Review Article

Impact of Temperature Difference on the Physicochemical Properties and Yield of Tomato: A Review

Amrutha Vijayakumar* and R Beena

Department of Plant Physiology, College of Agriculture, Vellayani, Thiruvananthapuram, Kerala, India

Abstract

Tomato is one of the most heat sensitive vegetable crops having high economical and commercial importance. Maximum daily temperature, minimum daily temperature, difference between day and night temperatures, average day time temperature and average night time temperature are the temperature factors that influence the plant growth potentials in a crop. The major effects of high temperature or high difference in day and night temperature (DIF) in plants include inhibition of seed germination, plant growth retardation, improper plant development, deterioration of fruit quality, alteration in photosynthesis, reduced dry matter production, water loss, oxidative stress and finally the yield reduction. This review focusses on the impacts of DIF on the different aspects of growth, development, quality and yield.

Keywords: Temperature differences, Tomato, physiological, quality, yield

***Correspondence**

Author: Amrutha Vijayakumar

Email: amritvjayraj@gmail.com

Introduction

The global human population is currently growing at an alarming rate and is expected to remain in such condition for at least 35 years [1]. An increasing population is associated with an increase in demand of food but the food production is not sufficient to feed the growing population. Global warming and associated heat stress due to climate change is a major threat which affects the crop production adversely [1]. The global climate change models predict an increase of 2°C daily mean temperature between year 2046 and 2065 and 3.7°C by 2100 [2]. This climate change is expected to affect the world in many ways, including the extinction of species that cannot escape their adverse environment and a decrease in food productivity.

High temperature stress/Heat stress

The rise in temperature beyond a threshold level for a period of time sufficient to cause irreversible damage to plant growth and development can be defined as heat stress. Heat stress due to high ambient temperature is a serious threat to crop production worldwide [3].

The vegetables are more prone to abiotic stresses and approximately 50% loss in yield is recorded due to various abiotic stresses [4]. The important effects of high temperature or high difference in day and night temperature (DIF) in plants are inhibition of seed germination, reduction of plant growth, improper development, reduction of produce quality, alteration in photosynthesis, phenology and dry matter production, water loss, oxidative stress and ultimately yield reduction. Tomato is one of the most heat sensitive vegetable crops having high economical and commercial importance (**Figure 1**). Temperature factors that influence plant growth potentials includes: maximum daily temperature, minimum daily temperature, difference between day and night temperature**,** average day time temperature and average night time temperature.

Day and night temperature difference (DIF)

DIF is defined as the difference between day temperature and night temperature. Positive DIF indicates day temperature is being higher than night temperature, while negative DIF indicates night temperature is being higher than day temperature. DIF can improve shoot length, leaf colour, and foliage density, and promote internode elongation when the DIF was more than 0°C [5, 6].

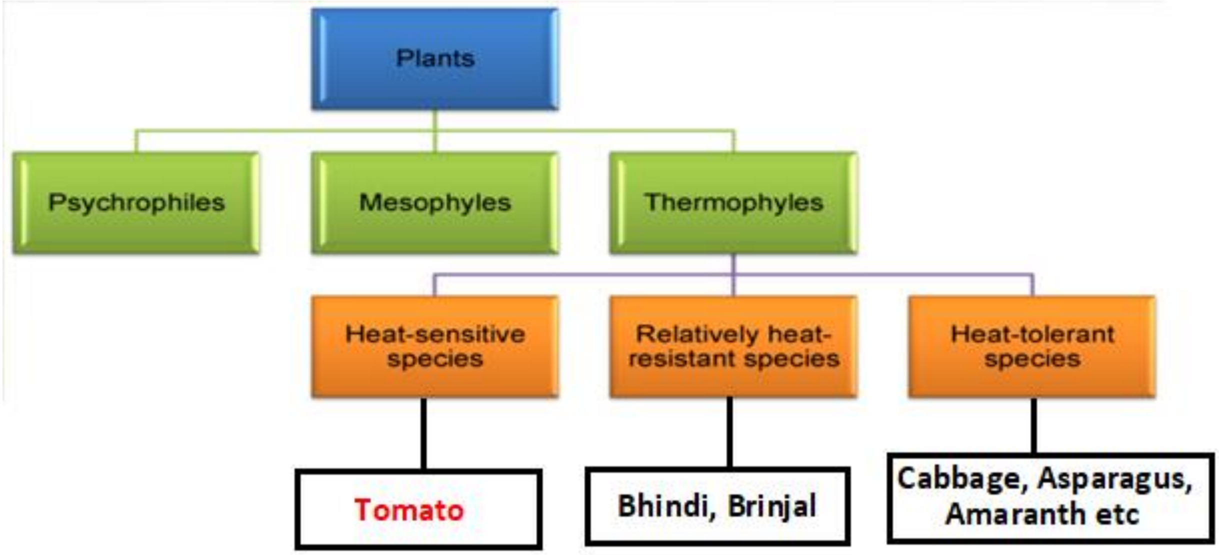

Figure 1 Classification of plants based on heat tolerance (adapted from [7])

Tomato

Tomato (*Solanum lycopersicum* L.) is considered as an important and economic vegetable crop worldwide. Tomato belongs to the Solanaceae family that includes several other crops, such as potato and pepper. Tomatoes are native to South America. Tomato is the second most consumed vegetable in the world after potato [8]. The biggest tomato producer, Asia represents 60.3% of tomato production. India it stands third in area (789 ha) and production (19759 MT) of tomato [8]. Currently, most of the tomato producing agro-climatic regions of India and world are facing the challenge of fluctuations in temperature conditions during tomato growing seasons [9].

The five different growth stages of tomato such as germination and early growth with initial leaves (between 25 and 35 days), vegetative period (20 to 25 days), flowering (20 to 30 days), early fruiting (20 to 30 days), and mature fruiting (15 to 20 days) depend on environmental factors such as air temperature, light condition, soil conditions and nutrients [7] (Figure 1 and **Figure 2**).

DIF can limit crop growth and yield [10], and must be considered in greenhouse production of tomato. Inthichack [11] found that −10°C DIF at an average temperature of 20°C increased the uptake of potassium (K), calcium (Ca) and magnesium (Mg) by roots and improved tomato quality. Positive DIF could increase carbohydrate, free amino acid and soluble protein contents in tomato fruits, which improved the fruit quality [12].

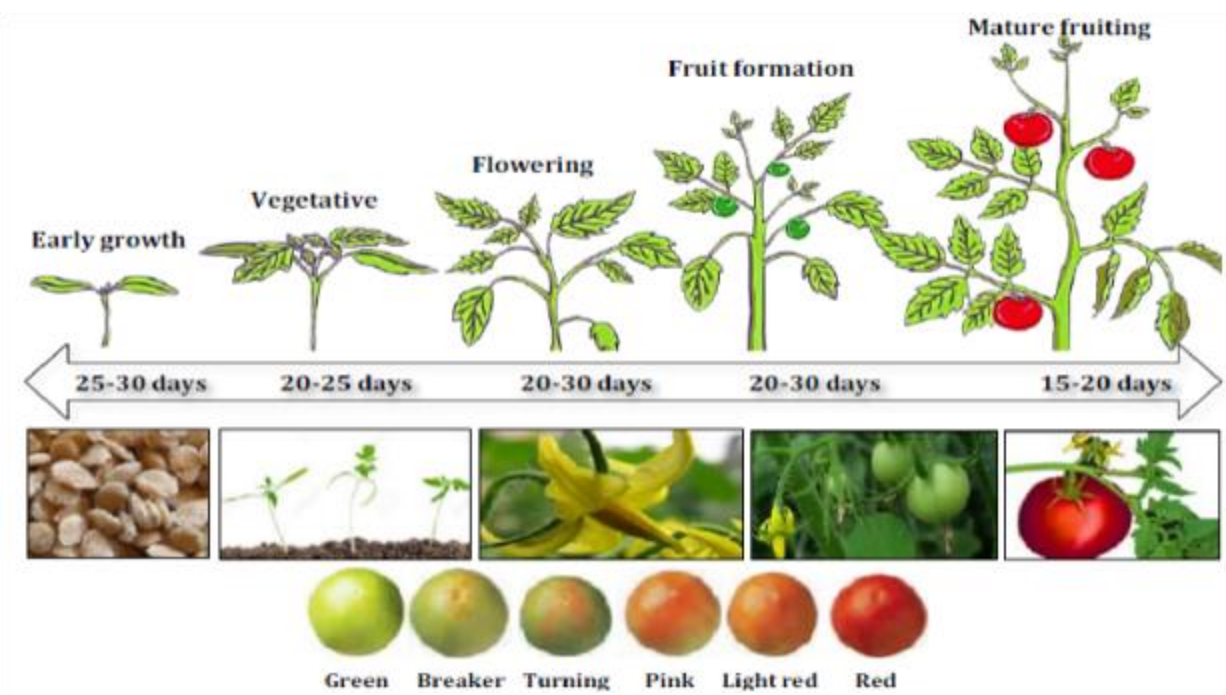

Figure 2 Different growth stages of tomato (adapted from Shamshiri [7])

Tomato and high temperature

The optimal growing temperature of tomato is 25°C to 30°C during day time and 20°C during night time [13]. A temperature above this threshold can lead to serious deleterious effects such as flower abscission, decrease of pollen quality, abnormal growth and reduced fruit set. Tomato plants when exposed to a long heat stress with an average temperature of 34°C/19°C shows flower drop of 34% and decrease of fruit set upto 71% [14].

