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Induction of heat stress tolerance in economically important Tomato (*Solanum lycopersicum*): A review on current knowledge

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Abstract

Tomatoes (*Solanum lycopersicum*) are common foods that provide essential calories, vitamins, and minerals to almost 80% of the global population. Concerns about the impact of rising temperatures on tomato production have intensified as a result of recent global climate change. Heat stress disrupts the plant's critical physiological and biochemical processes. High temperatures suppress photosynthetic activity and chlorophyll concentration, as well as pollen germination, fruit set, and ripening. Heat stress accumulates reactive oxygen species (ROS), which cause significant oxidative destruction to the crop. Heat shock proteins are produced swiftly by plants to reduce the effects of heat stress. A variety of factors determine heat tolerance including chlorophyll fluorescence, canopy temperature, membrane stability, plant water status, secondary metabolite synthesis, antioxidants, and associated enzymes. Knowledge of heat stress impact and tolerance at the biochemical, physiological, morphological, and molecular level at various growth phases (from seed germination to harvest) is critical for developing new crop types that can cope with future climate. To better understand the process underpinning stress tolerance and the generation of heat-tolerant cultivars, further research on the advanced genetic approaches like genome wide association mapping (GWAS), microarray, CRISPR Cas gene knockout editing and virus induced gene silencing (VIGS) in tomato seedlings under heat stress is required.

Keywords: Heat stress, *Solanum lycopersicum*, Heat tolerance, Next-generation sequencing technology, Genetic markers

List of abbreviations: Chl = Chlorophyl; ATP = Adenosine triphosphate; ROS = Reactive oxygen species; PT1 = Proline transporter 1 gene; SAMDC = S-adenosylmethionine decarboxylase; HSPs = Heat shock proteins; HSFs = Heat stress transcription factors; RAPDs = Randomly amplified polymorphic DNAs; AFLPs = Amplified fragment length polymorphisms; CAPS = Cleaved amplified polymorphic sequences; RFLPs = Restriction fragment length polymorphisms; VNTRs = Variable number of tandem repeats; SCARs = Sequence characterized amplified regions; ESTs = Expressed sequence tags; COS = Conserved ortholog sets; SSCPs = Single-strand conformation polymorphisms; InDels = Insertion deletions; SNPs = Single nucleotide polymorphisms; LD = Linkage disequilibrium; NGS = Next-generation sequencing technology; RADseq = Restriction site-associated DNA sequencing; GBS = Genotyping-by-sequencing

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Introduction

Agriculture is facing tremendous environmental pressure across the world. In terms of climate change, abiotic stresses are the most remarkable environmental concerns in agriculture which affects plant growth and production (Foley et al., 2011). Modern climate models indicate that by the turn of the 21st century, average world temperatures will rise by 1 °C to 6 °C, with frequent and severe heat waves (Thornton et al., 2021). Following the intensity of heat, drought, salt, and mineral toxicity stressors, rising global temperatures pose a significant danger to agricultural yield. Heat stress is categorized by a rise in ambient air temperature over the threshold level, which is coupled with the rise in soil temperature and a decrease in moisture level, which is sufficient to induce irreparable damage in plants (Liu et al., 2012). Although rising temperatures may be advantageous in certain colder locations, they have emerged as a main threat to the long-term production of crops in the world's warmer regions (Gourdji et al., 2013; Lobell & Gourdji, 2012). To reduce this environmental impact on agriculture for sustainable crop production, several management measures such as conservation tillage, yield gap adoption, and improving cropping efficiency were implemented.

Although the tomato is technically a berry fruit, it is often recognized as a vegetable with a vital role in olericulture (Shah et al., 2020). It originated in the Andes of South America (modern-day Peru), where it grew wild at the foot of mountains (Darboe, 2018) and taken to different regions of the world by an explorer (Arah et al., 2015). In ancient times, it was considered poisonous and grown as an ornamental plant in gardens. It was recognized as a food crop in 1840 in Europe (Paran & Van Der Knaap, 2007) but now after the potato, it is the world's second most consumed vegetable belonging to the family Solanaceae (El-Sappah et al., 2019). It is the most prominent garden plant and is also cultivated at a commercial scale all over the world as the demand is increasing day by day. Beefsteak, cherry, paste, san-Marzano, globe, green, pear, Roma, Milano, chonto, and industrial tomato are the main types of tomatoes. These are consumed as raw (pulp, salad and juice) or in various cooked (soup, sauce and ketchup etc) forms (Ahmed et al., 2012; Rowles et al., 2018).

Nutritional status

Tomato is a rich source of minerals, antioxidants (phenolics and lycopene) and vitamins (vitamin C and vitamin A), essential amino acids, sugars, iron phosphorous, and dietary fibers (Ayandiji et al., 2011; Perveen et al., 2015) that make it healthy item of the human diet (Golam et al., 2012). One average fresh tomato provides vitamin C (47 RDA), vitamin A (22 RDA) along with 25 calories of total energy (Arah et al., 2015; Pinela et al., 2012). Tomatoes are also a significant source of Potassium, protein, phylloquinone (vitamin K), folate (vitamin B9), Beta carotene, Naringenin, Chlorogenic acid, glycoalkaloids (tomatine), flavanones, phytoene and flavones (Masood et al., 2018; Setyorini, 2021). The quantity of main nutrients that can be derived from 100 g of ripened tomato is given below in the Table 1 (Bhowmik et al., 2012; Jaramillo et al., 2007).

