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Food crops face rising temperatures: An overview of responses, adaptive mechanisms, and approaches to improve heat tolerance

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Abstract: The rising temperatures are resulting in heat stress for various agricultural crops to limit their growth, metabolism, and leading to significant loss of yield potential worldwide. Heat stress adversely affects normal plant growth and development depending on the sensitivity of each crop species. Each crop species has its own range of temperature maxima and minima at different developmental stages beyond which all these processes get inhibited. The reproductive stage is on the whole more sensitive to heat stress, resulting in impaired fertilization to cause abortion of flowers. During seed filling, heat stress retards seed growth by affecting all the biochemical events to reduce seed size. Unfavorable temperature may significantly affect photosynthesis, respiration, water balance, and membrane stability of leaves. To combat heat stress, plants acquire various defense mechanisms for their survival such as maintaining membrane stability, and scavenging reactive oxygen species by generating antioxidants and stress proteins. Thermo-tolerance can be improved by the accumulation of various compounds of low molecular mass known as thermo-protectants as well as phyto-hormones. Exogenous application of these molecules has benefited plants growing under heat stress. Alternatively, transgenic plants over-expressing the enzymes catalyzing the synthesis of these molecules may be raised to increase their endogenous levels to improve heat tolerance. In recent times, various transgenics have been developed with improved thermo-tolerance having potential benefits for inducing heat tolerance in food crops. Updated information about of the effects of heat stress on various food crops and their responses as well as adaptive mechanisms is reviewed here.

ABOUT THE AUTHORS

We are evaluating the responses of food legumes to various environmental stresses, particularly heat and drought at different organizational levels. We work on these aspects in collaboration with International Crops Research Institute for Semi-arid Tropics (ICRISAT), International Center for Agricultural Research in Dry Areas (ICARDA), Asian Vegetable Research Development Center, and University of Western Australia. The work involves screening core-germplasm for heat and drought tolerance and exploring the mechanisms related to heat tolerance. Since rising temperatures pose a serious threat to agriculture, there is need to address issues related to heat tolerance in crops, which have been discussed in the present article.

PUBLIC INTEREST STATEMENT

Global temperatures are rising which would have serious implications in agriculture all over the world. There is need to understand how our food crops respond to increasing temperatures and what kind of mechanisms are activated to face heat stress. Identifying these mechanisms would help to devise suitable strategies to develop heat-tolerant crops to minimize the yield losses due to high-temperature stress.
1. Introduction

Plants, being sessile, face various forms of abiotic and biotic stresses in the environment (Iba, 2002). Environmental stresses such as drought, salt, cold, and temperature affect plants, individually, and in combination (Serrano et al., 1999). Climate change has increased the intensity of heat stress, with adverse effects on agricultural and horticultural crops, resulting in serious economic losses (Beck, Fettig, Knake, Hartig, & Bhattacharai, 2007). The global mean surface air temperature increased by 0.5°C in the twentieth century and is expected to increase a further 1.5–4.5°C by the late twenty-first century (IPCC, 2012; Karl et al., 1991). A temperature increase of 3–4°C could reduce crop yields by 15–35% in Africa and Asia and by 25–35% in the Middle East (Ortiz et al., 2008). Current speculation about global climate change is that most agricultural regions will experience more extreme environmental fluctuations in the future (Solomon et al., 2007). The increasing threat of climate change is already having a substantial impact on agriculture production worldwide as heat waves cause significant yield losses with great risks for future global food security (Christensen & Christensen, 2007). The rise in temperature, even by a single degree beyond the threshold level, is considered heat stress in plants (Hasanuzzaman, Nahar, Alam, Roychowdhury, & Fujita, 2013; Wahid, Gelani, Ashraf, & Foolad, 2007). Heat stress has harmful effects on plants by affecting growth, development, metabolism, and productivity of plants (Hasanuzzaman, Nahar, & Fujita, 2013). Exposure to high temperature shortens the life cycle, increases senescence, and severely affects potential yields (Porter, 2005).

2. Effects of heat stress

Transitory or constantly high temperatures cause an array of morpho-anatomical, physiological, and biochemical changes in plants, which affect their growth and development, thereby leading to drastic reductions in economic yield. Heat stress may cause either direct or indirect injury to the plant.

1. Direct injury: includes aggregation and denaturation of proteins as well as increased fluidity of membranes.

2. Indirect injury: includes inactivation of enzymes in chloroplasts and mitochondria, inhibition of protein synthesis, enhanced protein degradation and loss of membrane integrity (Howarth, 2005). All these alterations result in cell injury or even death within a few minutes, which ultimately leads to catastrophic collapse of cellular organization (Schoffl, Prandl, & Reindl, 1999).

Heat stress leads to morphological damage and hence reduced yield (Vollenweider & Günthardt-Goerg, 2005; Figure 1). Heat stress on plants reduces photosynthesis as this is the most thermosensitive part of plant function (Kim & Portis, 2005; Wise, Olson, Schrader, & Sharkey, 2004). High temperatures induce the production of reactive oxygen species (ROS), which at very high levels may lead to severe cell injury and even cell death (Apel & Hirt, 2004; Schoffl et al., 1999). Reproductive processes are adversely affected by high temperature, including pollen germination and pollen tube growth, ovule viability, stigmatic and style positions, number of pollen grains retained by the stigma, fertilization and post-fertilization processes, and growth of the endosperm, proembryo, and fertilized embryo (Foolad, 2005).

2.1. Germination and vegetative growth

Depending on the intensity, duration, and stage of exposure, heat stress can adversely affect the rate of growth and development of plants (Gan, Wang, Angadi, & Mcdonald, 2004; Wahid et al., 2007). Long-term effects of heat stress on developing seeds may include delayed germination or loss of vigor, which ultimately reduces emergence and seedling establishment. Reduced seed germination has been reported in many legumes including soybean (Glycine max L. Merrill; Ortiz &
Cardemil, 2001; Ren, Bilyeu, & Beuselinck, 2009), pea (Pisum sativum L.; Nemeskeri, 2004; Ren et al., 2009), lentil (Lens culinaris Medik; Chakraborty & Pradhan, 2011), mungbean (Phaseolus aureus Roxb.; Devasirvatham, Tan, Gaur, Roju, & Trethowan, 2012; Kumar et al., 2011), and chickpea (Cicer arietinum L.; Kaushal, Gupta, Bhandari, Kumar, & Thakur, 2011; Piramila, Prabha, Nandagopalan, & Stanley, 2012). Seed germination and vigor index decreased significantly when mungbean seeds were exposed to 10, 20, and 30 min of 50°C treatment (Piramila et al., 2012) which agreed with the findings of Mansoor and Naqvi (2011). Likewise, Senna (Cassia tora L.) seeds, when incubated under normal room temperature, exhibited 92% germination but exposure to 40, 50, and 60°C continuously for 10 days reduced the germination to 85, 63, and 32%, respectively (Pant, Malla, Aruna, & Chauhan, 2012). Essemine, Ammar, and Bouzid (2010) attributed inhibition of germination by heat stress (45°C) to cell death and embryo damage in wheat (Triticum aestivum L.) during early development (first 6 days of growth). There are conflicting reports about post-emergence seedling growth in maize under heat stress. Momcilovic and Ristic (2007) in their studies have shown that the maize coleoptile was heat tolerant at all stages of seedling development while in another study, exposure to 40°C substantially reduced maize coleoptile growth and at 45°C, growth completely stopped (Akman, 2009).

Vegetative plant parts may show various morphological symptoms in response to heat stress such as scorching and sun-burning of leaves, twigs, branches and stems, leaf senescence and abscission, shoot and root growth inhibition, fruit discoloration, and damage which ultimately reduces yield (Vollenweider & Günthardt-Goerg, 2005). For example, plant height in wheat decreased significantly under heat stress (Laghrí, Mahboob, & Arain, 2012) while long exposures to heat stress inhibited first leaf growth in wheat (Savicka & Škute, 2012). In a recent study, Al-Busaidi, Ahmed, and Chikara (2012) observed that high atmospheric temperature causes significant water loss which negatively influenced growth and biomass production in the bio-fuel plant (Jatropha curcas L.). Stunted growth has also been reported in alfalfa (Medicago sativa L.) plants exposed to high temperature (Mingpeng et al., 2010). High temperatures caused significant reductions in shoot dry mass, relative growth rate, and net assimilation rate in maize (Zea mays L.), pearl millet (Pennisetum glaucum L.), and sugarcane (Saccharum officinarum L.; Ashraf & Hafeez, 2004; Wahid, 2007). A major impact of high temperature on shoot growth is a severe reduction in the first internode length resulting in
premature death of plants (Hall, 1992). In cotton (Gossypium hirsutum L.), plants grown at 35/27 and 40/32°C, the length of fruiting branches decreased by about 25% due to shortened branch internodes (Reddy, Baker, & Hodges, 1990). Sugarcane plants grown under high temperatures exhibited smaller internodes, increased tillering, early senescence, and reduced total biomass (Ebrahim, Zingsheim, El-Shourbagy, Moore, & Komar, 1998). Emerging cotton seedlings had poorly developed roots and leaf burn, especially on younger leaves in response to heat stress (Lather, Saini, & Punia, 2001). Heat-induced chlorosis has been reported in maize (Karim, Fracheboud, & Stamp, 1997), wheat (Almeselmani, Deshmukh, & Sairam, 2009), mungbean (Kumar et al., 2011), and chickpea (Kumar et al., 2013). The negative effects of heat stress during vegetative and reproductive growth stages using agronomic, phenological, morphological, and physiological assessment have been studied in crops such as rice (Oryza sativa L.; Weerakoon, Maruyama, & Ohba, 2008) and cotton (Cottee, Tan, Bange, Cothren, & Campbell, 2010). During high temperatures, especially high night-time temperatures, tiller number decreased while shoot elongation was promoted in wheat plants (Johkan, Oda, Maruo, & Shinohara, 2011). In maize, high-temperature treatment (35/27°C day/night) promoted vegetative growth and plant biomass production (Suwa et al., 2010).

2.2. Reproductive growth

The reproductive stage is extremely sensitive to heat stress and suffers loss of buds, flowers, fruits (pods, siliqua, spikes, etc.), and seeds resulting in severe reductions in crop productivity (Thakur, Kumar, Malik, Berger, & Nayyar, 2010; Zinn, Tunc-Ozdemir, & Harper, 2010). Damage to male or female organs is determined at microsporogenesis or megasporogenesis stages (Devasirvatham et al., 2012; Nayyar, Bains, & Kumar, 2005; Figure 2).

Reproductive processes are adversely affected by high temperature, which causes structural and functional abnormalities leading to failure of pollen germination and pollen tube growth, loss of ovule viability, altered stigmatic and style positions, reduced number of pollen grains retained by the stigma, loss of stigma receptivity, impaired fertilization and post-fertilization processes, and abnormal growth of the endosperm, pro-embryo and fertilized embryo (Foolad, 2005; Zinn et al., 2010). Various reproduction-related events affected by heat stress are shown in Figure 3.

2.2.1. Flowering

Heat stress affects flowering by reducing flower number and size, and causing deformed floral organs (Morrison & Stewart, 2002; Takeoka, Hiroi, Kitano, & Wada, 1991) leading to loss of flowers and young pods and hence reduced yield (Saxena, Saxena, & Mohamed, 1988), as observed in mungbean and chickpea (Tickoo, Gajjar, & Manji, 1996), common bean (Phaseolus vulgaris L.; Suzuki, Tsukaguchi, Takeda, & Egawa, 2001), and rapeseed (Brassica napus L.; Angadi et al., 2000). Hall (1992) reported cowpea (Vigna unguiculata L. Walp) to be susceptible to high night temperatures during early flowering and pod set which suppressed pod set due to anther indehiscence and low pollen viability (Warrag & Hall, 1984). However, in pea, day temperature has a greater effect than night temperature on dry matter production (Stanfield, Ormrod, & Fletcher, 1966). Exposure to high temperature (32/27°C) for 10 days before and during anthesis reduced pod set in common beans (Gross & Kigel, 1994), which is in agreement with similar studies on cowpea (Hall, 1992), peanut (Arachis hypogaea L.; Prasad, Craufurd, & Summerfield, 1999), apricot (Prunus armeniaca L.; Rodrigo & Herrero, 2002), and sweet cherry (Prunus avium L.; Hedhly, Hormaza, & Herrero, 2007). Brown and Zeiher (1998) reported several flower abnormalities such as smaller flowers, asynchronous development of male and female reproductive structures, failure of anthers to release pollen and the presence of elongated stigmas in cotton plants under heat stress (above 32°C). Heat stress during the reproductive phase in legumes is generally linked with reduced or no pollination, and abscission of flower buds, flowers, and pods with substantial yield loss (Nakano, Kobayashi, & Terauchi, 1998).