The production of tomatoes requires fertilization of female egg by the pollen grain. The development of the pollen occurs inside flowers, inside the anthers. Anthers are considered as the supportive tissue that supplies with essential metabolites required for its development of pollen. The performance of tomato under heat stress is based on the vulnerability of the pollen grain which results in reduction of fruit yield [13].

Physiological responses in tomato under different DIF

1. Growth and development
2. Photosynthesis
3. Reproductive development
4. Quality parameters
5. Yield

Growth and development

Tomato production under high temperature more than the optimum temperature has got adverse effect on plant growth [15] and will decrease productivity. Basic physiological processes such as assimilate partitioning, growth and development are adversely affected by high temperature. Under heat stress condition a reduction in source and sink activities occur leading to severe reductions in growth, economic yield and harvest index. Assimilate partitioning, occur via apoplastic and symplastic pathways, under high temperatures, has significant effects on transport and transfer processes in plants [16]. Giri [17], studied that in tomato plants temperature above 35^0 C results in reduced shoot dry mass, root dry mass, total dry mass and root:shoot ratio (**Figure 3**).

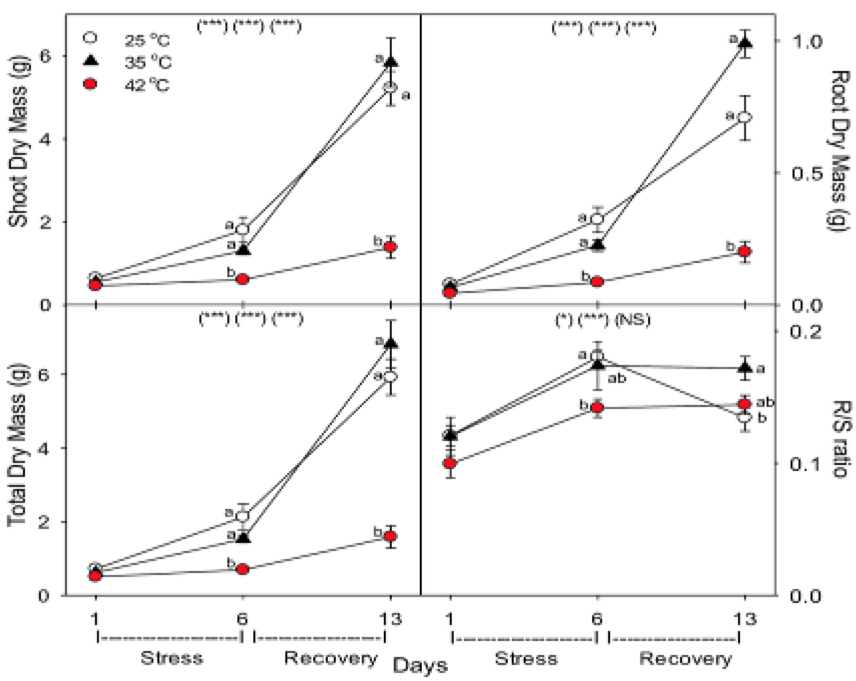

Figure 3 Effect of abrupt heat stress on biomass of tomato (adapted from Giri [17])

Plants were grown at different day/night conditions for one to six days, 25 ^{O}C /20^{O}C (control temperature); 35^{O}C / 30 ^{O}C (moderate temperature stress) and 42^{O}C / 37^{O}C (high temperature stress). These were returned to control conditions for seven days for recovery. Decrease in levels of nutrient uptake and assimilation proteins occur in tomato roots under temperature stress conditions.

Nafees [18] conducted an experiment to study influence of temperature on germination of tomato seeds. Germination rate at 40^{O}C was negligible than those at 10^{o}C (**Figure 4**). To improve the germination under 40 ^{o}C, seed priming was done as a treatment and superoxide dismutase (SOD) and protein were estimated. Increased SOD activity is an indicator of the stress tolerance capacity of a plant [19]. It can be suggested that priming of seed can be used to improve the stress tolerance capacity in case of tomato. The increment in the protein content in tomato leaf, obtained from primed sets may be resulted due to the overall growth of the crop [20].

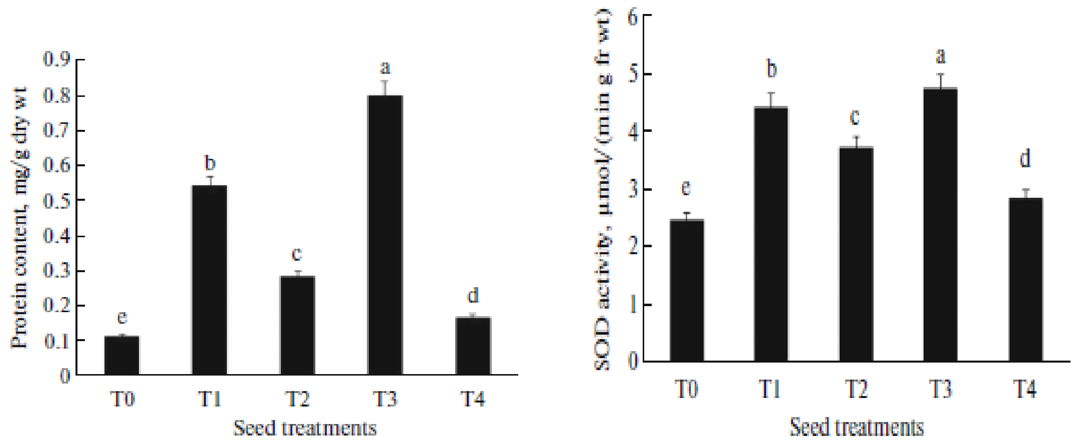

Figure 4 Effect of different temperatures on germination and seedling growth of primed seeds of tomato (T_0 - non-primed control; T_1 - hydro-primed; T_2, T_3 and T_4 - 5, 7.5 and 10 mM concentration of $Mg(NO_3)_2$ respectively [18])

Decrease in plant biomass and Mg uptake are observed in tomato plants when exposed to low temperature due to increased K uptake in tomato [21]. Tomato plants avoid chilling injury by increasing the root absorption area. They also slow down the respiration and decrease water content in plant [22]. Competition between K^+ and Mg^{2+} also occurs during ion transport from the roots to shoot. K/Mg ratio in the shoots increase significantly under high K and was higher than that of the roots, suggesting that high K inhibits the root to shoot transport of Mg in tomato. Although K and Mg both are highly mobile, they behave differently during xylem and phloem transport. Compared with K^+, Mg^{2+} is more easily absorbed by parenchymal cells because of its higher valency. When the K/Mg ratio becomes imbalanced because of high K concentrations, the transport rate of K^+ is far higher than that of Mg [23].

Wang and Camp [24] conducted an experiment to study the effect of DIF on tomato root activity and low molecular weight organic acid secretion in tomato (**Figure 5**). A fixed daily temperature of 25°C and five DIF treatments (−12, −6, 0, 6 and 12°C) were consructed to grow tomato under climate chamber conditions. Parameters like root/shoot ratio, leaf maximum photosynthetic rate (Pmax), root activity, total nitrogen (N), phosphorus (P) and potassium (K) concentrations in roots and LMWOAs produced their types and concentrations were measured at different growth stages of tomato (**Figure 6**).

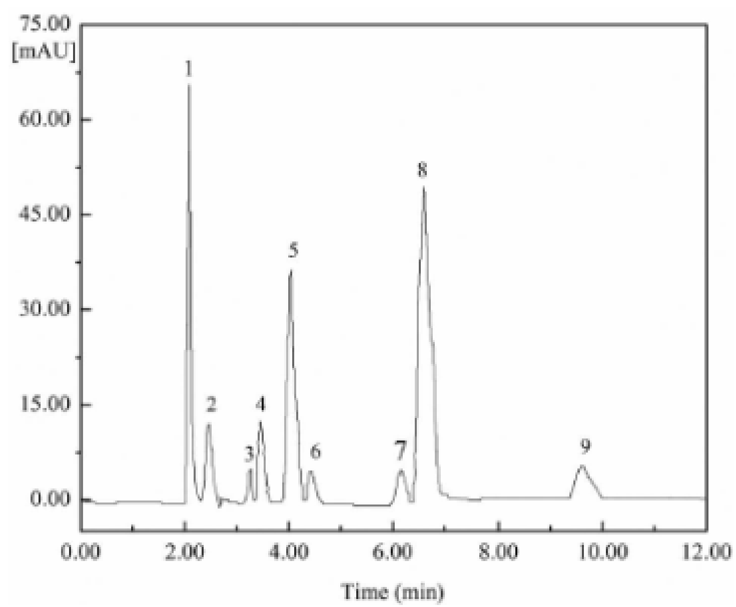

Figure 5 Chromatogram of mixing standard sample showing LMWOA. 1. oxalic acid; 2. formic acid; 3.malic acid; 4.malonic acid; 5. lactic acid; 6. acetic acid; 7.citric acid; 8.succinic acid; 9. propionic acid

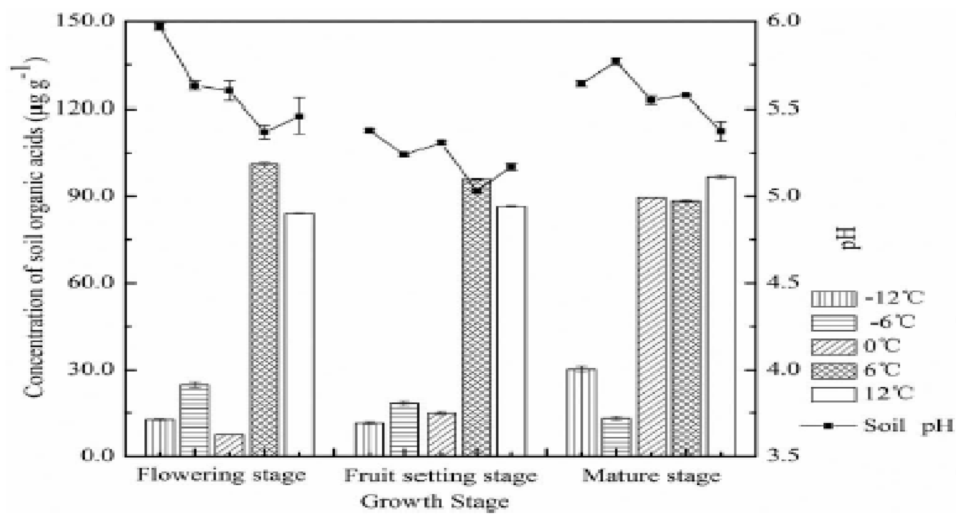

Figure 6 Effects of DIF on LMWOA and pH in rhizosphere soil at different growth stages [25].

