha, and ML1299) that performed better in terms of pollen viability, yield, and biomass under both normal and late-sown conditions. Likewise, in a study on lentil, Sita et al. (2017a, b) revealed five heat-tolerant genotypes (IG2507, IG3263, IG3745, IG4258, and FLIP2009) that had superior pollen function under heat stress (40/30 °C) and could be used in future breeding programs for developing heat tolerance. Similar results were obtained in chickpea, where two heat-tolerant genotypes (ICC15614 and ICCV92944) exhibited high pollen germination and pollen viability under heat stress (Kaushal et al. 2016). The evaluation of pollen sensitivity to high temperatures might be an important trait for plant breeders to unravel the existing germplasm for heat tolerance (Mesihovic et al. 2016). Despite, there is sufficient literature on pollen fertility and selection; the molecular mechanisms underpinning this selection are still controversial due to genetic variability among different crops.

Conventional breeding for heat tolerance

A simple method for identifying heat-resilient cultivars is the analysis of breeding material in a warmer environment and recognition of better performing lines (Jha et al. 2014). Several morphological and physiological attributes can be used as potential traits for identifying heat-tolerant cultivars (Jha et al. 2014; Fig. 2). Heat-stress resilience in

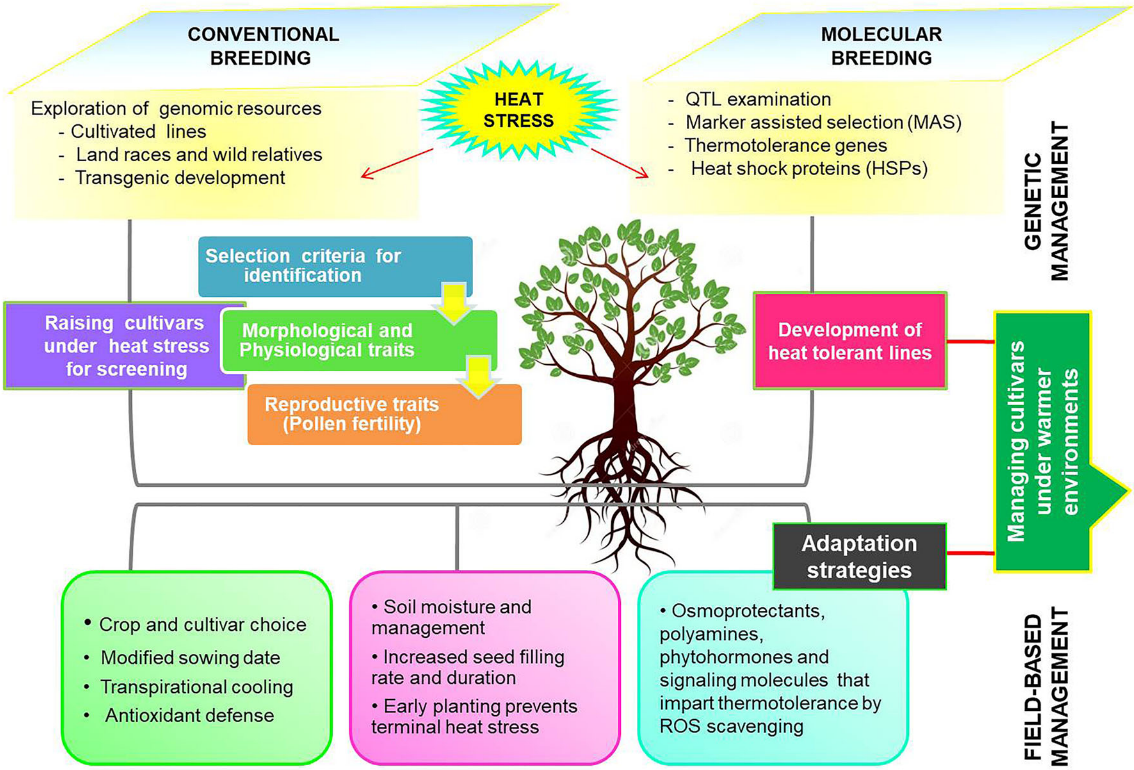

Fig. 2 Breeding strategies for heat-stress tolerance in crop plants. A schematic representation of conventional and molecular breeding methods involving exploitation of landraces and wild relatives for developing transgenic with improved thermotolerance. Adaptation strategies for managing genotypes under field conditions that involve various physiological and reproductive traits for heat tolerance are also illustrated

plants is generally characterized by a minimum loss of photosynthetic efficiency and enhanced synthesis of protective biomolecules (Bita and Gerats 2013). The reproductive development and photosynthetic ability of plants are highly susceptible to heat stress-induced damage. Heat-resilient lines should perform better in terms of photosynthesis, membrane thermostability, and pod set during the period of heat shock (Nagarajan et al. 2010). A few other components which could be used in selection and breeding include the grain-filling period, grain number and grain weight (Sharma et al. 2008). Further, the heat tolerance index is a suitable stress tolerance indicator to assess the ability to recover after heat shock (Setimela et al. 2005).

Through conventional breeding, novel heat-tolerant genotypes can be developed; for instance, an early maturing variety of broccoli with improved head quality will avoid exposure of the heat-sensitive floral stage to warmer days later in the season (Farnham and Bjorkman 2011). Repeated selection using *T. tauschii* as a gene donor was beneficial for enhancing wheat (BC1F6) yield in terms of increased grain filling and grain size (Gororo et al. 2002). In tropical legumes, direct selection for yield enhancement identified heat-stress tolerance in a cowpea species,'California Blackeye No. 27 (CB27)' during the reproductive stage in terms of high flower production and pods set under hot environments (Ehlers et al. 2005). Similarly, four common bean genotypes (SRC-1-12-1-48, SRC-1-12-1-182, 98020-3-1-7-2, and 98012-3-1-2-1) exhibited high heat resilience based on the evaluation of stress indicators including the heat susceptibility index, heat tolerance index, and geometric mean analysis (Porch 2006). Further, screening of various chickpea genotypes in the field identified the heat-tolerant genotype ICCV 92944 (Gaur et al. 2012) and others (Jha et al. 2014). Some hybrid varieties of maize (K J. Surabhi, YH-1898, NK 64017, and FH-793 ND-6339) also contributed to yield stability under heat stress (Rahman et al. 2013). In potato, genetic gain through breeding occurred after periodic selection for heat tolerance that also improved yields by up to 37.8% (Benites and Pinto 2011). Even though conventional breeding is a fundamental criterion in developing stress tolerance, its relevance and application in a wide range of crop species are still questionable (Jha et al. 2014).

Some potential traits related to physiology and reproductive biology of plants under heat stress can be used successfully to screen and breed for heat tolerance. For example, Zhou et al. (2015) screened four tomato genotypes (two heat-tolerant and two heat-sensitive) for maximum quantum efficiency (F_v/F_m) under heat stress; the heat-resilient group maintained high photosynthetic rates, gS, and total phenolic contents, suggesting that F_v/F_m is an important indicator of heat tolerance in plants. Further, the heat-resilient lines had better pollen germination, fruit set, and yield under heat stress than the heat-sensitive lines (Zhou et al. 2015). Analysis of yield-associated physiological traits for heat tolerance in 16 cotton (*Gossypium hirsutum* L.) cultivars identified two tolerant genotypes (Ersan92 and Sayar314) that performed well under heat stress and could be used in trait-associated breeding for improved yield (Demirel et al. 2016). Likewise, various pollen and physiological traits were assessed in 38 cotton cultivars for heat tolerance during the boll-filling stage; based on the screening details, genotype PX532211WRF was marked as tolerant to both heat and drought stress (Singh et al. 2018). Trait-based screening of potential heat-resilient genotypes indicates the likelihood of using genetic variation at both vegetative and reproductive stages of growth to improve heat adaptation under changing climate conditions.

Modern and advanced breeding

Need for molecular breeding

The identification of stable and stress-tolerant genomic resources and their introduction into elite cultivars via traditional breeding and advanced molecular and biotechnological approaches is crucial (Cabello et al. 2014). Recent efforts to generate plant cultivars with better heat tolerance via selection-dependent breeding methods have not been especially successful (Grover et al. 2013). Therefore, breeding successes for heat tolerance are limited. A unique approach to breeding stress tolerance by deciphering the genomic regions responsible for tolerance has promise and is particularly beneficial for creating stress-tolerant lines with high yield performance (Driedonks et al. 2016). Significant knowledge of marker-trait relations is required for effective marker-aided breeding related to terminal heat tolerance in commercially useful crop plants (Kato et al. 2000). Marker-aided selection (MAS) has been used extensively to expedite the efficiency of plant breeding. Some molecular markers have been used in MAS; however, simple sequence repeats and single nucleotide polymorphisms (SNPs) are being used extensively for mapping quantitative trait loci (QTL) (Das and Rao 2015). Molecular breeding has been recently used to pyramid genes conferring resistance to heat stress (Shamsudin et al. 2016). Some molecular traits with potential for molecular breeding are detailed below.

Quantitative trait loci

Novel breeding approaches using **quantitative trait loci** (QTLs) mapping are effective for identifying heat-stress endurance in plants (Jha et al. 2014). QTLs involving various traits such as grain filling and leaf senescence have been well characterized in heat-stressed wheat plants (Mason et al. 2010). In wheat, QTLs associated with grain filling under heat stress were characterized on chromosome number 5A and 1B (Yang et al. 2002b), and three QTL for green color and nine for tillering and grain filling have been identified (Kumar et al. 2010). Eleven QTLs in maize and four in *Arabidopsis* that play an essential role in thermotolerance have been characterized (Frova and Sari-Gorla 1994). In rice, a principal trait loci *OsHTAS* (*Oryza sativa* heat tolerance at the *s*eedling stage) has been isolated from the genotype HT54, which provides high temperature (48 °C) resilience particularly during the seedling stage and grain filling (Wei et al. 2012). Five QTLs for pollen germination and six for pollen tube growth under heat stress have been detected in maize using RFLP markers and mapping techniques (Frova and Sari-Gorla 1994) and, from the same mapping population, six QTL for cellular membrane stability were characterized (Ottaviano et al. 1991). Four QTL (Stg1–4) controlling the stay-green trait have been mapped on three LGs (A, D, and J) in sorghum (Xu et al. 2000), as have two QTL (*HQTL1* and *HQTL2*) for enhancing pollen viability under heat stress (Timmerman-Vaughan et al. 2005). Similarly, by testing SNP markers in a RIL population (CB27 × IT82E-18), Lucas et al. (2013) reported five essential genomic regions that conferred heat tolerance in cowpea. In tomato, six QTL were associated with fruit set under high-temperature stress (Grilli et al. 2007). In *Brassica campestris* L. ssp. *Pekinensis*, the use of amplified fragment length polymorphism (AFLP) and random amplified polymorphic DNA (RAPD) markers led to the discovery of five QTL for heat endurance (Shuancang et al. 2003). In another experiment, two recombinant inbred lines of rice were developed from an interspecific cross of the parental line *O. sativa* subsp. *japonica* SNU-SG1 with stay-green traits and *O. sativa* subsp. *japonica* Suweon490 or *O. sativa* subsp. *indica* Andabyeo (Fu et al. 2011). The authors identified two stay-green linked QTLs, cumulative chlorophyll content of flag leaf (*Csfl6*) and total cumulative SPAD value of the four upper leaves (*Tcs9*)—located on chromosomes 6 and 9, respectively (Fu et al. 2011). In maize, the SGR trait has been correlated with yield gain (Zheng et al. 2009). QTL examination of a maize line constructed from a cross between a stay-green inbred line Q319 and a normal inbred line Mo17 showed 14 QTL for post-anthesis stay-green traits that are linked to yield gains in maize (Zheng et al. 2009). QTL examination of cowpea led to the discovery of five genomic regions responsible for 11.5–18.1% of the phenotypic variation for heat tolerance along with three loci linked to the heat-induced browning of seed coats (Pottorff et al. 2014). Genome-associated mapping revealed five QTL regions in wheat that were strongly linked to post-anthesis heat resilience (Talukder et al. 2014a, b). Bac-molenaar et al. (2015) identified four QTLs for heat tolerance mainly during reproduction (before anthesis and after anthesis) in *Arabidopsis thaliana*. In wheat, 37 QTLs for genomic regions encoding ChlF were analyzed during heat stress that helps to improve crop yield through marker-assisted breeding (i Azam et al. 2015). Likewise, QTLs associated with early morning flowering and heat tolerance were identified on chromosomes 7 and 8 in rice through selective genotyping, which can be used for fine selection of heat tolerance and heat escape mechanisms in plants (Baliuag et al. 2015). Recently, QTL mapping in lentil characterized two primary QTL (qHt_ps and qHt_ss) with 9.23 and 12.1% phenotypic variation for pod set and seedling survival, respectively, under heat stress (Singh et al. 2017). Likewise, a genome-mapping study identified QTLs linked to heat stress resilience in *Brassica napus*. L. for various agronomic traits such as plant height, pod number, pod length, and proportion of sterile pods (Rahaman et al. 2017). Three QTLs encoding a gene, viz. *HSc70* (*HEAT-SHOCK COGNATE 70*) for thermotolerance and yield enhancement, have been identified in potato (Trapero-Mozos et al. 2018; Table 2). Recently, Shanmugavadivel et al. (2017) identified a putative QTL *qSTIPSS9*.1 on chromosome 9 of rice (Nagina22/IR64) for heat tolerance at the reproductive stage, which could be used in marker-assisted breeding to increase yield potential in rice. Twenty QTLs related to pollen infertility, aborted pods, and total number of pods were identified in a spring variety of mustard (*Brassica napus*), which can be used to develop tolerant cultivars (Rahaman et al. 2018). Similarly, CTM (composite interval mapping) analysis of chickpea genotypes led to the discovery of eight QTLs in CaLG05 and CaLG06 genomic regions for reproductive heat tolerance (Paul et al. 2018). A series of 296 F8-9 inbred recombinant lines from crossing heat-tolerant (ICC15614) and heat-sensitive (ICC4567) chickpea genotypes were assessed in the field to examine heat-responsive traits, genetic variability, and QTL associated with heat tolerance (Paul 2018a, b). Four important QTLs were located on the CaLG05 region for pod filling, grain yield, seed number and pod set, with a combined phenotypic variation of up to 50% (Paul 2018a, b).

