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Review

An overview of heat stress in tomato (*Solanum lycopersicum* L.)

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ABSTRACT

Heat stress has been defined as the rise of temperature for a period of time higher than a threshold level, thereby permanently affecting the plant growth and development. Day or night temperature is considered as the major limiting factor for plant growth. Earlier studies reported that night temperature is an important factor in the heat reaction of the plants. Tomato cultivars capable of setting viable fruits under night temperatures above 21 °C are considered as heat-tolerant cultivars. The development of breeding objectives is generally summarized in four points: (a) cultivars with higher yield, (b) disease resistant varieties in the 1970s, (c) long shelf-life in 1980s, and (d) nutritive and taste quality during 1990s. Some unique varieties like the dwarf "Micro-Tom", and the first transgenic tomato (FlavrSavr) were developed through breeding; they were distributed late in the 1980s.

High temperature significantly affects seed, pollen viability and root expansion. Researchers have employed different parameters to evaluate the tolerance to heat stress, including membrane thermo stability, floral characteristics (Stigma exertion and antheridia cone splitting), flower number, and fruit yield per plant. Reports on pollen viability and fruit set/plant under heat stress by comparing the pollen growth and tube development in heat-treated and non-heat-stressed conditions are available in literature. The electrical conductivity (EC) have been used to evaluate the tolerance of some tomato cultivars in vitro under heat stress conditions as an indication of cell damage due to electrolyte leakage; they classified the cultivars into three groups: (a) heat tolerant, (b) moderately heat tolerant, and (c) heat sensitive.

It is important to determine the range in genetic diversity for heat tolerance in tomatoes. Heat stress experiments under field conditions offer breeders information to identify the potentially heat tolerant germplasm.

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1. Introduction

Increasing the temperature 10–15 °C above the optimum temperature is generally termed as heat stress or heat shock (Wahid et al., 2007). Heat stress is a multifaceted function that depends on the speed of rise in temperature and the total period (Blum, 1988). The frequency of heat shocks and the duration of high day/night temperature mainly affect the intensity of heat stress in specific climatic zones. Thermotolerance indicates the capability of a plant to survive with extremely high or low temperature and produce economic yield.

Cherry tomato (*Solanum lycopersicum* var. *cerasiforme*), a wild relative of cultivated species, was first found in South America and Mexico (Bai and Lindhout, 2007). Reports show that the tomato crop frequently experiences high temperatures in some parts of the world. Tomato reproduction is extremely sensitive to heat stress. High temperature can cause abortion of the male gametophyte and lead to reduction in fruit set. The expected increase in atmospheric temperature (1.5–11 °C) by 2100 can severely affect crop productivity (Reddy and Kakani, 2007; Stainforth et al., 2005). Therefore, the reproductive behavior of crop plants under these extreme environments needs to be extensively studied (Karapanos et al., 2010).

A small increase in the average atmospheric temperature over the threshold may cause serious hazard to crop production in many parts of the world (Hall, 2010). Tomato (*Solanum lycopersicum* L.) belongs to the family Solanaceae, and it is a widely cultivated crop. Mexico, Brazil, Spain, and Italy are the major tomato producing countries where as Belgium and Netherlands lead in yield per hectare (Tubiello et al., 2013). Despite its capability to grow under variable climates, tomato fruit production is affected by high temperature stress because the increase in day/night temperatures above 26/20 °C, respectively, can significantly affect fruit setting and yield (Lohar and Peat, 1998).

Rhodes and Hanson (1993) reported that many plant species have developed defense mechanisms to cope with stressful conditions because they have been exposed to various stresses during their evolutionary history and the accumulation of sugars, amino acids, and betaines is one of the strategies that help plants to survive under stressful environments (Chen and Murata, 2002).

Tomato was introduced to Europe during the 16th century and it later spread to the Mediterranean area (Pék and Helyes, 2004). Through breeding programs a large number of cultivars have been developed since.