They observed that the N, P and K concentrations were maximum under +6°C DIF under different growth stages of tomato indicating that the root activity is maximum at this temperature difference and ability of roots to absorb plant available forms of nitrogen is also more at this temperature (**Figure 7**).

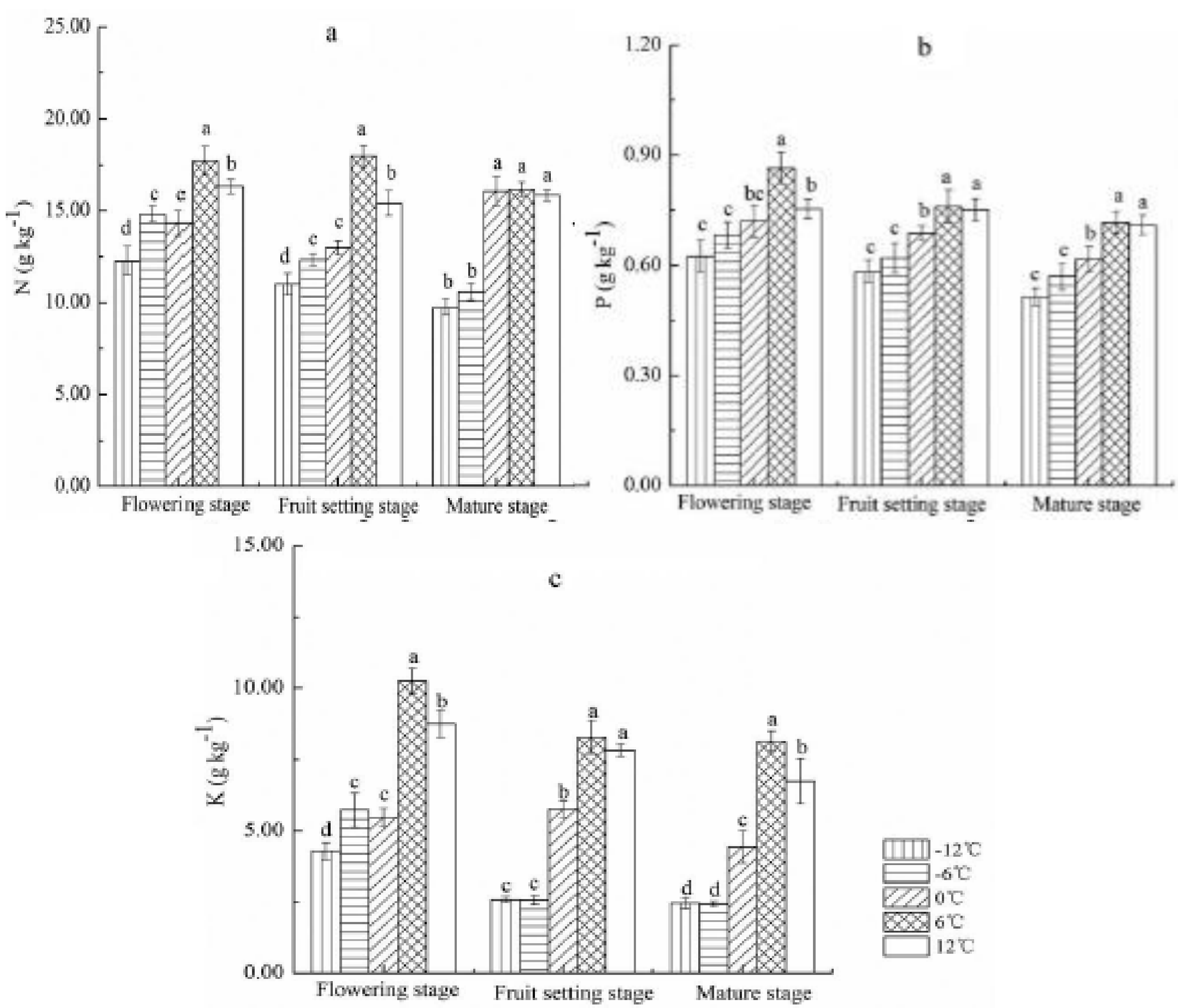

Figure 7 Effects of DIF on total N, P and K concentrations in tomato roots [25]

Table 1 Tomato root activity under different DIF treatment at different growth stages in tomato (μg g^{-1} h^{-1})

DIF	Flowering stage	Fruit setting stage	Mature stage
-12 °C	171	483	351
-6 °C	218	527	301
0 °C	194	505	398
+6 °C	274	674	402
+12 °C	306	567	416

For each DIF, root activity in different growth stages was found in the order, **fruit setting stage > mature stage > flowering stage** (**Table 1**).

Positive DIFs increase leaf photosynthesis, root dry matter accumulation, enhances root activity and nutrient uptake which promote tomato growth. Negative DIFs negatively affect tomato growth. Root activity and Pmax are correlated with LMWOA secretion by roots. Positive DIFs promote secretion of oxalic acid, formic acid, malonic acid, lactic acid, acetic acid and propionic acid by tomato roots, whereas negative DIFs promote secretion of malic acid, citric acid and propionic acid. Total LMWOA concentrations under positive DIFs are significantly higher than under 0°C DIF in the flowering and fruit setting stages, while negative DIFs significantly have low total LMWOA concentrations in the mature stage compared with 0°C DIF.

Photosynthesis

Photosynthesis is one of the most important growth factor highly sensitive to high temperature and decline in assimilation with every single degree of temperature after 30^0 C where its rate is at its peak [26]. With increasing temperature, photosynthetic rate and respiratory rate decline and the photosynthetic rate declines before respiratory rate [16]. Plants differ with respect to their heat tolerance and the threshold temperature and in all plants net photosynthetic rate significantly decrease when exposed to temperature greater than threshold temperatures. The biochemical reactions of photosynthesis are affected by heat stress by irreversible damage of RuBisCO, oxygen complexes, thylakoid membrane, chloroplast ultrastructure and PSII reaction centres. Any constraints in photosynthesis can limit plant growth at high temperatures (**Figure 8**).

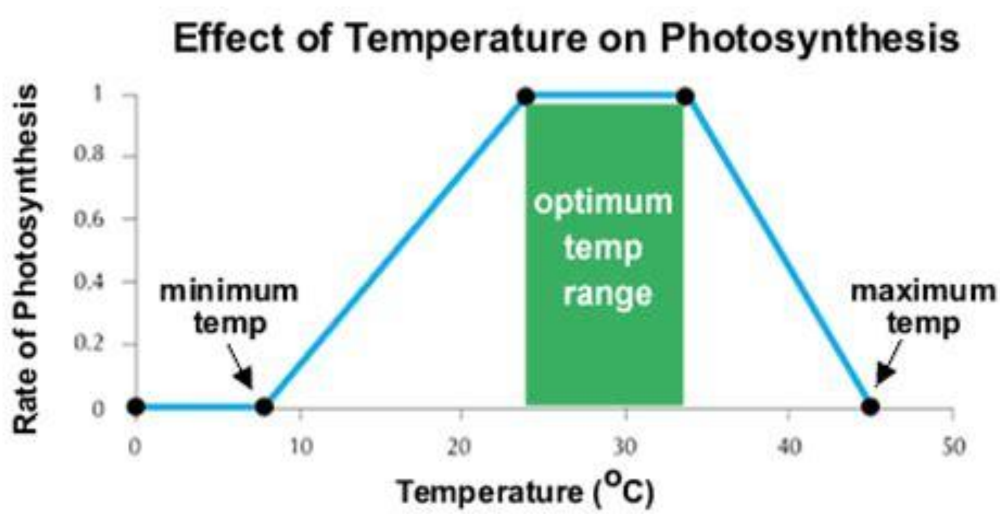

Figure 8 Effect of temperature on the photosynthetic rate of tomato [25]

Chloroplast structure

Exposure of tomato varieties for 30 days at 30^o C lead to the changes in the leaf microstructure and chloroplast ultrastructure. Disordering of chloroplast lamella, increased number of plastoglobulus, loss of grana stacking, swelling of grana and altered organization of thylakoids are the major changes occuring in chloroplast under heat stress conditions [26]. Photochemical reactions in thylakoid lamellae and carbon metabolism in the stroma of chloroplast is the primary site of injury at high temperature condition. Zhou [27] observed swollen chloroplast and decomposed starch grain in heat susceptible genotypes under heat stress condition and the chloroplast ultrastructure and grana stacking are completely destroyed in sensitive genotypes than tolerant genotypes (**Figure 9**).