Table 1 Nutritional contents per 100 grams of tomato (Ali et al., 2021)

Principal	**Element**	**Quantity**
Energy	…..	34 Kcal
Water	……	91 %
Proteins	……	17.7 g
Fats	Myristic acid	0.56 g
	Palmitic acid	18 g
	Stearic acid	4.81 g
	Palmitoleic acid	0.25 g
	Oleic acid	14 g
	Linoleic acid	49 g
	Linolenic acid	10 g
	Caproic acid	0.03 g
	Caprylic acid	0.06 g
	Capric acid	0.04 g
	Heptadecanoic acid	0.26 g
	Lauric acid	0.09 g
	Pentadecanoic acid	0.12 g
	Arachidic acid	0.88 g
	Eicosadienoic acid	0.04 g
	Arachidonic acid	0.04 g
	Eicosapentaenoic acid	0.05 g
	Erucic acid	0.02 g
	Docosadienoic acid	0.07 g
	Behenic acid	0.59 g
	Tricosanoic acid	0.68 g
	Lignoceric acid	0.74 g
	Saturated fatty acid	27.4 g
	Monounsaturated fatty acid	13.8 g
	Polyunsaturated fatty acid	57.55 g
	Vaccenic acid	0.53 g
	Eicosanoic acid	0.10 g

Carbohydrates	……..	5.96 g
	Total sugars	50.6%
	Reducing sugars	35.8%
	Fructose	2.8%
	Glucose	2.4%
	Sucrose	0.02%
Fiber	…..	11.4 g
Vitamins	Vitamin A	614 IU
	Vitamin B1 (Thiamine)	0.66 mg
	Vitamin B2 (Riboflavin)	0.48 mg
	Vitamin B3 (Niacin)	9.68 mg
	Vitamin B5 (Pantothenic acid)	4.93 mg
	Vitamin B6 (Pyridoxin)	1.51 mg
	Vitamin B7 (Biotin)	68.97 µg
	Vitamin B9 (Folate)	14 mg
	Vitamin C (Ascorbic acid)	36 mg
	Vitamin E	15 µg
	Vitamin K	98 µg
Minerals	Sodium	70 mg
	Potassium	403 mg
	Calcium	105 mg
	Magnesium	172 mg
	Phosphorus	300 mg
	Chlorine	517 µg
	Boron	36 µg
	Nickel	0.66 mg
	Nitrate	274 mg
	Iron	4.55 mg
	Zinc	2.48 mg
	Cobalt	19.6 mg
	Copper	0.67 mg
	Manganese	0.60 mg
	Chromium	193 µg
	Iodine	2.65 mg
	Fluorine	413 µg
	Aluminum	1241 µg
	Silicon	46.5 µg
	Selenium	13 µg
	Lead	1.21 µg
	Cadmium	0.17 µg
	Arsenic (As)	0.2 µg
Amino acids	Threonine	1.37 g/ 100 g Protein
	Valine	2.49 g/ 100 g Protein
	Methionine	0.57 g/ 100 g Protein
	Isoleucine	2.13 g/ 100 g Protein
	Leucine	2.80 g/ 100 g Protein
	Phenylalanine	1.77 g/ 100 g Protein
	Histidine	1.93 g/ 100 g Protein
	Lysine	2.45 g/ 100 g Protein
	Arginine	2.33 g/ 100 g Protein
	Aspartic Acid	1.40 g/ 100 g Protein
	Serine	1.78 g/ 100 g Protein
	Glutamic Acid	10.13 g/ 100 g Protein
	Proline	1.53 g/ 100 g Protein
	Glycine	2.30 g/ 100 g Protein
	Alanine	2.74 g/ 100 g Protein
	Cystine	0.21 g/ 100 g Protein
	Tyrosine	1.82 g/ 100 g Protein

Carotenoids	β-carotene α-carotene Lycopene Lutein + zeaxanthin Phytoene Phytofluene	9942.16 µg 101.00 µg 8002.50 µg 60.67 µg 668.33 µg 500.00 µg

Health benefits of tomato

Antioxidant, anti-proliferative, anti-carcinogenic, anti-tumorigenic, anti-inflammatory, anti-mutagenic, and anti-atherogenic phytonutrients are present in tomatoes. Tomato is enriched with lycopene along with a lesser amount of other anti-oxidants like lutein*α*- carotene, phytofluene, *β*-carotene, phytoene, *γ*- carotene, and neurosporene (Chaudhary et al., 2018). Balanced tomato consumption is beneficial to reducing the risk of various cancer diseases especially prostate cancer (Sharma et al., 2021). Lycopene also improves vision and fertility in males by increasing sperm quality and swimming efficiency while decreasing the quantity of defective sperms (Innes, 2014; Leong et al., 2018). Tomato consumption can prevent various old-age diseases like Parkinson's, osteoporosis, Alzheimer's and dementia (Arah et al., 2015).

It is reported that Supplementing with lycopene (2.5–10 M) lowers total cholesterol through inhibiting HMG-CoA reductase expression (Palozza et al., 2010). The amount of lycopene in a person's blood is known to be inversely linked to the risk of heart disease (Costa-Rodrigues et al., 2018). Tomato intake is associated with a lower risk of inflammatory diseases such as atherosclerosis (Casas et al., 2018; Cheng et al., 2019). Quercetin aids in chromatin remodelling, which helps to prevent epigenetic changes as cancer progresses (Martí et al., 2016). Similarly, high carotenoid intake in the human diet has been linked to a lower risk of chronic diseases (Bohn, 2019). Carotenoids modulate the immune response, stimulate intercellular signaling (gap junction) pathways, have pro-vitamin A activity, regulate cell cycle and apoptosis, and modulate a variety of physiological processes, resulting in disease resistance (Milani et al., 2017; Sathasivam & Ki, 2018). Carotenoids such as α-carotene, β-carotene and β-cryptoxanthin serve as precursors to vitamin A, hence a reduction in their levels in the blood leads to vitamin A insufficiency (Fernández-García et al., 2012; Tanumihardjo, 2013). The rutin found in tomato (vitamin P) has previously shown significant anti-oxidant, anti-inflammatory and anti-carcinogenic potential (Kelebek et al., 2017; Li et al., 2014; Navarro-González et al., 2011; Röhlen-Schmittgen et al., 2020). The healthy benefits of tomatoes (Table 2) make it the most demanding vegetable in the world (Ali et al., 2021; Bhowmik et al., 2012).