2.2.2. Male gametophyte development

Generally, pollen grain development is more sensitive to heat stress, at all stages, compared to the female gametophyte as reported in maize (Herrero & Johnson, 1980), cowpea (Ahmed, Hall, & DeMason, 1992), chickpea (Clarke & Siddique, 2004; Devasirvatham et al., 2012, 2013; Kaushal et al.,...
The number and morphology of pollen grains, anther dehiscence, pollen viability, metabolism, and composition are affected by heat stress, as observed in common beans (Gross & Kigel, 1994), groundnut (A. hypogaea L.; Prasad et al., 1999), soybean (Djanaguiraman, Prasad, Boyle, & Schapaugh, 2013; Koti, Reddy, Kakani, Zhao, & Reddy, 2005), and chickpea (Devasirvatham et al., 2013). Endo et al. (2009) found that although high-temperature-treated pollen grains had a normal round shape, some tapetal functions, and pollen adhesion to the stigma and its subsequent germination were negatively affected. In chickpea, reduced pollen germination and tube growth in the style was observed in the heat-sensitive genotype ICC 5912 at 35/20°C due to sterile pollen (Devasirvatham, Tan, Trethowan, Gaur, & Mallikarjuna, 2010; Kaushal et al., 2013). Recently, Djanaguiraman et al. (2013) observed significant reductions in in vitro pollen germination in soybean plants when exposed to 38/28°C for 14 days at flowering. In cowpea, anthers were rendered indehiscent under heat stress (33/30°C) condition which was attributed to degeneration of the tapetal layer (Ahmed et al., 1992). Heat stress decreased the concentration of soluble sugars in the anther walls of developing and mature pollen grains in cowpea (Ismail & Hall, 1999) and the findings were further confirmed by Suzuki et al. (2001) in common bean.

Female gametophyte development
Female gametophytic tissue is less sensitive to heat stress than male gametophytic tissue (Devasirvatham et al., 2012, 2013; Kaushal et al., 2013; Saini & Aspinall, 1981). Saini, Sedgley, and Aspinall (1983) reported that heat stress (30°C) during meiosis in wheat can reduce yield due to abnormal ovary development resulting in reduced pollen growth and seed set. Heat stress can potentially harm style length and induce abnormalities in ovary development, as reported in mango.
(Mangifera indica L.; Sukhvibul, Whiley, Smith, Hetherington, & Vithanage, 1999), chickpea (Srinivasan, Saxena, & Johansen, 1999), and apricot (Rodríguez & Herrero, 2002; Table 1). The pistil is sporophytic tissue which provides nutrition to developing male and female gametophytes; a lack of nutrients from the style to the growing pollen tube, possibly due to lack of transport, might also contribute toward impaired tube growth (Snider, Oosterhuis, Loka, & Kawakami, 2011). Stigma receptivity significantly reduced at 40/30 and 45/35°C in chickpea (Kumar et al., 2013). A reduction in carbohydrate reserves and ATP production in the style resulted in reduced photosynthesis in cotton under heat stress (38/20°C) (Snider, Oosterhuis, Skulman, & Kawakami, 2009). Unfavorable high temperature (30°C) reduced ovule number and viability in common beans (Suzuki et al., 2001) and Arabidopsis (Arabidopsis thaliana L. Heynh; Whittle, Otto, Johnston, & Krochko, 2009). Reduced length of stigmatic receptivity under temperature stress has been reported in sweet cherry (Hedhly, Hormaza, & Herrero, 2003) and peach (Prunus persica L. Stokes; Hedhly, Hormaza, & Herrero, 2005). High temperature results in an exserted style which in turn inhibits pollen germination and thus the reproductive process (Wahid et al., 2007). Abnormal embryo sac development reduced seed set in rapeseed under heat stress (32/26°C) (Polowick & Sawhney, 1987, 1988). When the temperature increased from 5 to 25°C, reduced ovule length was observed in sweet and sour cherry under controlled growth temperature of 20°C (Postweiler, Stösser, & Anvari, 1985). Likewise, degeneration or suppression of the embryo sac was observed in response to heat stress in peach (Kozai et al., 2004) and rapeseed (Polowick and Sawhney 1987, 1988). Young, Wilen, and Bonham-Smith (2004) studied the response of both microgametophytes and megagametophytes to heat stress (28/23°C) in rapeseed. When male gametes were subjected to heat stress (35/18°C) and female gametes were unaltered, seed set decreased by 88% whereas, in case of unaltered male gametes and heat-stressed female gametes, seed set decreased by 37% but when both male and female gametes were subjected to high temperature, seed set loss was the highest, i.e. it decreased by 97%.

2.2.4. Fertilization

Depending on the time, duration, and severity, heat stress could limit fertilization by inhibiting male (Jain, Prasad, Boote, Hartwell, & Chourey, 2007) and female (Saini et al., 1983; Snider et al., 2009) gametophytic development. Heat stress reduces fertilization efficiency due to increased oxidative
stress in the pistil, reduced soluble carbohydrate and ATP content in the pistil, and decreased leaf photosynthesis, as observed in studies on mungbean (Suzuki et al., 2001), cotton (Snider et al., 2009, 2011), soybean (Board & Kahlon, 2011), and chickpea (Kumar et al., 2013). High-temperature stress (>30°C) from early meiosis to pollen maturity has a damaging effect on the viability of pollen grains in wheat, resulting in failure of fertilization and thus reduced seed set (Saini & Aspinall, 1981). Increased temperature mid-anthesis decreased the grain number per year at maturity in spring wheat (Ferris, Ellis, Wheeler, & Hadley, 1998), indicating the heat sensitivity of fertilization and grain setting.

2.2.5. Grain filling and yield
Heat stress causes yield loss in legumes, cereals, and other crops due to poor vegetative and reproductive development (Hall, 2004; Paulsen, 1994). Heat stress may accelerate seed filling, thereby reducing the duration of this stage and limiting yield potential (Boote et al., 2005). The relative sensitivity of reproductive stages such as flowering and seed filling to heat stress may vary according to crop species (Sung, Kaplan, Lee, & Guy, 2003). Yield reductions reported in many food crops like cowpea (Hall, 1992), rice (Baker, Allen, & Boote, 1992; Islam, 2011; Peng et al., 2004), canola (Morrison, 1993), pea (Guilioni, Wery, & Tardieu, 1997), common beans (Prasad et al., 1999; Rainey & Griffiths, 2005), peanut (Prasad et al., 1999), wheat (Guedira, McCluskey, MacRitchie, & Paulsen, 2002; Zhong et al., 2013), soybean (Board & Kahlon, 2011), lentil (Barghi, Mostafaii, Peighami, & Zakaria, 2012), and chickpea (Kumar et al., 2013) have been attributed to reductions in seed filling.

In response to heat stress, Shah and Paulsen (2003) observed decreased leaf area, and shoot and grain biomass in wheat. Reduced grain yield and grain weight has been reported in wheat at temperatures above 25°C (Blumenthal, Bekes, Gras, Barlow, & Wrigley, 1995; Gibson & Paulsen, 1999; Refay, 2011; Wardlaw, Blumenthal, Larroque, & Wrigley, 2002). Exposure of wheat plants to heat stress post-anthesis reduced grain number per spike, kernel weight per spike, harvest index and yield (Dias & Lidon, 2009; Taghizadeh & Sharifi, 2010) and agreed with earlier reports on peanut (Prasad, Craufurd, Summerfield, & Wheeler, 2000). Similarly, subjecting wheat to heat stress at anthesis and grain filling also reduced grain yield (Farooq, Bramley, Palta, & Siddique, 2011; Gibson & Paulsen, 1999). In another study, reduced yield in wheat under heat stress was due to the production of immature grains as a result of increased dark respiration (Johkan et al., 2011). Heat stress (15/10°C and 21/16°C day/night) during grain filling resulted in smaller and shrivelled grains which further reduced yield in wheat (Maçãs, Gomes, Dias, & Coutinho, 2000). In tomato, heat stress adversely affected pollen and anther development which, in turn, contributed to reduced fruit set (Peet, Sato, & Gardner, 1998). Exposing chickpea to high temperatures during flower and pod development markedly reduced seed yield and harvest index (Gan et al., 2004; Kumar et al., 2013; Wang, Gan, Clarke, & McDonald, 2006) and plants were forced to mature earlier under high temperature, thereby further reducing the yield (Kausaloh et al., 2013; Krishnamurthy et al., 2011). Likewise, reduced grain yield in maize under heat stress has been reported by Khodarahmpour (2011). Suwa et al. (2010) attributed it to effects on sink activity rather than source activity. In canola (Brassica spp.), reduced seed yield was reportedly due to infertile pods, reduced seed weight, and less seeds per pod (Sinsawat, Leipner, Stamp, & Fracheboud, 2004). In sorghum (Sorghum bicolor L.) under heat stress, filled seed weight and seed size decreased by 53 and 51%, respectively, hence reducing yield (Mohammed & Tarpley, 2010).

2.3. Physiology

2.3.1. Photosynthesis
Photosynthesis is the most thermo-sensitive part of plant function (Kim & Portis, 2005; Wise et al., 2004) and hence is adversely affected at supra-optimal temperatures. Photosynthesis tolerates temperatures of 30-35°C, but is adversely affected above 40°C (Schuster & Monson, 1990). Chloroplast stroma and thylakoid membranes are damaged by high temperatures (Wang et al., 2010; Wise et al., 2004). Photosystem II (PSII) in the light reaction (Heckathorn et al., 2002) and RUBISCO (ribulose1,5-bisphosphate carboxylase/oxygenase) activase in the Calvin cycle (Crafts-Brandner & Salvucci, 2000) are both thermo-labile. Heat stress thus impairs the electron transport
chain (ETC) and affects the activation and activity of enzyme RUBISCO (Ahmad, Diwan, & Abrol, 2010; Prasad, Boote, Vu, & Allen, 2004). Although photosystem I and II both are damaged under high temperature, PSII is more sensitive to heat stress. All this may lead to the production of ROS (Camejo et al., 2006; Guo, Yu, Tao, Su, & Zhang, 2009) which at very high levels may result in severe cell injury and even cell death (Apel & Hirt, 2004). The reaction center and donor side of PSII

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soybean leaves exhibited inconsistent changes under high-temperature treatments (Li, Fu, Huang, & Yu, 2009; Mathur, Jajoo, Mehta, & Bharti, 2011), whereas net photosynthesis (Pn) was inhibited at leaf temperatures above 38°C in maize (Crafts-Brandner & Salvucci, 2002). Wheat plants subjected to heat stress of 40–55°C, even for a short period, reduced photosynthetic activity (Kaur, Sheoran, & Nainawatee, 1988). In chickpea, chlorophyll content and photochemical efficiency were inhibited by increased temperatures (Kumar et al., 2013). Long-term high-temperature stress (45 days, 40/30°C day/night) reduced photosynthetic rate, Fv/Fm, and antioxidant enzymes activities in sorghum leaves (Djanaguiraman, Prasad, & Seppanen, 2010; Table 2). The rate of photosynthesis in maize was unaffected by heat stress (Suwa et al., 2010), but in tomato, Islam (2011) reported reduced photosynthetic rates with high temperature (32°C) at both pre-flowering and flowering stages. In potato (Solanum tuberosum L.), heat stress damaged the antenna complex of PSII and reduced photosynthetic behavior. In tobacco (Nicotiana tabacum L.) leaves, heat stress (43°C for 2 h) decreased the rate of photosynthesis by 38% compared with an optimal temperature (25°C; Tan, Meng, Brestic, Olsowska, & Yang, 2011). Greer and Weedon (2012) observed that the average rates of photosynthesis in grapes (Vitis vinifera L.) leaves decreased by 60% with increasing temperature from 25 to 45°C, which was attributed to 15–30% stomatal closure. Fingered citron (Citrus medica var. Sarcodactylis swingle) leaves exposed to 40 and 45°C for 6 h significantly reduced their photosynthetic rate (Chen, Zheng, Li, & Guo, 2012), while there was no effect on photosynthetic capacity at 35°C for 6 h or 40°C for 4 h. Heat stress has reportedly reduced chl content, chl a/b ratio, and chl:carotenoid ratio in Solanum spp. (Aien, Khetarpal, & Pal, 2011) and wheat (Reda & Mandoura, 2011); however, in sugarcane, heat stress increased chlorophyll a:b ratio (Wahid, 2007). Another study on wheat revealed that the amount of chlorophyll a, b, and carotenoids did not significantly change at 30/25°C, but decreased at higher temperatures 35/30°C, while the chl a/b and chlorophyll/ carotenoids ratios remained unaltered under heat stress (Amirjani, 2012). Kaushal et al. (2013) reported significantly reduced RUBISCO activity and sucrose content in leaves due to heat stress (>32/20°C) in all of the tested chickpea genotypes (heat-tolerant ICC 15614, ICCV 92944 and heat-sensitive ICC 5912, ICC 10685). However, tolerant genotypes had 20–38% higher RUBISCO activity and 21–30% higher sucrose content than their sensitive counterparts.