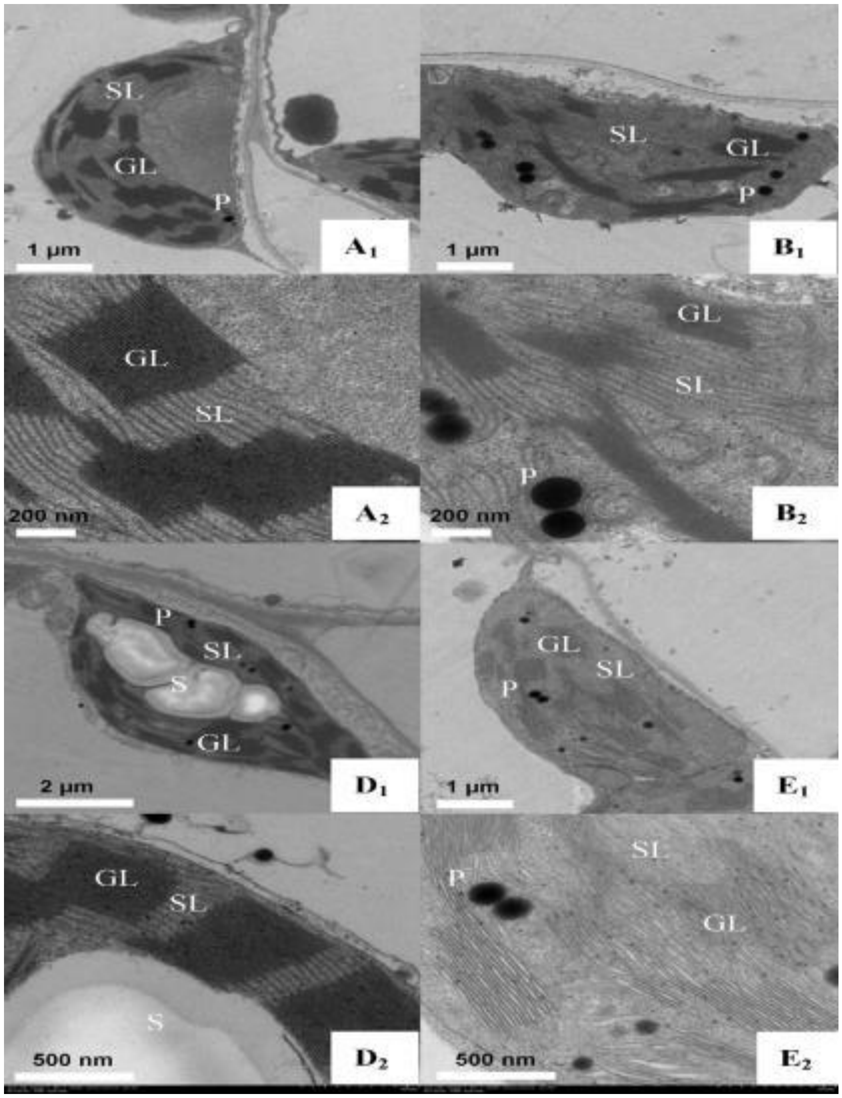

Figure 9 The chloroplast ultrastructure of leaf mesophyll cell from tolerant genotype under control 26/18^{O}C (A1, A2) and under heat stress 36/28^{O}C for four days (B1, B2) and susceptible under control (D1, D2) and under heat stress for four days (E1, E2). GL- grana lamella; SL- stroma lamella: P- plastoglobulus: S- starch [27]

Photosynthetic apparatus

One of the main reasons for the decline of net photosynthesis at elevated temperature is due to the changes in the structural organisation of photosynthetic apparatus. Photosynthetic apparatus especially photosystem II is the most sensitive element of photosynthetic apparatus and the damage to it is often the first response under heat stress. PSII is highly thermolabile and its activity is fully reduced or partially reduced under high temperatures, which may be due to the properties of thylakoid membranes where PSII is located.

Heat stress lead to the dissociation of oxygen evolving complex (OEC), resulting in an imbalance between the electron flow from OEC toward the acceptor side of PSII in the direction of PSI reaction centre. Heat stress causes dissociation of a manganese (Mn) stabilizing 33-kDa protein in PSII reaction centre complex followed by the release of Mn atoms and it destroy other parts of the reaction centre like the D1 and/or the D2 proteins. Damaged PSII units causes loss of the capacity of oxygen evolution leading to damage in electron transport [28]. Hence the electron transport play a crucial role in limiting photosynthesis at heat stress condition.

Chlorophyll fluorescence

Chlorophyll fluorescence is the ratio of variable fluorescence to maximum fluorescence (Fv/Fm) and the base fluorescence (F_0) are physiological parameters used to correlate heat tolerance. Chlorophyll fluorescence used as a tool to study the alterations of photosystem I and photosystem II activity [29]. The ratio between variable fluorescence and maximum fluorescence i.e. chlorophyll fluorescence (Fv/ Fm) will give appraise of the maximum quantum efficiency of PSII, and is the best tool to phenotype different tomato genotypes for heat tolerance [27].

Under abiotic stress condition especially heat stress, a decline in chlorophyll fluorescence is observed (**Figure 10**). Non-photochemical quenching under stress condition leading to decrease in Fm and the following increase in Fo, due to the photo-inactivation of PS II, is the main reason for the decline of Fv/Fm. It was observed that in tomato, Fv/Fm under control condition was higher than Fv/Fm under stress condition [27].

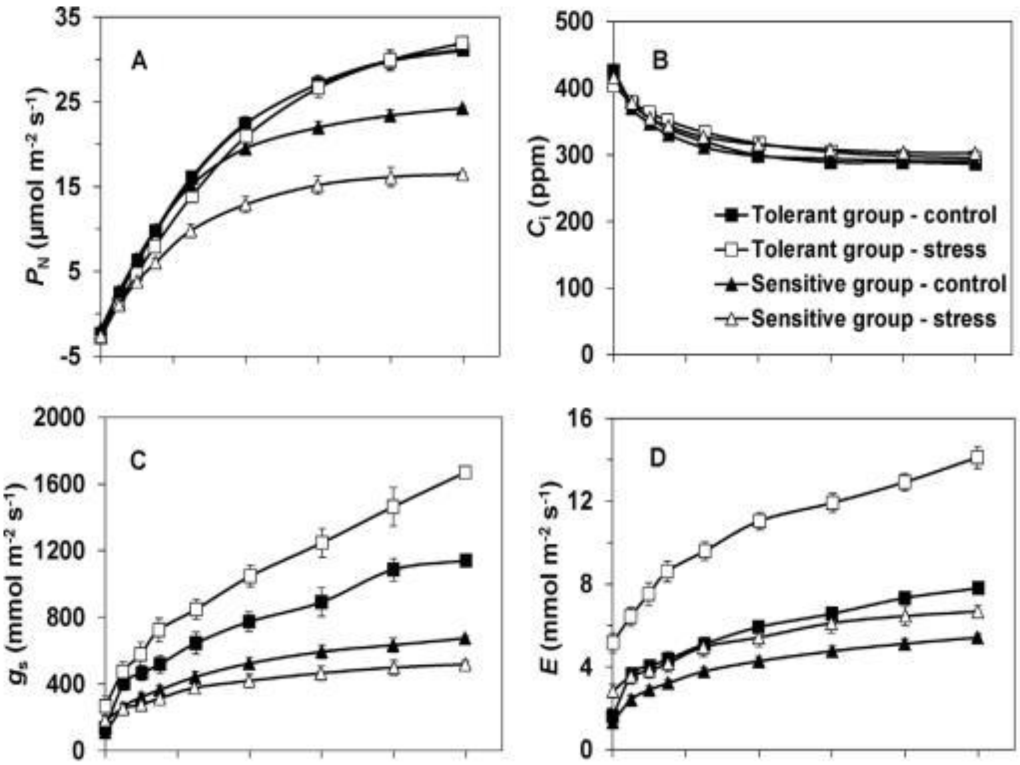

Figure 10 The net photosynthesis rate (P_N), (B) intracellular CO2 (Ci), (C) stomatal conductance (gs), (D) transpiration rate of the leaf under control (26/18^{o}C) and heat stress (36/28^{o}C) [27]

Chlorophyll content

Photosynthetic pigments play an important role in the adaptation and survival of plants under different DIF [30]. Reduction in photosynthesis under heat stress is linked to the decrease in chlorophyll content; lipid peroxidation of chloroplast and lipid peroxidation of thylakoid membrane are the main reason for the reduced chlorophyll content [31]. Under stress condition the enzyme which form carbon-carbon and carbon-nitrogen bonds in the pyrrole ring of porphobilinogen i.e, 5-aminolevulinic acid dehydratase (porphobilinogen synthase) is inactivated which lead to decrease in the chlorophyll content [16].