With climate change, the priority is to develop heat-tolerant varieties that can survive high temperature and other abiotic stresses. Different from *Solanum chilense*, commercial tomatoes have limited heat tolerance potential. As a result of global warming, the main threat to crop production in many parts of the world is heat stress (Sato et al., 2000; Hedhly et al., 2009). Increasing the

day temperature above 25 °C significantly decreases fruit numbers, the weight of the fruit, and seed number per fruit (Peet et al., 1998). Short term exposure to extremely high temperature (45 °C) can lead to programmed cell death (PCD), release of cytochrome c, and induced production of caspase-like enzymes (Qu et al., 2009). The reproductive stage in the plant is generally more susceptible to high temperature than the vegetative stage (Ruan et al., 2010; Zinn et al., 2010).

Summer heat stress in many countries terminates tomato production (Saeed et al., 2007). The deficiency of heat tolerance in most tomato cultivars presents a major restriction on growing them in regions where temperatures during part of the growing season, even for short duration, reach 38 °C or higher (Dinar and Rudich, 1985b; Sung et al., 2003). High temperature affects physiological and biochemical development and thus leads to fruit yield reduction (Singh et al., 2017; Dinar and Rudich, 1985a).

Tomato plants are sensitive to high temperatures and heat stress can stimulate flower abscission (Camejo et al., 2005) and limit the fruit yield (Driedonks, 2018). Increase in temperature negatively affected the pollen grain, especially at the first stage, leading to poor pollen germination and impaired pollen tube development (Raja et al., 2019). High temperature dose not just reduce the flowering and fruit set of the plant, but also affects the development and maturity of the fruit and consequently reduces the crop yield.

High temperature also affects photosynthesis (Nankishore and Farrell, 2016; Salvucci and Crafts-Brandner, 2004; Poreek et al., 2009), changes the membrane fluidity, disrupts the general stability of metabolic mechanism, and thus causes over-production of reactive oxygen species and oxidative stress (Larkindale et al., 2005).

2. Tomato responses to heat stress

Tomato heat tolerance is a quantitative trait (Wen et al., 2019). A number of studies have evaluated heat tolerance in tomato using various parameters. The phenotypic index is a direct diagnostic tool that can directly reflect the degree of heat damage (Wu and Zhang, 2013). Therefore, the heat injury index is a preferred and the most reliable index for the degree of heat damage to tomato seedlings under high-temperature stress (Min et al., 2012). Membrane damage is a primary symptom of heat injury, and heat tolerance is positively correlated with the electrolytic leakage rate (Xu et al., 2017). Physiological and biochemical indexes (Siddiqui et al., 2017; Zhou et al., 2018) are also reliable evaluation tools especially that these changes respond faster than morphological changes to high temperature stress. High-temperature stress leads to the inhibition of chlorophyll biosynthesis (Berova et al., 2013); hence, chlorophyll content can also be used as an effective evaluation index for high-temperature stress. In other studies (Srivastava