The QTLs described above, and discovered through marker-assisted breeding in diverse crop species, may help in transferring heat-resilient gene(s)/QTLs to well-bred cultivars. Further, fine mapping followed by cloning of representative QTL will be beneficial for breeders to initiate marker-assisted breeding for conferring heat tolerance in major crop plants. Studies related to the identification of marker genes associated with heat resilience have more scope these days and require better vision in this field. A comprehensive account of different QTLs associated with heat stress tolerance is in Table 1.

Heat shock proteins

Heat shock proteins (Hsps) were initially reported in plants under high-temperature stress and act as strong buffers in maintaining cellular stability under optimal and stressful conditions (Wang et al. 2015). It is well documented that they prevent protein misfolding during plant metabolism (Wang et al. 2004), and stabilize proteins and membranes during heat stress (Hüttner and Strasser 2012). Considering their molecular weight, HSPs are generally divided into six subfamilies viz., Hsp60, Hsp70 (DnaK family), Hsp90, Hsp100 (Clp), the small HSPs (sHsp) and the chaperonins (GroEL family) (Park and Seo 2015). Of these, the chaperonins and HSP70 family impart thermotolerance in plants (Jacob et al. 2017). Moreover, under stressed conditions, the lineages of Hsp90, Hsps70, and Hsp60 are recruited as stress chaperones that communicate with a diverse array of co-chaperone proteins, hence regulating their activity (Liberek et al. 2008). Genomic analysis validated the occurrence of 13 sHsps members, 7Hsp60 members, 18 Hsp70 members, seven Hsp90 members and eight Hsp100 in *Arabidopsis thaliana* (Zhang et al. 2015). The enhanced expression of HSPs has been observed in other crop plants (maize, wheat, rice, and legumes) during episodes of heat stress (Kumar et al. 2012). By modulating the genetic composition of HSPs, novel heat-tolerant varieties can be developed; for instance, enhanced expression of Hsp101 in *Arabidopsis* and rice conferred resilience to extreme temperatures (Katiyar-Agarwal et al. 2003). Another group of HSPs, characterized as small heat shock proteins, are a remarkably diverse and abundant category of proteins that can emulate their response immediately to counteract transient changes in the external environment (Sun et al. 2002). The significance of chloroplast sHsps was delineated in *Agrostis stolonifera* grass by introducing sHsp26.2 into susceptible variants to provide heat tolerance (Zhu et al. 2012). Further, *TaHsfA6f* (a transcriptional regulator) upregulated wheat TaHsp, TaGAAP, and TaRof1 (*Triticum aestivum*) genes, imparting thermotolerance during heat stress (Xue et al. 2013). Similarly, over-expression of OsHsp18.6 (a small heat shock protein in rice) reduced sterility under heat conditions without altering other agronomic traits (Wang et al. 2015). Differential expression of MsHsp23 in creeping bentgrass (*Agrostis stolonifera*) provided high thermotolerance against heat stress, possibly via enhanced chaperone activity and induction of enzyme

Table 1 QTLs for heat stress tolerance in plants

QTL	Trait	Chromosome	Plant cultivar	References
qHbs-1 qHbs-2	Heat-induced browning of seed coat	2 and 14	IT93K-503-1/CB46 (cowpea)	Pottoroff et al. (2014)
qF_v/F_m.cgb-5B	Chlorophyll fluorescence	91	Lumai14 (wheat)	i Azam et al. (2015)
qHTSF6.1	Flowering	6	Giza 178 (rice)	Ye et al. (2015)
qHTCo5 qHTCo3	Head quality	5 and 3	USVL138 (broccoli)	Branham et al. (2017)
qHSI:DYb qHSI:DYAb	Dry grain yield	3	Dent (maize)	Frey et al. (2016)
stg QTL	Stay-green	4B and 7D	Seri/Babax (wheat)	Pinto et al. (2016)
qPV11	Pollen viability	11	Nagcarlang (tomato)	Xu et al. (2017)
qHTSF4	Flowering	4	N22 (rice)	Lafarge et al. (2017)
qTDgh3-74	Canopy temperature depression	3	BTx642/RTx7000 (sorghum)	Awika et al. (2017)
ft QTL	Early flowering	9	CB27/IT82E − 18 (cowpea)	Hunyh et al. (2018)
qCHC.iiwbr2A	Chlorophyll content	2A	HD 2808/HUW510 (wheat)	Bhusal et al. (2017)

ascorbate peroxidase (Lee et al. 2015). A small heat shock protein (sHsp26) is highly abundant in maize leaves and reported to confer heat tolerance by interacting with different chloroplast proteins (Hu et al. 2015a, b). Similarly, transgenic tobacco plants developed through over-expression of the chloroplast heat shock protein (*LeHsp21*) from tomato (*Lycopersicon esculentum* cv PKM-1) exhibited better tolerance to both heat and oxidative stress (Zhang et al. 2016). Likewise, increased expression of *Brassica campestris* heat shock protein (BcHsp70) in tobacco provided endurance to heat stress by modulating various physiological parameters (Wang et al. 2016). A study by Wang et al. (2016) indicated that FaHsfA2c might act as a positive player in conferring improved thermotolerance in *Arabidopsis* and tall fescue, and could be potentially used as a novel gene for genetic and molecular breeding to produce heat-tolerant cool-season grass species. Individually, each member of the Hsps/chaperones has a particular role, but the coordinated function of different Hsp/chaperone networks emerges as the key principle of stress tolerance. However, elucidation of the role of Hsps/chaperones as regulatory and sensing molecules in signal transduction and transcription pathways in response to stress remains unclear; contemporary research in relation to functional aspects of HSPs/chaperones in stress tolerance is underway.

Thermotolerance-linked genes

Plants as sessile organisms regulate the expression of a myriad of genes in response to adverse environmental stimuli, especially heat waves (de Souza et al. 2012). The expression and characterization of these genes could assist in the identification of plant processes that are activated or repressed during adaptation and as a defense to heat stress (Frey et al. 2015). Diverse genes have been identified through transcriptomics, genomics, and proteomics analyses in various plant species, which are engaged in heat resilience mechanisms and essential for developing stable cultivars (Zhang et al. 2017a, b). Transcriptional profiling during the induction and recovery of a heat period has been undertaken in various crop plants, e.g., grapes, brassica, rice, tomato, maize and barley (Liu et al. 2012; Dong et al. 2015; Sarkar et al. 2014; Frank et al. 2009; Frey et al. 2015; Mangelsen et al. 2011). Lavania et al. (2015) summarized various transcriptomic studies related to heat-stress tolerance and concluded that plants remodel different signaling cascades and transcription networks linked to metabolic activities in a conserved manner in response to heat stress. Studies on various crops exposed to varied heat regimes are remarkably analogous in the heat-responsive genes (Lavania et al. 2015) and can be exploited to induce heat tolerance. For instance, transgenic *Arabidopsis* plants over-expressing the wheat heat-responsive ferritin gene (*TaFER*) had enhanced resilience to heat stress (Zang et al. 2017) and could be used in future breeding programs. Transgenic rice plants over-expressing *TaMBF1c* (*Multiprotein binding factor1c*) isolated from wheat exhibited high heat resilience in comparison to the control (Qin et al. 2015). Moreover, *TaMBF1c* over-expressers showed high transcript levels of two trehalose phosphate synthase genes and six HSPs, suggesting their crucial role in heat tolerance (Qin et al. 2015). Hu et al. (2015) revealed that *GCN5* (histone acetyltransferase) plays a critical role in imparting thermotolerance in *Arabidopsis*; over-expression of the wheat (*TaGCN5*) gene restored heat tolerance in *gcn5* mutants of *Arabidopsis,* suggesting *GCN5*-regulated thermotolerance is conserved between wheat and *Arabidopsis*. Recently, a heat-responsive *TaGASR1* gene was characterized from heat-tolerant cultivar TAM107 (Zhang et al. 2017); further analysis revealed that enhanced expression of *TaGASR1* in transgenic *Arabidopsis* imparted high tolerance to heat stress by decreasing ROS production. Transcriptional analysis of 20-day-old siliquae of *Brassica napus* identified various heat-responsive candidate genes such as ROF2, DREB2a, MBF1c and Hsa32 that were upregulated during heat stress to impart thermotolerance (Yu et al. 2014). Similarly, upregulation of a putative DPB3-1 (transcriptional regulator DNA polymerase II subunit B3-1) gene can positively regulate the dehydration-responsive element binding protein 2A (DREB2A) in *Arabidopsis thaliana* to further increase heat tolerance without growth retardation (Sato et al. 2016). In a recent study, 26 cultivars of tall fescue species grown in growth chambers (*Festuca* spp.) were exposed to heat stress (38/33 °C, day/night temperature) to identify candidate genes and their associated markers for heat tolerance (Xu et al. 2018). Their findings validated that transcript levels of novel genes regulating in carbohydrate metabolism (sucrose synthase), energy production (ATP synthase), photosynthesis (RuBisCO activase,), oxidative response (catalase), stress protection (HSP90) and growth regulation (Actin) are positively correlated with physiological traits for heat tolerance (Xu et al. 2018) and could be utilized to construct heat-tolerant germplasm through marker-assisted breeding. Significant progress has been made to enhance photosynthetic ability under heat stress by engineering genes related to photosynthesis, viz. chloroplastic Fe superoxide dismutase (FeSOD), chloroplastic glutamine synthetase (GS2), ω3fattyaciddesaturase (FAD7), sedoheptulose1, 7bisphosphatase (SBPase), transcription factors ABA-responsive 17 (ABR17), and phosphoenolpyruvate carboxylase (C_4-PEPC) (Ashraf and Harris 2013; Grover et al. 2013). Moreover, genes related to calcium or calmodulin-regulated signaling pathways, viz. CDPKs, annexin, CBPs, Ca^{2+} binding protein EF hand, CBL (calcineurin-B like proteins), and CIPK (CBL-interacting protein kinase) are also induced by heat, indicating the involvement of Ca^{2+}-mediated signal transduction in the heat-stress response (Wu et al. 2012).

The heat-tolerant germplasm can be explored further to identify possible DNA-linked markers associated with heat tolerance via marker-assisted breeding (Burke and Chen 2015). The application of DNA markers and the integration of modern genomic tools in breeding would help to meet future global food demands. The advent of next-generation sequencing approaches has simplified the deployment of these assays for exploring the rice genome.

Epigenetics of heat tolerance

Epigenetics is a term generally applied to histone-induced modifications in chromatin structure by histone variants, DNA methylation, RNA interference, and histone chaperones; however, these variations may not be epigenetic as they are highly stable via cell division (Lämke and Bäurle 2017). Immense progression in the field of epigenomics has refined our knowledge of epigenetic control of heat-stress responses in plants (Sahu et al. 2013). As outlined by various biologists (Li et al. 2017; Chen et al. 2016; Liu et al. 2015; Ohama et al. 2017), the contribution of chromatin modification, DNA methylation, and ncRNAs is evident in the regulation of heat-responsive gene(s) and their complex circuit providing acclimation to heat stress (Jha et al. 2017). Several epigenetically induced heat-responsive master genes have been unveiled in various crop species including cotton (Min et al. 2014), rice (Folsom et al. 2014), mustard (Gao et al. 2014) and *Arabidopsis* (Naydenov et al. 2015). In plants, DNA methylation is mostly induced by DOMAINS REARRANGED METHYLTRANSFERASE 2 (DRM2) and is regulated by three major pathways, viz. CG methylation via METHYLTRANSFERASE 1 (MET1), CHG methylation via CHROMOMETHYLASE 3 (CMT3), and DECREASE IN DNA METHYLATION 1 (DDM1) (Liu et al. 2015). Heat stress influences DNA methylation differently in different species; for instance, in *Arabidopsis*, heat waves enhanced global methylation and the HRF (homologous recombination frequency) level (Boyko et al. 2010). Likewise, high methylation has been observed in oak (*Quercus suber* L.) plants raised at high temperature, i.e., 55 °C (Correia et al. 2013). At high temperature, a significant decrease in the expression of DNA methyltransferases (DRM1 and DRM3) and S-ADENOSYL-L-HOMOCYSTEINE HYDROLASE1 (SAHH1) was observed in cotton (*Gossypium hirsutum*) anthers, causing genome-wide methylation during tetrad formation and the tapetal degradation phase (Min et al. 2014). Naydenov et al. (2015) showed that the enhanced activity of DRM2 and NUCLEAR RNA POLYMERASE D 1(NRPD1) in *Arabidopsis* plants facing heat stress might facilitate genome methylation (Naydenov et al. 2015). High-temperature stress can affect global DNA methylation and methyltransferase expression at specific pollen developmental stages (Solis et al. 2012) or regulate methylation of genes encoding relevant heat shock proteins (McCue et al. 2014). Weng et al. (2014) unraveled the involvement of a histone chaperone (ANTI-SILENCING FUNCTION 1 (ASF1)

AtASF1A/B) in heat-stress responses in *Arabidopsis*, suggesting that *AtASF1A/B* transcriptionally activates some *HSF* and *HSP* genes via H3K56ac acetylation and nucleosome modifications. Apart from this, heat stress is expected to modulate the chromatin structure of pollen by increasing the frequency of chromatin modifications (Pecinka and Mittelsten Scheid 2012). These findings validated that epigenetic regulation of gene expression occurs in response to adverse environmental changes; however, understanding heat responses at the epigenetic level demands further knowledge and vision for developing heat-tolerant crops.