Stomatal closure

In tomato stay- green or delayed senescence is one of the character of heat tolerance and under high temperatures, tomato genotypes cannot stay green due to decrease in chlorophyll a, chlorophyll b and carotenoid content and shows early chlorosis and withered leaves [27]. Leaf water content, leaf stomatal conductance and intercellular CO_2 concentration are highly affected by heat stress. The reduction in intercellular CO_2 concentration due to stomatal closure under heat stress reduces photosynthetic rate. Stomatal conductance and net photosynthesis are impaired by high temperature stress due to decreased Rubisco activase enzyme. However, high temperature increases Rubisco catalytic activity, low affinity between enzyme and CO2 and enhanced oxygenase – type activity decreases and net photosynthetic rate.

Yuan [32], conducted an experiment in five temperature conditions (16/34, 19/31, 25/25, 31/19, and 34/16°C) with respective DIFs of -18, -12, 0, +12, and +18^{o}C with mean daily temperature of 25°C. Results showed that chlorophyll Chl *a*, Chl *b*, net photosynthetic rate (P_N), stomatal conductance (*g*s), maximum quantum yield of PSII photochemistry (Fv/Fm), effective quantum yield of PSII photochemistry (ΦPSII) and photochemical quenching (qp) increases under positive DIF, while these reduces with negative DIF. Contrarily the Chl *a*/*b* ratio and non-photochemical quenching (NPQ) decrease under positive DIF, while increase with negative DIF (Figure 10).

Oxidative stress

Reactive oxygen species (ROS) is defined as oxygen derived free radicals (superoxide, hydroxyl, hydroperoxyl radical) and non-radical oxygen derivatives of high reactivity (singlet oxygen, hydrogen peroxide). Under oxidative stress, the production of reactive oxygen species (ROS) is more and this causes membrane damage that eventually lead to cell death.

Heat stress increases the generation of ROS including singlet oxygen (O_2), superoxide radical (O2•–), hydrogen peroxide (H_2O_2) and hydroxyl radical (OH•), thereby induced oxidative stress [32]. ROS results in the autocatalytic peroxidation of membrane lipids and pigments leading to the loss of membrane semi-permeability and changes its functions (**Figure 11**).

To scavenge excess ROS, plants develop complex antioxidant defense systems involving several enzymes and metabolites (Figure 11). The antioxidants can be enzymatic and non-enzymatic. Enzymatic antioxidants includes, Superoxide dismutase (SOD), catalase (CAT), Peroxidase (POD), Ascorbic acid peroxidase (APX), Glutathione reductase (GR), Dehydroascorbate reductase (DHAR) and Monodehydroascorbate reductase (MDHAR). And reduced glutathione (GSH), ascorbic acid (AsA), α-tocopherol and carotenoids are the non-enzymatic ones [16].

Superoxide radical is synthesized in the chloroplast and mitochondrion and in micro bodies. The scavenging of O2− by superoxide dismutase (SOD) results in the generation of H_2O_2, which is eliminated by APX or CAT. Both O^{2-} and H_2O_2 are not as toxic as the (OH−), which is produced by the combination of O^{2-} and H_2O_2 in the presence of little amounts of Fe^{2+} and Fe^{3+}. The OH− damage chlorophyll, protein, DNA, lipids and other macromolecules, thus affecting plant metabolism and limiting growth and yield.

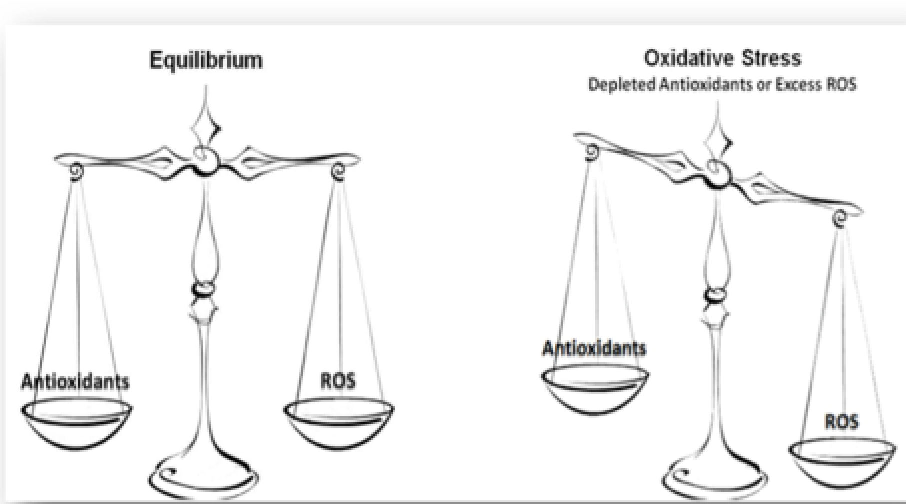

Figure 11 When ROS and antioxidants are in equilibrium the plant is said to be in normal condition and if production of ROS is more than the antioxidants in plant system, the plant is under oxidative stress [16]

Decrease in antioxidant activity in stressed plants result in higher levels of ROS that lead to injury. Heat tolerant cultivars of tomato exhibit greater antioxidant activity than heat sensitive ones. There is a strong correlation between the ability of antioxidant defence system and the ability of tomatoes to produce greater yields [33].

Cell membrane integrity

Temperature stress results in membrane disruption because of protein denaturation or melting of membrane lipids, leading to membrane rupture and loss of cellular contents. The primary symptom of heat stress is membrane disruption and the thermo stability of plasmalemma is considered as measure of thermo tolerance. The percent of electrolyte leakage shows the extent of membrane damage or cell membrane stability when exposed to high temperature. The varieties which are tolerant to high temperature have high membrane thermo-stability and showed less electrolyte leakage than sensitive genotypes under stress condition [27]. The level of ion leakage through the membrane is negatively correlated with the pollen viability, fruit setting and flower per inflorescence. Fruit set is reduced as a result of membrane damage [34].

Membrane thermo-stability has correlation with photosynthetic activity and respiratory activity under temperature stress condition. Heat stress disrupted the ion homeostasis by altering ion transport and compartmentalization [15]. Ion homeostasis specifically, Na^+ and K^+ homeostasis maintained the biological membrane potential, the activities of enzymes and osmotic concentration to adjust with the cell volume. Membrane lipid peroxidation and disruption of cell membrane stability by protein denaturation during heat stress causes oxidative stress [31].

Reproductive development

The major determinant of fruit production and the most sensitive process in plant is pollen development phase (**Figure 12**).

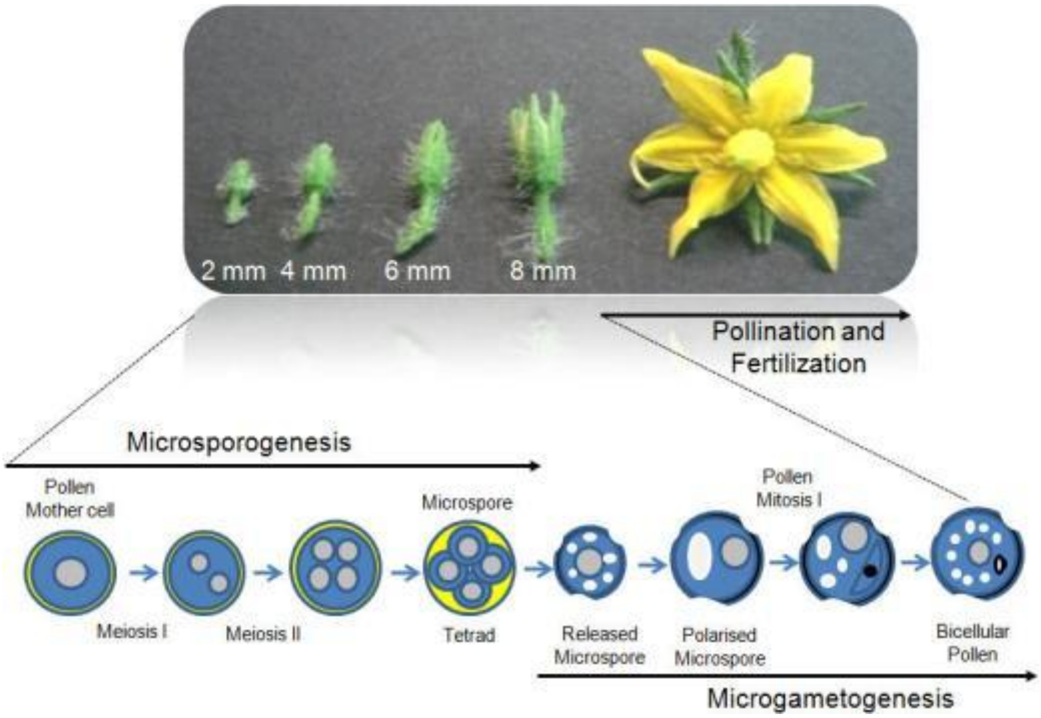

Figure 12 The different stages of pollen development [32]

Impaired meiosis

The pollen is sensitive to heat and sensitivity occur at pollen meiosis to pollen mitosis I [32], exposure of heat at microspore stage results in microspore abortion, reduced number of pollen grains at anthesis and less number of mature viable pollen grains which can germinate (**Figure 13**). High temperature results in the defective microsporogenesis and the defects in development of staminate or pistillate organs [34]. Different stages of the pollen development are sensitive to high temperatures during the meiosis stage and a defect of microsporogenesis occurs with defects of the tapetum cells [36].