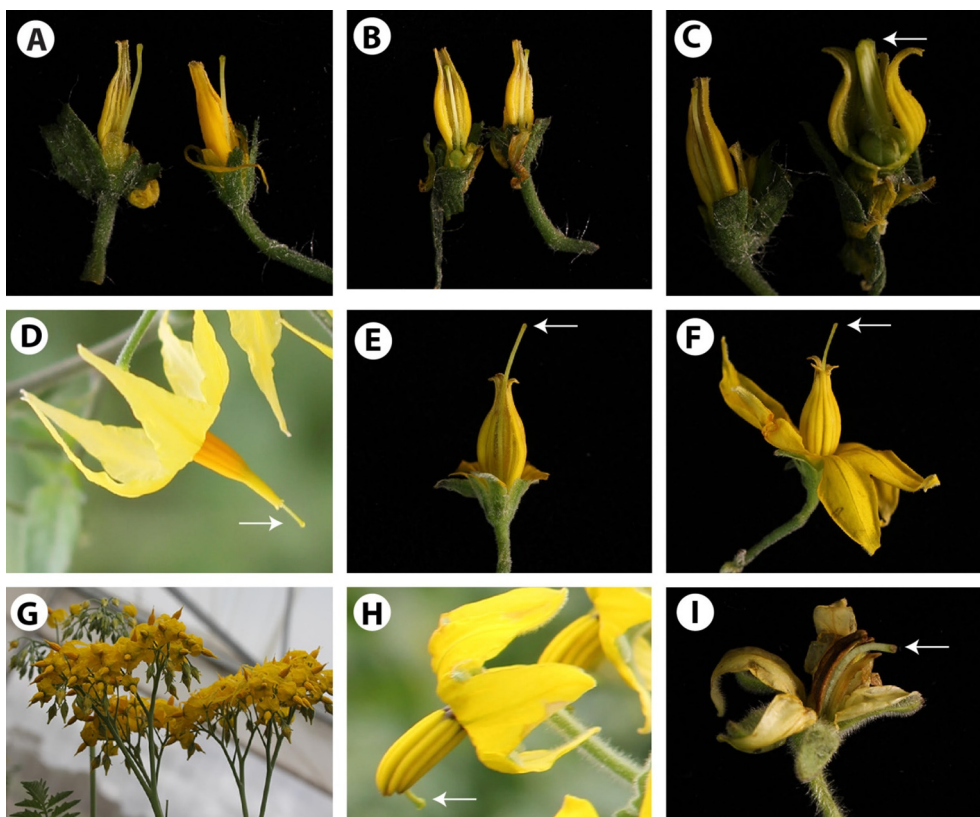


Fig. 1. The effect of high-temperature on floral structure including the size and morphology of the floral constituents. A-B. LA3847 and LA4284, respectively, showing flowers under control (flower on the left) and heat conditions (flower on the right) without noticeable stigma exertion under heat. C. LA4256 accession with stigma exertion and deformation of the style as a sign of sensitivity to heat (flower on the right). D. LA0373 showing stigma exertion above the anther cone similarly under control and heat conditions. E-G. LA1930 showing the mostly exserted stigmata among all accession. E. Flower with dissected anthredial cone showing the long style exserted above the level of anthers. F. Non-dissected flower showing the exserted stigma. G. Prolific production of self-incompatible flowers with exserted stigmata under control condition. H-I. LA0716 showing exserted stigmata under control and high temperature conditions, respectively (Alsamir et al., 2017d).

et al., 2017), microscopic observation index has been used in heat tolerance evaluations.

2.1. Pollen development

Many studies have focused on the effects of heat stress on pollen development (Raja et al., 2019; Pressman et al., 2002; Firon et al., 2006; Frank et al., 2009). Pressman et al. (2002) reported that heat stress in tomato caused male sterility but that the male sterile plants growing at 29 °C were able to bear fruits once they received pollen developed at 25 °C.

In tomato, the pollen germination and pollen tube development are reduced at temperatures above 30 °C (Vasil, 1987). Kakani et al. (2005) reported that the optimal temperature for pollen germination in vitro was 15–22 °C, whereas 25 °C was the best temperature for pollen germination in vivo (Dempsey, 1970). The heat stress significantly affects the male reproductive organs (Fig. 1) as it decreases the number of pollen grains developed and released in the anther, pollen viability, and germination (Alsamir et al., 2017d; Rieu et al., 2017).

Increasing temperature up to 35 °C damaged both the physiological and biochemical activities of the plant (Singh, et al. 2017; Al-Khatib and Paulsen, 1999; Rivero et al., 2001). Heat stress reduced flower pollination rate in tomato and thus lead to low fruit setting and low yield; this phenomenon also affected the lycopene content, causing high evaporation and low fruit quality.

2.2. Fruit development

Sucrose cleavages enzymes are one of the main compounds found in tomato fruit and are an ideal system to study fruit development under heat stress. McLaughlin and Boyer (2004) reported that sucrose and cell wall invertase are highly susceptible to abiotic stresses, causing ovary abortion under drought in maize. Li et al. (2011b) reported that high sucrose availability, and invertase activity at the reproductive stage in tomato contributed to heat tolerance in young fruit.

2.3. Fruit production

High temperature affects the physiological functions of roots alongside the development of the aboveground plant parts such as fruits. However, plant responses to higher temperatures are difficult to assess by measuring the physiological processes of intact roots, especially when a minor change in root temperature (12 °C to 15 °C) can significantly reduce fruit yield (Driedonks, 2018; Bar Tsur et al., 1985; Bitá and Gerats, 2013; Sato et al., 2000). The high temperature affected the morphology of the tomato flowers and its physiological metabolism, and altered the production of compounds, such as carbohydrates, polyamines, and proline (Alsamir et al., 2017b; Pressman et al., 2002; Sato et al., 2006; Song et al., 2002).