Genetic engineering for heat tolerance

Engineering crops involving transgenic approaches is a relatively quick way of developing heat tolerance and has tremendous potential to contribute to the sustainability of food security (Teixeira et al. 2013). Significant research in the identification of genes linked with heat tolerance and their manipulation via various transgenic methods has been undertaken (Bohnert et al. 2006). A transgenic tobacco produced by altering the composition of chloroplast membranes had improved photosynthetic efficiency under heat stress (Murakami et al. 2000). In tobacco, increased tolerance against heat stress has been observed by introgressing the *Dnak1* (chaperone protein) gene (Ono et al. 2001). Similarly, introduction of the BADH (betaine-aldehyde dehydrogenase) gene in transgenic plants produced more glycine betaine, thus conferring enhanced resilience to heat stress (Yang et al. 2005). Genetic alteration for over-expression of SOD (superoxide dismutase, an antioxidant) has been beneficial under heat-stress conditions (Sairam et al. 2000). In rice, the constitutive high expression of manganese superoxide dismutase (MSD1) helps in ROS-detoxification, increases chaperone activity, and improves grain quality (Shiraya et al. 2015). Likewise, enhanced expression of broccoli catalase (BoCAT) provided heat resilience in transgenic *Arabidopsis* by scavenging H_2O_2 (Chiang et al. 2014). Over-expression of HSPs through genetic engineering has been particularly beneficial for transgenic plants. Thus, transgenic tobacco for thermotolerance was produced by introducing *MT-sHSP* from tomato (Sanmiya et al. 2004). A stress protein from *Medicago sativa* (MsHsp23), when introduced in creeping bentgrass, resulted in thermotolerance, and transgenic plants had less wilting of leaves and high ascorbate peroxidase (APX) activities (Lee et al. 2015). Wang et al. (2016) showed that *BcHSP70* cDNA from young seedlings of *Brassica campestris* enhanced heat tolerance in transgenic tobacco lines, which will be beneficial for culturing novel heat-resistant *Brassica campestris* varieties via molecular breeding.

Few transcription factors have been tested using transgenic means to introduce heat tolerance. Thus, over-expression of *TaNAC2L* (*Triticum aestivum*) in wheat and transgenic *Arabidopsis* during heat stress increased thermotolerance without altering phenotype expression relative to the wild-type, possibly by up-regulating the heat-responsive genes (Guo et al. 2015). Enhanced expression of *Arabidopsis* thaliana dehydration-responsive element binding protein 2A (DREB2A) and DPB3-1 conferred heat resilience in rice without affecting growth (Sato et al. 2016). A study by Wang et al. (2017a, b) revealed that the FaHsfA2c gene from tall fescue served as an absolute regulator of thermotolerance in *Arabidopsis* and tall fescue, and could be used as a master gene for breeding and genetic manipulation to yield heat-resilient cool-season grass varieties. Similar thermotolerance could be achieved in perennial grasses using expansins, as studied by Xu et al. (2014) in tobacco plants. The PpEXP1 (expansin) over-expresser tobacco plants had low membrane lipid per-oxidation and electrolyte leakage, less hydrogen peroxide, more chlorophyll content and antioxidant activity than wild relatives (Xu et al. 2014). Likewise, DREB2A and HSF2 genes can produce heat-resilient transgenic plants (Ohama et al. 2017). Various reports have highlighted the enhanced production of osmolytes, cell detoxification enzymes, and HSPs in heat-tolerant transgenic plants raised through different routes (Grover et al. 2013), as given in Table 2.

As heat tolerance is a multigenic trait governed by composite genotype-environment interactions, it is likely that over-expression of individual genes is not sufficient to confer heat tolerance through transgenic approaches (Lavania et al. 2015). Hence, it is crucial to decode the heat-stress responsive ‘candidate’ genes as putative thermosensors. Despite extensive experimentation, expansion of laboratory outcomes to the field has not yet been fulfilled.

Conclusions and future outlook

Despite the immediate need to improve plant thermotolerance in the face of climate change, little progress has been made in raising heat-tolerant cultivars with improved performance. Engineering of novel varieties through molecular breeding is time-consuming and tedious (Driedonks et al. 2016); hence, identification of genetic variation for heat tolerance is essential. For this purpose, different physiological and reproductive traits could be explored and characterized effectively for introgression in a breeding program. As heat-stress responses are generally governed by QTL/thermotolerance genes, concerted efforts should be

Table 2 Transgenic developed for heat tolerance through various routes

Gene	Source plant	Target plant	Promotor	Functional aspects	References
By using proteins involved in osmolyte synthesis					
1. *BADH* (*betaine*				*aldehydedehydrogenase*)	*Spinacia oleracea*
Nicotiana tabacum	35S-CaMV	Transgenic plants showed high		thermotolerance due to PSII repairment	Yang et al. (2007)
2. *BADH* (*betaine aldehyde dehydrogenase*)	*Spinacia oleracea*	*Lycopersicon esculentum*	35S-CaMV	Transgenic plants over-accumulating glycine betaine showed high antioxidant activity and heat tolerance	Li et al. (2014a, b)
By using proteins involved in ROS scavenging system					
1. *CuZnSOD* (*copper zinc superoxide dismutase*)	*Solanum tuberosum*	*Solanum tuberosum*	SWPA2 (oxidative stress inducible)	CuZnSOD is involved in ROS scavenging and transgenic plants were more tolerant	Kim et al. (2010)
2. *BcAPX1* (*ascorbate peroxidase*)	*Brassica campestris*	*Arabidopsis thaliana*	Ubi (Ubiquitin)	High antioxidant activity chlorophyll content, and germination rate in transgenic plant	Chiang et al. (2015)
3. *SOD* (*superoxide dismutase*) (*MSD1*)	*Oryza sativa*	*Oryza sativa*	PUbi1 (ubiquitin)	Grain quality of rice plants with over-expression of MSD1 was better than wild plants	Shiraya et al. (2015)
By using proteins associated with lipid metabolism and membranes					
1. *fad8* (*desaturase*)	*Brassica napus*	*Nicotiana tobacum*	35S-CaMV	Enhanced expression of FAD3 resulted in high heat sensitivity	Zhang et al. (2005)
2. *fad7* (*ω-3-fatty acid desaturase*)	*Arabidopsis thaliana*	*Oryza sativa*	Ubi1 (Ubiquitin)	Transgenics showed high photosynthetic efficiency chlorophyll content under heat stress	Sohn and Bach (2007)
3. *GPAT* (*glycerol-3 phosphate acyltransferase*)	*Capsicum annum*	*Nicotiana tobacum*	Ubi1 (Ubiquitin)	Over-expressors have high membrane thermostability under heat stress	Yan et al. (2008)
By using heat shock proteins (HSPs) and heat shock factors (HSFs)					
1. *BcHsp70* (*heat shock Protein*)	*Brassica compestris*	*Nicotiana tobacum*	35S-CaMV	Increased accumulation of osmolytes and decreased MDA levels in transgenics under heat stress	Wang et al. (2016)
2. *CsHsp17.7, CsHsp18.1, CsHsp21.8* (*small heat shock Proteins*)	*Camellia sinensis*	*Arabidopsis thaliana*	35S-CaMV	Transformants were highly tolerant to heat stress and had high proline content, low ion leakage and high level of stress-related genes	Wang et al. (2017)
3. *MsHsp23* (*heat-shock protein*)	*Medicago sativa*	*Medicago sativa*	35S-CaMV	Enhanced tolerance to heat and oxidative stress	Lee et al. (2017)
4. *LiHsfA2b* (*heat shock Factor 2b*)	*Lilium lingiflorum*	*Arabidopsis thaliana*	35S-CaMV	Increased thermotolerance via upregulation of chaperone machinery	Xin et al. (2017)
5. *ZmHsf04* (*heat shock factor*)	*Zea mays*	*Arabidopsis thaliana*	35S-CaMV	ZmHsf04 is a transcriptional activator, that enhances thermotolerance by up-regulating the expression of HSP genes	Jiang et al. (2018)
Others					
1. *TaFER-5B* (*ferritin gene*)	*Triticum aestivum*	*Arabidopsis thaliana*	Ubi (Ubiquitin)	Enhanced tolerance to heat stress via ROS scavenging	Zang et al. (2017)
2. *Hsc70* (*heat-shock cognate 70*)	*Potato*	*Nicotiana benthamiana*	35S-CaMV	Upregulation of Hsc70 increases tolerance to heat stress	Trapero-Mozos et al. (2018)
3. *MsDLSP* (*DnaJ-like Protein*)	*Medicago sativa*	*Nicotiana tobacum*	35S-CaMV	Transgenics showed better chlorophyll content and low MDA accumulation under heat stress	Lee et al. (2018)
4. *TaFBA1* (*F-box protein*)	*Triticum aestivum*	*Nicotiana tobacum*	Ubi (Ubiquitin)	TaFBA1 improved antioxidant activity by interacting with other stress-related proteins, that enhances heat tolerance in transgenics	Li et al. (2018)
5. HTR1 (*high temperature resistance 1*)	*Oryza sativa*	*Arabidopsis and Festuca arundinacea*		Transformants with HTR1 exhibited high tolerance to heat stress	Lin et al. (2018)

made to understand the tolerance mechanisms at molecular and physiological levels. Discovery of putative genes and molecular markers by assessing available generic resources as well as cloning and mapping should be emphasized. Elementary research has offered information on molecular aspects of the plant heat-stress response, which will accelerate gene cloning after identification and localization of QTLs. The identified thermotolerance genes and QTL can be introgressed to generate transgenic plants via genetic engineering to impart high levels of thermotolerance. Moreover, the gathered information can be applied to generate leads for the genetic modification of heat tolerance traits. This review has highlighted the recent attempts to improve heat-stress tolerance in plants via conventional and molecular breeding programs employing various QTL, thermotolerance genes, and HSPs, which would facilitate further studies in this aspect.

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References

Abro, S., Rajput, M. T., Khan, M. A., Sial, M. A., & Tahir, S. S. (2015). Screening of cotton (*Gossypium hirsutum* L.) genotypes for heat tolerance. *Pakistan Journal of Botany, 47*(6), 2085–2091.

Ahmad, P., & Prasad, M. N. V. (2011). Environmental adaptations and stress tolerance of plants in the era of climate change. *Springer Science & Business Media*. pp. (1–19).

Ahlawat, S., Chhabra, A. K., Behl, R. K., & Bisht, S. S. (2008). Genotypic divergence analysis for stay green characters in wheat (*Triticum aestivum* L. em. Thell). *The South Pacific Journal of Natural and Applied Sciences, 26*(1), 73–81.

Almeida, G. D., Nair, S., Borém, A., Cairns, J., Trachsel, S., Ribaut, J.-M., et al. (2014). Molecular mapping across three populations reveals a QTL hotspot region on chromosome 3 for secondary traits associated with drought tolerance in tropical maize. *Molecular Breeding, 34*(2), 701–715.

Amani, I., Fischer, R. A., & Reynolds, M. P. (1996). Canopy temperature depression association with yield of irrigated spring wheat cultivars in a hot climate. *Journal of Agronomy and Crop Science, 176*(2), 119–129.

Arbona, V., Manzi, M., de Ollas, C., & Gómez-Cadenas, A. (2013). Metabolomics as a tool to investigate abiotic stress tolerance in plants. *International Journal of Molecular Sciences, 14*(3), 4885–4911.

Ashraf, M., & Harris, P. J. C. (2013). Photosynthesis under stressful environments: an overview. *Photosynthetica, 51*(2), 163–190.

Asthir, B. (2015). Protective mechanisms of heat tolerance in crop plants. *Journal of Plant Interactions, 10*(1), 202–210.

Awasthi, R., Kaushal, N., Vadez, V., Turner, N. C., Berger, J., Siddique, K. H. M., et al. (2014). Individual and combined effects of transient drought and heat stress on carbon assimilation and seed filling in chickpea. *Functional Plant Biology, 41*(11), 1148–1167.

Awika, H. O., Hays, D. B., Mullet, J. E., Rooney, W. L., & Weers, B. D. (2017). QTL mapping and loci dissection for leaf epicuticular wax load and canopy temperature depression and their association with QTL for staygreen in Sorghum bicolor under stress. *Euphytica, 213*(9), 207.

Bac-Molenaar, J. A., Fradin, E. F., Becker, F. F. M., Rienstra, J. A., van der Schoot, J., Vreugdenhil, D., et al. (2015). Genome-wide association mapping of fertility reduction upon heat stress reveals developmental stage-specific QTLs in *Arabidopsis thaliana*. *The Plant, Cell,* tpc-15.