Table 2 Health benefits of tomato (Bhowmik et al., 2012; Ali et al., 2021)

Bioactive Compound	**Use**
Lycopene	To cure prostate, stomach, and colorectal cancer; Boost immune system of males against flue and cold; Natural sunscreen protects from dangerous UV rays
Calcium and vitamin K	To strengthen and repair bone and bone tissues
Coumaric acid	Protect lungs from damaging effects of cigarette smoke
Vitamin A and C	Neutralize free radicals in the blood; Prevent night blindness; Reduce lead toxicity in the blood; Stimulate production neurotransmitters for the proper functioning of the brain; Reduce the risk of scurvy; Strengthen bone, skin, hairs and teeth
Vitamin B and potassium	Lowers the cholesterol level; Lowers blood pressure and prevent heart attack and stroke; Reduce migraine attacks
Chromium	Prevent diabetes and maintain blood sugar level
Quercetin	antioxidant and anti-inflammatory effects that might help reduce swelling, kill cancer cells, control blood sugar, and help prevent heart disease
Kaempferol	Reduces the risk of chronic diseases, especially cancer. Kaempferol augments human body's antioxidant defense against free radicals. Kaempferol modulates apoptosis, angiogenesis, inflammation, and metastasis
Naringenin	Promotes carbohydrate metabolism, increases antioxidant defenses, scavenges reactive oxygen species, modulates immune system activity
caffeic acid	Reduce inflammation; Prevent cancer; Prevent toxicity associated with chemotherapy and radiation; Prevent diabetes; Prevent premature aging; Prevent neurodegenerative diseases, like Parkinson's disease; Reduce exercise-related fatigue
Rutin	Helps blood circulation; Prevents blood clots; Lowers cholesterol; Reduces arthritis pain.
Chlorogenic acid	It has anti-diabetic, anti-carcinogenic, anti-inflammatory and anti-obesity potential
Ferulic acid	Anti-inflammatory, antioxidant, antimicrobial activity, anticancer, and antidiabetic effect
P-coumaric acid	Inhibit proliferation and migration of cancer cells and promote apoptotic cancer cell death, supporting its potential anticancer effects
Resveratrol	Antioxidant and anti-inflammatory properties against diseases like cancer, diabetes, and Alzheimer's

	disease; The anti-inflammatory effects of resveratrol make it a good remedy for arthritis, and skin inflammation
Chrysin	Used for bodybuilding; for treating anxiety, inflammation, gout, HIV/AIDS, erectile dysfunction (ED), and baldness; and for preventing cancer
Epicatechin	Reducing the risks of diabetes mellitus and cardiovascular diseases. Anti-hyperlipidaemic, anti-inflammatory, antioxidative, anticarcinogenic, and cytoprotective
Catechin	Aids in weight loss; Catechins may help to prevent certain types of cancer including breast cancer and prostate cancer; Protects brain health; May offer sun protection
Luteolin	Anti-oxidant, anti-inflammatory, microglia inhibition, neuro-protection, and memory increase
Cinnamic acid	Reduced inflammation, lower blood sugar and cholesterol levels, improved memory, and the increased growth of "good" gut bacteria
Sinapic acid	Antioxidant, anti-inflammatory, anticancer, antimutagenic, anti-glycemic, neuro-protective, and antibacterial activities

Global tomato production

Tomato is adapted to grow from tropics to arctic regions of the world with diverse climatic conditions. Tomato production increased in the last two decades from 1994 to 2018 (Fig. 1). Asia is a major tomato producer with a total share of 53.7% in the global market, followed by America (17.9%), Europe (16%), Africa (11.9%), and Oceania (0.4%) from 1994 to 2018 (Fig. 2). Turkey, China, India, USA, Brazil, Egypt, Iran, Mexico, Italy and Spain are the top ten tomato producers in the world (FAOSTAT, 2020). Global production of tomatoes is almost 160.0 million tons (Qasim et al., 2018) whereas China is the "Global King" of tomato growing countries with an average annual production of million tons. Although, the tomato has good potential to grow in diverse climates global average yield of tomato is low and not sufficient to meet the current market demand (Alsamir et al., 2019) because it confronts severe heat stress at different growth stages of lifecycle (Ruggieri et al., 2019).

Tomatoes are a vegetable crop with high economic significance in Asian countries. In certain sections of Pakistan, tomatoes are produced throughout the year. It is mainly cultivated in thirteen districts of Punjab and other provinces (Table 3, 4). Tomato yield may be limited due to viral (TMV and TYLCV), fungal (early and late blights, blossom end rot), and bacterial wilt illnesses, nematode and Orobanchi (parasitic plant) assaults, a lack of indigenous hybrids, and a lack of different germplasm sources. Besides this, the prevalence of high temperature during the long summer is a major abiotic factor that catastrophically hinders tomato production (Jahan et al., 2019).