2.3.2. Membranes
Plasma membranes are considered the most heat-sensitive among all components of a plant cell as they are the primary sites for injury (Blum, 1988). During heat injury, the membranes of sensitive plants undergo a phase transition from solid–gel structure to flexible liquid–crystalline structure. This denaturation of proteins or increase in unsaturated fatty acids results in increased fluidity of the membrane (Savchenko, Klyuchareva, Abramchik, & Serdyuchenko, 2002). Highly unsaturated fatty acids are less rigidly packed into a membrane due to the non-linearity of fatty acid chains introduced by the presence of double bonds (Cyril, Powell, Duncan, & Waird, 2002; Horváth et al., 2012), which further results in activation of lipid-based signaling cascades, increased Ca^{2+} influx, and cytoskeletal reorganization (Bita & Gerats, 2013). During heat stress, the injury can be assessed by the loss of membrane integrity that is reflected in organic and inorganic ion leakage from cells (Levitt, 1980; Salvucci & Crafts-Brandner, 2004; Sullivan, 1972). Severe cellular injury and even cell death may occur within minutes under heat stress, which has been attributed to a catastrophic collapse of cellular organization (Schoffl et al., 1999). Electrolyte leakage is thus a measure of reduced cell membrane thermo-stability and reflects stress-induced changes (Liu & Huang, 2000; Xu, Li, Zhang, Wei, & Cui, 2006). Electrolyte leakage is influenced by plant/tissue age, sampling organ, developmental stage, growing season, degree of hardening, and plant species. The maintenance of high membrane thermo-stability is thus related to thermo-tolerance (Howarth, Pollock, & Peacock, 1997). In soybean, heat stress enhanced membrane permeability and electrolyte leakage, which in turn reduced the ability of the plasma membrane to retain solutes and water (Lin, Roberts, & Key, 1984). Likewise, higher membrane damage was observed in sensitive chickpea genotypes at 40/30°C which was further aggravated at 45/35°C (Kumar et al., 2013). When compared with other grain legumes such as pigeonpea, groundnut, and soybean, chickpea was the most sensitive in terms of membrane thermo-stability and PSII function (Srinivasan, Takeda, & Senboku, 1996). Membrane thermo-stability has thus been successfully employed to assess thermo-tolerance in many food crops worldwide.
Heat-induced electrolyte leakage has been reported in soybean (Martineau, Specht, Williams, & Sullivan, 1979), sorghum (Sullivan & Ross, 1979), potato and tomato (Chen, Shen, & Li, 1982), wheat (Dias & Lidon, 2009; Saadalla, Quick, & Shanahan, 1990; Savicka & Škute, 2010), cowpea (Ismail & Hall, 1999), cotton (Rahman, 2004), barley (Hordeum vulgare L.; Wahid & Shabbir, 2005), rice (Mohammed & Tarpley, 2010), and mungbean (Egorova, Yin-Shan, & Hwa, 2011; Kumar et al., 2011).

2.2.3. Respiration
Heat stress affects respiration as it retards or increases mitochondrial activity depending on the crop (Paulsen, 1994; Stone, 2001). Initially, the rate of respiration increases exponentially with increasing temperature but beyond threshold levels, respiration decreases due to damage to respiratory mechanisms (Prasad, Staggenborg, & Ristic, 2008). Decreased respiration under high temperature has been reported in chickpea (Kumar et al., 2013), and was most likely due to the impaired structure and function of mitochondria and proteins and the effect on the electron transport rate. The rate of both photorespiration and dark respiration of cotton leaf increased with increasing temperature (Salvucci & Crafts-Brandner, 2004). Prasad et al. (1999) found that increase in respiration rate especially during the night can increase ROS, resulting in cell damage and reduced pollen viability. Respiration, particularly the mitochondrial ETC, is responsible for the production of ROS in the dark (Kromer, 1995).

### Table 2. Impact of heat stress on photosynthesis in some crops

<table>
<thead>
<tr>
<th>Plant</th>
<th>Temperature</th>
<th>Effects</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soybean (<em>Glycine max</em>)</td>
<td>42–43°C</td>
<td>Damaged PSII; Decreased Fv/Fm</td>
<td>Ferris et al. (1998) and Li et al. (2009)</td>
</tr>
<tr>
<td>Broadbean (<em>Vicia faba</em>)</td>
<td>42°C</td>
<td>Decreased photosynthesis</td>
<td>Hamada (2001);</td>
</tr>
<tr>
<td>Oak (<em>Quercus pubecens</em>)</td>
<td>45°C</td>
<td>Photosynthesis reduced by 90%</td>
<td>Haldimann and Feller (2005)</td>
</tr>
<tr>
<td>Rice (<em>Oryza sativa</em>)</td>
<td>33°C for 5 d</td>
<td>Decreased photosynthesis</td>
<td>Asseng, Cao, Zhang, and Ludwig (2009); Hurkman, Vensel, Tanaka, Whitehand, and Altenbach (2009)</td>
</tr>
<tr>
<td>Sorghum (<em>Sorghum bicolor</em>)</td>
<td>40/30°C for 45 d</td>
<td>Decreased photosynthetic rate</td>
<td>Djanaguiraman et al. (2010)</td>
</tr>
<tr>
<td>Potato (<em>Solanum spp.</em>)</td>
<td>Above 20°C</td>
<td>Decreased chlorophyll content and chl a/b ratio</td>
<td>Aien et al. (2011)</td>
</tr>
<tr>
<td>Tomato (<em>Lycopersicon esculentum</em>)</td>
<td>32°C</td>
<td>Decreased chlorophyll content and chl a/b ratio</td>
<td>Islam (2011)</td>
</tr>
<tr>
<td>Wheat (<em>Triticum aestivum</em>)</td>
<td>45°C and 55°C</td>
<td>Photosynthesis decreased by 5.8 and 1.12%, respectively</td>
<td>Reda and Moudoura (2011)</td>
</tr>
<tr>
<td>Grapes (<em>Vitis vinifera</em>)</td>
<td>25–45°C</td>
<td>Reduced photosynthesis (by 60%) and stomatal conductance</td>
<td>Tan et al. (2011), Greer and Weedon (2012)</td>
</tr>
<tr>
<td>Tomato (<em>Lycopersicon esculentum</em>)</td>
<td>35°C for 2 h</td>
<td>Decreased chi a and b</td>
<td>Jie, Xiaodong, Tianlai, and Zaigiang (2012)</td>
</tr>
<tr>
<td>Chickpea (<em>Cicer arietinum</em>)</td>
<td>45/35°C</td>
<td>Inhibited chlorophyll content and photochemical efficiency</td>
<td>Kumar et al. (2013)</td>
</tr>
<tr>
<td>Chickpea (<em>Cicer arietinum</em>)</td>
<td>Above 32/20°C</td>
<td>Decreased RUBISCO and sucrose activity</td>
<td>Kaushal et al. (2013)</td>
</tr>
</tbody>
</table>
2.3.4. Water imbalance

Heat stress is frequently associated with rapid loss of water from the plant surface resulting in dehydration (Simoes-Araujo, Rumjanek, & Margis Pinheiro, 2003), as reported in wheat, sorghum (Machado & Paulsen, 2001), tomato (Mazorra, Nunez, Echerarria, Coll, & Sánchez-Blanco, 2002), sugarcane (Wahid & Close, 2007), and beans (Koini et al., 2009). Heat stress affects water availability, uptake, and its translocation along with ions and organic solutes across the plasma membrane resulting in impaired photosynthesis (especially damage to PSII) and reduced leaf osmotic potential (Huve, Bichele, Tobias, & Niinemets, 2005). Water loss is more frequent during the day than at night due to enhanced transpiration reducing water potential (Tsukaguchi, Kawamitsu, Takeda, Suzuki, & Egawa, 2003). Heat stress is closely related to the rate of transpiration, so evaporation from the leaf surface increases leaf cooling. Leaves subjected to heat stress exhibit increased transpiration once the threshold temperature is reached (Levitt, 1980). The ability to maintain high stomatal conductance at high temperatures promotes transpirational heat dissipation, as observed in heat-tolerant bread and durum wheat genotypes (Dias et al., 2011) and various heat-tolerant and sensitive chickpea genotypes (Kaushal et al., 2013). However, under severe heat stress, loss of stomatal conductance has been reported in tobacco (Tan et al., 2011). Plants maintain nearly stable water relations regardless of temperature when moisture is adequate, but high temperature strongly affects water relations when water is limiting. Hence, drought and heat stress in combination have more detrimental effects on plant growth and development as observed at grain filling in wheat (Nicolas, Gleadow, & Dalling, 1984). Constant hydraulic resistance to water flow may substantially reduce water absorption and transpiration (Morales et al., 2003), as observed in wheat and sorghum. Both these crops were grown in well-watered and water-stressed soils under control conditions in growth chambers at 15/10, 25/20, 35/30, and 40/35°C (day/night). Observations on soil water content, leaf relative water content, leaf water potential, leaf osmotic potential, leaf turgor potential, and osmotic adjustment at two-day intervals remained nearly constant at all temperatures in well-watered soil but were affected strongly by high temperature in water-stressed soil (Machado & Paulsen, 2001).