Bala, P., & Sikder, S. (2017). Heat stress indices, correlation and regression analysis of wheat genotypes for yield potential. *International Journal of Current Agricultural Sciences, 7*(4), 190–194.

Baliuag, N. N. A., Redona, E. D., Hernandez, J. E., Cruz, P. C. S., & Ye, C. (2015). Genetic analysis for heat tolerance and early morning flowering traits at flowering stage in rice (*Oryza sativa* L.). *Philippine Journal of Crop Science (PJCS), 40*(3), 62–72.

Balota, M., Payne, W. A., Evett, S. R., & Peters, T. R. (2008). Morphological and physiological traits associated with canopy temperature depression in three closely related wheat lines. *Crop Science, 48*(5), 1897–1910.

Barnabás, B., Jäger, K., & Fehér, A. (2008). The effect of drought and heat stress on reproductive processes in cereals. *Plant, Cell and Environment, 31*(1), 11–38.

Benites, F. R. G., & Pinto, C. A. B. P. (2011). Genetic gains for heat tolerance in potato in three cycles of recurrent selection. *Crop Breeding and Applied Biotechnology, 11*(2), 133–140.

Bhusal, N., Sarial, A. K., Sharma, P., & Sareen, S. (2017). Mapping QTLs for grain yield components in wheat under heat stress. *PLoS ONE, 12*(12), e0189594.

Bishop, J., Potts, S. G., & Jones, H. E. (2016). Susceptibility of faba bean (*Vicia faba* L.) to heat stress during floral development and anthesis. *Journal of Agronomy and Crop Science, 202*(6), 508–517.

Bita, C., & Gerats, T. (2013). Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. *Frontiers in Plant Science, 4,* 273.

Blum, A., Klueva, N., & Nguyen, H. T. (2001). Wheat cellular thermotolerance is related to yield under heat stress. *Euphytica, 117*(2), 117–123.

Bohnert, H. J., Gong, Q., Li, P., & Ma, S. (2006). Unraveling abiotic stress tolerance mechanisms–getting genomics going. *Current Opinion in Plant Biology, 9*(2), 180–188.

Boote, K. J., Allen, L. H., Prasad, P. V. V., Baker, J. T., Gesch, R. W., Snyder, A. X., Pan, D., & Thomas, J. M. G. (2005). Elevated Temperature and CO_2 Impacts on Pollination, Reproductive Growth, and Yield of Several Globally Important Crops. *Journal of Agricultural Meteorology 60*(5), 469–474.

Borrell, A. K., Oosterom, E. J., Mullet, J. E., George-Jaeggli, B., Jordan, D. R., Klein, P. E., et al. (2014). Stay-green alleles individually enhance grain yield in sorghum under drought by modifying canopy development and water uptake patterns. *New Phytologist, 203*(3), 817–830.

Boyko, A., Blevins, T., Yao, Y., Golubov, A., Bilichak, A., Ilnytskyy, Y., et al. (2010). Transgenerational adaptation of *Arabidopsis* to stress requires DNA methylation and the function of Dicer-like proteins. *PLoS ONE, 5*(3), e9514.

Branham, S. E., Stansell, Z. J., Couillard, D. M., & Farnham, M. W. (2017). Quantitative trait loci mapping of heat tolerance in broccoli (*Brassica oleracea* var. italica) using genotyping-by-sequencing. *Theoretical and Applied Genetics, 130*(3), 529–538.

Brestic, M., Zivcak, M., Olsovska, K., & Repkova, J. (2013). Involvement of chlorophyll a fluorescence analyses for identification of sensitiveness of the photosynthetic apparatus to high temperature in selected wheat genotypes. *Photosynthesis* *research for food, fuel and the future* (pp. 510–513). Berlin: Springer.

Burke, J. J., & Chen, J. (2015). Enhancement of reproductive heat tolerance in plants. *PLoS ONE, 10*(4), e0122933.

Cabello, J. V., Lodeyro, A. F., & Zurbriggen, M. D. (2014). Novel perspectives for the engineering of abiotic stress tolerance in plants. *Current Opinion in Biotechnology, 26,* 62–70.

Cairns, J. E., Crossa, J., Zaidi, P. H., Grudloyma, P., Sanchez, C., Araus, J. L., et al. (2013). Identification of drought, heat, and combined drought and heat tolerant donors in maize. *Crop Science, 53*(4), 1335–1346.

Camejo, D., Rodríguez, P., Morales, M. A., Dell'Amico, J. M., Torrecillas, A., & Alarcón, J. J. (2005). High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. *Journal of Plant Physiology, 162*(3), 281–289.

Chandra, K., Prasad, R., Thakur, P., Madhukar, K., & Prasad, L. C. (2017). Heat tolerance in wheat-a key strategy to combat climate change through molecular markers. *International Journal of Current Microbiology and Applied Sciences, 6*(3), 662–675.

Chauhan, S., Srivalli, S., Nautiyal, A. R., & Khanna-Chopra, R. (2009). Wheat cultivars differing in heat tolerance show a differential response to monocarpic senescence under high-temperature stress and the involvement of serine proteases. *Photosynthetica, 47*(4), 536–547.

Chebrolu, K. K., Fritschi, F. B., Ye, S., Krishnan, H. B., Smith, J. R., & Gillman, J. D. (2016). Impact of heat stress during seed development on soybean seed metabolome. *Metabolomics, 12*(2), 28.

Chen, L.-S., Li, P., & Cheng, L. (2009). Comparison of thermotolerance of sun-exposed peel and shaded peel of 'Fuji'apple. *Environmental and Experimental Botany, 66*(1), 110–116.

Chen, Y., Müller, F., Rieu, I., & Winter, P. (2016). Epigenetic events in plant male germ cell heat stress responses. *Plant Reproduction, 29*(1–2), 21–29.

Chiang, C.-M., Chen, S.-P., Chen, L.-F. O., Chiang, M.-C., Chien, H.-L., & Lin, K.-H. (2014). Expression of the broccoli catalase gene (BoCAT) enhances heat tolerance in transgenic *Arabidopsis*. *Journal of Plant Biochemistry and Biotechnology, 23*(3), 266–277.

Chiang, C. M., Chien, H. L., Chen, L. F. O., Hsiung, T. C., Chiang, M. C., Chen, S. P., et al. (2015). Overexpression of the genes coding ascorbate peroxidase from *Brassica campestris* enhances heat tolerance in transgenic *Arabidopsis thaliana*. *Biologia Plantarum, 59*(2), 305–315.

Condon, A. G., Reynolds, M. P., Rebetzke, G. J., Van Ginkel, M., Richards, R. A., & Farquhar, G. D. (2007). *Using stomatal aperture-related traits to select for high yield potential in bread wheat. Wheat production in stressed environments* (pp. 617–624). Berlin: Springer.

Cornish, K., Radin, J. W., Turcotte, E. L., Lu, Z., & Zeiger, E. (1991). Enhanced photosynthesis and stomatal conductance of Pima cotton (*Gossypium barbadense* L.) bred for increased yield. *Plant Physiology, 97*(2), 484–489.

Correia, B., Valledor, L., Meijón, M., Rodriguez, J. L., Dias, M. C., Santos, C., et al. (2013). Is the interplay between epigenetic markers related to the acclimation of cork oak plants to high temperatures? *PLoS ONE, 8*(1), e53543.

Cottee, N. S., Tan, D. K. Y., Bange, M. P., Cothren, J. T., & Campbell, L. C. (2010). Multi-level determination of heat tolerance in cotton (*Gossypium hirsutum* L.) under field conditions. *Crop Science, 50*(6), 2553–2564.

Das, G., & Rao, G. J. N. (2015). Molecular marker assisted gene stacking for biotic and abiotic stress resistance genes in an elite rice cultivar. *Frontiers in plant science, 6,* 698.

Das, S., Krishnan, P., Nayak, M., & Ramakrishnan, B. (2014). High temperature stress effects on pollens of rice (*Oryza sativa* L.) genotypes. *Environmental and Experimental Botany, 101,* 36–46.

de Luche, H. S., da Silva, J. A. G., da Maia, L. C., & de Oliveira, A. C. (2015). Stay-green: A potentiality in plant breeding. *Ciência Rural, 45*(10), 1755–1760.

de Souza, M. A., Pimentel, A. J. B., & Ribeiro, G. (2012). *Breeding for heat-stress tolerance. Plant breeding for abiotic stress tolerance* (pp. 137–156). Berlin: Springer.

Debnath, S., Gazal, A., Yadava, P., & Singh, I. (2016). Identification of contrasting genotypes under heat stress in maize (*Zea mays* L.). *Maize Journal, 5*(1–2), 14–24.

Demİrel, U., Çopur, O., & Gür, A. (2016). Early-stage screening for heat tolerance in cotton. *Plant Breeding, 135*(1), 80–89.

Devasirvatham, V., Gaur, P. M., Mallikarjuna, N., Raju, T. N., Trethowan, R. M., & Tan, D. K. Y. (2013). Reproductive biology of chickpea response to heat stress in the field is associated with the performance in controlled environments. *Field Crops Research, 142,* 9–19.

Devasirvatham, V., Gaur, P. M., Mallikarjuna, N., Tokachichu, R. N., Trethowan, R. M., & Tan, D. K. Y. (2012). Effect of high temperature on the reproductive development of chickpea genotypes under controlled environments. *Functional Plant Biology, 39*(12), 1009–1018.

Devasirvatham, V., Tan, D. K. Y., & Trethowan, R. M. (2016). *Breeding strategies for enhanced plant tolerance to heat stress. Advances in plant breeding strategies: Agronomic, abiotic and biotic stress traits* (pp. 447–469). Berlin: Springer.

Dias, M. C., & Brüggemann, W. (2010). Limitations of photosynthesis in Phaseolus vulgaris under drought stress: Gas exchange, chlorophyll fluorescence and Calvin cycle enzymes. *Photosynthetica, 48*(1), 96–102.

Djanaguiraman, M., Prasad, P. V. V., Boyle, D. L., & Schapaugh, W. T. (2011). High-temperature stress and soybean leaves: Leaf anatomy and photosynthesis. *Crop Science, 51*(5), 2125–2131.

Dong, X., Yi, H., Lee, J., Nou, I.-S., Han, C.-T., & Hur, Y. (2015). Global gene-expression analysis to identify differentially expressed genes critical for the heat stress response in *Brassica rapa*. *PLoS ONE, 10*(6), e0130451.

Driedonks, N., Rieu, I., & Vriezen, W. H. (2016). Breeding for plant heat tolerance at vegetative and reproductive stages. *Plant Reproduction, 29*(1–2), 67–79.

Ehlers, R.-U., Oestergaard, J., Hollmer, S., Wingen, M., & Strauch, O. (2005). Genetic selection for heat tolerance and low temperature activity of the entomopathogenic nematode–bacterium complex Heterorhabditis bacteriophora–*Photorhabdus luminescens*. *BioControl, 50*(5), 699–716.

Erice, G., Irigoyen, J. J., Pérez, P., Martínez-Carrasco, R., & Sánchez-Díaz, M. (2006). Effect of elevated CO_2, temperature and drought on dry matter partitioning and photosynthesis before and after cutting of nodulated alfalfa. *Plant Science, 170*(6), 1059–1067.

Fahad, S., Bajwa, A. A., Nazir, U., Anjum, S. A., Farooq, A., Zohaib, A., et al. (2017). Crop production under drought and heat stress: Plant responses and management options. *Frontiers in Plant Science, 8,* 1147.

Farnham, M. W., & Bjorkman, T. (2011). Breeding vegetables adapted to high temperatures: a case study with broccoli. *Hort Science, 46*(8), 1093–1097.

Feng, B., Liu, P., Li, G., Dong, S. T., Wang, F. H., Kong, L. A., et al. (2014). Effect of heat stress on the photosynthetic characteristics in flag leaves at the grain-filling stage of different heat-resistant winter wheat varieties. *Journal of Agronomy and Crop Science, 200*(2), 143–155.

Fischer, R. A., Rees, D., Sayre, K. D., Lu, Z.-M., Condon, A. G., & Saavedra, A. L. (1998). Wheat yield progress associated with higher stomatal conductance and photosynthetic rate, and cooler canopies. *Crop Science, 38*(6), 1467–1475.

Folsom, J. J., Begcy, K., Hao, X., Wang, D., & Walia, H. (2014). Rice FIE1 regulates seed size under heat stress by controlling early endosperm development. *Plant Physiology, 165,* 238.

Frank, G., Pressman, E., Ophir, R., Althan, L., Shaked, R., Freedman, M., et al. (2009). Transcriptional profiling of maturing tomato (*Solanum lycopersicum* L.) microspores reveals the involvement of heat shock proteins, ROS scavengers, hormones, and sugars in the heat stress response. *Journal of Experimental Botany, 60*(13), 3891–3908.

Frey, F. P., Presterl, T., Lecoq, P., Orlik, A., & Stich, B. (2016). First steps to understand heat tolerance of temperate maize at adult stage: Identification of QTL across multiple environments with connected segregating populations. *Theoretical and Applied Genetics, 129,* 945–961.

Frey, F. P., Urbany, C., Hüttel, B., Reinhardt, R., & Stich, B. (2015). Genome-wide expression profiling and phenotypic evaluation of European maize inbreds at seedling stage in response to heat stress. *BMC Genomics, 16,* 123.

Frova, C., & Sari-Gorla, M. (1994). Quantitative trait loci (QTLs) for pollen thermotolerance detected in maize. *Molecular and General Genetics MGG, 245,* 424–430.