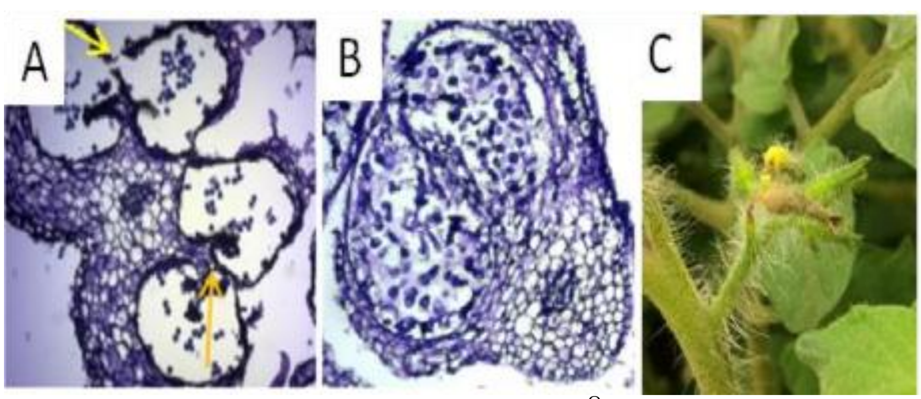

Figure 13 Effect of high temperature (32/26 ^{O}C) on anther of tomato

The tapetum is a key tissue that provides nutrition to the pollen at early stages before it degenerates when the microspore cell starts to vacuolate and form the polarized microspore [28]. After the release of the tetrad, the tapetum layer degenerate prematurely under high temperature and lead to a decrease of nutrition to the pollen this cause pollen sterility [36]. Several metabolites show a drop in production during the microspore stage, specifically like sugars, the main energy source for the pollen maturation. The high number of tapetal mitochondria increases the need for sugars, which lead to an unbalanced homeostasis under heat stress. Tolerant tomato genotypes have higher levels of sugars [37].

Picture A shows anther at mature stage of pollen development under control conditions. The opening of locule is indicated with an arrow. Picture B shows a severe anther deformation and four distinct locules are no longer visible. Picture C tomato shows flower abscission under mild high temperatures [38].

Pollen germination percentage

High temperature has great impact on pollen development and the pollen germination percentage which are drastically lowered under high temperature [35]. Pollen maturation, pollen viability, pollen germination and pollen tube growth are affected negatively with high temperature. The poor pollen germination is the major reason for reduced fruit set. Pollen maturation require the accumulation of starch, which provide energy for the germination and tube growth of pollen but the reduced assimilate translocation under heat stress results in poor germination [39]. The energy sources for the development and germination of pollen are sucrose and hexoses, this act as osmolytes. Heat tolerant varieties have processes to control the loss of carbohydrates. Pollen of heat tolerant genotypes has greater concentration of glucose when compared to sucrose and fructose and it can also retain higher amounts of carbohydrates.

With increase in temperature above 34°C, the pollen germination and pollen tube growth decreases [40]. In heat tolerant genotype, pollen tube growth is unaffected by heat stress and give high fruit set than control. The fruit set is influenced by pollen tube growth. Bita et al. [38] observed that the pollen germination percentage and pollen tube growth observed from non-stressed condition of both heat tolerant and sensitive genotypes are high, while those from heat stress condition showed small sized flowers with malformed anther cones and exhibited reduced pollen germination in heat sensitive genotypes. Heat tolerant genotypes produced higher number of pollen grains than the heat sensitive genotypes. The number of pollen grains released is lesser under high temperature stress but are not affecting the time of pollen release.

Pollen viability

The competition for nutrients in the locular fluid of anther during high temperature stress, results in small difference in the metabolic performance of microspores, outcomes dead and fully viable pollen from same anther locule. Reduced carbohydrate metabolism in the tomato anther during heat stress results in poor pollen development and viability [28]. The pollens are highly sensitive to mild changes in the environment, can be used to study the whole plant nature under different conditions. The genotypes which show tolerance to high temperature have high pollen viability than the sensitive genotypes under high temperature. So the high temperature tolerance in the tomato can be correlated with the pollen viability under high temperature (**Figure 14**).

Ploeg and Heuvelink [41] reported that temperature had a large impact on several aspects of growth and development. At lower optimal temperatures, fruit set decreases as a result of poorer pollen quality.

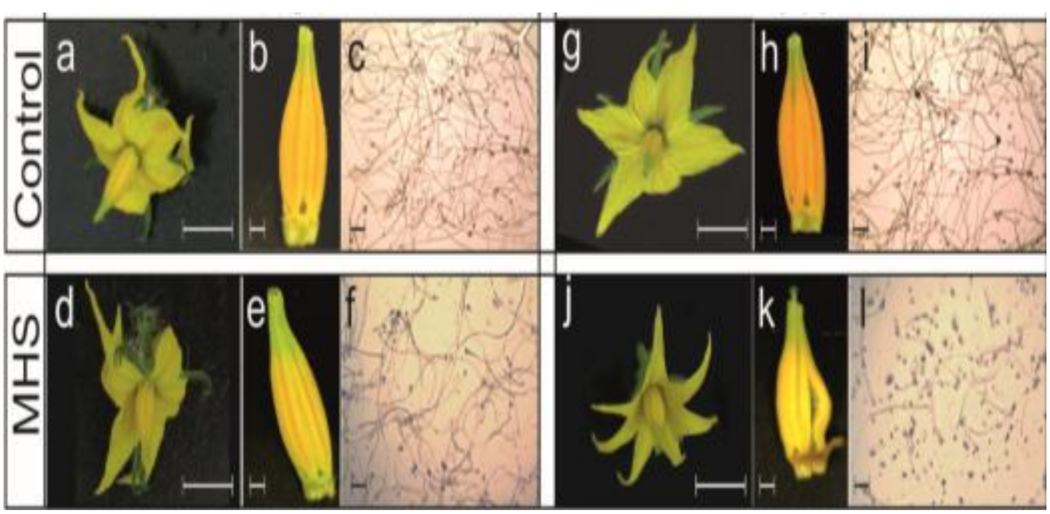

Figure 14 The comparison of flower and anther development of the tomato genotypes under control and heat stress conditions (two weeks) in tolerant genotype HT and sensitive genotype HS. Panels a, d, g, j; whole flowers: panels b, e, h and k: isolated anther cones; panels c, f, I, l: germinating pollen [38]

Stigma exertion

Tomato is a highly self-pollinated plant; stigma exertion at high temperature prevents self-pollination and reduces productivity. The exerted style (i.e., stigma is elongated than the anther cone) during reproductive stage is the important effect of high temperature in tomato, that reduces self-pollination [42]. The stigma and style exertion under high temperature affect fruit setting ability. Stigma tube elongation and cone splitting occur in tomato under high temperature. Unnecessary elongation of style in most flowers reduces the pollen access to stigma in heat sensitive genotypes and reduces fertilization [34]. Under high temperature stress, the stigma as well as the anther shows a reduced elongation in length called anther shortening [43]. The genotypes producing flowers having no stigma exertion at high temperature is stable and produce high fruit yield. The viability of male and female organs and style protrusion level are the major factors ascertaining the reproductive success under high temperature [44]. The heritability of fruit setting is less while the heritability of style exertion is relatively high. Temperatures greater than 40° C for 4 hours cause the flowers to abort. If the night temperature is less than 12° C or if the day temperature is greater than 29° C, pollen becomes tacky and nonviable, pollination cannot occur and the flowers will die and fall off [45].

Hormonal interactions

Plants have the ability to identify and cope up with adverse environmental conditions, and the degree of adaptability or tolerance to specific stresses differs within species and genotypes. Hormones play a crucial role in this response. Cross-talk with in hormone signalling can influence an organism's ability to sense different inputs and respond properly. Hormonal homeostasis, stability, biosynthesis and compartmentalization are changed under stress conditions.

Hormones influences processes like regulation of flowering time, leaf senescence, fruit ripening and in pollen development. Auxin, gibberellins and abscisic acid plays a crucial role in the development of the tapetum, which is essential for the distribution of metabolites to the pollen. Other hormones like ethylene, jasmonic acid and brassinosterioids also regulates pollen development.

Auxin regulates plant development by influencing plant growth, senescence, fruit formation, leaf abscission and apical dominance. Blocking of auxin biosynthesis pathway leads to abnormalities in floral organ development and defective pollen production. Auxin is necessary in the process of pollen maturation and anther dehiscence [36].

GA_3 functions to promote stem growth by increasing both cell division and cell elongation. Plant height development is positively related to IAA. Zeatin is positively correlated with stem diameter development according to Wu [46], reported that higher level of cytokinin involve in stem swelling process. Similar to plant height increase, leaf area increment, and fruit diameter increment are also influenced synchronously with GA_3, IAA and ZT. Li [47] indicated that a higher amount of endogenous ZT improved sugar accumulation. The soluble sugars content of tomato fruit is positively related with GA_3, IAA and ZT. But soluble sugars are not correlated with ABA. Similar to soluble sugars, vitamin C and soluble protein are positively correlated with GA_3, IAA and ZT [48] Tm or DIF and interaction of both Tm and DIF influences the GA_3, IAA, and ZT [49].

Hormones under high DIF

Auxin production decreases with high level of ABA in the plant at high temperatures. Gibberellins (GA) are known to act in hypocotyl elongation, floral transition, fruit patterning and plant defence. GA mutation results in defective pollen germination, elongation and pollen development. And the GA content in plants reduced under temperature conditions [32].