Changing the temperature to suboptimal temperature conditions significantly affected the reproductive growth of the tomato, causing comparatively higher damage to anthers than to female

organs (Peet et al., 1998; Sato et al., 2000; Xu et al., 2017). Failure in pollen development causes loss in fruit setting (Sato et al., 2000).

Giri et al. (2017) reported that increase in the temperature can decrease root growth, the concentration of nutrient-uptake, nutrient-assimilation proteins, and the rate of nutrient uptake by roots. Heat stress can also change the sink-source association among roots and shoots, which affects the vegetative and the reproductive growth in tomato plants leading to reduced yield and fruit quality (Abdul-Baki and Stommel, 1995; Zinn et al., 2010; Wahid et al., 2007). Furthermore, high temperature has been reported to affect floral abortion causing 80% flower loss in tomato plants leading to reduced fruit set (Ruan et al., 2010; Rieu et al., 2017).

Hanson et al. (2002) suggested that the flowering and fruit set are the most important parameters in the evaluation of different tomato cultivars under heat stress as they are very sensitive towards high temperature. Camejo et al. (2005) reported that high temperature affected photosynthetic activity and the subsequent development and maturity of the fruit thereby reducing the crop yield. High temperature significantly affected morpho-physiological parameters, such as plant height, number of branches, and total plant biomass (Shaheen et al., 2016).

2.4. Respiration

The relationship between respiration rates and growth rates can affect the balance of physiological activities in the plant and this can help define temperature effects on plant growth. Gary et al. (2003) explained the effects of high temperature on respiration and growth of the tomato plant and reported that the temperature affected both metabolic rates and metabolic efficiency. High and low temperatures not only affected the membrane integrity or enzyme denaturation but also caused loss of substrate carbon level efficiency (Holladay et al., 2004).

Loka and Oosterhuis (2010) reported that higher difference between day and night temperatures might increase the seed germination. Heat shock protein 70 is synthesized when the plants are exposed to environmental stresses (Sung et al., 2001). Increasing the night temperature to 30 °C might stimulate mechanisms to fixing damage at 40 °C during the days.

2.5. Nutrient uptake

Heat stress affected both the nutrient metabolism and ammonium assimilation in tomatoes (Giri, 2013; Hungria and Kaschuk, 2014). Bassirirad (2000) reported that many factors causing decrease in nutrient absorption under heat stress including the decrease in root growth or a reduction in nutrient absorption per unit root.

2.6. Cell wall invertase (CWIN)

Liu et al. (2016) reported that reduced CWIN activity was observed to be related with poor seed and fruit set under high temperature. They found that the rise of CWIN activity led to automatic cell death in fruits.

Firon et al. (2006) and Li et al. (2011b) reported that higher CWIN activity in the anther and fruit of tomato plants decreased the fruit abortion under extreme high temperature compared to lower CWIN activity in other cultivars. Additionally, a rise in CWIN activity was noticed in ovary-to-fruit transition (Palmer et al., 2015).

3. Mechanisms of heat tolerance in tomato

Chen et al. (2007) reported that one of the basic strategies for the defense and survival of plants under heat stress was the accumulation of proline, sugars, and polyols. Environment changes can cause a significant change in the levels of phenolics and flavonoids contents in tomato (Ilahy et al., 2016).

3.1. Sugar level

Sugar level is affected by heat stress treatment in tomatoes (Harsh et al., 2016). Significant variation between the studied genotypes was observed and sugar level reduced in affected pollen grains before anthesis resulting in decreased fruit set and lower accumulation of total sugar (Raja et al., 2019; Driedonks, 2018; Mazzeo et al., 2018).

Zhou et al. (2017a,b) reported that soluble sugar content increased in the leaves of heat-tolerant tomato plants under heat stress compared with sensitive plants at the flowering and anthesis stages. This was largely because the sensitive genotypes could not regulate carbohydrate synthesis under heat stress.

3.2. Polyamine (PA) changes

Polyamines (PAs) are small ubiquitous chemicals that play a key role in the regulation of physiological activities and a range of stress reactions in plants; they accumulate under abiotic stress (heat stress) (Bouchereau et al., 1999; Yang et al., 2007). Increased PA level significantly increased the protective reaction of plants to different abiotic stresses (Kumar et al., 2006). PA played an important role in abiotic stress tolerance through osmotic modification, membrane stability, and balancing the stomatal movements (Liu et al., 2007).