Fu, J.-D., Yan, Y.-F., Kim, M. Y., Lee, S.-H., & Lee, B.-W. (2011). Population-specific quantitative trait loci mapping for functional stay-green trait in rice (*Oryza sativa* L.). *Genome, 54,* 235–243.

Gao, G., Li, J., Li, H., Li, F., Xu, K., Yan, G., et al. (2014). Comparison of the heat stress induced variations in DNA methylation between heat-tolerant and heat-sensitive rapeseed seedlings. *Breeding Science, 64,* 125–133.

Gaur, P. M., Jukanti, A. K., Samineni, S., Chaturvedi, S. K., Basu, P. S., Babbar, A., et al. (2013). Climate change and heat stress tolerance in chickpea. *Climate Change and Plant Abiotic Stress, Tolerance,* 837–856.

Gaur, P. M., Jukanti, A. K., & Varshney, R. K. (2012). Impact of genomic technologies on chickpea breeding strategies. *Agronomy, 2*(3), 199–221.

Gautam, A., Agrawal, D., SaiPrasad, S. V., & Jajoo, A. (2014). A quick method to screen high and low yielding wheat cultivars exposed to high temperature. *Physiology and Molecular Biology of Plants, 20*(4), 533–537.

Gororo, N. N., Eagles, H. A., Eastwood, R. F., Nicolas, M. E., & Flood, R. G. (2002). Use of *Triticum tauschii* to improve yield of wheat in low-yielding environments. *Euphytica, 123*(2), 241–254.

Gottardini, E., Cristofori, A., Cristofolini, F., Nali, C., Pellegrini, E., Bussotti, F., et al. (2014). Chlorophyll-related indicators are linked to visible ozone symptoms: evidence from a field study on native *Viburnum lantana* L. plants in northern Italy. *Ecological Indicators, 39,* 65–74.

Gous, P. W., Hickey, L., Christopher, J. T., Franckowiak, J., & Fox, G. P. (2016). Discovery of QTL for stay-green and heat-stress in barley (*Hordeum vulgare*) grown under simulated abiotic stress conditions. *Euphytica, 207*(2), 305–317.

Greer, D. H., & Weedon, M. M. (2012). Modelling photosynthetic responses to temperature of grapevine (*Vitis vinifera* cv. Semillon) leaves on vines grown in a hot climate. *Plant, Cell and Environment, 35*(6), 1050–1064.

Grilli, G. V. G., Braz, L. T., & Lemos, E. G. M. (2007). QTL identification for tolerance to fruit set in tomato by fAFLP markers. *Crop Breeding and Applied, Biotechnology,* 234–241.

Grover, A., Mittal, D., Negi, M., & Lavania, D. (2013). Generating high temperature tolerant transgenic plants: Achievements and challenges. *Plant Science, 205,* 38–47.

Guanter, L., Zhang, Y., Jung, M., Joiner, J., Voigt, M., Berry, J. A., et al. (2014). Global and time-resolved monitoring of crop photosynthesis with chlorophyll fluorescence. In *Proceedings of the national academy of sciences* (p. 201320008).

Guo, W., Zhang, J., Zhang, N., Xin, M., Peng, H., Hu, Z., et al. (2015). The wheat NAC transcription factor TaNAC2L is regulated at the transcriptional and post-translational levels and promotes heat stress tolerance in transgenic *Arabidopsis*. *PLoS ONE, 10*(8), e0135667.

Gupta, N. K., Agarwal, S., Agarwal, V. P., Nathawat, N. S., Gupta, S., & Singh, G. (2013). Effect of short-term heat stress on growth, physiology and antioxidative defence system in wheat seedlings. *Acta Physiologiae Plantarum, 35*(6), 1837–1842.

Guy, C., Kaplan, F., Kopka, J., Selbig, J., & Hincha, D. K. (2008). Metabolomics of temperature stress. *Physiologia Plantarum, 132*(2), 220–235.

Han, F., Chen, H., Li, X.-J., Yang, M.-F., Liu, G.-S., & Shen, S.-H. (2009). A comparative proteomic analysis of rice seedlings under various high-temperature stresses. *Biochimica et Biophysica Acta (BBA)-Proteins and Proteomics, 1794*(11), 1625–1634.

Harsant, J., Pavlovic, L., Chiu, G., Sultmanis, S., & Sage, T. L. (2013). High temperature stress and its effect on pollen development and morphological components of harvest index in the C3 model grass *Brachypodium distachyon*. *Journal of Experimental Botany, 64*(10), 2971–2983.

Hatfield, J. L., & Prueger, J. H. (2015). Temperature extremes: Effect on plant growth and development. *Weather and Climate Extremes, 10,* 4–10.

Hemantaranjan, A., Bhanu, A. N., Singh, M. N., Yadav, D. K., Patel, P. K., Singh, R., et al. (2014). Heat stress responses and thermotolerance. *Advances in Plants and Agricultural Research, 1*(12), 10–15406.

Hofmann, G. E., & Todgham, A. E. (2010). Living in the now: physiological mechanisms to tolerate a rapidly changing environment. *Annual Review of Physiology, 72,* 127–145.

Hu, Z., Song, N., Zheng, M., Liu, X., Liu, Z., Xing, J., et al. (2015a). Histone acetyltransferase GCN 5 is essential for heat stress-responsive gene activation and thermotolerance in Arabidopsis. *The Plant Journal, 84*(6), 1178–1191.

Hu, X., Yang, Y., Gong, F., Zhang, D., Zhang, L., Wu, L., et al. (2015b). Protein sHSP26 improves chloroplast performance under heat stress by interacting with specific chloroplast proteins in maize (*Zea mays*). *Journal of Proteomics, 115,* 81–92.

Hüttner, S., & Strasser, R. (2012). Endoplasmic reticulum-associated degradation of glycoproteins in plants. *Frontiers in Plant Science, 3,* 67.

Huynh, B., Ehlers, J. D., Huang, B. E., Muñoz-Amatriaín, M., Lonardi, S., Santos, J. R. P., et al. (2018). A multi-parent advanced generation inter-cross (MAGIC) population for genetic analysis and improvement of cowpea (*Vigna unguiculata* L. Walp.). *The Plant Journal, 93*(6), 1129–1142.

i Azam, F., Chang, X., & Jing, R. (2015). Mapping QTL for chlorophyll fluorescence kinetics parameters at seedling stage as indicators of heat tolerance in wheat. *Euphytica, 202*(2), 245–258.

Ismail, A. M., & Hall, A. E. (1999). Reproductive-stage heat tolerance, leaf membrane thermostability and plant morphology in cowpea. *Crop Science, 39*(6), 1762–1768.

Jacob, P., Hirt, H., & Bendahmane, A. (2017). The heat-shock protein/chaperone network and multiple stress resistance. *Plant Biotechnology Journal, 15*(4), 405–414.

Jagadish, S. V. K., Cairns, J., Lafitte, R., Wheeler, T. R., Price, A. H., & Craufurd, P. Q. (2010). Genetic analysis of heat tolerance at anthesis in rice. *Crop Science, 50*(5), 1633–1641.

Jagadish, K. S. V., Craufurd, P., Shi, W., & Oane, R. (2014). A phenotypic marker for quantifying heat stress impact during microsporogenesis in rice (*Oryza sativa* L.). *Functional Plant Biology, 41*(1), 48–55.

Jagadish, S. V. K., Craufurd, P. Q., & Wheeler, T. R. (2008). Phenotyping parents of mapping populations of rice for heat tolerance during anthesis. *Crop Science, 48*(3), 1140–1146.

Jenks, M. A., & Hasegawa, P. M. (2008). *Plant abiotic stress*. London: Wiley.

Jha, U. C., Bohra, A., Parida, S. K., & Jha, R. (2017). Integrated "omics" approaches to sustain global productivity of major grain legumes under heat stress. *Plant Breeding, 136*(4), 437–459.

Jha, U. C., Bohra, A., & Singh, N. P. (2014). Heat stress in crop plants: Its nature, impacts and integrated breeding strategies to improve heat tolerance. *Plant Breeding, 133*(6), 679–701.

Jiang, H., Li, M., Liang, N., Yan, H., Wei, Y., Xu, X., et al. (2007). Molecular cloning and function analysis of the stay green gene in rice. *The Plant Journal, 52*(2), 197–209.

Jiang, Y., Zheng, Q., Chen, L., Liang, Y., & Wu, J. (2018). Ectopic overexpression of maize heat shock transcription factor gene ZmHsf04 confers increased thermo and salt-stress tolerance in transgenic *Arabidopsis*. *Acta Physiologiae Plantarum, 40*(1), 9.

Joshi, A. K., Kumari, M., Singh, V. P., Reddy, C. M., Kumar, S., Rane, J., et al. (2007). Stay green trait: variation, inheritance and its association with spot blotch resistance in spring wheat (*Triticum aestivum* L.). *Euphytica, 153*(1–2), 59–71.

Kalaji, H. M., Jajoo, A., Oukarroum, A., Brestic, M., Zivcak, M., Samborska, I. A., et al. (2016). Chlorophyll a fluorescence as a tool to monitor physiological status of plants under abiotic stress conditions. *Acta Physiologiae Plantarum, 38*(4), 102.

Karademir, E., Karademir, Ç., Ekinci, R., Başbağ, S., & Başal, H. (2012). Screening cotton varieties (*Gossypium hirsutum* L.) for heat tolerance under field conditions. *African Journal of Agricultural Research, 7* (47), 6335–6342.

Katiyar-Agarwal, S., Agarwal, M., & Grover, A. (2003). Heat-tolerant basmati rice engineered by over-expression of hsp101. *Plant Molecular Biology, 51*(5), 677–686.

Kato, K., Miura, H., & Sawada, S. (2000). Mapping QTLs controlling grain yield and its components on chromosome 5A of wheat. *Theoretical and Applied Genetics, 101*(7), 1114–1121.

Kaur, R., Bains, T. S., Bindumadhava, H., & Nayyar, H. (2015). Responses of mungbean (*Vigna radiata* L.) genotypes to heat stress: Effects on reproductive biology, leaf function and yield traits. *Scientia Horticulturae, 197,* 527–541.

Kaushal, N., Awasthi, R., Gupta, K., Gaur, P., Siddique, K. H. M., & Nayyar, H. (2013). Heat-stress-induced reproductive failures in chickpea (*Cicer arietinum*) are associated with impaired sucrose metabolism in leaves and anthers. *Functional Plant Biology, 40*(12), 1334–1349.

Kaushal, N., Bhandari, K., Siddique, K. H. M., & Nayyar, H. (2016). Food crops face rising temperatures: An overview of responses, adaptive mechanisms, and approaches to improve heat tolerance. *Cogent Food and Agriculture, 2*(1), 1134380.

Kim, M. D., Kim, Y., Kwon, S., Yun, D., Kwak, S., & Lee, H. (2010). Enhanced tolerance to methyl viologen-induced oxidative stress and high temperature in transgenic potato plants overexpressing the CuZnSOD, APX and NDPK2 genes. *Physiologia Plantarum, 140*(2), 153–162.

Kumar, R. R., Goswami, S., Sharma, S. K., Singh, K., Gadpayle, K. A., Kumar, N., et al. (2012). Protection against heat stress in wheat involves change in cell membrane stability, antioxidant enzymes, osmolyte, H_2O_2 and transcript of heat shock protein. *International Journal of Plant Physiology and Biochemistry, 4*(4), 83–91.

Kumar, U., Joshi, A. K., Kumari, M., Paliwal, R., Kumar, S., & Röder, M. S. (2010). Identification of QTLs for stay green trait in wheat (*Triticum aestivum* L.) in the 'Chirya 3' × 'Sonalika' population. *Euphytica, 174*(3), 437–445.

Kumar, S., Thakur, P., Kaushal, N., Malik, J. A., Gaur, P., & Nayyar, H. (2013). Effect of varying high temperatures during reproductive growth on reproductive function, oxidative stress and seed yield in chickpea genotypes differing in heat sensitivity. *Archives of Agronomy and Soil Science, 59*(6), 823–843.

Kumari, M., Pudake, R. N., Singh, V. P., & Joshi, A. K. (2013). Association of staygreen trait with canopy temperature depression and yield traits under terminal heat stress in wheat (*Triticum aestivum* L.). *Euphytica, 190*(1), 87–97.

Kumari, M., Singh, V. P., Tripathi, R., & Joshi, A. K. (2007). *Variation for staygreen trait and its association with canopy temperature depression and yield traits under terminal heat stress in wheat. Wheat production in stressed environments* (pp. 357–363). Berlin: Springer.

Kusaba, M., Tanaka, A., & Tanaka, R. (2013). Stay-green plants: What do they tell us about the molecular mechanism of leaf senescence. *Photosynthesis Research, 117*(1–3), 221–234.

Lafarge, T., Bueno, C., Frouin, J., Jacquin, L., Courtois, B., & Ahmadi, N. (2017). Genome-wide association analysis for heat tolerance at flowering detected a large set of genes involved in adaptation to thermal and other stresses. *PLoS ONE, 12*(2), e0171254.

Lämke, J., & Bäurle, I. (2017). Epigenetic and chromatin-based mechanisms in environmental stress adaptation and stress memory in plants. *Genome Biology, 18*(1), 124.