Table 3 Pakistan's major tomato-growing regions

Zones	**Agro-ecological zones/divisions**
Southern Punjab	Bahawalnagar, Khanewal, Muzaffargarh, Bahawalpur, and Rahim Yar Khan,
Central Punjab	Sargodha, Khushab, Sahiwal, Okara, Faisalabad and Sheikhupura
Northern Punjab	Sialkot and Gujranwala
Sindh	Larkana Hyderabad, Karachi, Badin, SakkurThatta, NowsheroFeroz, Mirpurkhas and Nawabshah
KPK	Nowshera, Swat, Swabi, Malakand, South Waziristan, Charsadda, North Waziristan, Kurram, Tank, and Mardan
Balochistan	Killa Saifulla, Pislin, Loralai, Khuzdar and Awaran

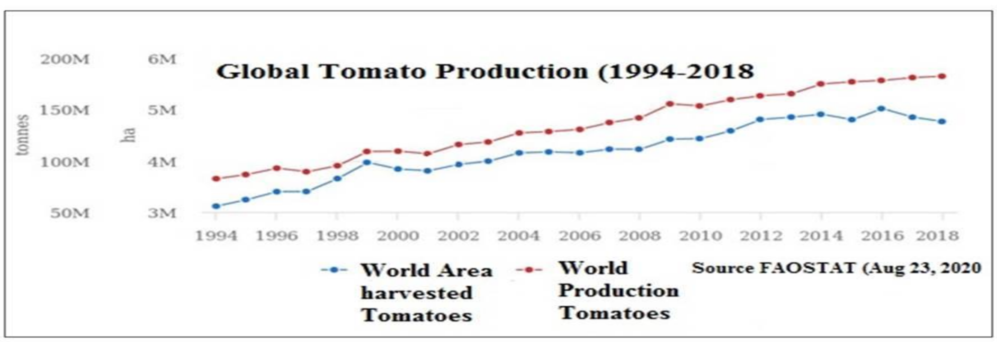

Fig. 1 Global tomato production (1994-2018); Source (FAOSTAT, 2020)

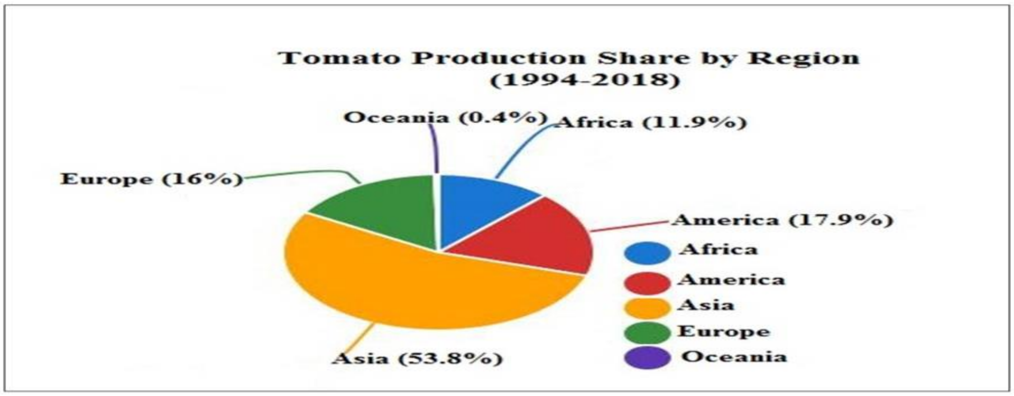

Fig. 2 Tomato production share by region (1994-2018), adopted from (FAOSTAT, 2020)

Effect of temperature

Tomato is a day-neutral plant and thrives best at pH 5.5 to 6.5 is fairly fertile, well-drained sandy loam or heavier soils containing 1.5% organic matter content. It requires 460mm of rainfall per cropping season, sensitive to water logging and heat stress. It is cultivated in different seasons in four provinces of Pakistan (Table 4). It requires diverse temperature regimes at various growth stages from seed germination to harvest (Table 5). It is hard to identify a steady overhead threshold temperature because crop behavior varies according to other environmental factors (Golam et al., 2012). Average day temperatures above 35ºC adversely affect the seed germination and seedling establishment, above 40ºC aborts the flowers due to the physical destruction of pollen grains, pollen tube germination and growth and above 25ºC can drastically reduce yield by affecting fruit set in tomato (Firon et al., 2012). Thus, sustainable tomato production in the prevailing hot environment is the exigent and main thrust of tomato breeders.

Heat stress tolerance is a very complex phenomenon because high temperature causes variations in various biochemical and physiological processes that directly or indirectly affect plant growth and development which leads to significant yield reduction (Zhang et al., 2019). Heat stress disturbs plant water relations (Hussain et al., 2019), reduction of photosynthetic capacity (Ashraf & Harris, 2013; Chovancek & Zivcak, 2019), decreases of metabolic activities (Zhou et al., 2019), and changes in the level of endogenous hormones (Ahammed et al., 2019), the generation of oxidative reactive species (Wang et al., 2019), ethylene production stimulation (Pan et al., 2019), pollen tube formation is reduced, and pollen loss is increased (Luria et al., 2019) in plants. Thus, it is necessary to study the response of tomatoes in terms of physiology, biochemistry, reproductive and vegetative growth to understand the basic mechanism involved in tomato heat tolerance.