The genetic control of PA metabolism is important to determine its role in drought and salt stress. Increased tolerance to abiotic stress was reported when PA biosynthetic genes were over expressed, including arginine decarboxylase (Capell et al., 2004; Masgrau et al., 1997; Roy and Wu, 2001), ornithine decarboxylase (Kumria and Rajam, 2002), S-adenosyl-methionine decarboxylase (Torrighiani et al., 2005), and spermidine synthase (Kasukabe et al., 2004; Kasukabe et al., 2006) in rice, tobacco, *Arabidopsis*, and sweet potato plants. S-Adenosyl-L-methionine decarboxylase (SAMDC) is an important enzyme regulating the biosynthesis of PAs. SAMDC over expression in plants led to improved tolerance to abiotic stresses, such as salt (Roy and Wu, 2002), drought (Waie and Rajam, 2003), acidic oxidative stress (Wi et al., 2006) and heat stress (Berberich et al., 2015).

3.3. Polyphenol oxidase activity

Rivero et al. (2001) reported a significant change in metabolite content of phenolics, and enzymatic function under heat stress in tomato. They reported that decreased biomass weight increased the concentration of soluble phenolics, and decreased peroxidase and polyphenol oxidase function under heat stress at 35 °C.

3.4. Fatty acid and cellular membrane

Membrane lipid composition changes under heat stress, helping to maintain membrane integrity (Iba, 2002). Liu et al. (2006) and Murakami et al. (2000) reported a rise in concentration of saturated fatty acids in polar lipids involved in protection of membrane integrity in tomato plants. Fatty acids are affected under stress and a change is reflected in membrane-bound proteins, and photosyn-

thetic function and mitochondrial respiration in Arabidopsis (Kim and Portis, 2005).

Membrane damage leads to starvation, decreasing the ion mutability, creation of toxic compounds, and rise in oxidative compounds (Schöffl et al., 1999; Howarth, 2005). Change in saturated fatty acids is one of the important mechanisms in the plant when exposed to heat stress (Wakita et al., 2001; Anai et al., 2003; Orlova et al., 2003; Sakurai et al., 2003). The change in membrane fatty acids help the plant maintain an environment appropriate for the activity of important proteins under heat stress (Upchurch, 2008).

High content of polyunsaturated fatty acids, 70% of the total, composed of dienoic and trienoic fatty acids (TAs) are available in the leaf cellular membrane lipids whereas the other fatty acid was found in diverse intracellular membrane systems (Kodama et al., 1997; McConn, 1996; Ohlrogge and Browse, 1995). Several authors (Anai et al., 2003; Matos et al., 2007; Orlova et al., 2003; Zhang et al., 2005; Kodama et al., 1995) reported that Accumulation of TAs in membrane lipids was associated with tolerance under chilling stress.

Membrane lipid concentration is an important factor linked to many biological and physiological activities and plays a key role in recovering the chloroplast activity, pollen growth, temperature tolerance and hormone synthesis (Gibson et al., 1994; Xu et al., 2017; Kodama et al., 1995; McConn, 1996; Routaboul and Fischer, 2000).

The continued activity of cellular membranes under stress is necessary for physiological functions, like photosynthesis and respiration (Blum, 1988). Photosystem II (PSII) is very sensitive to the change in temperature and its function significantly declines or stops under heat stress (Camejo et al., 2005), because of the direct effect of heat stress on the thylakoid membranes where PSII is located (McDonald and Paulsen, 1997).

Electrolyte leakage has been used in many studies to measure the tolerance and sensitivity towards heat stress and distinguish between the plant genotypes. The thermo stability of the cell membrane affecting the electrolyte leakage has been studied in tomato (Biswas et al., 2012), wheat and barley (Wahid and Shabbir, 2005). The cellular membrane integrity gets decreased and cell electrolytes flow out under heat stress. Bajji et al., (2002) suggested electrolyte leakage as a useful parameter to discriminate between the genotypes under heat stress. Alsadon et al. (2006) used electrical conductivity as a method in detecting genetic variability in heat tolerance by measuring the amount of leakage from injured cells. Kumar et al. (2012); Wahid et al. (2007) reported a decrease in membrane thermo stability under heat stress in tomato and recorded that the tolerant genotypes had higher membrane thermo stability.