Lavania, D., Siddiqui, M. H., Al-Whaibi, M. H., Singh, A. K., Kumar, R., & Grover, A. (2015). Genetic approaches for breeding heat stress tolerance in faba bean (*Vicia faba* L.). *Acta Physiologiae Plantarum, 37*(1), 1737.

Lee, K. W., Cha, J. Y., Mun, J. Y., Lee, B. H., Kim, Y. G., & Lee, S. H. (2015). Heterologous expression of Mshsp23, a *Medicago Sativa* small heat shock protein, enhances heat stress tolerance in creeping bentgrass. *Journal of Animal and Plant Sciences, 25,* 884–891.

Lee, K.-W., Rahman, M., Choi, G. J., Kim, K.-Y., Ji, H. C., Hwang, T. Y., et al. (2017). Expression of small heat shock protein23 enhanced heat stress tolerance in transgenic alfaalfa plants. *JAPS: Journal of Animal and Plant Sciences, 27*(4), 1238.

Lee, K.-W., Rahman, M. A., Kim, K.-Y., Choi, G. J., Cha, J.-Y., Cheong, M. S., et al. (2018). Overexpression of the alfalfa DnaJ-like protein (MsDJLP) gene enhances tolerance to chilling and heat stresses in transgenic tobacco plants. *Turkish Journal of Biology, 42*(1), 12–22.

Li, S., Fu, Q., Chen, L., Huang, W., & Yu, D. (2011). *Arabidopsis thaliana* WRKY25, WRKY26, and WRKY33 coordinate induction of plant thermotolerance. *Planta, 233*(6), 1237–1252.

Li, H., Hu, T., Amombo, E., & Fu, J. (2017). Genome-wide identification of heat stress-responsive small RNAs in tall fescue (*Festuca arundinacea*) by high-throughput sequencing. *Journal of Plant Physiology, 213,* 157–165.

Li, X., Lawas, L. M. F., Malo, R., Glaubitz, U., Erban, A., Mauleon, R., et al. (2015). Metabolic and transcriptomic signatures of rice floral organs reveal sugar starvation as a factor in reproductive failure under heat and drought stress. *Plant, Cell and Environment, 38*(10), 2171–2192.

Li, M., Li, Z., Li, S., Guo, S., Meng, Q., Li, G., et al. (2014a). Genetic engineering of glycine betaine biosynthesis reduces heat-enhanced photoinhibition by enhancing antioxidative defense and alleviating lipid peroxidation in tomato. *Plant Molecular Biology Reporter, 32*(1), 42–51.

Li, S., Liu, J., Liu, Z., Li, X., Wu, F., & He, Y. (2014b). Heat-induced tas1 target1 mediates thermotolerance via heat stress transcription factor A1a–directed pathways in *Arabidopsis*. *The Plant, Cell,* tpc-114.

Li, Q., Wang, W., Wang, W., Zhang, G., Liu, Y., Wang, Y., et al. (2018). Wheat F-box protein gene TaFBA1 is involved in plant tolerance to heat stress. *Frontiers in Plant Science, 9,* 521.

Liao, J., Zhang, H., Shao, X., Zhong, P., & Huang, Y. (2011). Identification for heat tolerance in backcross recombinant lines and screening of backcross introgression lines with heat tolerance at milky stage in rice. *Rice Science, 18*(4), 279–286.

Liberek, K., Lewandowska, A., & Ziętkiewicz, S. (2008). Chaperones in control of protein disaggregation. *The EMBO Journal, 27*(2), 328–335.

Lin, H., Li, X., Gao, J., Junxiang, S., & Shi, M. (2018). New rice high temperature resistance gene and use in crop breeding resistance to high temperature thereof. Google Patents.

Liu, J., Feng, L., Li, J., & He, Z. (2015). Genetic and epigenetic control of plant heat responses. *Frontiers in Plant Science, 6,* 267.

Liu, G.-T., Wang, J.-F., Cramer, G., Dai, Z.-W., Duan, W., Xu, H.-G., et al. (2012). Transcriptomic analysis of grape (*Vitis vinifera* L.) leaves during and after recovery from heat stress. *BMC Plant Biology, 12*(1), 174.

Lucas, M. R., Ehlers, J. D., Huynh, B. L., Diop, N. N., Roberts, P. A., & Close, T. J. (2013). Markers for breeding heat-tolerant cowpea. *Molecular breeding, 31*(3), 529–536.

Maavimani, M., & Saraswathi, R. (2014). Anther characteristics and spikelet fertility in rice (*Oryza sativa* L.) under high temperature stress at anthesis. *Indian Journal of Genetics and Plant Breeding (The), 74*(3), 300–308.

Madan, P., Jagadish, S. V. K., Craufurd, P. Q., Fitzgerald, M., Lafarge, T., & Wheeler, T. R. (2012). Effect of elevated CO_2 and high temperature on seed-set and grain quality of rice. *Journal of Experimental Botany, 63*(10), 3843–3852.

Malaspina, P., Giordani, P., Faimali, M., Garaventa, F., & Modenesi, P. (2014). Assessing photosynthetic biomarkers in lichen transplants exposed under different light regimes. *Ecological Indicators, 43,* 126–131.

Mangelsen, E., Kilian, J., Harter, K., Jansson, C., Wanke, D., & Sundberg, E. (2011). Transcriptome analysis of high-temperature stress in developing barley caryopses: Early stress responses and effects on storage compound biosynthesis. *Molecular Plant, 4*(1), 97–115.

Marcum, K. B. (1998). Cell membrane thermostability and whole-plant heat tolerance of Kentucky bluegrass. *Crop Science, 38*(5), 1214–1218.

Martineau, J. R., Specht, J. E., Williams, J. H., & Sullivan, C. Y. (1979). Temperature tolerance in soybeans. I. Evaluation of a technique for assessing cellular membrane thermostability 1. *Crop Science, 19*(1), 75–78.

Mason, R. E., Mondal, S., Beecher, F. W., Pacheco, A., Jampala, B., Ibrahim, A. M. H., et al. (2010). QTL associated with heat susceptibility index in wheat (*Triticum aestivum* L.) under short-term reproductive stage heat stress. *Euphytica, 174*(3), 423–436.

Mason, R. E., & Singh, R. P. (2014). Considerations when deploying canopy temperature to select high yielding wheat breeding lines under drought and heat stress. *Agronomy, 4*(2), 191–201.

Mathur, S., Agrawal, D., & Jajoo, A. (2014). Photosynthesis: Response to high temperature stress. *Journal of Photochemistry and Photobiology B: Biology, 137,* 116–126.

Matsui, T., & Omasa, K. (2002). Rice (*Oryza sativa* L.) cultivars tolerant to high temperature at flowering: anther characteristics. *Annals of Botany, 89*(6), 683–687.

McCue, A. D., Panda, K., Nuthikattu, S., Choudury, S. G., Thomas, E. N., & Slotkin, R. K. (2014). ARGONAUTE 6 bridges transposable element mRNA-derived siRNAs to the establishment of DNA methylation. *The EMBO Journal, 34,* e201489499.

Mesihovic, A., Iannacone, R., Firon, N., & Fragkostefanakis, S. (2016). Heat stress regimes for the investigation of pollen thermotolerance in crop plants. *Plant Reproduction, 29*(1–2), 93–105.

Min, L., Li, Y., Hu, Q., Zhu, L., Gao, W., Wu, Y., et al. (2014). Sugar and auxin signaling pathways respond to high temperature stress during anther development as revealed by transcript profiling analysis in cotton. *Plant Physiology, 178,* 113.

Mittler, R. (2006). Abiotic stress, the field environment and stress combination. *Trends in Plant Science, 11*(1), 15–19.

Mittler, R., Finka, A., & Goloubinoff, P. (2012). How do plants feel the heat? *Trends in Biochemical Sciences, 37*(3), 118–125.

Morrison, M. J., & Stewart, D. W. (2002). Heat stress during flowering in summer *Brassica*. *Crop Science, 42*(3), 797–803.

Muchero, W., Roberts, P. A., Diop, N. N., Drabo, I., Cisse, N., Close, T. J., et al. (2013). Genetic architecture of delayed senescence, biomass, and grain yield under drought stress in cowpea. *PLoS ONE, 8*(7), e70041.

Murakami, Y., Tsuyama, M., Kobayashi, Y., Kodama, H., & Iba, K. (2000). Trienoic fatty acids and plant tolerance of high temperature. *Science, 287*(5452), 476–479.

Nagarajan, S., Jagadish, S. V. K., Prasad, A. S. H., Thomar, A. K., Anand, A., Pal, M., et al. (2010). Local climate affects growth, yield and grain quality of aromatic and non-aromatic rice in northwestern India. *Agriculture, Ecosystems & Environment, 138*(3–4), 274–281.

Naveed, M., Ahsan, M., Akram, H. M., Aslam, M., & Ahmed, N. (2016). Genetic effects conferring heat tolerance in a cross of tolerant × susceptible maize (*Zea mays* L.) genotypes. *Frontiers in Plant Science, 7,* 729.

Nawaz, A., Farooq, M., Cheema, S. A., & Wahid, A. (2013). Differential response of wheat cultivars to terminal heat stress. *International Journal of Agriculture and Biology, 15*(6), 1354.

Naydenov, M., Baev, V., Apostolova, E., Gospodinova, N., Sablok, G., Gozmanova, M., et al. (2015). High-temperature effect on genes engaged in DNA methylation and affected by DNA methylation in *Arabidopsis*. *Plant Physiology and Biochemistry, 87,* 102–108.

Norvie, L. M., Lambio, L. A. F., Luvina, B., & Cardenas, C. C. (2014). Germplasm innovation of heat tolerance in rice (*Oryza sativa*) for irrigated lowland conditions in the Philippines. *Rice Science, 21,* 162.

Obata, T., & Fernie, A. R. (2012). The use of metabolomics to dissect plant responses to abiotic stresses. *Cellular and Molecular Life Sciences, 69*(19), 3225–3243.

Ohama, N., Sato, H., Shinozaki, K., & Yamaguchi-Shinozaki, K. (2017). Transcriptional regulatory network of plant heat stress response. *Trends in Plant Science, 22*(1), 53–65.

Ono, K., Hibino, T., Kohinata, T., Suzuki, S., Tanaka, Y., Nakamura, T., et al. (2001). Overexpression of DnaK from a halotolerant cyanobacterium *Aphanothece halophytica* enhances the high-temperatue tolerance of tobacco during germination and early growth. *Plant Science, 160*(3), 455–461.

Ottaviano, E., Gorla, M. S., Pe, E., & Frova, C. (1991). Molecular markers (RFLPs and HSPs) for the genetic dissection of thermotolerance in maize. *Theoretical and Applied Genetics, 81*(6), 713–719.

Panigrahy, M., Neelamraju, S., Rao, D. N., & Ramanan, R. (2011). Heat tolerance in rice mutants is associated with reduced accumulation of reactive oxygen species. *Biologia Plantarum, 55*(4), 721.

Park, C.-J., & Seo, Y.-S. (2015). Heat shock proteins: A review of the molecular chaperones for plant immunity. *The Plant Pathology Journal, 31*(4), 323.

Parry, M. A. J., Reynolds, M., Salvucci, M. E., Raines, C., Andralojc, P. J., Zhu, X.-G., et al. (2010). Raising yield potential of wheat. II. Increasing photosynthetic capacity and efficiency. *Journal of Experimental Botany, 62*(2), 453–467.

Paul, S., Das, M. K., Baishya, P., Ramteke, A., Farooq, M., Baroowa, B., et al. (2017). Effect of high temperature on yield associated parameters and vascular bundle development in five potato cultivars. *Scientia Horticulturae, 225,* 134–140.

Paul, P. J., Samineni, S., Sajja, S. B., Rathore, A., Das, R. R., Chaturvedi, S. K., et al. (2018a). Capturing genetic variability and selection of traits for heat tolerance in a chickpea recombinant inbred line (RIL) population under field conditions. *Euphytica, 214*(2), 27.

Paul, P. J. N., Samineni, S., Thundi, M., Sajja, S. B., Rathore, A., Das, R. R., et al. (2018b). Molecular mapping of QTLs associated with heat tolerance in chickpea. *Internnational Journal of Molecular Science, 19,* E2166. https://doi.org/10.3390/ijms19082166.

Paupière, M. J., van Haperen, P., Rieu, I., Visser, R. G. F., Tikunov, Y. M., & Bovy, A. G. (2017). Screening for pollen tolerance to high temperatures in tomato. *Euphytica, 213*(6), 130.

Pecinka, A., & Mittelsten Scheid, O. (2012). Stress-induced chromatin changes: a critical view on their heritability. *Plant and Cell Physiology, 53*(5), 801–808.

Petolino, J. F., Cowen, N. M., Thompson, S. A., & Mitchell, J. C. (1992). *Gamete selection for heat stress tolerance in maize. Angiosperm pollen and ovules* (pp. 355–358). Berlin: Springer.

Peverelli, M. C., & Rogers, W. J. (2013). Heat stress effects on crop performance and tools for tolerance breeding. *Revista de la FCA UNCUYO, 45*(2), 349.

Pinto, R. S., Lopes, M. S., Collins, N. C., & Reynolds, M. P. (2016). Modelling and genetic dissection of staygreen under heat stress. *Theoretical and Applied Genetics, 129*(11), 2055–2074.

Poli, Y., Basava, R. K., Panigrahy, M., Vinukonda, V. P., Dokula, N. R., Voleti, S. R., et al. (2013). Characterization of a Nagina22 rice mutant for heat tolerance and mapping of yield traits. *Rice, 6*(1), 36.