Table 4 Sowing, transplanting, and harvesting time of tomato in Pakistan (Khokhar & HRI, 2013)

Province	Nursery sowing	Transplanting	Harvesting
Punjab	(i) July/August (Katha Saghral) (ii) October (Central Plains) (iii) November to December (Hilly Areas)	(i) August/ September (ii) November (iii) February/March	(i) December to February (ii) April to May (iii) May to June
KPK	(i)August (Dargai) (ii) April to May (Northern Areas) (iii) May to June	(i) October (ii) May to June (iii) June to July	(i) December to January (ii) July to August (iii) October to November
Sindh	(i) June/July (ii) August to October (iii) December	(i) July/August (ii) September to November (iii) February	(i) September to November (ii) December to February (iii) May to June
Balochistan	(i) November /December (Plains) (ii) March /April (Hilly Areas)	(i) March (ii) April/May	(i) May to June (ii) June to August

Table 5 Optimum temperature ranges at different growth stages of tomato (Khokhar & HRI, 2013)

Growth Stage	Optimum Temperature
Seed germination	15.5ºC to 29ºC
Seedling growth	25ºC to 26ºC
Pollen tube germination	22ºC to 27ºC
Fruit setting	18ºC to 20ºC
Fruit ripening	24ºC to 28ºC

Heat-stressed tomato responses

Responses in morphology and growth

High temperatures can cause significant pre-harvest and post-harvest losses in tomatoes. Heat stress causes burning of leaves, twigs, stems, and branches, leaf senility, and abscission, prohibition of the shoot and root development, fruit discoloration, and diminished production (Abdalla et al., 2020). Other morphological characteristics, such as fruit set, quantity of fruits per plant, fruit weight, and days to fruit maturity, differ between heat resistant and sensitive tomato cultivars. Heat stress negatively affects pollen viability, female fertility that fruit development reduces or even fails (Pham et al., 2020).

High temperature beyond the optimum regimes decreases floral bud development, flower abortion, gamete development, and formation of seeded fruits from pollinated flowers that diminished crops yields (Pham et al., 2020). Heat stress also influences meiosis in micro-and mega-gametophytes (Hassan et al., 2021), pollen tube development and pollen germination, a number of pollen grains, pH in stigma, style and ovule, the viability of embryo and ovule, fertilization of gametes, development of endosperm, (Pan et al., 2017). Under heat, there is an aberrant formation of exerted style (stigma is stretched beyond the anther cone) in tomato, which inhibits self-pollination. All of these changes, whether in vegetative or reproductive development, result in significant yield loss.

Physiological responses

Plant water status

Turgor pressure and water status of plants are the most sensitive to elevated ambient temperature. Plant tissue dehydrates as a result of high temperatures, and disturbs the turgidity of cells which subsequently restricts plant growth and development. The temperature of 31˚C is considered as the threshold for various cool-season crops to maintain their water status and cell turgidity during the flowering stage (Atkinson & Urwin, 2012), while arise in leaf temperature in response to heat stress lowers the relative water contents and subsequently affects the photosynthesis and transpiration (Zhou et al., 2019). Heat tolerant genotypes show less reduction in leaf water contents than heat-sensitive ones (Zhou et al., 2017) because the production of different antioxidants associated with dehydration tolerance is stimulated intolerant genotypes in response to heat stress (Rezaei et al., 2010). In addition, the increased activity of aquaporins and hydraulic conductivity of cell membranes in heat-tolerant genotypes help to maintain the water status reported by (Akter & Islam, 2017).

Photosynthesis and respiration

Photosynthesis and respiration are the most vulnerable physiological processes in tomatoes, resulting in low development (Huther et al., 2013). Heat stress decreases leaf area, impairs the photosynthetic machinery which lowers the rate of photosynthesis and ultimate crop yield reduction (Wassie et al., 2020). Heat stress injures the stroma and thylakoid lamellae in chloroplast which are the main reaction sites of carbon metabolism and photochemical reactions. High temperatures cause oxidative stress, which breaks thylakoid membranes and restricts membrane-associated electron transporters and enzymes, lowering photosynthesis rates (Nouri et al., 2015).

Photosystem-II, Rubisco, and Rubisco binding proteins are much sensitive to heat stress and are the major cause of reduced photosynthetic events (Tan et al., 2020). Leaves exposed to a elevated temperature of 40˚C either in dark or light cause irreversible changes in photosystem-II, Rubisco, and Rubisco activase (Chen et al., 2017). Due to the inactivation of Rubisco binding proteins, heat stress disrupts the complex processes of photosystem-II, which reduces carbon absorption. The light-harvesting complex-II Chl a/b-proteins are likewise separated from the photosystem-II by high temperatures (Galka et al., 2012).

Heat stress affects the respiration process by affecting mitochondrial activities. In contrast to photosynthesis, the rate of respiration rises under elevated temperature, however, at a certain temperature, it decreases owing to injury to the respiratory system (Prasad et al., 2008). The increased rate of respiratory carbon loss in response to heat stress makes significant reductions in the production of ATP and enhanced production of ROS because heat stress affects the solubility of CO_2 and O_2, and the kinetics of Rubisco (Cossani & Reynolds, 2015). Heat-sensitive genotypes show a higher respiration rate compared to controls when subjected to heat stress (Zhou et al., 2017).

Leaf senescence

Due to structural alterations in the chloroplast and plasma membranes, vacuolar collapse, and subsequent interference with cellular homeostasis, leaf senescence is one of the most common signs of heat injuries (Khanna-Chopra, 2012). Heat stress inhibits the biosynthesis of chlorophyll which may accelerate leaf senescence in tomatoes (Megahed et al., 2008). A substantial diurnal temperature range is also responsible for the enhancement of flag leaf senescence in tomatoes, as plants exposed to heat stress during maturity accelerated leaf senescence (Hassan et al., 2021). Thus, heat-stressed plants experienced senescence-related changes in various metabolites such as carbohydrates, proteins, lipids, osmolytes, and hormones (Ciucă & Petcu, 2009).