3.5. Glycinebetaine (GB) level

Characteristic compatible solutes, in different species, include polyols, sugars, amino acids, betaines, and associated compounds (Bita and Gerats, 2013; Rhodes and Hanson, 1993). Glycinebetaine is low-molecular-weight metabolite and plays an important role in tolerance against abiotic stress and helps the plant survive (Bita and Gerats, 2013; Bohnert et al., 1995; Chen and Murata, 2002).

McCue and Hanson (1990); Bohnert et al. (1995); Rhodes and Hanson (1993) reported that under biotic stress the glycinebetaine (GB) level increased rapidly. Accumulation of GB in vivo, in tobacco, led to improved tolerance to heat stress and improved growth and photosynthesis (Shi et al., 2006).

Bita and Gerats (2013) reported that maize and sugarcane lines tolerant to high temperature stress had high level of GB. Adcox et al. (2005), Chen and Murata (2008), Park et al. (2006) and Yang and Lu (2006) reported that exogenous application of GB

increased tolerance in maize plants to different abiotic stresses due to heat, drought, salt and freezing.

Rivero et al. (2013) found that GB accumulation increased under a combination of heat and salt stress in tomato plants. Einset et al. (2007) exogenously applied GB in Arabidopsis and reported that it improved the genes expression for transcription factors, membrane moving mechanisms, reactive oxygen, and plasma membrane functions.

Hayashi et al. (1998); Yang et al. (2005) and Yang et al. (2007) reported the importance of GB in increasing the heat stress tolerance. GB is important metabolite associated with the activation of HSPs under heat shock and increased the thermo tolerance of the plant, thus clarifying that GB and HSP70 had role in protecting and improving the Krebs cycle enzyme functions. Diamant et al. (2003) stated that GB activated ClpB (HSP100) which helped increase competence for disaggregation of proteins under heat shock (Chou et al., 1989; Lin et al., 1984; Allakhverdiev et al., 2008; Lui and Shono, 1999; Sanmiya et al., 2004).

3.6. Salicylic acid (SA)

Salicylic acid (SA) (2-hydroxybenzoic acid) plays an important role in systemic acquired resistance and hypersensitive response, and contributes to basal and acquired thermo tolerance (Dat et al., 1998a; Dat et al., 2000; Lopez-Delgado et al., 1998).

Salicylic acid was important for plant growth, and resistance responses, and played important role in inducing specific enzymes (Chen and Gallie, 2006). SA regulated the enzyme activity, like biosynthetic enzyme, catalyzed biosynthetic reactions for generating protective compounds (Solecka and Kacperska, 2003). SA standardized the protective enzymes, like SOD and POD, that were important to increase plant's tolerance to abiotic stresses (Shim et al., 2003).

Raskin (1992) and Conrath et al., (1995) found that SA enhanced induced HSP accumulation in plants. Raskin (1992) and Snyman and Cronjé (2008) reported that SA influenced the heat shock response in tomato plant. The phenolic compounds and antioxidative enzymes' function increased when SA was applied in the *Salvia miltiorrhiza* cell culture (Dong et al., 2010). Shinwari, et al., (2018) reported increased tomato thermo tolerance when treated with SA.

3.7. Proline level

Proline works as an osmolyte and a molecular chaperone regulating the structure of protein and protecting the cells from damage under stress conditions (Verbruggen and Hermans, 2008 ; Szabados and Savouré, 2010). Proline accumulated during heat stress in tolerant tomato plant to protect the cell wall from damage (Mazzeo et al., 2018).

Claussen (2005) and Singh et al. (2017) found an increase in the proline level in tomato leaves under heat stress and it was positively associated with the pollen viability.

Proline level increased in many plants in response to abiotic stresses, however, in tobacco and Arabidopsis plants, proline did not accumulate under heat stress (Rizhsky et al., 2004; Dobra et al., 2010). Gholi-Tolouie et al. (2018) reported an increase in the proline level under biotic stress in tomato leaves. The proline level was controlled by the regulation of biosynthesis and catabolism (Szabados and Savouré, 2010).