2.3.5. Oxidative stress and antioxidant defense

Increased formation of ROS is a general feature of abiotic stress, such as extreme temperature, high light, and drought (Lopez-Delgado, Dat, Foyer, & Scott, 1998). Heat stress induces production of ROS, including singlet oxygen (\( ^1O_2 \)), superoxide radical (\( O_2^- \)), hydrogen peroxide (\( H_2O_2 \)), and hydroxyl radical (\( OH^- \)), which at very high level are responsible for oxidative stress and lead to severe cell injury and even cell death (Apel & Hirt, 2004; Potters, Pasternak, Guisez, Palme, & Jansen, 2007). Oxidative stress is a common adverse effect of heat stress in cells due to the production of superoxides, lipid peroxides, and hydrogen peroxides (Yin, Chen, & Yi, 2008). Major sites of ROS production under heat stress include PSI and PSII of chloroplasts, plasma membrane, mitochondria, peroxisomes, apoplasts, and endoplasmic reticulum, while a small amount of ROS are also produced in microbodies (Soliman, Fujimori, Tose, & Sugiya, 2011). For example, heat shock treatments at different temperatures (22, 30, 35, and 40°C) to 8-day-old wheat seedlings resulted in the accumulation of \( H_2O_2 \) (Kumar, Gupta, & Nayyar, 2012). ROS have toxic potential effects as they can induce protein oxidation, DNA damage, lipid peroxidation of membranes (malondialdehyde content), and destruction of pigments (Apel & Hirt, 2004; Hasanuzzaman, Hossain, da Silva, & Fujita, 2012; Xu et al., 2006). Heat stress-induced membrane peroxidation and aggravated membrane injury was observed in soybean (Young et al., 2004), cotton (Mohammed & Tarpley, 2010), wheat (Savicka & Škute, 2010), rice and maize (Kumar, Sirhindi, Bhardwaj, Kumar, & Arora, 2012), and sorghum (Tan et al., 2011). Tolerant plants tend to combat ROS production by inducing an antioxidant system consisting of enzymatic and non-enzymatic components. The enzymatic system includes superoxide dismutase (SOD), catalase (CAT), peroxidase (POX), glutathione reductase (GR), and ascorbate peroxidase (APX) and the non-enzymatic system includes reduced glutathione (GSH), ascorbic acid (ASA), tocopherols, and carotenoids. SOD is a primary antioxidant enzyme, which converts \( O_2^- \) to \( H_2O_2 \) and \( O_2 \). CAT breaks down \( H_2O_2 \), APX uses ascorbate as a substrate to neutralize \( H_2O_2 \) and GR reduces glutathione disulfide (GSSG) to the sulfhydryl from GSH. Babu and Devraj (2008) reported that heat stress drastically reduced the activities of GR and CAT in french beans. Likewise, in chickpea, the oxidative stress assessed by measuring the activity of enzymatic antioxidants such as SOD, CAT, APX, and GR
elevated in plants grown at 40/35°C but decreased at 45/40°C (Kaushal et al., 2011); similar findings have been observed in sorghum (Djanaguiraman et al., 2010). Almeselmani et al. (2009) observed that the activity of SOD, APX, CAT, GR, and POX increased significantly at all stages of growth in wheat cultivar C306 (HT) in response to heat stress, whereas CAT, GR, and POX activity decreased significantly in the susceptible cultivar PB343. In a similar fashion, exposure of a thermo-tolerant (BPRS426) and thermo-sensitive (NPJ119) Indian mustard (Brassica juncea) genotype to high temperature (45°C) revealed higher SOD, CAT, APX, and GR activities in tolerant genotypes (Rani, Dhawan, Jain, Chhabra, & Singh, 2013). In lentil, Chakraborty and Pradhan (2011) observed initial increases in CAT, APX, and SOD activities as temperature increased from 20 to 50°C, before declining at 50°C while POX and GR activities decreased at all temperatures. In pearl millet plantlets, heat stress significantly increased SOD, CAT, and peroxidase activities (Kolupaev, Yastreb, Karpets, & Miroshnichenko, 2011). Under heat stress conditions, activity of antioxidant enzymes such as SOD, APX, POX, and CAT increased, while H$_2$O$_2$ and MDA decreased, which increased shoot weight in tomato (Ogweno et al., 2008). These studies imply that maintaining redox homeostasis is vital to tolerate mild heat stress, while severe stress, even for short periods, impairs this ability. One approach to induce heat tolerance requires a thorough understanding of the expression of antioxidants in heat-stressed plants of various crops, which may be a significant step toward improving heat tolerance.

3. Threshold temperature of various crops
Threshold temperature is the temperature above which the growth and development of a crop ceases. Every crop has its own threshold temperature at which maximum vegetative and reproductive growth occurs (Hatfield et al., 2011; Zinn et al., 2010). If the temperature of a crop exceeds the threshold range, then its seed germination, seedling and vegetative growth, flowering, fruit set, and fruit ripening are adversely affected. The threshold temperature range during different stages of plant growth and development of some legumes, cereals, and other crops are summarized below.

3.1. Legumes
Legumes rank third in world crop production and form an important part of world production after cereals and oilseeds (Popelka, Terryn, & Higgins, 2004). Legumes are major sources of proteins and complement the staple cereals in diets by providing proteins, essential amino acids, micronutrients, vitamins, minerals, and fibers (Gowda, Upadhaya, Sharma, Varshney, & Dwivedi, 2013; Shanmugasundaram, 2003). Legumes are also required for crop rotation worldwide but are temperature susceptible (McDonald & Paulsen, 1997). Legumes, including chickpea, common bean, cowpea, groundnut, pigeon pea (Cajanus cajan L.), broad beans/faba beans, soybean, and many other podded plants, are grown across the Mediterranean and subtropical countries for food security, improved nutrition and to maintain soil fertility (Reddy, Bhatnagar-Mathur, et al., 2012). Legumes play an important role in nitrogen fixation due to their symbiotic association with several rhizobial species thereby increasing soil fertility (Abd-Alla, Issa, & Ohyama, 2014). Nodule formation, function, and structure along with the nitrogen fixation efficiency of legumes are affected under temperature stress (Kurdali, 1996; Minchin, Summerfield, Hadley, & Roberts, 1980) as reported for chickpea (Rodrigues, Laranjo, & Oliveira, 2006). Daily maximum temperatures above 25°C are considered the threshold level for heat stress in cool-season legume crops. Productivity of these food legumes is affected by both high and low temperature stresses. In legumes, heat stress during post-anthesis results in poor pollen germination on the stigma and reduced pollen tube growth in the style (Taiwar & Yanagihara, 1999), reduced or no fertilization (Ormrod, Woolley, Eaton, & Stobbe, 1967) and embryo abortion (Gross & Kigel, 1994). High-temperature stress is an important limiting factor in the production of faba bean, chickpea, and lentil (Ibrahim, 2011). Critical temperatures appear to be higher in chickpea than in lentil, pea, or faba beans (Saxena et al., 1988).

3.1.1. Common bean (P. vulgaris L.)
Common beans originated in the highlands of Central America and the Andes and are adapted to moderate temperatures (Wallace, 1980). Beans have been called the “poor man’s meat.” Many crop species are damaged by high temperatures, and heat stress particularly affects the development of reproductive organs (Hall, 1992). High temperature has caused abortion of floral buds and flowers in
several species of beans (Konsens, Ofir, & Kigel, 1991). The physiological stress that results when flowering beans are subjected to high night temperatures (20°C), and, to a lesser degree, high day temperatures (above 30°C) results in excessive abscission of reproductive organs and reduced crop yields (Kigel, Konsens, & Ofir, 1991; Konsens et al., 1991). Studies have indicated that the reproductive stage is more sensitive to heat stress than the vegetative stage (Giorno et al., 2013). Heat stress is more damaging to the male reproductive phase (microsporogenesis) than the female reproductive phase (megasporogenesis; Dickson & Boetegger, 1984; Monterroso & Wien, 1990); during anthesis, megasporogenesis becomes more sensitive under heat stress (Gross & Kigel, 1994). Beans yield has a threshold temperature of 24°C (Laing, Jones, & Davis, 1984).

3.1.2. Mungbean (P. aureus Roxb.)
Mungbean originated in India and is an important legume crop cultivated mainly in the Indian subcontinent (Mohammad, Shehzadi, Shah, & Shah, 2010). The optimum temperature for growth of mungbean is 28–30°C (Poehlman, 1991) and temperatures above these limits are expected to drastically inhibit its potential yield. Tickoo et al. (1996) reported that mungbean thrives best at 30–40°C but above 40°C, there is significant flower shedding.

3.1.3. Pea (P. sativum L.)
Pea is a cool-season food legume grown worldwide. Stanfield et al. (1966) reported that pea yield is affected at temperatures above 16°C, Nonnecke, Adedipe, and Omrod (1971) suggested that the critical temperature for pea production is 27°C, and Fletcher, Omrod, Maurer, and Stanfield (1966) considered 20–21°C best for pea production. According to Mahoney (1991), the optimum temperature for vegetative growth of pea is 15–20°C. Humphrey (1990) reported that temperatures above 25.6°C depressed seed yield in peas, while exposure to heat stress (>30°C) at flowering and podding significantly reduced seed yield. Ridge and Pye (1985) reported yield reductions in some pea cultivars of 0.6 t ha⁻¹ for every 1°C increase at flowering time. Deactivation of the RUBISCO enzyme in pea has been reported at temperatures above 38°C (Haldimann & Feller, 2005).

3.1.4. Soybean (G. max L. Merr.)
Soybean originates from tropical and subtropical regions, as it requires warm growing conditions; however, soybean yield reportedly decreased by 13% with a 1°C rise in temperature (Lobell & Field, 2007). Exposure of soybean to temperatures above 35°C inhibited pollen germination and pollen tube growth with complete failure reported at 47°C (Koti, Reddy, Kakani, Zhao, & Reddy, 2004; Salem, Kakani, Koti, & Reddy, 2007). Flower initiation decreased above 32°C and seed formation was delayed at 30–40°C (Thomas, Boote, Allen, Gallo-Meagher, & Davis, 2003). Soybean yield decreased by 27% when exposed to 35°C for 10 h (Gibson & Mullen, 1996). In soybean, post-anthesis and reproductive development thrives between 23 and 26°C (Boote et al., 2005; Boote, Jones, & Hoogenboom, 1998) with 30.2°C considered optimum for pollen germination (Boote et al., 2005). Maximum pollen tube growth was reportedly at 36.1°C (Hatfield et al., 2008).

3.1.5. Peanut/groundnut (A. hypogaea L.)
Groundnut is an important oilseed legume grown particularly in semi-arid regions of India and Africa (FAO, 2001). Some workers have proposed that heat stress (30–35°C) does not affect photosynthesis and vegetative growth (Prasad et al., 2000; Talwar, Takeda, Yashima, & Senboku, 1999). In contrast, some other studies have indicated that reproductive phase particularly microsporogenesis and anthesis of groundnuts are quite sensitive stages to higher temperature (Prasad, Craufurd, Kakani, Wheeler, & Boote, 2001).

3.1.6. Lentil (L. culinaris Medik.)
Lentil is an important food legume of South Asia, West Asia, and North Africa (Ferguson & Robertson, 1999). It is presumably the most ancient legume to have been domesticated (Bohl, Lal, & Sharma, 1993). Lentil requires a cold climate and is sown as a winter-season crop. It is very hardy and can tolerate frost and severe winters but is quite sensitive to heat. It requires cold temperatures during vegetative growth and warm temperatures at maturity; the optimum temperature for growth is
The heat sensitivity of lentil is supported by various studies worldwide (Barghi et al., 2012; Roy, Tarafdar, Das, & Kundagrami, 2012; Sinsawat et al., 2004).

### 3.2. Cereals

Increasing temperatures are threatening the yield of cereals such as rice, wheat, maize, and sorghum. With the increase in population and to maintain global food security, cereal production needs to improve substantially (Reynolds et al., 2012). Sudden increases in heat stress at grain filling reduced seed weights in cereals (rice, wheat, maize, and sorghum) more than gradual heat stress, resulting in yield loss (Wardlaw, 1994). Heat stress reduced starch, protein, and oil contents in the maize kernel (Wilhelm, Mullen, Keeling, & Singletary, 1999) and other grain quality-related attributes in other cereals (Maestri et al., 2002).

#### 3.2.1. Rice (O. sativa L.)

Rice yields are estimated to decrease by 41% by the end of the twenty-first century (Ceccarelli et al., 2010). The threshold temperature for normal growth and development of rice ranges from 27 to 32°C (Yin, Kroff, & Goudriann, 1996). Increased temperature or exposure of plants to heat stress even for short durations resulted in reduced grain yield. For every 1°C rise in temperature, grain rice yield decreased by 10% (Peng et al., 2004). Both flowering and booting stages (microsporogenesis) are highly heat sensitive (Farrell, Fox, Williams, & Fukai, 2006) with the lethal temperature for flowering >41°C. The production and viability of pollen also decreases at temperatures above 25°C (Kim, Horie, Nakagawa, & Wada, 1996; Prasad, Boote, & Allen, 2006). Complete sterility resulted in reduced yield at temperatures above 35°C (Matsui, Omasa, & Horie, 1999). The duration of grain filling decreased with temperatures above 25°C (Chowdhury & Wardlaw, 1978; Snyder, 2000).