Carbohydrates

Carbohydrates play an important role in plant homeostasis as a major energy source available during seed germination and pollen development, also stabilize the cell membranes and osmotic balance during stress signaling. Plant nutrition, performance, and health are all affected by disruptions in carbohydrate metabolism in exposure to abiotic and biotic stress (De Storme & Geelen, 2014). Negative impacts of heat stress on carbohydrate metabolism during reproductive growth of different crops such as pepper, tomato, chickpea, and sorghum have been reported in the previous several years. Flower development in tomato under high temperature of 32˚C affects the pollen viability, pollen and anther wall soluble carbohydrates are reduced, whereas locular fluid (fluid found in the ovary of angiosperms) soluble sugars are increased (Pressman et al., 2002) suggest that soluble sugars are blocked in locular fluid in response to heat stress and cannot move to pollen for its proper development. High starch contents accumulate in pollen three days before the anthesis (period in which flower is fully open) and then converted to soluble sugars for normal pollen development but under heat stress, less accumulation of starch led to a lack of soluble sugar contents ultimately causing abnormal pollen development. Moreover, the activity of hexose producing invertase enzyme in tomato flowers of heat-sensitive genotypes was lower than heat-tolerant genotypes exposed to high temperature of 32˚C/26˚C for thirty days (Firon et al., 2006) and at 36˚C/28˚C for 24 hours (Sun et al., 2011). Heat tolerant genotypes had higher hexose contents than heat-sensitive genotypes which play a protective role under heat stress. So, with an increase in the activity of hexose producing invertases, pollen formation with excellent viability relies heavily on the presence of soluble sugars and starch.

Osmolytes

Proline is a stress-responsive osmolyte that plays a protective role in cellular homeostasis by scavenging reactive oxygen species and membrane integrity (Hayat et al., 2012). Heat stress decreases the pollen germination but proline exposure can restore the germination potential of pollen grains under high temperature by stabilizing the conformation of the protein (Hong-qi & Croes, 1983). Under high temperature of 45˚C, heat-tolerant cultivars of tomato showed an abundance of proline contents in mature pollens while heat-sensitive had more proline contents in anthers than pollens because heat stress inhibits the transfer of proline from anthers to pollens by decreasing the proline transporter 1 gene (PT1) expression in crops such as tomato (Hanif et al., 2021; Tan et al., 2020).

Lipids

Lipids are important constituents of membranes and stress-responsive metabolites to maintain the membrane fluidity. High temperature-induced oxidative stress increases reactive oxygen species and disturbs membranes stability in crops such as sorghum (Prasad & Djanaguiraman, 2011), wheat (Akter & Islam, 2017), rice (Kilasi et al., 2018), tomato (Xu, Wolters-Arts, et al., 2017), and carrot (Nijabat et al., 2020). Disruption of membrane stability leads to a decrease in pollen viability and saturated phospholipids in pollens. An increase in unsaturated fatty acids under high temperatures leads to an increase in membrane fluidity and makes the membranes vulnerable to oxidative damages (Djanaguiraman et al., 2013; Prasad et al., 2008). Polyamines also act as ROS scavengers (Fariduddin et al., 2013) and are known as membrane-stabilizing metabolites (Alcázar-Román et al., 2006). As *in vitro* pollen germination of tomato was inhibited at 33˚C in response to decrease in polyamine contents but the exposure of various polyamines spermidine and spermine restore the germination potential (Song et al., 1999). Furthermore, exposure to high temperatures (38˚C) for four hours decreases the level of spermidine and spermine while increasing the putrescine in germinating pollen of tomato (Song et al., 2002). Inhibited pollen germination and decrease in spermidine and spermine contents are attributed to reduced activity of the S-adenosyl-methionine decarboxylase (SAMDC) enzyme in response to heat stress.

Hormones

Various hormones like brassinosteroids, ethylene, auxins, gibberellins, and abscisic acid play their role in responses to heat stress. Brassinosteroids are ROS scavengers and increase the pollen germination in tomatoes under a high temperature of 35˚C (Singh & Shono, 2005). Mutation in ethylene receptor and ethylene spray increases the pollen viability under heat stress (Larkindale & Knight, 2002). Auxins help the plants to tolerate heat and drought stress (Sharma et al., 2015). Reduction in auxin gibberellins and contents with increased concentration of ABA in response to heat stress cause pollen abnormality and male sterility (Sakata et al., 2014) but exogenous auxin application prevents male sterility and improves pollen germination (Fahad et al., 2018). Plants must maintain metabolic equilibrium in order to avoid disruption of biochemical processes, which might result in excessive accumulation or decrease of chemicals required for pollen formation. To better understand the heat tolerance mechanism in tomatoes, it is necessary to understand the genetics involved in these processes.

Heat stress tolerance

The ability of plants to survive and maintain stable production even under extremely elevated temperatures is termed heat tolerance (Nahar et al., 2015). Heat tolerance is a multi-complex, polygenic trait that varies from species to species. Abiotic factors like intensity and exposure period of stress at various growth stages of the crop (seed germination, seedling emergence, vegetative and reproductive phase) during the life cycle also affect the physiology and yield of the crop (Chaudhry & Sidhu, 2021).