3.8. Myo-inositol

Myo-inositol plays an important role as a junction position for abiotic and biotic stress responses and its accumulation under abiotic stresses has a positive correlation with plant tolerance to abiotic stress (Tan et al., 2013).

3.9. Gamma-aminobutyric acid (GABA)

Gamma-aminobutyric acid (GABA) increased in many plants under heat, osmotic and salt stress as it regulates effector proteins (Pareeket al., 2009; Kinnersley and Turano, 2000). GABA is mostly created by glutamate decarboxylase in the cytosol, and transferred to the mitochondria. GABA succinic semi-aldehyde dehydrogenase transfer GABA into succinate in the TCA phase (Fait et al., 2008; Shelp et al., 1999). GABA metabolism was linked with carbon–nitrogen constancy (Bouche and Fromm, 2004; Song et al., 2002). The role of GABA was important for salt stress tolerance in *Arabidopsis thaliana* (Renault et al., 2010).

3.10. Abscisic acid (ABA)

Abscisic acid (ABA) is an important controller of abiotic stress tolerance and is up-regulated rapidly under stress. ABA has a role in opening and closing of stomata to regulate water loss by transpiration (Cutler et al., 2010; Hubbard et al., 2010; Raghavendra et al., 2010).

3.11. Ca^{2+} and root uptake

Calcium acts as a cellular messenger in plant physiological function, affects the integrity of cell walls, maintains the cell contact, and inhibits ion leakage caused by stress (Fortes et al., 2017).

Changing the amount of calcium in the plant tissue is affecting biochemical and physiological proceedings. Hepler (2005) mentioned that calcium looks to be the first transducer of hormonal and ecological indicators. Akula and Ravishankar (2011) reported the increased level of Ca^{2+} in the cytoplasm under abiotic stress. They also suggested that induced variations in microsomal membrane role characteristic of enhanced senescence could happen under ecological stresses like physical damage, chilling wound, and heat shock.

Heat stress affects negatively root nutrient uptake and nutritional quality which lead to reduced crop production (Giri et al., 2017).

The high temperature over a longer period caused lower oxygen availability and led to the root browning, thus affecting membrane integrity (Fukuoka and Enomoto, 2001; Wells and Eissenstat, 2002). Saidi et al. (2010) reported that high solution temperature in both short and long term treatment affected membrane transport (as it was affected by many environmental factors), and heat stress caused damage to membrane fluidity and permeability of cells.

3.12. Heat shock proteins (HSP)

As discussed above, heat shock proteins play an important role in regulating plant thermo tolerance and enhancing the survival of the plant under extreme heat exposure (Howarth and Ougham, 1993; Lin et al., 1984; Vierling, 1991).

There are two types of thermotolerance; acquired thermotolerance and basal thermotolerance (Suzuki et al., 2008). The capability for acquired thermotolerance can be increased by increasing the expression levels of protective genes before exposing to heat stress (Larkindale and Vierling, 2008).

Tomato thermo tolerance is controlled by 21 heat stress transcription factors (Hsfs) (Scharf et al., 1998). Heat stress transcription factor A-2 (HsfA2) and Hsf B1 are heat inducible (Scharf et al., 1998), but the activity is organized by HsfA1 playing a role as main controller of the heat shock response (Mishra et al., 2002).

Scharf et al., (1998) reported the importance of the collaboration of HsfA2 and HsfA1 for the co-localization of HsfA2 in the nucleus. HsfA2 plays a key role for controlling Hsfs under heat

stress (Mishra et al., 2002). The heat stress induced creation of HSP70 and the gene expression of HSP70 in *Arabidopsis* improved at maturation and germination of seeds under controlled conditions (Sung et al., 2001). HSP70 is important for thermo-tolerance in seed germination (Su and Li, 2008).

Li et al. (2011a) found that the increase in night temperatures increased the respiration rate, leading to decreased levels of ATP and carbohydrates. Heat shock proteins70 is created and accumulated in dry seeds of *Arabidopsis* when plants are under environmental stresses and at seed maturation but they are down-regulated quickly through seed germination (Sung et al. 2001).