Porch, T. G. (2006). Application of stress indices for heat tolerance screening of common bean. *Journal of Agronomy and Crop Science, 192*(5), 390–394.

Pottorff, M., Roberts, P. A., Close, T. J., Lonardi, S., Wanamaker, S., & Ehlers, J. D. (2014). Identification of candidate genes and molecular markers for heat-induced brown discoloration of seed coats in cowpea [*Vigna unguiculata* (L.) Walp]. *BMC Genomics, 15*(1), 328.

Pradhan, G. P., Prasad, P. V. V., Fritz, A. K., Kirkham, M. B., & Gill, B. S. (2012). High temperature tolerance in *Aegilops* species and its potential transfer to wheat. *Crop Science, 52*(1), 292–304.

Prasad, P. V. V., Bheemanahalli, R., & Jagadish, S. V. K. (2017). Field crops and the fear of heat stress: Opportunities, challenges and future directions. *Field Crops Research, 200,* 114–121.

Prasad, P. V. V., Boote, K. J., Allen, L. H., Jr., & Thomas, J. M. G. (2002). Effects of elevated temperature and carbon dioxide on seed-set and yield of kidney bean (*Phaseolus vulgaris* L.). *Global Change Biology, 8*(8), 710–721.

Qin, D., Wang, F., Geng, X., Zhang, L., Yao, Y., Ni, Z., et al. (2015). Overexpression of heat stress-responsive TaMBF1c, a wheat (*Triticum aestivum* L.) multiprotein bridging factor, confers heat tolerance in both yeast and rice. *Plant Molecular Biology, 87*(1–2), 31–45.

Qu, A.-L., Ding, Y.-F., Jiang, Q., & Zhu, C. (2013). Molecular mechanisms of the plant heat stress response. *Biochemical and Biophysical Research Communications, 432*(2), 203–207.

Rahaman, M., Mamidi, S., & Rahman, M. (2017). Association mapping of agronomic traits of canola ("*Brassica napus*" L.) subject to heat stress under field conditions. *Australian Journal of Crop Science, 11*(9), 1094.

Rahaman, M., Mamidi, S., & Rahman, M. (2018). Genome-wide association study of heat stress-tolerance traits in spring-type *Brassica napus* L. under controlled conditions. *The Crop Journal, 6*(2), 115–125.

Rahman, S. U., Arif, M., Hussain, K., Hussain, S., Mukhtar, T., Razaq, A., et al. (2013). Evaluation of maize hybrids for tolerance to high temperature stress in central Punjab. *Columbia International Publishing American Journal of Bioengineering and Biotechnology, 1*(1), 30–36.

Ramani, H. R., Mandavia, M. K., Dave, R. A., Bambharolia, R. P., Silungwe, H., & Garaniya, N. H. (2017). Biochemical and physiological constituents and their correlation in wheat (*Triticum aestivum* L.) genotypes under high temperature at different development stages. *International Journal of Plant Physiology and Biochemistry, 9*(1), 1–8.

Ray, J., & Ahmed, J. J. (2015). Canopy temperature effects on yield and grain growth of different wheat genotypes. *IOSR Journal of Agriculture and Veterinary Science, 8*(7), 2319–2380.

Rekika, D., Kara, Y., Souyris, I., Nachit, M. M., Asbati, A., & Monneveux, P. (2000). The tolerance of PSII to high temperatures in durum wheat (*T. turgidum* conv. durum): Genetic variation and relationship with yield under heat stress. *Cereal Research Communications, 28,* 395–402.

Reynolds, M. P., Balota, M., Delgado, M. I. B., Amani, I., & Fischer, R. A. (1994). Physiological and morphological traits associated with spring wheat yield under hot, irrigated conditions. *Functional Plant Biology, 21*(6), 717–730.

Reynolds, M. P., Singh, R. P., Ibrahim, A., Ageeb, O. A. A., Larque-Saavedra, A., & Quick, J. S. (1998). Evaluating physiological traits to complement empirical selection for wheat in warm environments. *Euphytica, 100*(1–3), 85–94.

Rodziewicz, P., Swarcewicz, B., Chmielewska, K., Wojakowska, A., & Stobiecki, M. (2014). Influence of abiotic stresses on plant proteome and metabolome changes. *Acta Physiologiae Plantarum, 36*(1), 1–19.

Roychoudhury, A., Datta, K., & Datta, S. K. (2011). *Abiotic stress in plants: From genomics to metabolomics. Omics and Plant Abiotic Stress Tolerance* (pp. 91–120). Chicago: Bentham Science Publishers.

Sage, T. L., Bagha, S., Lundsgaard-Nielsen, V., Branch, H. A., Sultmanis, S., & Sage, R. F. (2015). The effect of high temperature stress on male and female reproduction in plants. *Field Crops Research, 182,* 30–42.

Sahu, P. P., Pandey, G., Sharma, N., Puranik, S., Muthamilarasan, M., & Prasad, M. (2013). Epigenetic mechanisms of plant stress responses and adaptation. *Plant cell reports, 32*(8), 1151–1159.

Saint Pierre, C., Crossa, J., Manes, Y., & Reynolds, M. P. (2010). Gene action of canopy temperature in bread wheat under diverse environments. *Theoretical and Applied Genetics, 120*(6), 1107–1117.

Sairam, R. K., Srivastava, G. C., & Saxena, D. C. (2000). Increased antioxidant activity under elevated temperatures: a mechanism of heat stress tolerance in wheat genotypes. *Biologia Plantarum, 43*(2), 245–251.

Salem, M. A., Kakani, V. G., Koti, S., & Reddy, K. R. (2007). Pollen-based screening of soybean genotypes for high temperatures. *Crop Science, 47*(1), 219–231.

Sanmiya, K., Suzuki, K., Egawa, Y., & Shono, M. (2004). Mitochondrial small heat-shock protein enhances thermotolerance in tobacco plants. *FEBS Letters, 557*(1–3), 265–268.

Sarkar, N. K., Kim, Y.-K., & Grover, A. (2014). Coexpression network analysis associated with call of rice seedlings for encountering heat stress. *Plant Molecular Biology, 84*(1–2), 125–143.

Sato, H., Todaka, D., Kudo, M., Mizoi, J., Kidokoro, S., Zhao, Y., et al. (2016). The Arabidopsis transcriptional regulator DPB 3-1 enhances heat stress tolerance without growth retardation in rice. *Plant Biotechnology Journal, 14*(8), 1756–1767.

Savchenko, G. E., Klyuchareva, E. A., Abramchik, L. M., & Serdyuchenko, E. V. (2002). Effect of periodic heat shock on the inner membrane system of etioplasts. *Russian Journal of Plant Physiology, 49*(3), 349–359.

Saxena, D. C., Prasad, S. V. S., Chatrath, R., Mishra, S. C., Watt, M., Prashar, R., et al. (2014). Evaluation of root characteristics, canopy temperature depression and stay green trait in relation to grain yield in wheat under early and late sown conditions. *Indian Journal of Plant Physiology, 19*(1), 43–47.

Setimela, P. S., Andrews, D. J., Partridge, J., & Eskridge, K. M. (2005). Screening sorghum seedlings for heat tolerance using a laboratory method. *European Journal of Agronomy, 23*(2), 103–107.

Shamsudin, N. A. A., Swamy, B. P. M., Ratnam, W., Cruz, M. T. S., Raman, A., & Kumar, A. (2016). Marker assisted pyramiding of drought yield QTLs into a popular Malaysian rice cultivar, MR219. *BMC Genetics, 17*(1), 30.

Shanmugavadivel, P. S., Sv, A. M., Prakash, C., Ramkumar, M. K., Tiwari, R., Mohapatra, T., et al. (2017). High resolution mapping of QTLs for heat tolerance in rice using a 5 K SNP array. *Rice, 10*(1), 28.

Sharma, D. K., Andersen, S. B., Ottosen, C., & Rosenqvist, E. (2015). Wheat cultivars selected for high Fv/Fm under heat stress maintain high photosynthesis, total chlorophyll, stomatal conductance, transpiration and dry matter. *Physiologia Plantarum, 153*(2), 284–298.

Sharma, D. K., Fernández, J. O., Rosenqvist, E., Ottosen, C.-O., & Andersen, S. B. (2014). Genotypic response of detached leaves versus intact plants for chlorophyll fluorescence parameters under high temperature stress in wheat. *Journal of Plant Physiology, 171*(8), 576–586.

Sharma, L., Priya, M., Bindumadhava, H., Nair, R. M., & Nayyar, H. (2016). Influence of high temperature stress on growth, phenology and yield performance of mungbean [*Vigna radiata* (L.) Wilczek] under managed growth conditions. *Scientia Horticulturae, 213,* 379–391.

Sharma, R. C., Tiwary, A. K., & Ortiz-Ferrara, G. (2008). Reduction in kernel weight as a potential indirect selection criterion for wheat grain yield under terminal heat stress. *Plant Breeding, 127*(3), 241–248.

Shi, P., Tang, L., Lin, C., Liu, L., Wang, H., Cao, W., et al. (2015). Modeling the effects of post-anthesis heat stress on rice phenology. *Field Crops Research, 177,* 26–36.

Shi, J., Yan, B., Lou, X., Ma, H., & Ruan, S. (2017). Comparative transcriptome analysis reveals the transcriptional alterations in heat-resistant and heat-sensitive sweet maize (*Zea mays* L.) varieties under heat stress. *BMC Plant Biology, 17*(1), 26.

Shiraya, T., Mori, T., Maruyama, T., Sasaki, M., Takamatsu, T., Oikawa, K., et al. (2015). Golgi/plastid-type manganese superoxide dismutase involved in heat-stress tolerance during grain filling of rice. *Plant Biotechnology Journal, 13*(9), 1251–1263.

Shuancang, Y., Yongjian, W., & Xiaoying, Z. (2003). Mapping and analysis QTL controlling heat tolerance in *Brassica campestris* L. ssp. Pekinensis. *Acta Horticulturae Sinica, 30*(4), 417–420.

Shukla, N. (2013). Flower numbers, pod production, pollen viability are reduced with flower and pod abortion increased in Chickpea (*Cicer arietinum* L.) under heat stress. *Research Journal of Recent Sciences, 2,* 116–119.

Sikder, S., & Paul, N. K. (2010). Effects of post-anthesis heat stress on stem reserves mobilization, canopy temperature depression and floret sterility of wheat cultivars. *Bangladesh Journal of Botany, 39*(1), 51–55.

Singh, A., & Grover, A. (2008). Genetic engineering for heat tolerance in plants. *Physiology and Molecular Biology of Plants, 14*(1–2), 155.

Singh, D., Singh, C. K., Singh Tomar, R. S., & Pal, M. (2017). Genetics and molecular mapping of heat tolerance for seedling survival and pod set in lentil. *Crop Science, 57*(6), 3059–3067.

Singh, K., Wijewardana, C., Gajanayake, B., Lokhande, S., Wallace, T., Jones, D., et al. (2018). Genotypic variability among cotton cultivars for heat and drought tolerance using reproductive and physiological traits. *Euphytica, 214*(3), 57.

Sita, K., Sehgal, A., Hanumantha Rao, B., Nair, R. M., Vara Prasad, P. V., Kumar, S., et al. (2017a). Food legumes and rising temperatures: effects, adaptive functional mechanisms specific to reproductive growth stage and strategies to improve heat tolerance. *Frontiers in Plant Science, 8,* 1658.

Sita, K., Sehgal, A., Kumar, J., Kumar, S., Singh, S., Siddique, K. H. M., et al. (2017b). Identification of high-temperature tolerant lentil (*Lens culinaris* Medik.) genotypes through leaf and pollen traits. *Frontiers. Plant Science, 8,* 744.

Sohn, S. O., & Back, K. (2007). Transgenic rice tolerant to high temperature with elevated contents of dienoic fatty acids. *Biologia Plantarum, 51*(2), 340–342.

Solís, M.-T., Rodríguez-Serrano, M., Meijón, M., Cañal, M.-J., Cifuentes, A., Risueño, M. C., et al. (2012). DNA methylation dynamics and MET1a-like gene expression changes during stress-induced pollen reprogramming to embryogenesis. *Journal of Experimental Botany, 63*(18), 6431–6444.

Stefanov, D., Petkova, V., & Denev, I. D. (2011). Screening for heat tolerance in common bean (*Phaseolus vulgaris* L.) lines and cultivars using JIP-test. *Scientia Horticulturae, 128*(1), 1–6.

Stratonovitch, P., & Semenov, M. A. (2015). Heat tolerance around flowering in wheat identified as a key trait for increased yield potential in Europe under climate change. *Journal of Experimental Botany, 66*(12), 3599–3609.

Sun, W., Van Montagu, M., & Verbruggen, N. (2002). Small heat shock proteins and stress tolerance in plants. *Biochimica et Biophysica Acta (BBA)-Gene Structure and Expression, 1577*(1), 1–9.

Suwa, R., Hakata, H., Hara, H., El-Shemy, H. A., Adu-Gyamfi, J. J., Nguyen, N. T., et al. (2010). High temperature effects on photosynthate partitioning and sugar metabolism during ear expansion in maize (*Zea mays* L.) genotypes. *Plant Physiology and Biochemistry, 48*(2–3), 124–130.

Suzuki, K., Takeda, H., Tsukaguchi, T., & Egawa, Y. (2001). Ultrastructural study on degeneration of tapetum in anther of snap bean (*Phaseolus vulgaris* L.) under heat stress. *Sexual Plant Reproduction, 13*(6), 293–299.