Heat tolerance involves changes in many morphological, biochemical, physiological, and genetic characters of the plant. For example, accumulation of antioxidants (Bita & Gerats, 2013), osmolytes (Sakamoto & Murata, 2002), carotenoid contents (Savchenko et al., 2010), and heat shock proteins (Bowen et al., 2002) have already been reported due to heat stress in plants. Heat shock proteins (HSPs) or molecular chaperons assist the plant to prevent denaturation and aggregation of target protein molecules in their cells (Scharf et al., 2012). As plant cells receive high-temperature stimulus in the plasma membrane that activates signaling cascade reaction by stimulating calcium sensors like Ca^{2+}, calmodulins (Ranty et al., 2016), and calcium-dependent protein kinases (Das & Pandey, 2010) leading to the synthesis of heat shock proteins (HSPs) or molecular chaperons. These molecular chaperones protect the plant against heat stress by continuing the process of protein folding, refolding, and stabilizing their function (Neta-Sharir et al., 2005). Protein structure stabilization by HSPs and scavenging of ROS by the production of antioxidant compounds help the plant to maintain redox balance, cellular membranes, and homeostasis in cells even under heat stress (Sachdev et al., 2021).

Heat tolerance includes the control of gene expression via transcriptional repression of other genes, DNA methylation and DNA polymerases (Sakata & Higashitani, 2008). High temperature stimulates the expression of genes that encode regulatory proteins (Semenov & Halford, 2009), heat stress transcription factors (HSFs), heat shock proteins (HSPs) and suppresses genes encoding hydrolytic enzymes (Giorno et al., 2013) in heat-tolerant species. Plant breeders are working hard to promote heat stress tolerance in plants. However, the precise mechanism of heat stress resistance in plants via gene induction is yet unclear (Frank & Hutchison, 2009). Due to the general intricacy of features and their interaction with environmental variables, the short-term remedy to heat stress is uncertain (Rahaman et al., 2017). Recently, crop simulation modeling along with genetic information has become an additional approach to dissecting the complexity of traits (Semenov & Halford, 2009). It may be useful in identifying heat stress-related complex characteristics and developing heat stress tolerance in plants.

Molecular and classical genetic markers

Improvements in genetics makeup led to the development of cultivars that can withstand environmental challenges, increasing economic output. It entails the introduction of a single gene of interest into the recipient genotypes, which aids in the improvement of heat tolerance. The genetic markers known as isozymes were famous in the 1970s and early 1980s for genetic modifications. In tomatoes, 41 isozymic genes have been detected that are responsible for fifteen different kinds of enzymatic responses (Tanksley, 1993). Isozyme markers are extremely limited in number and, in some cases, are not polymorphic even between closely related lines (Tanksley, 1993; Tanksley & Orton, 2012). With the arrival of highly heritable molecular marker technique inthe1980s (Botstein et al., 1980) and early 1990s, molecular genetics took the advantage of testing dissimilarities within a single species, and genetic mapping entered a new exciting and developed era with the promise to remarkably enhanced efficiency of crop breeding. These molecular markers are non-coding or coding repetitive segments from the small area of DNA. They may or may not have an actual effect on the phenotype of a trait but are closely positioned to a gene controlling a specific phenotypic trait (Collard et al., 2005). These phenotypically neutral and identically unconstrained in number markers have enabled scanning of the whole genome and assigning landmarks in high density on each chromosome in a variety of crop species. As a result, molecular markers aid in the identification and mapping of genes related with a desired phenotypic feature, such as tomato (Chaudhary et al., 2019; Jiang, 2013; Thoday, 1961).

In some crops, the protein synthesis elongation factor in chloroplast (Ef-Tu) has been linked to heat tolerance (Fu et al., 2012). Cultural methods like as planting time, soil and irrigation management, and plant density may all be adjusted to reduce stress. Although the application of molecular marker technologies and genetic alterations has resulted in the generation of plants with enhanced heat tolerance, further progress in stress tolerance breeding is dependent on physiological mechanisms, and the genetic foundation of heat tolerance remains rare. Several molecular markers, such as randomly amplified polymorphic DNAs (RAPDs), have been refined and used in various crops over the last two decades (Williams & Smith, 1993), simple sequence repeats (SSRs or microsatellites) (He et al., 2003), amplified fragment length polymorphisms (AFLPs) (Vos et al., 1995), cleaved amplified polymorphic sequences (CAPS) (Konieczny & Ausubel, 1993), restriction fragment length polymorphisms (RFLPs) (Botstein et al., 1980), variable number of tandem repeats (VNTRs or minisatellites) (Jeffreys, 1985), sequence characterized amplified regions (SCARs) (Paran & Michelmore, 1993), expressed sequence tags (ESTs), conserved ortholog sets (COS), single-strand conformation polymorphisms (SSCPs) (Orita et al., 1989), insertion deletions (InDels), and single nucleotide polymorphisms (SNPs) (Landegren et al., 1998).

Monomorphic markers cannot expose the variation between the genotypes while the valuable polymorphic markers usually help to find out the variation and discrepancies between same or dissimilar species at a genetic level (Sofi et al., 2021). A polymorphic marker can be dominant or co-dominant, depending upon its ability to express variation between the heterozygotic or homozygotic individuals. A dominant marker can amplify only two allele sizes and can be detected by its presence or absence while a co-dominant marker amplifies many alleles and can show variation to size (Litvinov et al., 2020). All these markers such as RFLP with low genomic coverage to SSR with medium genomic coverage made it possible to assess the genetic diversity between individuals of the same or dissimilar species. This diluted marker application has a drawback of genomic coverage (usually low) therefore cannot narrow down the distance between the responsible gene and marker (Table 6). Thus, it is impossible to perform fine gene mapping for a phenotypic trait of interest using marker application with low genomic coverage.