Giorno et al. (2009) and Sun et al. (2002) reported that the activation of heat shock gene expression through plant growth is more associated with developmental programme than the reaction of the plant under stress conditions.

Giorno et al. (2009); Nover et al. (1989); Scharf et al. (1998); Heerklotz et al. (2001); Heerklotz et al. (2001) and Port et al. (2004) explained the main role of HsfA2 in three phases: (1) a soluble nuclear phase, (2) a soluble cytoplasmic phase, and (3) a stored phase.

The development of pollen grain is highly sensitive to heat shock and it is partially due to failure in increase of Hsf and Hsp mRNAs (Frova et al., 1989; Gagliardi et al., 1995; Giorno et al., 2009; Mascarenhas and Crone, 1996; Paupière et al., 2017).

4. Breeding for high temperature stress

Data on global temperatures show a rising trend in temperatures thus making heat stress on tomatoes a critical issue to address. High temperature negatively affects tomato growth resulting in lower yield and productivity (Sato et al., 2006). For a sustainable crop system the understanding of the genetic and physiological responses in tomatoes is crucially important.

Tomato being a major vegetable crop is important in terms of its food and economic value. Also the tomato is a suitable model plant species having a moderately compact genome (950 Mb) and genetic linkage map, wide germplasm resources (<http://tgrc.uc-davis.edu>), diploidy, and moderately short life cycle (Pujar et al., 2013). Due to the diversity in germplasm resources and plant characters including photoperiod, flowering and the development of fruits, compound leaves and mycorrhizal roots, it offers itself as an alternative model plant to *Arabidopsis thaliana* (Carvalho et al., 2011). The massive availability of mutants in tomato is also another beneficial characteristic of a model plant (Emmanuel and Levy, 2002). The modern tomato cultivars may be employed for genomic studies (Sun et al., 2006). The availability of genetic variation in fruit set under heat stress may help selection for heat tolerance. The capacity to tolerate heat stress can be enhanced through modifying the expression levels of “receptive” genes before the heat shock (Frank et al., 2009). The genes conferring stress tolerance are available in germplasm collections, wild relatives, and materials surviving in extreme environments (Krishna et al., 2019).

Transgenic technology could be an important tool to improve the tolerance of tomato to heat stress, particularly if combined with conventional approaches. Transgenic technology including transformation and re development procedures and gene editing (CRISPR-CAS9) may play important role in developing the cultivars tolerant to heat stress (Krishna et al., 2019 ; Brooks et al., 2014). A limited number of studies to incorporate heat tolerance in tomato are available compared to many more studies aiming tolerance to drought, salt and cold (Marco et al., 2015). Several proteins are reported to be related to enhanced tomato thermo-tolerance (Cheng et al., 2009).

The cultivated tomatoes can be enriched with desired traits from wild sources but it is often associated with agronomic inferi-

ority in the offspring. The major complications arise due to the quantitative nature of the traits with many genes involved. Earlier reports (Grandillo et al., 1999; Saliba-Colombani et al., 2001; Van der Knaap and Tanksley, 2003) highlighted that yield and yield contributing traits in tomato were the polygenic characters. These reports also indicated the existence of continuous selection pressure for yield related traits through the progression of domestication.

The information gained on chromosomal segments related to intricate traits, the simultaneous effects of the chromosomal segments on other characters, or the genetic control of traits (dominance or over-dominance etc.) through conventional breeding is generally insufficient (Semel et al., 2006). Researchers also agree that depending only on phenotypic criteria for selection was less precise under high $G \times E$ effects. Identification of genetic markers may improve the selection and breeding of polygenic traits of interest. DNA markers have enabled identification of quantitative trait loci (QTLs) to improve the traits of interest (Gur and Zamir, 2004).

Molecular mapping established on crosses between the cultivated tomato and the related wild species is valuable to make use of the variation existing in the available genetic resources. Data on tomato introgression lines assayed for fruit related traits is available (Gur et al., 2004). However, limited molecular work on the effect of heat stress on tomato fruit has been reported. A suitably designed molecular genetics investigation may help identify genes for heat tolerance response in tomato. Ibrahim (2016) reported that the genotypes considered as heat tolerant can make important genetic resource for introgression of heat tolerance genes, and recommended breeding programs to improve the fruit quality using backcross hybridization.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

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