Talukder, S. K., Babar, M. A., Vijayalakshmi, K., Poland, J., Prasad, P. V. V., Bowden, R., et al. (2014a). Mapping QTL for the traits associated with heat tolerance in wheat (*Triticum aestivum* L.). *BMC Genetics, 15*(1), 97.

Talukder, A., McDonald, G. K., & Gill, G. S. (2014b). Effect of short-term heat stress prior to flowering and early grain set on the grain yield of wheat. *Field Crops Research, 160,* 54–63.

Tan, W., Wei Meng, Q., Brestic, M., Olsovska, K., & Yang, X. (2011). Photosynthesis is improved by exogenous calcium in heat-stressed tobacco plants. *Journal of Plant Physiology, 168*(17), 2063–2071.

Team, C. W., Pachauri, R. K., & Meyer, L. A. (2014). IPCC, 2014: climate change 2014: synthesis report. Contribution of Working Groups I. *II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland, 151.*

Teixeira, E. I., Fischer, G., van Velthuizen, H., Walter, C., & Ewert, F. (2013). Global hot-spots of heat stress on agricultural crops due to climate change. *Agricultural and Forest Meteorology, 170,* 206–215.

Tenorio, F. A., Ye, C., Redoña, E., Sierra, S., Laza, M., & Argayoso, M. A. (2013). Screening rice genetic resources for heat tolerance. *SABRAO Journal of Breeding and Genetics, 45*(3), 371–381.

Thomas, H., & Ougham, H. (2014). The stay-green trait. *Journal of Experimental Botany, 65*(14), 3889–3900.

Tian, Y., Chen, J., Chen, C., Deng, A., Song, Z., Zheng, C., et al. (2012). Warming impacts on winter wheat phenophase and grain yield under field conditions in Yangtze Delta Plain, China. *Field Crops Research, 134,* 193–199.

Timmerman-Vaughan, G. M., Mills, A., Whitfield, C., Frew, T., Butler, R., Murray, S., Lakeman, M., McCallum, J., Russell, A., & Wilson, D. (2005) Linkage Mapping of QTL for Seed Yield, Yield Components, and Developmental Traits in Pea. *Crop Science, 45*(4):1336.

Trapero-Mozos, A., Morris, W. L., Ducreux, L. J. M., McLean, K., Stephens, J., Torrance, L., et al. (2018). Engineering heat tolerance in potato by temperature-dependent expression of a specific allele of HEAT-SHOCK COGNATE 70. *Plant Biotechnology Journal, 16*(1), 197–207.

Usman, M. G., Rafii, M. Y., Ismail, M. R., Malek, M. A., Latif, M. A., & Oladosu, Y. (2014). Heat shock proteins: functions and response against heat stress in plants. *International Journal of Scientific and Technology Research, 3*(11), 204–218.

Vignjevic, M., Wang, X., Olesen, J. E., & Wollenweber, B. (2015). Traits in spring wheat cultivars associated with yield loss caused by a heat stress episode after anthesis. *Journal of Agronomy and Crop Science, 201*(1), 32–48.

Vijayalakshmi, K., Fritz, A. K., Paulsen, G. M., Bai, G., Pandravada, S., & Gill, B. S. (2010). Modeling and mapping QTL for senescence-related traits in winter wheat under high temperature. *Molecular Breeding, 26*(2), 163–175.

Wahid, A., & Shabbir, A. (2005). Induction of heat stress tolerance in barley seedlings by pre-sowing seed treatment with glycinebetaine. *Plant Growth Regulation, 46*(2), 133–141.

Wang, X., Huang, W., Liu, J., Yang, Z., & Huang, B. (2017a). Molecular regulation and physiological functions of a novel FaHsfA2c cloned from tall fescue conferring plant tolerance to heat stress. *Plant Biotechnology Journal, 15*(2), 237–248.

Wang, W., Vinocur, B., Shoseyov, O., & Altman, A. (2004). Role of plant heat-shock proteins and molecular chaperones in the abiotic stress response. *Trends in Plant Science, 9*(5), 244–252.

Wang, X., Yan, B., Shi, M., Zhou, W., Zekria, D., Wang, H., et al. (2016). Overexpression of a *Brassica campestris* HSP70 in tobacco confers enhanced tolerance to heat stress. *Protoplasma, 253*(3), 637–645.

Wang, A., Yu, X., Mao, Y., Liu, Y., Liu, G., Liu, Y., et al. (2015). Overexpression of a small heat-shock-protein gene enhances tolerance to abiotic stresses in rice. *Plant Breeding, 134*(4), 384–393.

Wang, M., Zou, Z., Li, Q., Xin, H., Zhu, X., Chen, X., et al. (2017b). Heterologous expression of three *Camellia sinensis* small heat shock protein genes confers temperature stress tolerance in yeast and *Arabidopsis thaliana*. *Plant Cell Reports, 36*(7), 1125–1135.

Wei, H., Liu, J., Wang, Y., Huang, N., Zhang, X., Wang, L., et al. (2012). A dominant major locus in chromosome 9 of rice (*Oryza sativa* L.) confers tolerance to 48 C high temperature at seedling stage. *Journal of Heredity, 104*(2), 287–294.

Weng, M., Yang, Y. U. E., Feng, H., Pan, Z., Shen, W., Zhu, Y. A. N., et al. (2014). Histone chaperone ASF1 is involved in gene transcription activation in response to heat stress in *Arabidopsis thaliana*. *Plant, Cell and Environment, 37*(9), 2128–2138.

Wu, H., Luo, D., Vignols, F., & Jinn, T. (2012). Heat shock-induced biphasic Ca^{2+} signature and OsCaM1-1 nuclear localization mediate downstream signalling in acquisition of thermotolerance in rice (*Oryza sativa* L.). *Plant, Cell and Environment, 35*(9), 1543–1557.

Wu, T., Weaver, D. B., Locy, R. D., McElroy, S., & van Santen, E. (2014). Identification of vegetative heat-tolerant upland cotton (*Gossypium hirsutum* L.) germplasm utilizing chlorophyll fluorescence measurement during heat stress. *Plant Breeding, 133*(2), 250–255.

Xin, H., Zhang, H., Zhong, X., Lian, Q., Dong, A., Cao, L., et al. (2017). Over-expression of LlHsfA2b, a lily heat shock transcription factor lacking trans-activation activity in yeast, can enhance tolerance to heat and oxidative stress in transgenic *Arabidopsis* seedlings. *Plant Cell, Tissue and Organ Culture (PCTOC), 130*(3), 617–629.

Xu, J., Driedonks, N., Rutten, M. J. M., Vriezen, W. H., de Boer, G.-J., & Rieu, I. (2017). Mapping quantitative trait loci for heat tolerance of reproductive traits in tomato (*Solanum lycopersicum*). *Molecular Breeding, 37*(5), 58.

Xu, W., Subudhi, P. K., Crasta, O. R., Rosenow, D. T., Mullet, J. E., & Nguyen, H. T. (2000). Molecular mapping of QTLs conferring stay-green in grain sorghum (*Sorghum bicolor* L. Moench). *Genome, 43*(3), 461–469.

Xu, Y., Wang, J., Bonos, S. A., Meyer, W. A., & Huang, B. (2018). Candidate genes and molecular markers correlated to physiological traits for heat tolerance in fine fescue cultivars. *International Journal of Molecular Sciences, 19*(1), 116.

Xu, Q., Xu, X., Shi, Y., Xu, J., & Huang, B. (2014). Transgenic tobacco plants overexpressing a grass PpEXP1 gene exhibit enhanced tolerance to heat stress. *PLoS ONE, 9*(7), e100792.

Xue, G.-P., Sadat, S., Drenth, J., & McIntyre, C. L. (2013). 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. *Journal of Experimental Botany, 65*(2), 539–557.

Yan, K., Chen, N., Qu, Y., Dong, X., Meng, Q., & Zhao, S. (2008). Overexpression of sweet pepper glycerol-3-phosphate acyltransferase gene enhanced thermotolerance of photosynthetic apparatus in transgenic tobacco. *Journal of Integrative Plant Biology, 50*(5), 613–621.

Yang, X., Liang, Z., & Lu, C. (2005). Genetic engineering of the biosynthesis of glycinebetaine enhances photosynthesis against high temperature stress in transgenic tobacco plants. *Plant Physiology, 138*(4), 2299–2309.

Yang, J., Sears, R. G., Gill, B. S., & Paulsen, G. M. (2002a). Genotypic differences in utilization of assimilate sources during maturation of wheat under chronic heat and heat shock stresses. *Euphytica, 125*(2), 179–188.

Yang, J., Sears, R. G., Gill, B. S., & Paulsen, G. M. (2002b). Quantitative and molecular characterization of heat tolerance in hexaploid wheat. *Euphytica, 126*(2), 275–282.

Yang, X., Wen, X., Gong, H., Lu, Q., Yang, Z., Tang, Y., et al. (2007). Genetic engineering of the biosynthesis of glycinebetaine enhances thermotolerance of photosystem II in tobacco plants. *Planta, 225*(3), 719–733.

Ye, C., Tenorio, F. A., Argayoso, M. A., Laza, M. A., Koh, H.-J., Redoña, E. D., et al. (2015). Identifying and confirming quantitative trait loci associated with heat tolerance at flowering stage in different rice populations. *BMC Genetics, 16*(1), 41.

Yu, E., Fan, C., Yang, Q., Li, X., Wan, B., Dong, Y., et al. (2014). Identification of heat responsive genes in *Brassica napus* siliques at the seed-filling stage through transcriptional profiling. *PLoS ONE, 9*(7), e101914.

Yuan, L., Yuan, Y., Liu, S., Wang, J., Zhu, S., Chen, G., et al. (2017). Influence of high temperature on photosynthesis, antioxidative capacity of chloroplast, and carbon assimilation among heat-tolerant and heat-susceptible genotypes of nonheading Chinese cabbage. *HortScience, 52*(11), 1464–1470.

Zang, X., Geng, X., Wang, F., Liu, Z., Zhang, L., Zhao, Y., et al. (2017). Overexpression of wheat ferritin gene TaFER-5B enhances tolerance to heat stress and other abiotic stresses associated with the ROS scavenging. *BMC Plant Biology, 17*(1), 14.

Zarei, B., Naderi, A., Jalal Kamali, M. R., Lack, S., & Modhej, A. (2013). Determination of physiological traits related to terminal drought and heat stress tolerance in spring wheat genotypes. *International Journal of Agriculture and Crop Sciences, 5*(21), 2511–2520.

Zhang, M., Barg, R., Yin, M., Gueta-Dahan, Y., Leikin-Frenkel, A., Salts, Y., et al. (2005). Modulated fatty acid desaturation via overexpression of two distinct ω-3 desaturases differentially alters tolerance to various abiotic stresses in transgenic tobacco cells and plants. *The Plant Journal, 44*(3), 361–371.

Zhang, J., Chen, H., Wang, H., Li, B., Yi, Y., Kong, F., et al. (2016). Constitutive expression of a tomato small heat shock protein gene LeHSP21 improves tolerance to high-temperature stress by enhancing antioxidation capacity in tobacco. *Plant Molecular Biology Reporter, 34*(2), 399–409.

Zhang, K., Ezemaduka, A. N., Wang, Z., Hu, H., Shi, X., Liu, C., et al. (2015). A novel mechanism for small heat shock proteins to function as molecular chaperones. *Scientific Reports, 5,* 8811.

Zhang, L., Geng, X., Zhang, H., Zhou, C., Zhao, A., Wang, F., et al. (2017a). Isolation and characterization of heat-responsive gene TaGASR1 from wheat (*Triticum aestivum* L.). *Journal of Plant Biology, 60*(1), 57–65.

Zhang, H., Liang, W., Yang, X., Luo, X., Jiang, N., Ma, H., et al. (2010). Carbon starved anther encodes a MYB domain protein that regulates sugar partitioning required for rice pollen development. *The Plant Cell, 22*(3), 672–689.

Zhang, Y.-J., Zhou, L.-Y., Bai, Y.-X., Yi, W.-B., Cu, K., Nie, X., et al. (2017b). Development of plant expression vector with Taq DNA polymerase gene to yield heat-tolerant maize lines. *International Journal of Agriculture and Biology, 19*(3), 523.

Zheng, H. J., Wu, A. Z., Zheng, C. C., Wang, Y. F., Cai, R., Shen, X. F., et al. (2009). QTL mapping of maize (*Zea mays*) stay-green traits and their relationship to yield. *Plant Breeding, 128*(1), 54–62.

Zhou, R., Yu, X., Kjær, K. H., Rosenqvist, E., Ottosen, C.-O., & Wu, Z. (2015). Screening and validation of tomato genotypes under heat stress using Fv/Fm to reveal the physiological mechanism of heat tolerance. *Environmental and Experimental Botany, 118,* 1–11.

Zhu, X., Thalor, S. K., Takahashi, Y., Berberich, T., & Kusano, T. (2012). An inhibitory effect of the sequence-conserved upstream open-reading frame on the translation of the main open-reading frame of HsfB1 transcripts in Arabidopsis. *Plant, Cell and Environment, 35*(11), 2014–2030.

Zinn, K. E., Tunc-Ozdemir, M., & Harper, J. F. (2010). Temperature stress and plant sexual reproduction: Uncovering the weakest links. *Journal of Experimental Botany, 61*(7), 1959–1968.