#### 3.2.2. Wheat (T. aestivum L.)

Wheat is a winter-season crop, widely grown in tropical and subtropical regions of the world. Heat stress is an important constraint to wheat productivity at different growth stages, especially anthesis and grain filling (Rehman et al., 2009). Wardlaw, Dawson, Munibi, and Fewster (1989) reported 3–4% reductions in yield for every 1°C rise in temperature. Photosynthesis is maximized at a threshold temperature of 20–22°C, but inhibited at 30–32°C (Al-Khatib & Paulsen, 1999). The vegetative development of wheat has a threshold temperature of 20–30°C (Kobza & Edwards, 1987), whereas reproductive growth, grain yield, and single grain growth occur best at 15°C (Chowdhury & Wardlaw, 1978). The threshold temperature for anthesis and grain filling ranges from 12 to 22°C, beyond which grain yield is significantly reduced (Tewolde, Fernandez, & Erickson, 2006). Heat stress during grain filling resulted in lower yields (Guedira et al., 2002; Maçãs et al., 2000), especially with high night temperatures, i.e. above 20°C (Prasad, Dey, Shakarad, & Joshi, 2003).

#### 3.2.3. Maize (Z. mays L.)

Maize, a C$_4$ plant, is the principal staple food and world's most extensively grown cereal (Cassman, 1999; Morris, Risopoulos, & Beck, 1999). Climate change poses a serious threat to maize production and productivity (Porter, 2005; Wahid et al., 2007). Lobell, Schlenker, and Roberts (2011) reported 1% yield reduction with every °C rise above 30°C. High temperatures adversely affect the growth and development of plants leading to reduced yield (Noohi, Fatahi, & Kamali, 2009; Smith, 1996). Optimum germination and growth in maize occurs at 20–30°C and 28–31°C, respectively (Wahid et al., 2008). Heat stress increased flower abortion, caused fertilization failure, and decreased seed size (Dupuis & Dumas, 1990; Taiwar et al., 1999). The threshold temperature for leaf growth is up to 35°C while beyond 35°C is considered lethal (Dubey, 2005). However, Crafts-Brandner and Salvucci (2002) reported that photosynthesis thrives at 33–38°C and is inhibited at 45°C (Smith, 1996). Temperatures above 35°C are lethal to maize pollen viability and even short exposure of maize plants beyond the threshold temperature during flowering resulted in a significant loss of yield (Luo, 2011).

#### 3.2.4. Sorghum (S. bicolor L.)

Sorghum, a C$_4$ grass, is the fifth most economically important cereal crop grown worldwide after wheat, rice, maize, and barley (Reddy, Kumar, et al., 2012). Climate change, especially short episodes
of heat stress (above threshold temperature), is projected to affect sorghum yield considerably (AICSIP, 2012–2013). Sorghum is grown mainly in semi-arid regions of the world. Kusewa (1978) suggested that optimum germination in sorghum occurs at 22–35°C (Peacock & Heinrich, 1984), while the lethal temperature for germination is >40°C (Singh & Dhaliwal, 1972). For vegetative development, threshold temperatures range from 26 to 34°C; however, optimum reproductive development occurs at 25–28°C. Quinby, Hesketh, and Voigt (1973) indicated that temperatures of 32/28 and 32/29°C delayed floral initiation, but temperatures from 25/20 to 35/25°C increased floral initiation. Sumayao, Kanemasu, and Hodges (1977) reported a decline in photosynthesis in sorghum above 33°C, and Yan, Chen, Shao, Shao, and Zhao (2013) reported reduced leaf photosynthesis and pollen function above 48°C at night. Heat stress reduced seed filling duration, decreased seed size, and lowered seed yields in sorghum (Chowdhury & Wardlaw, 1978; Prasad et al., 2006). Increasing the temperature from 36/26 to 40/30°C delayed panicle emergence by 20 days and completely inhibited it at 44/34°C (Prasad et al., 2006). Heat stress during flowering resulted in poor pollen viability and dehiscence, reduced pollen germination and pollen tube growth leading to failed fertilization. Unfavorably high temperatures may even lead to early embryo abortion resulting in reduced seed set percentage, seed number, and seed yield (Prasad, 2010). High temperatures resulted in poor pollen germination and reduced seed set due to reduced sucrose and starch content of microspores in sorghum (Jain et al., 2007).

3.3. Some other crops

3.3.1. Cotton (G. hirsutum L.)
Cotton is a tropical crop grown in hot and semi-arid areas of the world, where temperatures may reach 48–50°C. However, with every 1°C increase in daily maximum temperature, the yield of cotton fiber harvested per hectare reportedly decreased by 110 kg ha⁻¹ (Singh, Shambhoo, Singh, & Randhir, 2007). The threshold temperature for seed germination and seedling development in cotton ranges from 28 to 30°C, whereas maximum leaf area development occurs at 26°C (Reddy, Vara Prasad, & Kakani, 2005). Threshold temperatures for pollen viability, vegetative biomass, photosynthesis, and seed size are proposed to be 32/22, 40/30, 44/34, and 36/26°C, respectively (Prasad et al., 2006). Vegetative growth is unaffected by moderately high temperatures, while the reproductive process is highly sensitive to heat stress (Reddy et al., 2005). The threshold temperature for pollen germination ranges from 28 to 37°C, while pollen tube growth needs temperatures between 28 and 32°C (Kakani et al., 2005). High-temperature stress prior to and during flowering significantly influences several reproductive processes leading to reduced fruit set in cotton. Liu et al. (2006) found that the temperature required for pollen tube growth and cotton boll retention is 27.8°C. However, Rahman (2004) reported reduced vegetative growth and boll production in cotton under heat stress (27.8°C). Oosterhuis (1999) observed that high temperatures decreased pollen viability and fertilization which was later confirmed by Burke, Velten, and Oliver (2004) who reported that the maximum pollen germination at 28°C was reduced to 40% when cotton plants were exposed to 39°C. On the other hand, Kakani et al. (2005) reported reduced pollen viability above 32°C and reduced pollen tube elongation above 29°C.

3.3.2. Brassica spp.
Rapeseed–mustard is the third most important source of edible oil next to soybean and groundnut in India, and is grown in certain tropical and subtropical regions as a cold-season crop (Shekhawat, Rathore, Premi, Kandpal, & Chauhan, 2012). The rapeseed–mustard group broadly includes Indian mustard, yellow sarson, brown sarson, raya, and toria crops. High temperatures affect plant growth and development, and therefore yield (Boyer, 1982). A 17% yield reduction has been reported in brassica plants exposed to a 1°C rise in temperature (Lobell & Asner, 2003). Heat stress in Brassica accelerated plant development and aborted flowers causing significant losses in seed yield (Rao, Jain, & Shivanna, 1992). The threshold temperature for flowering was proposed as 29.5°C by Angadi et al. (2000) beyond which seed yield decreased in B. napus L., B. rapa L., and B. juncea L. However, Shekhawat et al. (2012) suggested that the threshold temperature for flowering was 3.9–25.4°C. High mean maximum temperatures during vegetative development reduced flower numbers for all
Brassica species (Morrison & Stewart, 2002). Seed yield decreased as heat stress increased during flowering (Morrison & Stewart, 2002). The reduction in seed yield was primarily due to fewer flowers as well as fewer and smaller seeds produced per flower. A reduction in the rate of seed production occurred when Brassica spp. were exposed to 7 days of heat stress (35/15°C) during flowering (Angadi et al., 2000). Hall (1992) reported that flowering is the most sensitive stage in Brassica resulting in reduced pollen development, anthesis and fertilization leading to reduced crop yield. A rise of 3°C in the maximum daily temperature (21–24°C) during flowering reduced canola seed yield by up to 430 kg ha⁻¹ (Nuttall, Moulin, & Townley Smith, 1992).

3.3.3. Tomato (L. esculentum L.)
Tomato is an important vegetable crop grown worldwide. The threshold temperatures for vegetative and reproductive growth are about 37 and 28–30°C, respectively (Reddy, Davidonis, Johnson, & Vinyard, 1999; Reddy et al., 2005). Heat stress affects both the vegetative and reproductive stage, hampering photosynthesis and leading to reduced yield and fruit quality even when exposed for short periods above 38°C (Stevens & Rudich, 1987). Likewise, Sato, Peet, and Thomas (2000) reported that an increase in temperature from 28/22 to 32/26°C significantly reduced fruit set, but physiological processes like photosynthesis and night respiration were not affected. Reduced fruit set has been attributed to impaired pollen development under supra-optimal temperatures (Sakata & Higashitani, 2008); however, other studies have attributed this reduction to changes in the carbohydrate profile (Firon et al., 2006; Pressman, Peet, & Masonpharr, 2002; Sato et al., 2006).

3.3.4. Potato (S. tuberosum L.)
Potato productivity may decrease in tropical regions as a result of the higher temperatures as it grows best within a narrow temperature range of 18–20°C (FAO, 2008). When grown at 20–25°C, the net assimilation rate of potato decreased by 20–25% (Burton, 1972). The threshold temperature for photosynthesis in potato is 20°C, above which photosynthesis starts decreasing (Burton, 1981). Maximum biomass accumulation has also been reported at similar temperatures (Timlin et al., 2006). Prange, McRae, Midmore, and Deng (1990) reported a reduction in net photosynthesis at 30/25°C due to reduced activity of PSII. The findings were further confirmed by Havaux (2006), but the proposed threshold temperature was 38°C in this case.

A summarized list of some crops and their optimum temperature range during vegetative and reproductive periods along with the temperature at which reproductive yield failed is shown in Table 3.

4. Multiple defense responses to heat stress
Plants combat heat stress using various defense mechanisms for their survival within a physiological tolerance limit. Plants show varying responses to heat stress depending on the intensity, duration, and rate of temperature change (Wahid, 2007). The various mechanisms include changes at the molecular, cellular, biochemical, physiological, and whole-plant levels (Sung et al., 2003; Wahid, 2007; Yeh, Kaplinsky, Hu, & Charrng, 2012). It is well established that plants can respond defensively to heat stress. A preliminary treatment with a moderately elevated, non-lethal temperature can temporarily render plants more resistant to a subsequent potentially lethal heat shock and this phenomenon is known as heat acclimation. Tolerance and acclimation to heat stress are important for crops. Acquisition of thermo-tolerance is particularly important for plants that experience daily temperature fluctuations and are unable to escape to more favorable environments. Short-term avoidance or acclimation mechanisms include changing leaf orientation, transcriptional cooling, altering membrane lipid composition, reflecting solar radiation, leaf shading of tissues that are sensitive to sunburn, and extensive rooting (Lehman & Engelke, 1993; Wahid, 2007; Figure 4). Under heat stress, early maturation is closely related to smaller yield losses in many crops, which may be attributed to the engagement of an escape mechanism (Adams, Cockshull, & Cave, 2001; Toker, Lluch, Tejera, Serraj, & Siddique, 2007). At supra-optimal temperatures, heat-tolerant grass species and cultivars exhibit higher activity in the photosynthetic apparatus (Allakhverdiev et al., 2008; Ristic, Bukovnik, & Prasad, 2007) and higher carbon allocation and nitrogen uptake rates (Xu et al., 2006). Other major tolerance mechanisms—including ion transporters, osmoprotectants, free-radical scavengers, late
embryogenesis (LEA) abundant proteins and factors, ubiquitin, dehydrins involved in signaling cascades and transcriptional control—are essentially significant to counteract stress effects (Wang, Vinocur, Shoseyov, & Altman, 2004). LEA proteins can prevent protein aggregation and protect citrate synthesis under heat and drought stress (Goyal, Walton, & Tunnacliffe, 2005). When exposed to drought and heat stress, dehydrin protein expression was observed in leaves of geranium (Arora,