Single nucleotide polymorphisms (SNPs) markers are a good source of sequence variation in the plant genome. These are the most often utilized in genome-wide association mapping research, genetic diversity analysis, population structure, linkage map building, Quantitative trail locus (QTL) mapping, association mapping, and linkage disequilibrium (LD) investigations (Chagné et al., 2008). Four genetic loci (QTLs) in Arabidopsis have been identified to acquire the plant from acquiring thermo-tolerance. Using restriction fragment length polymorphism, 11 QTLs for pollen germination and pollen tube expansion under heat stress in maize were discovered. Heat tolerance QTL mapping experiments have been carried out on a variety of rice populations at various phases of flowering. However, there has yet to be any validation or precise mapping of the discovered QTLs for heat tolerance (Ye et al., 2012). In wheat and maize, many loci for heat tolerance have been discovered (Bai, 2003; Bennett et al., 2012). QTLs important in gaining thermo-tolerance were initially discovered in Arabidopsis mutants sensitive to heat (Bac-Molenaar et al., 2015). In a genetic investigation of lettuce seed thermo-inhibition, a large QTL for heat tolerance germination as well as another QTL with minor effects were discovered (Argyris et al., 2008). Heat tolerance in current germplasm might be improved using the markers associated to these QTLs. Currently, multiple measures such as thousand-grain weight, grain-filling period, canopy temperature detection, yield, or senescence-related variables are used to identify heat tolerance QTLs (Pinto et al., 2010; Vijayalakshmi et al., 2010).

High-throughput SNPs array is an efficient technique and more reliable option but high cost per sample limits its use in plant breeding. In recent years, cost-effective, high-throughput next-generation sequencing technology (NGS) has widely been used in plant breeding programs (Edae et al., 2014; Poland & Rife, 2012). Recent advancements in NGS technology, such as restriction site-associated DNA sequencing (RADseq) and genotyping-by-sequencing (GBS), have boosted not only its reliability but also its cost-effectiveness. GBS is a high-throughput, cost-effective, robust, multi-complexed approach that can be used for SNPs discovery and genotyping of thousands of samples simultaneously in various crop species (Elshire et al., 2011). The use of restriction enzyme digestion reduces the complexity of the genome which makes GBS more effective and efficient for genetic analysis of plant species with complex and large genome sizes. GBS has been widely used for genetic diversity analysis, marker-trait association, and genome-wide association studies in tomato crops (Table 7). In tomato, various studies have been reported about QTLs detection conferring to yield, quality, and tolerance to abiotic stress such as salinity, drought, low temperature but little has been reported about high temperature (Ashraf & Foolad, 2005). From seed germination to fruit production, this scenario advocated a stronger emphasis on breeding and detecting QTLs for heat tolerance in tomatoes.

Table 6 Advantages and disadvantages of genetic markers

Marker	Type	DNA required(μg)	Advantages	Disadvantage
AFLP	Dominant	0.5-1.0	Robust, High reliability, and reproducibility, A high level of polymorphism and a large number of loci can be detected at the same time.	Random, High quality, and a large amount of DNA is required. Cannot be sequenced
RAPD	Dominant	0.01-0.1	Inexpensive, quick, simple. A high level of polymorphism and a large number of loci can be generated from a single primer.	Low reliability; Reproducibility is low; Cannot be sequenced.
RFLP	Co-dominant	5.0-50.0	Robust, High reliability, reproducibility Specific loci can be detected Can be cloned/sequenced	High quality and a large amount of DNA is required. A low level of polymorphism can be generated. Time-consuming and expensive
SSR	Co-dominant	0.05-0.12	Robust, High reliability, reproducibility Genome-specific: Particular loci can be detected. A high level of polymorphism can be generated. Can be cloned/sequenced	High to moderate quality of DNA is required. Polyacrylamide electrophoresis is required. Time-consuming, laborious, and expensive

SNP	Co-dominant	0.05	Robust, High reliability, reproducibility High level of polymorphism can be generated. Can be cloned/sequenced Small amount of DNA is required	High-quality DNA is required

Table 7 Use of genotyping-by-sequencing (GBS) in tomato crops for various trait by Qualitative Trait Locus (QLTs)

Trait	QTLs	Reference
Tomato flavor	37	(Zhao et al., 2019)
Fruit metabolic traits	44	(Sauvage et al., 2014)
Fruit quality	19	(Ruggieri et al., 2014)
Fruit diameter	22	(Zhang et al., 2016)
Fruit ascorbic acid	22	(Zhang et al., 2016)
Fruit weight	17	(Zhang et al., 2016)
Heat tolerancefor yield contributing fruit traits	17	(Ruggieri et al., 2019)
Water deficit tolerance for yield contributing fruit traits	31	(Albert et al., 2016)
Heat tolerance for reproductive traits	22	(Gonzalo et al., 2020)
Heat tolerance for reproductive traits		(Xu, Driedonks, et al., 2017)

Conclusion and future prospect

Climate change and global warming are wreaking havoc on the universe, raising atmospheric temperatures. These extreme temperature regimes cause severe difficulty in tomato seedlings rising and yield losses during the hottest months (mostly July and August) which ultimately lower the farmers' livelihood. Frequent heat waves affect tomato growth at all developmental stages from seed germination to fruit production by disturbing plant physiological, biochemical and anatomical processes at molecular level, especially by producing large quantity of ROS. Heat stress has different impacts depending on the genotype and also on the severity, timing, and duration of the stress. Consequently, numerous advanced approaches were carried out to incur heat tolerance in tomato but results were not satisfactory. To better understand the process underpinning stress tolerance and the generation of heat-tolerant cultivars, further research on the advanced genetic approaches like genome wide association mapping (GWAS), microarray, CRISPR Cas gene knock out editing and virus induced gene silencing (VIGS) in tomato seedlings under heat stress is required.

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