Ethylene, the gaseous hormone regulates different growth and developmental processes in plants such as from seed germination to flowering and fruiting and also tolerance to environmental stresses. High temperature hinders ethylene production which results in defective ripening and failure in anther locule opening. Abscisic acid is important for seed development, plant growth and in adapting under environmental stresses [16]. ABA induction is an important for thermotolerance mechanism, as it involved in the generation of several HSPs.

Jasmonic acid is involved in processes like fruit ripening, seed germination, root growth, resistance to biotic stresses, protein storage and in pollen fertility. Any defects in the biosynthesis of jasmonic acid cause abnormalities in anther dehiscence causing inhibition of pollen release.

Other hormone, salicylic acid (SA) is the one involved in heat-stress responses exhibited by plants. SA is important for signalling pathways in response to systemic acquired resistance (SAR) and the hypersensitive response (HR). SA stabilizes production of heat shock transcription factors and helps them bind to the promoter of heat shock related genes.

Yield

Small rise in temperature above optimum have significant negative effects on yield [50]. All the physiological responses like inability of pollen to form elongation tube, pollen development impairment, reduction of reproductive success, reduced photosynthesis, oxidative stress and altered membrane stability reduce yield of crop (**Figure 15**). In tomato yield decreases with increase in temperature [51].

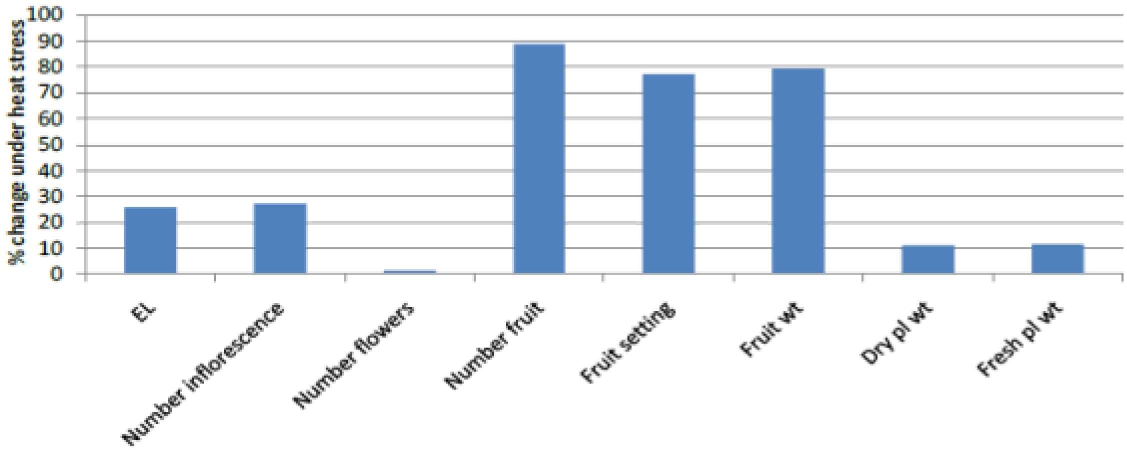

Figure 15 Alsamir [51] studied the change in various plant characters under high temperature stress and found that the fruit number, fruit setting and fruit weight are highly affected

Adams [52] studied the impact of temperature on growth and development of tomato fruits and results showed that when plants were grown under controlled environmental conditions at 14, 18, 22 and 26 ^{0}C respectively, tomato fruits ripened at 95, 65, 46 and 42 days after flower opening

Quality parameters

Pre harvest factors and post harvest factors influences the tomato fruit quality. To obtain good quality produce, optimize growth condition and to preserve the produce under proper storage conditions [53].The longer continuous days exposure to high temperatures during growth, caused the worst fruit yield and quality [54]. Khanal [55] studied the relationship between the temperature conditions with varieties and storage days. The different varieties showed significant differences in physical characteristics like firmness, dry matter, soluble solids, percentage of acid and pH content which is due to genetic differences [56-58].

In the study conducted by Khanal [55], the influence of pre-harvest growing conditions of tomato plants with the shelf life of tomato fruits are studied. He used plants grown under three temperature regimes i.e. 24/17°C, 27/14°C and 30/11°C. Tomato firmness is affected by different pre-harvest temperature regimes. Firmness was found to be increasing at temperature range (27/14˚C) and further increase in difference between day and night temperatures (30/11˚C) resulted in decrease in firmness value. The polysaccharides and cell wall enzymes have important role in firmness, certain temperature can limit the activity of polysaccharides and cell wall enzymes. After attaining optimal temperature further increase in temperature results in deactivation of enzymes like galactosyl and arabinosyl and accumulation of polyuronides in plants. Decrease in tomato firmness may be due to changes in cell wall number, cell turgor properties and cell wall composition.

A temperature increase from 26 to 30˚C increases the amount of soluble solids, resulting from the carbohydrate biosynthetic enzyme activity [59]. With the increase in temperature, soluble solid content increased [60]. Citric acid and malic acid are present in tomato fruit. Citric acid increases from maturation to end of postharvest period and malic acid decreases from maturation to end of postharvest period [61].The amount of acid content in tomato fruit is found to be increased with the increase in temperature. The pH is inversely related with acid content. The titrable acids and other organic acids like ascorbic acid, dehydroascorbic acid, citramalic, shikimic, fumaric, isocitric, succinic, lactic, malic, saccharic, gluconic, gulonic and tartaric acids contribute to pH content of the fruit [62]. With the increase in temperature, pH of the fruit content decreases [62]. Higher percentage of titrable acid are found in fruits grown at lower night temperature (12˚C) [26], because the amount of organic acid decreases with increase in temperature regimes during growing period. Increase in day temperatures and decrease in night temperatures have negative impacts on organic acid content in tomato.

Under positive DIF, compared to 0^o DIF, soluble sugar content is more (**Table 2**). The plants grown under positive DIF show higher photosynthetic rate than those grown in a negative DIF or constant temperature. The response of vitamin C and soluble protein content to DIF is similar to soluble sugars (**Table 3**). Vitamin C content increases initially but deceases at the end. The amount of soluble sugars and soluble solid concentration are correlated with IAA, GA_3 and ZT concentration in plants [63].

Table 2 Effect of different DIF on concentrations of soluble sugars (mg/g FW) in tomato fruit (Khanal, [55])

DIF	28 days after treatment	35 days after treatment	42 days after treatment
-18 °C	40.12	48.27	52.78
-12 °C	49.24	60.57	64.42
0 °C	63.37	78.34	83.74
+12 °C	79.45	91.78	96.42
+18 °C	74.69	88.45	92.68

Table 3 Effect of different DIF on concentrations of vitamin C (mg/100 g FW) in tomato fruit (Khanal, [55])

DIF	28 days after treatment	35 days after treatment	42 days after treatment
-18 °C	17.52	15.36	13.23
-12 °C	20.74	18.48	16.35
0 °C	25.56	22.45	20.74
+12 °C	31.44	29.35	27.46
+18 °C	28.49	25.43	23.74

Conclusion

Poor fruit set of tomato caused by heat stress is a major reason of low yield in the tropical and subtropical regions or tomato growing areas of the world. DIF strongly affected tomato growth. Positive DIFs increase tomato leaf photosynthesis and root dry matter accumulation, and increase root activity and nutrient uptake, which promote tomato growth. Negative DIFs negatively influences tomato growth.

Development of heat tolerant tomato lines has to be the major objective in tomato breeding and biotechnology particularly in the present global warming scenario. So a line that possesses all the model traits should be developed to increase the thermo-tolerance so that the plant can give moderately higher yield even under high temperature.

Future Prospects

Identification and characterization of pollen genes sensitive to heat stress as well as those genes involved in pollen defense mechanisms will help in developing better genotypes. By using molecular breeding as well as transgenic techniques the heat resistant genes could be incorporated to develop heat tolerant genotypes. Identification and characterization of genes that are involved in heat stress sensing and signal transduction and these genes can be used for the production of more heat tolerant and heat resistant genotypes.

References

[1] Ainsworth, D.J. and Ort, D.R. 2010. Impacts of chilling temperatures on photosynthesis in warm-climate plants. Trends Plant Sci., 6: 36–42.

[2] IPCC. 2013. Summary of policymakers. In: Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nouels, A. and Xia, Y. (eds), Climate Change: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, UK, 1535 p.

[3] Kaushal, N., Bhandari, K., Siddique, K.H.M. and Nayyar, H. 2016. Food crops face rising temperatures: An overview of responses, adaptive mechanisms, and approaches to improve heat tolerance. Cogent Food Agric., 2: 1134380.

[4] Bray, E.A., Bailey-serres, J. and Weretilnyk, E. 2011. Responses to abiotic stresses. Biochemistry Molecular Biology of Plants In: Gruissem, W., Buchannan, B. and Jones, R. (eds), Am. Soc. Plant Physiologists Rockville, pp 1158-1203.