<table>
<thead>
<tr>
<th>Plant species</th>
<th>Threshold temperature (°C)</th>
<th>Developmental stage</th>
<th>References</th>
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<tbody>
<tr>
<td>Cereals</td>
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<td></td>
<td>15</td>
<td>Reproductive</td>
<td>Chowdhury and Wardlaw (1978)</td>
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<tr>
<td></td>
<td></td>
<td>Pollen viability</td>
<td>Dupuis and Dumas (1990)</td>
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<tr>
<td>Rice (Oryza sativa)</td>
<td>33</td>
<td>Biomass</td>
<td>Matsushima, Ikewada, Maeda, Honma, and Niki (1982)</td>
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<tr>
<td></td>
<td>25</td>
<td>Grain formation and yield</td>
<td>Baker et al. (1992)</td>
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<tr>
<td>Sorghum (Sorghum bicolor)</td>
<td>26–34</td>
<td>Vegetative</td>
<td>Maiti (1996)</td>
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<tr>
<td></td>
<td>25–28</td>
<td>Reproductive</td>
<td></td>
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<tr>
<td>Legumes</td>
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<tr>
<td>Peanut/groundnut (Arachis hypogaea)</td>
<td>29–33</td>
<td>Vegetative development</td>
<td>Bolhuis and De Groot (1959)</td>
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<td></td>
<td>23</td>
<td>Anthesis</td>
<td>Hatfield et al. (2008)</td>
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<td>Soybean (Glycine max)</td>
<td>26</td>
<td>Reproductive development</td>
<td>Boote et al. (1998)</td>
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<td></td>
<td>23</td>
<td>Post-anthesis</td>
<td>Boote et al. (2005)</td>
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<td>Pollen germination</td>
<td>Boote et al. (2005)</td>
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<td></td>
<td>36.1</td>
<td>Pollen tube growth</td>
<td>Hatfield et al. (2008)</td>
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<td>Pea (Pisum sativum)</td>
<td>15–20</td>
<td>Vegetative growth</td>
<td>Mahoney (1991)</td>
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<td></td>
<td>28–30</td>
<td>Growth</td>
<td>Poehlman (1991)</td>
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<tr>
<td>Mungbean (Phaseolus aureus)</td>
<td>10–30</td>
<td>Flowering</td>
<td>Vander Moesen (1972)</td>
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<td></td>
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<td>Pod development</td>
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<tr>
<td>Chickpea (Cicer arietinum)</td>
<td>15–30</td>
<td>Growth</td>
<td>Singh and Dhaliwal (1972)</td>
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<td></td>
<td>25</td>
<td>Reproductive growth</td>
<td>Singh and Dhaliwal (1972)</td>
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<td></td>
<td>22–25</td>
<td>Fruit growth</td>
<td>Adams et al. (2001)</td>
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<td></td>
<td>17–18</td>
<td>Fruit size</td>
<td>Adams et al. (2001)</td>
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<td>Other crops</td>
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<tr>
<td>Tomato (Lycopersicon esculentum)</td>
<td>37</td>
<td>Vegetative development</td>
<td>Reddy et al. (1999), (2005)</td>
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<tr>
<td></td>
<td>28–30</td>
<td>Reproductive development</td>
<td></td>
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<tr>
<td>Cotton (Gossypium hirsutum)</td>
<td>32/22</td>
<td>Pollen viability</td>
<td>Prasad et al. (2006)</td>
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<tr>
<td></td>
<td>40/30</td>
<td>Vegetative biomass</td>
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<td></td>
<td>44/34</td>
<td>Photosynthesis</td>
<td></td>
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<td></td>
<td>36/26</td>
<td>Seed size</td>
<td></td>
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<tr>
<td>Brassica spp.</td>
<td>29.5</td>
<td>Flowering</td>
<td>Angadi et al. (2000)</td>
</tr>
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</table>
Pitchay, & Bearce, 1998) and sugarcane (Wahid & Close, 2007). Ubiquitin and conjugated ubiquitin synthesis also emerged as important mechanisms of heat tolerance in mesquite (Prosopis spp.) and soybean under heat stress (Huang & Xu, 2008).

Heat stress alters the stability, compartmentalization, content, and homeostasis of many molecules, especially hormones (Maestri et al., 2002). In response to stresses, plants accumulate various thermo-protectants such as proline (Pro), glycine betaine (GB), and trehalose (Tre) (Hare, Cress, & Staden, 1998; Sakamoto & Murata, 2002). Heat tolerance is induced by many other phyto-hormones such as salicylic acid (SA), abscisic acid (ABA), polyamines (PA), brassinosteroids (BRs), and ethylene (Eth) and putative signaling components such as nitric oxide (NO). The level of ABA rises under heat stress, which helps in thermo-tolerance through up- or down-regulation of various genes (Xiong, Lee, Ishitani, & Zhu, 2002). The rise in ABA further increases the production of heat shock proteins (HSPs), e.g. HSPs 70 (Pareek, Singhla, & Grover, 1998). HSPs act as molecular chaperones and serve to attain a proper folding of misfolded or aggregated proteins and to prevent misfolding of proteins depending on the level and duration of heat stress (Hartl, Bracher, & Hayer-Hartl, 2011). HSPs may be induced or enhanced when plants are exposed to elevated temperatures (Blumenthal, Batey, Bekes, Wrigley, & Barlow, 1990; Vierling, 1991). The expression of HSPs positively correlates with the acquisition of thermo-tolerance, and the over-expression of HSPs often results in enhanced thermo-tolerance (Scholl et al., 1999) and ultimately improves physiological parameters such as photosynthesis, assimilate partitioning, along with water and nutrient efficiency of the plants (Camejo et al., 2006; Momcilovic & Ristic, 2007). The production of ethylene (Eth) also varies in different plant species in response to heat stress (Arshad & Frankenberger, 2002), for example, in the case of wheat leaves, Eth levels decreased at 40°C. Increased formation of ROS is a general feature of abiotic stresses, such as extreme temperature, high light, and drought (Dash & Mohanty, 2002; Lopez-Delgado et al., 1998). In order to limit oxidative damage under stress conditions, plants have developed a series of detoxification systems which include enzymes such as POX, APX, CAT, and SOD (Dat, Lopez-Delgado, Foyer, & Scott, 2000; Jiang & Haung, 2001).

4.1. Thermo-tolerance

Heat tolerance can be induced in a plant by prior exposure to moderately high temperatures, which enables the plant to cope with subsequent, potentially lethal, heat exposure (Howarth & Ougham, 1993) and this acclimatization is termed as thermo-tolerance. When plants are exposed to excessive heat, a characteristic set of cellular and metabolic response is triggered. Plants accumulate various compounds of low molecular mass, known collectively as compatible solutes such as Pro, GB, and Tre, as an adaptive mechanism against stress conditions. These solutes have several protective roles in heat-stressed cells (Jain et al., 2007; Rasheed, Wahid, Ashraf, & Basra, 2010), which have been related to acquisition of thermo-tolerance (Rasheed et al., 2010). Besides these molecules, some phyto-hormones like SA, ABA, BRs, and PAs play an important role in thermo-tolerance. NO has emerged as a putative signaling molecule in response to heat stress (Hasanuzzaman, Hussain, & Fujita, 2010; Larkindale & Knight, 2002; Wang et al., 2010). Abscisic acid, a stress-related hormone, is reported to confer heat tolerance, but its mechanism is not fully known, especially whether osmolytes are involved in its action or not (Kumar, Kaushal, Nayyar, & Gaur, 2012). There is relatively little information on the involvement of such molecules in the heat stress response. An overview of these molecules as well as their emerging roles in heat tolerance is presented below.

4.1.1. Thermo-protectants

4.1.1.1. Heat shock proteins. HSPs act as molecular chaperones as they play a vital role in protecting plant cells from the deleterious effects of heat stress (Rousch, Bingham, & Sommerfeld, 2004). Under heat stress, the synthesis of transcription and translation of HSPs increases manifold. HSPs protect the stability and functional confirmation of proteins through folding and refolding of non-native proteins under stress conditions (Tripp, Mishra, & Scharf, 2009; Wang et al., 2004). HSPs are found in all groups of living organisms and are classified into five different types according to their molecular weight, HSP 100, HSP 90, HSP 70, HSP 60, and small HSPs.
In response to sudden exposure to high temperature, the production of normal plant proteins decreases while that of HSPs increases at all stages of plant development. HSPs are implicated in acquired thermo-tolerance, maintenance of cell integrity, prevention of protein denaturation, and protection of PSII but none of these roles nor any involvement in inheritance of high-temperature hardiness has been documented (Vierling, 1991). The presence of HSPs providing thermo-tolerance has been reported in crops such as tobacco (Barnett, Altschuler, McDaniel, & Mascarenhas, 1980), soybean (Hernandez & Vierling, 1993; Lin et al., 1984; Ortiz & Cardemil, 2001), and maize (Queitsch, Hong, Vierling, & Lindquest, 2000). Similarly, Kee and Nobel (1986) reported increased thermo-tolerance (6–8°C) in succulent plants like Agave deserti, Carnegiea gigantea, and Ferocactus acanthodes at temperatures up to 40/50°C. Some examples have been summarized in Table 4. HSPs have been reviewed extensively elsewhere (Hasanuzzaman, Nahar, Alam, et al., 2013; Larkindale & Knight, 2002; Wang et al., 2004), so will not be dealt here.

4.1.1.2. Proline. Proline (Pro), a non-essential amino acid, i.e. having amino group (–NH) instead of the usual amino group (–NH2), is one of the most studied and extensively reported thermo-protectant. Many studies have indicated a positive relationship between the accumulation of Pro and plant stress tolerance; however, some have argued that increased Pro concentration under stress is a product and not an adaptive response to stress (Ashraf & Foolad, 2005). Chickpea plants growing in the presence of Pro accumulated this molecule up to 63 μmol g⁻¹ DW and also reported less injury to membranes, and improved chlorophyll and water contents especially at 45/40°C. Additionally, oxidative injury was significantly reduced along with elevated levels of enzymatic and non-enzymatic antioxidants (Kaushal et al., 2011). Pro accumulation has been reported in barley and radish (Chu, Aspinall, & Paleg, 1974), tomato floral buds and leaves (Kou, Chen, & Ma, 1986), mulberry (Morus alba L.) leaves (Chaitanya, Sundar, & Reddy, 2001), Brassica vegetables (Takeda et al., 1999), cotton leaves (Ronde, Mescht, & Steyn, 2001), Chinese cabbage (Brassica rapa L.; Hossain, Takeda, & Senboku, 1995), apple (Pyrus malus L.; Park, Ro, Hwang, & Yiem, 2001), wheat (Ahmed & Hasan, 2011), maize (Kumar, Gupta, et al., 2012), and tobacco (Cvikrova et al., 2012). In suspension cells of cowpea and tobacco, Pro biosynthesis increased under heat stress (Mayer, Cherry, & Rhodes, 1990). In chickpea, the heat treatment resulted in a marginal increase in Pro content compared with the control; the increase was more significant after pretreatment with SA (Chakraborty & Tongden, 2005). However, no Pro accumulation has been observed in Arabidopsis (Rizshky et al., 2004), while a slight decrease was observed in germinating wheat seeds under heat stress (Song, Lei, & Tian,
Exogenous Pro application to chickpea plants during heat stress imparted significant protection against high temperature 45/40°C (Kaushal et al., 2011). In sugarcane, bud sprouting was observed after presoaking buds with GB and Pro individually under heat stress. Bud biomass increased when treated with both Pro and GB but individually Pro was more effective than GB. GB proved more effective at increasing leaf width than Pro (Rasheed, Wahid, Farooq, Hussain, & Basra, 2011).

4.1.1.3. Glycine betaine. GB (N, N, N-trimethylglycine), a quaternary ammonium compound, is one of the most effective osmolytes (Chen & Murata, 2002). A foliar spray of GB at 8 and 2 mM concentrations was sufficient to enhance rice seed germination and hence yield under heat stress (Naidu & Williams, 2004). High GB accumulation under heat stress has been observed in various crops like maize (Quan, Shang, Zhang, Zhao, & Zhang, 2004) and sugarcane (Wahid & Close, 2007), but other crops such as rice, mustard, soybean, potato, tobacco, and Arabidopsis do not accumulate GB and are therefore potential targets for engineering GB biosynthesis (McCue & Hanson, 1990). Exogenous application of 20 mM GB to heat-stressed barley seedlings effectively promoted seed germination and yield due to improved shoot water content compared with untreated seedlings (Wahid & Shabbir, 2005). The findings were further corroborated by Li et al. (2011) in tomato seedlings. Exogenous application of GB protected PSII in tomato plants and increased yield due to increased carbon assimilation under heat stress. Exogenous application of Pro and GB (10 μM) also promoted growth in heat-stressed chickpea plants (Kumar, Kaushal, et al., 2012).

4.1.1.4. Trehalose. There is little information on the role of trehalose (Tre) on heat-stressed plants. Luo, Li, Wang, Yang, and Wang (2010) observed the effects of Tre pretreatment on thylakoid membranes of winter wheat under heat stress. Under normal growth conditions, winter wheat synthesized 502 μg g⁻¹ Tre, which increased to 1250 μg g⁻¹ under heat stress and 1658 μg g⁻¹ in Tre pretreated seedlings. Under heat stress, Tre pretreatment protected proteins in the thylakoid membranes and the photosynthetic capacity, reduced electrolyte leakage, MDA content, superoxide anion and hydrogen peroxide levels, and lipoxygenase activity. Exogenous application of Tre (1, 10, 25, 50, and 100 μM) to leaf discs of fava beans resulted in significantly higher effective photochemical efficiency of PSII and increased photochemical quenching (Gao et al., 2013). The potential of Tre to induce heat tolerance in other crops needs to be examined as has been reported for inducing cold tolerance.

4.1.1.5. brassinosteroids. BRs have a protective function under various abiotic stresses (Vardhini & Rao, 2003). Exogenous application of BRs has a promotory effect on the growth of wheat (Shahbaz, Ashraf, & Athar, 2008), french bean (Upreti & Murti, 2004) and is involved in stimulating cell elongation (Salchert, Bhalerao, Koncz-Kalman, & Koncz, 1998). As far as agricultural crops are concerned, BRs not only enhance yield but also crop quality (Prusakova, Ezhov, & Salnikov, 1999). BRs also enhance pollen germination and yield in sweet cherry (Hewitt et al., 1985), tomato (Singh & Shono, 2005), and rice (Thussaganpanit, Jutmanee, Chai-Arree, &

### Table 4. List of some HSPs produced in plants under heat stress

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<thead>
<tr>
<th>Plant species</th>
<th>HSPs</th>
<th>Reference</th>
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<tr>
<td>Babul (Prosopis chilensis)</td>
<td>HSP 70</td>
<td>Medina and Cardemil (1993)</td>
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<tr>
<td>Arabidopsis thaliana</td>
<td>HSP70</td>
<td>Lee and Schöffl (1996)</td>
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<tr>
<td>Carrot (Daucus carota)</td>
<td>HSP 17.7</td>
<td>Malik, Slovin, Hwang, and Zimmerman (1999)</td>
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<tr>
<td>Maize (Zea mays)</td>
<td>HSP 100</td>
<td>Queitsch et al. (2000)</td>
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<tr>
<td>Soybean (Glycine max)</td>
<td>HSP 70</td>
<td>Ortiz and Cardemil (2001)</td>
</tr>
<tr>
<td>Maize (Zea mays)</td>
<td>sHSP</td>
<td>Moriarty, West, Small, Rao, and Ristic (2002)</td>
</tr>
<tr>
<td>Rice (Oryza sativa)</td>
<td>HSP 101</td>
<td>Hang and Vierling (2000)</td>
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Kaveeta, 2012). When supplied with exogenous 24-BR’s, tomato plants showed better response for 8 days under heat stress (40/30°C) and then for 4 days under normal conditions increased photosynthesis. Activity of antioxidant enzymes such as SOD, APX, GPOD, and CAT increased and decreased H2O2 and MDA content resulting in increase of shoot weight (Ogweno et al., 2008). A significant increase in net photosynthetic rate was reported by epibrassinosteroid (EBR) application to cucumber (Cucumis sativum L.; Yu et al., 2004) and tomato (Singh & Shono, 2005). The treatment of rapeseed and tomato seedlings with 24-epibrassinolide (a type of brassionosteroid) increased their basic thermo-tolerance (Dhaubhadel, Chaudhary, Dobinson, & Krishna, 1999). In Indian mustard, application of different concentrations of 24-epibrassinolide (0, 10−6, 10−8, and 10−10 M) on 10-day-old seedlings at 40°C identified that 10−8 M was most effective for temperature amelioration due to enhanced activity of antioxidant enzymes (SOD, CAT, APX; Kumar, Sirhindi, et al., 2012). Application of homobrassinolide (HBR) at 0.1 and 0.2 μg ml−1 as a pretreatment on 4-day-old Brassica seedlings before exposure to lethal temperatures increased seedling length, vigor index, total soluble sugar content, and enzymatic activities, and reduced the relative injury of membranes measured by electrolyte leakage. Exogenous application of BRs retarded the rate of chlorophyll degradation and proteins associated with these pigments particularly those associated with chloroplast thylakoid membranes (Hola, 2011).

4.1.1.6. Salicylic acid. SA is an important endogenous signal induced by heat stress; its level (1 μM–1 mM) increases within 30 min after heat stress and is reported to induce heat resistance as in the case of mustard seedlings (Dat, Lopez-Delgado, Foyer, & Scott, 1998). SA plays the role of natural inducer of thermo-genesis in arum lily and also induces flowering in a range of plants. Additionally, SA controls ion uptake by roots and stomatal conductivity (Raskin, 1992). An increase in endogenous SA levels in response to heat was reported in pea plants (Pan et al., 2006). Exogenous application of SA has mitigated various biotic and abiotic stresses like heat stress (Dat et al., 1998; Senaratna et al., 2003). Laminaria japonica sporophytes were treated with 0.5 mM L−1 of SA under heat stress (25°C for 16 h) which increased chlorophyll a and soluble protein content while the malondialdehyde (MDA) content decreased (Zhou et al., 2010). In grape plants, exogenous pretreatment with 0.1 mM SA maintained relatively higher activities of peroxidase (POX), SOD, ascorbate peroxidise (APX), GR, and MDHAR (monodehydroascorbate reductase) indicating that SA can induce intrinsic heat tolerance in grapevines (Wang & Li, 2006). In another study on grapes treated with 100 μM SA, exposure to 43°C resulted in higher RUBISCO activity, increased PSII function and hence photosynthesis (Wang et al., 2010). In rice, 0.5 mM SA reduced electrolyte osmosis, MDA content, and superoxide radical (O2−) production rate under heat stress at 35°C (Lu, Gao, Zheng, & Han, 2009). Likewise, 10−5 M SA significantly increased all growth parameters, antioxidant activity, and Pro levels in Indian mustard growing under heat stress, i.e. 30 and 40°C (Hayat, Masood, Yusuf, Fariduddin, & Ahmad, 2009). The results were confirmed by Kaur, Gha, and Sangha (2009) who reported improved antioxidative abilities of CAT and POX in Brassica species after exogenous application of 10 and 20 μMSA at high temperatures (40–55°C). Similarly, 100 μM SA alleviated reductions in photosynthesis under heat stress and to recover in grapevine leaves (Wang et al., 2010). The heat tolerance of Kentucky bluegrass (Poa pratensis L.) was enhanced when exposed to 46°C for 72 h in a growth chamber after application of 0.25 mM SA. SA application suppressed the increase in O2− generating rate and enhanced SOD activity significantly at 2- and 12-h heat stress and increased CAT activity within 12 h (He et al., 2005). Mustard (Sinapis alba L.) seedlings were sprayed with 100 μM solution of SA at 45°C; after a 6-h heat treatment, the level of ascorbic acid had significantly reduced, while DHAR and MDHAR content were enhanced. In addition, GR activity declined while APX remained stable (Dat et al., 1998). Potato plantlets when supplemented exogenously with lower concentrations of acetyl SA (10−6 and 10−5 M) for 5 weeks at 35°C significantly increased their survival rate to 44 and 55%, respectively (Lopez-Delgado et al., 1998). Exogenous application of 10 μM L−1 SA to creeping bentgrass (Agrotis stolonifera L.) under heat stress (35°C) induced heat tolerance by reducing oxidative damage (Larkindale & Huang, 2004). In a study on six chickpea genotypes, seedlings were sprayed with
100 μM L⁻¹ SA at 46°C which significantly reduced membrane injury, and enhanced protein and Pro contents which were accompanied by increased POX and APX activities. However, CAT activity decreased (Chakraborty & Tongden, 2005). Exogenous application of 150 μM SA induced a rapid and substantial increase in phenylalanine ammonia-lyase (PAL), a key enzyme in phenyl propanoid metabolism of grape berry under heat stress (Wen et al., 2008). In another case, exogenous application of 0.1–0.5 mM SA/ASA (acetyl salicylic acid) prevented wilting in common beans and tomato under high-temperature stress (Senaratna, Touchell, Bunn, & Dixon, 2000). Pretreatment of heat-stressed mungbean seedlings with SA reduced lipid peroxidation but improved membrane thermo-stability and antioxidant activity (Saleh, Abdel-Kader, & El Elish, 2007). Likewise, in cucumber, 1 mM SA foliar spray reduced electrolyte leakage and H₂O₂ level, and increased catalase activity (Shi, Bao, Zhu, Ying, & Qian, 2006).

4.1.1.7. Abscisic acid. Abscisic acid (ABA) is a naturally occurring compound that helps to regulate plant growth and development. ABA levels are elevated under various abiotic stresses such as heat, cold, salt, drought, and high irradiance (Pospisilova, Synkova, Haisel, & Batkova, 2009). Despite reports of increased ABA levels in plants exposed to high temperatures, little is known about ABA accumulation in plants during heat acclimation (Penfield, 2008). Increased ABA levels in pea plants occurred when exposed to constant stressful temperatures (Daie & Campbell, 1981). The role of ABA in inducing thermo-tolerance has been recognized in maize (Gong, Li, & Chen, 1998) and bromegrass (Bromus inermis L.; Robertson, Ishikawa, Custa, & Mackenzie, 1994). A significant increase in free and conjugated ABA was observed in tomato seedlings at 45/35°C compared to control plants (25/15°C) which increased heat tolerance. (Daie & Campbell, 1981) and likewise, ABA levels increased in response to heat treatment in tobacco (Teplova et al., 2000). Enhanced ABA levels in leaves of dwarf bean seedlings increased leaf resistance under high air temperature (38°C) and similar results were reported for tomato and wheat plants (Hiron & Wright, 1973). In pepper seedlings, ABA levels in the nucleus increased significantly due to de novo synthesis of ABA in root cap cells under heat stress (40°C; Tong-Xiang, Zong-Shen, Jian-Bo, & Rong-Qian, 2009). ABA is a signaling molecule, but it is reported to induce thermo-tolerance by raising the level of other signaling molecule like NO as observed in common/giant reed (Phragmites communis Trin.; Song et al., 2008). In Indian mustard, ABA applied at 0.5 and 1 μM decreased seedling mortality and increased growth at 47 ± 5°C (Chhabra, Dhawan, Sangwan, Dhawan, & Singh, 2009). Exogenous application of ABA alleviated heat stress symptoms by increasing SOD, CAT, APX, and POX and decreasing H₂O₂ and MDA contents (Ding, Song, Wang, & Bi, 2010). In heat-stressed chickpea, exogenous application of 2.5 μM ABA increased growth which was associated with enhanced endogenous ABA levels (Kumar, Kaushal, et al., 2012). Maize seedlings grown for 1–4 days in the presence of ABA responded better when roots and shoots were subjected to 3-h sub-lethal (40°C) and lethal (45°C) heat shocks, respectively. (Bonham-Smith, Kapoor, & Bewley, 1988). Pretreatment of maize with 0.3 mM L⁻¹ ABA at 46°C improved the thermo-tolerance under heat stress (Gong et al., 1998). Heat tolerance increased significantly within 24 h of ABA application at 7.6 or 9.5 μM in leaves and cell tissue culture in grapes (Abass & Rajshekhar, 1993). An ABA concentration of 10⁻⁵ M inhibited heat-induced effects and enhanced thermo-stability of thylakoid organization in barley in response to heat stress (Ivanov, Kitcheva, Christov, & Popova, 1992).

4.1.1.8. Polyamines. There is a growing appreciation of the role of polyamines (PAs) in plant stress responses (Kakkar & Sawhney, 2002), but their role in heat shock protection of higher plants is less understood. Exogenous application of 1 mM putrescine (Put), spermidine (Spd), and spermine (Spm) in mungbean at 50°C for 2 h increased root and hypocotyl growth, and protected membranes from peroxidation (Basra, Basra, Malik, & Grover, 2001). Pretreatment with Spm and Spd reduced peroxidase and increased catalase activities of beans under heat stress (Velikova, Yordanov, & Edreva, 2000). Exogenous application of 4 mM Spd improved the heat resistance in both heat-sensitive and heat-tolerant cultivars of tomato by enhancing resistance to thermal damage of pigment protein complexes structure and activity of PSII (Mukowski, 2001). El-Bassiouny (2004) suggested that improved heat tolerance in response to
Put application might be attributed to the induction of new protein biosynthesis in shoots of pea plants. Also, Bekheta and El-Bassiouny (2005) found that foliar application of Put on wheat plants increased SOD and CAT activities, increased RNA/DNA content and reduced MDA levels (Khalil et al., 2009). Exogenous application of Put, Spd, and Spm (1 mM) at high temperature enhanced growth, protected membranes, and minimized oxidative damage in soybean (Amooaigaie & Moghym, 2011). Tomato, when supplied with 1 mM Spm, increased expression of ethylene-related genes, PAs biosynthesis genes, hormone pathways, and oxidation/reduction genes thus imparting heat tolerance (Cheng et al., 2012). Increased endogenous Put content was reported in cotton, when supplied with 10 mM Put (Bibi, Oosterhuis, Goniasand, & Mattice, 2012), while 10 μM Put application on wheat-elevated activities of enzymatic and non-enzymatic antioxidants, and reduced lipid peroxidation in roots and shoots (Asthir, Koundal, & Bains, 2012). Wheat supplied with arginine (Arg) and Put (1.25/2.5 mM) acquired heat tolerance by increasing endogenous Put, Spd, and total PAs contents, total amino acids and the ratio of essential to non-essential amino acids (Hassanein et al., 2013). Exogenous application of 0.05 and 0.1 mM Spm reduced oxidative damage and increased chlorophyll content in Arabidopsis (Sagor et al., 2013).

4.1.1.9. Nitric oxide. NO is considered a signaling molecule involved in the regulation of physiological processes and stress responses in plants. NO is a highly reactive, membrane-permeant free radical which plays a crucial role in many physiological processes such as seed germination, reduction of seed dormancy, leaf expansion, regulation of plant maturation and senescence (Mishina, Lamb, & Zeier, 2007), suppression of floral transition (He et al., 2005), ethylene emission, stomatal closure (Garcia-Mata & Lamattina, 2002; Guo, Okamoto, & Crawford, 2003; Neill, Desikan, Clarke, & Hancock, 2002), programmed cell death, and light-mediated greening (Zhang et al., 2006). The effect of exogenous application of NO donors such as sodium nitroprusside (SNP) and S-nitroso-N-acetyl penicillamine (SNAP) was examined in common reed (Phragmites communis) at 45°C: ion leakage, growth suppression, cell viability, and MDA content increased as a result of heat stress (Song, Ding, Zhao, Sun, & Zhang, 2006). In another study, the application of 50 and 100 μM SNP on two cultivars of wheat-C306 (heat-tolerant) and PBW550 (heat-sensitive) at 33°C increased the activities of all antioxidant enzymes along with increased membrane thermo-stability and cellular viability (Bavita, Shashi, & Navtej, 2012). Application of exogenous NO in the form of SNP during heat shock in mungbean helped to maintain the stability of chlorophyll a fluorescence, membrane integrity, H₂O₂ content, and antioxidant enzyme activity (Yang, Yun, Zhang, & Zhao, 2006). Similarly, exogenous application of 0.5 mM SNP on 8-day-old heat-treated seedlings (38°C) of wheat for 24 and 48 h significantly reduced the high-temperature-induced lipid peroxidation and H₂O₂ content but increased the chlorophyll content, ascorbic acid, reduced glutathione (GSH), and the oxidized glutathione (GSSG) ratio (Hasanuzzaman et al., 2012). In wheat, exogenous application of NO decreased the effects of heat stress by up-regulating the antioxidant and glyoxalase system (Hasanuzzaman, Nahar, & Fujita, 2013c). The effect of exogenously applied NO on the heat tolerance of hardy garden mum (Chrysanthemum morifolium Ramat.) was investigated by applying SNP. SNP alleviated the heat stress by slowing down the reductions in photosynthetic pigment content and net photosynthetic rate. It also decreased MDA content and maintained higher activities of SOD, CAT, POX, and APX (Yang, Wu, & Cheng, 2011). Low levels of NO resulted in more green leaf tissue and photosynthesis under heat stress in barley (Uchida, Jagendorf, Hibino, Takabe, & Takabe, 2002). SNP pretreatment reduced the heat-induced damage in rice seedlings (Uchida et al., 2002) and increased the survival rate of wheat leaves and maize seedlings (Lamattina, Beligni, Garcia-Mata, & Laxalt, 2001). The model in Figure 5 depicts the involvement of various thermo-protectants and their mechanisms linked to the acquisition of heat tolerance.
5. Perception and signaling in plants under heat stress

Plants have sensing mechanisms on their membranes to detect even mild increase in temperature (Wise et al., 2004). Under heat stress, membrane fluidity increases, and therefore sensors present in membranes detect physical phase transition, which eventually leads to conformational changes and phosphorylation/dephosphorylation events when the temperature changes (Plieth, Hansen, Knight, & Knight, 1999). The heat shock stimulus is perceived by four sensors (Mittler, Finka, & Goloubinoff, 2012) which include plasma membrane-bound Ca\(^{2+}\) channels (Saidi et al., 2009), histone sensor in the nucleus (Kumar & Wigge, 2010), two unfolded protein sensors—one in the endoplasmic reticulum (Deng et al., 2011; Srivastava, Deng, & Howell, 2014) and the other in cytosol (Sugio, Dreos, Aparicio, & Maule, 2009; Figure 6). Membranes play a key role in heat sensing as they are first to sense temperature stress which results in the activation of calcium channels to induce Ca\(^{2+}\) influx across the plasma membrane leading to the heat shock response (Gong et al., 1998; Liu et al., 2006; Saidi et al., 2009; Wu & Jinn, 2010). Ca\(^{2+}\) concentration increases in cytoplasm and combines with calmodulin at CaM3 calcium-dependent kinases, which in turn activates various transcription factors like MAPKs and CDPKs or ROS-producing NADPH oxidase (Zhang, Chen, Zhang, & Liu, 2009). Signaling of these cascades at nuclear level leads to the production of antioxidants and compatible osmolytes for cell water balance and osmotic adjustment. Production of ROS is significant for signaling as well as production of antioxidants (Bohnert, Gong, Li, & Ma, 2006). The antioxidant defense mechanism is a part of the heat-stress adaptation leading to thermo-tolerance (Maestri et al., 2002).

Increased membrane fluidity in response to high temperature also induces lipid signaling where phospholipase D (PLD) and phosphatidylinositol-4,5-bisphosphate kinase (PIPK) are activated, leading to phosphatidic acid (PA) and D-myo-inositol-1,4,5-triphosphate (IP\(_3\)) accumulation (Mishkind, Vermeer, Darwish, & Munnik, 2009). These accumulated lipid molecules result in further activation of Ca\(^{2+}\) channels and inward flux of Ca\(^{2+}\). Additionally, increased heat shock tolerance can be obtained by heat-induced accumulation of other metabolites such as NO and H\(_2\)O\(_2\), which may activate similar signaling cascades or other molecular mechanisms (Hua, 2009). Changes in plasma membrane fluidity lead to the accumulation of ROS resulting in more Ca\(^{2+}\) influx into cells. ROS accumulation may...
lead to programmed cell death (Mathur & Jajoo, 2014). Heat stress leads to the activation of unfolded proteins (UPR) present in endoplasmic reticulum (ER-UPR) and cytosol (Cyt-UPR) (Deng, Srivastava, & Howell, 2013; Mittler et al., 2012). Activated ER-UPR splices the bZIP transcription factor that enters into the nucleus and leads to the expression of specific genes to BR signaling (Che et al., 2010; Deng et al., 2013). Alternatively, Cyt-UPR is activated by the heat shock factor (HSF, HSFA2) capable of binding the HSF-binding element at the promoter region of HSR genes (Sugio et al., 2009). Heat stress affects histone occupancy by replacing H2A by H2A.Z in the nucleosome as reported in Arabidopsis where ARP6 (actine-related protein 6) is involved in replacing histone (Clapier & Cairns, 2009; Erkina, Zou, Freeling, Vorobyev, & Erkine, 2010).

### 6. Transgenic approach to improve heat tolerance in crops

As discussed above, HSPs and biomolecules play an important role as thermo-protectants to mitigate thermal stress; various transgenics have been developed with improved thermo-tolerance, which have potential benefits for inducing heat tolerance in food crops. Increased thermo-tolerance has been achieved in plant species such as Arabidopsis (Alia, Sakamoto, & Murata, 1998), maize (Queitsch et al., 2000), tobacco (Alia et al., 1998; Park & Hong, 2002; Yang, Liang, & Lu, 2005), rice (Katiyar-Agarwal, Agarwal, & Grover, 2003), and alfalfa (Saurez, Calderon, & Iturriaga, 2008). Thermo-tolerance in Arabidopsis was induced by over-expression of the APX1 gene taken from pea and the HvAPX1 gene from barley (Shi, Muramoto, Ueda, & Takabe, 2001). Over-expression of
stay-green genes delayed senescence in sorghum under heat stress (Nyugen, 1999). Rehman et al. (2009) also reported some heat-tolerant genotypes in wheat due to the stay-green feature. Recently, Folsom, Begcy, Hao, Wang, and Walia (2014) reported that the FIE 1 (Fertilization independent endosperm 1) gene from Arabidopsis regulates seed size under heat stress by controlling early endosperm development in rice. Some examples where heat-tolerant crops have been developed are listed in Table 5.

### 7. Conclusions
Currently, global warming is a worldwide concern; rising temperatures are posing a severe threat for sustainable crop yields and global food production. High-temperature stress is the second most important stress after drought, which can strike crop plants at any time and impose severe limitations to crop growth and development. Hence, concern over temperature has increased due to the expected increase in the frequency and amplitude of heat stress in the near future. Heat stress affects plant growth and development; plants exposed to high temperature during reproduction have increased flower and fruit abortion leading to low yields. All food crops need to be examined for their responses to supra-optimal temperatures at various levels of their organization at various locations. Knowledge on the sensitivity of each growth stage to heat stress is needed to develop appropriate

<table>
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<th>Transgenic crop</th>
<th>Gene transferred</th>
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<td>Soybean (Glycine max)</td>
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<td>Eggplant (Salanum</td>
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<td>Agrobacterium tumifaciens</td>
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<td>Alfalfa (Medicago</td>
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Abbreviations: MT-sHSP, Mitochondrial small heat shock proteins; ATHSF, Arabidopsis thaliana Transcription factor; gusA, β-glucuronidase; Cod A, Choline oxidase; BADH, Betaine aldehyde dehydrogenase; APX1, ascorbate peroxidase; HvAPX1, (Hordeum vulgare) ascorbate peroxidase gene; ScTPS1, (Saccharomyces cerevisae) trehalose-6-phosphate synthase1; ScTPS2, (Saccharomyces cerevisae) trehalose-6-phosphate synthase2; ADC, Oat arginine deboxyylase; ySAMdc, yeast S-adenosyl methionine decarboxylase; PSCR, Pyrroline-5-carboxylate reductase; EsDREB2B, Eremosparton songoricum (Dehydration-Responsive Element-Binding Protein2); SP1, Stable protein 1; FIE 1, Fertilization independent endosperm1.
strategies for inducing heat tolerance. Plants may accumulate various thermo-protectants phyto-
hormones and signaling molecules under heat stress which contribute to impart thermo-tolerance
through up- and down-regulation of various genes. The metabolic pathways and their genes need to
be identified especially in reproductive components to address heat tolerance in the future.

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