[5] Twumasi, P., Schel, J.H.N. and Ieperen, W. 2009. Differential effects of temperature on stem length and xylem

vessel length distribution in Zinnia elegans. J. Hortic. Sci. and Biotechnol., 84: 531–553.
[6] Blanchard, M.G. and Runkle, E.S. 2011. The influence of day and night temperature fluctuations on growth and flowering of annual bedding plants and greenhouse heating cost predictions. Hortscience., 46: 599–603.
[7] Shamshiri, R.R., Jones, J.W., Thorp, K.R., Ahmad, D., Man, H.C., and Taheri, S. 2018. Review of optimum temperature, humidity, and vapour pressure deficit for microclimate evaluation and control in greenhouse cultivation of tomato: A review. Int. Agrophysics., 32(2): 287-302.
[8] National horticultural board. 2018. Horticultural statistics at a glance. Ministry of Agriculture & Farmer's Welfare, Department of Agriculture, Govt. of India, 490p.
[9] Ayyogari, K., Sidhya, P. and Pandit, M.K. 2014. Impact of climate change on vegetable cultivation - A review. Int. J. Agric. Environ. Biotechnol., 7(1): 145-155.
[10] Li, G.J., Benoit, F. and Ceustermans, N. 2004. Influence of day and night temperature on the growth, development and yield of greenhouse sweet pepper. J. Zhejiang University-Agric. Life Sci., 30: 487–491.
[11] Inthichack, P., Nishimura, Y. and Fukumoto, Y. 2013. Diurnal temperature alternations on plant growth and mineral absorption in eggplant, sweet pepper and tomato. Hortic. Environ. Biotechnol., 54: 37–43.
[12] Yang, Z.Q., Wang, X.L., Peng, X.D., Zhao, X., Yuan, X.K. and Han, X.J. 2014. Effect of difference between day and night temperature on nutrients and dry mass partitioning of tomato in climate chamber. Transactions of the Chinese Soc. Agric. Eng., 30: 138–147.
[13] Camejo, D., Morales, M.A., Amico, J.M., Torrecillas, A. and Alarcon, J.J. 2005. High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. J. Plant Physiol., 162: 281-289.
[14] Hazra, P., Ansary, S.H., Dutta, A.K., Balacheva, E. and Atanassova, B. 2009. Breeding tomato tolerant to high temperature stress. Acta Horticulturae., 830: 241-248.
[15] Zhang, J., Jiang, X.D., Li, T.L. and Cao, X.J. 2014. Photosynthesis and ultrastructure of photosynthetic apparatus in tomato leaves under elevated temperature. Photosynthetica., 52: 430- 436.
[16] Taiz, L., Zeiger, E., Moller, I.M. and Murphy, A. 2015. Plant Physiology and Development. Sinauer Associates, Massachusetts, 761p.
[17] Giri, A., Heckathorn, S., Mishra, S. and Krause, C. 2017. Heat stress decreases levels of nutrient uptake and assimilation proteins in tomato roots. Plants., 6(6): 143-151.
[18] Nafees, K., Kumar, M. and Bose, B. 2019. Effect of different temperatures on germination and seedling growth of primed seeds of tomato. Russian J. Plant Physiol., 66(5): 778–784.
[19] Vaktabhai CK, Kumar S (2017). Seedling invigouration by halo priming in tomato against salt stress. Journal of Pharmacology and Phytochemistry. 6: 716–722.
[20] Vassilevska-ivanova, R. and Tcekova, Z. 2002. Effect of temperature on seed germination and seedling growth of sunflower (*Helianthus annuus* L.). Comptes Rendus de l Academie Bulgare des Sciences. 55: 10–67.
[21] Li, H., Chen, Z., Zhou, T., Liu, Y., Raza, S. and Hou. J. 2018. Effects of high potassium and low temperature on the growth and magnesium nutrition of different tomato cultivars. Hortscience., 53(5): 710–714.
[22] Hund, A.W., Richner, A., Soldati, Y. and Stamp, P. 2007. Root morphology and photosynthetic performance of maize inbred lines at low temperature. Eur. J. Agron., 27: 52–61.
[23] Tromp J. and Vuure J.V. 2010. Accumulation of calcium, potassium and magnesium in apple fruits under various conditions of humidity. Physiol. Plant., 89:149–156.
[24] Wang, S.Y. and Camp, M.J. 2009. Temperatures after bloom affect plant growth and fruit quality of strawberry. Scientia Horticulturae., 85(3): 183-199.
[25] Yang, Z., Li, Y., Li, P., Zhang, F. and Thomas, B.W. 2016. Effect of difference between day and night temperature on tomato (*Lycopersicon esculentum* Mill.) root activity and low molecular weight organic acid secretion. Soil Sci. Plant Nutr., 62(6):423-431.
[26] Salvucci, M.E. and Crafts-brandner, S.J. 2004. Relationship between the heat tolerance of photosynthesis and the thermal stability of Rubisco activase in plants from contrasting thermal environments. Plant Physiol., 134: 1460-1470.
[27] Zhou, R., Xiaqing,Y., Katrine, H.K., Eva, R., Carl-otto, O. and Zhen, W. 2015. Screening and validation of tomato genotypes under heat stress using Fv/Fm to reveal the physiological mechanism of heat tolerance. Environ. Exp. Bot. 118: 1-11.
[28] Pressman E, Shaked R, Firon N (2007). Tomato (*Lycopersicon esculentum*) response to heat stress: Focus on pollen grains. Plant Stress., 1(2): 216-227.
[29] Gerganova, M., Antoaneta, V., Popova, D.S. and Maya, V. 2016. Tomato plants acclimate better to elevated temperature and high light than to treatment with each factor separately. Plant Physiol. Biochem., 104: 234-241.

[30] Veatch, B., Ray, D.T. and Gehrels, A. 2007. Night temperature, rubber production, and carbon exchange in guayule. Industrial Crops and Prod. 25: 34–43.

[31] Camejo, D., Jimenez, A., Alarcon, J.J., Torres, W., Gomez, J.M. and Sevilla, F. 2006. Changes in photosynthetic parameters and antioxidant activities following heat-shock treatment in tomato plants. Functional Plant Biol. 33: 177–187.

[32] Hazra, P., Ansary, S.H., Sikder, D.E. and Peter, K.V. 2007. Breeding tomato (*Lycopersicon esculentum* Mill.) resistant to high temperature stress. Int. J. Plant Breed., 1(1): 31-40.

[33] [32] Rainwater, D.T., Gosset, D.R., Millhollon, E.P., Hanna, H.Y., Banks, S.W. and Lucas, M.C. 1996. The relationship between yield and the antioxidant defense system in tomatoes grown under heat stress. Free Radical Res. 25: 421-435.

[34] Alsamir, M., Ahmad, N.M., Keitel, C., Mahmood, T. and Trethowan, R. 2017. Identification of high-temperature tolerant and agronomically viable tomato (*Solanum lycopersicum*) genotypes from a diverse germplasm collection. Adv. Crop Sci. Technol. 5(4): 299-309.

[35] Rieu, I., Twell, D. and Firon. N. 2017. Pollen Development at high temperature: from acclimation to collapse. Plant Physiol. 173: 1967–1976.

[36] Marine, J.P., Haperen, P.V., Rieu, I., Richard, G.F.V., Yury, M.T. and Arnaud, G.B. 2017. Screening for pollen tolerance to high temperatures in tomato. Euphytica. 213: 130-138.

[37] Firon, N., Shaked, R., Peet, M., Pharr, D., Zamski, E., Rosenfeld, K., Althan, L. and Pressman, E. 2006. Pollen grains of heat tolerant tomato cultivars retain higher carbohydrate concentration under heat stress conditions. Scientia Horticulturae. 109 (3): 212-217.

[38] Bita, C.E., Zenoni, S., Vriezen, W.H., Mariani, C., Pezzotti, M. and Gerats, T. 2011. Temperature stress differentially modulates transcription in meiotic anthers of heat-tolerant and heat-sensitive tomato plants. Genomics. 12: 384- 402.

[39] Filomena, G., Wolters-arts, M., Mariani, C. and Rieu, I. 2013. Ensuring reproduction at high temperatures: The heat stress response during anther and pollen development. Plants. 2: 489-506.

[40] Song, J., Nada, K. and Tachibana, S. 2002. Suppression of S-adenosylmethionine decarboxylase activity is a major cause for high-temperature inhibition of pollen germination and tube growth in tomato (*Lycopersicon esculentum* Mill.). Plant and Cell Physiol. 43 (6):619.

[41] Ploeg, A.V. and Heuvelink, E. 2005. Influence of sub-optimal temperature on tomato growth and yield. J. Hortic. Sci. Biotechnol. 80:652-659.

[42] Faruq, G., Zaakaria, H.P. and Arasg, N. 2012. Heat tolerance in tomato. Life Sci. J. 9(4): 1936-1950.

[43] Sato, S., Kamiyama, M., Iwata, T., Makita, N., Furukawa, H. and Ikeda, H. 2006. Moderate increase of mean daily temperature adversely affects fruit set of *Lycopersicon esculentum* by disrupting specific physiological processes in male reproductive development. Ann. Bot. 97 (5): 731.

[44] Bhattarai, U., Sharma, A., Das, R. and Talukdar, P. 2016. Genetic analysis of yield and yield attributing traits for high temperature resistance in tomato. Int. J. Veg. Sci. 5260: 1-13.

[45] Mohan, A. and Senthilkumar, D. 2019. A survey of tomato blossom and flower drop to the influence of environmental phenomena (*Solanum lycopersicum* L.). Int. J. Agric. Environ. Food Sci., 3(1): 15-20.

[46] Wu, C.T., Zhou, B.L. and Zhang, T.Z. 2009. Isolation and characterization of a sterile-dwarf mutant in Asian cotton (Gossypium arboreum L.). J. Genet. Genomics., 36: 343–353.

[47] Li, H., Chen, Z., Zhou, T., Liu, Y., Raza, S. and Hou, J. 2018. Effects of high potassium and low temperature on the growth and magnesium nutrition of different tomato cultivars. Hortscience. 53(5): 710–714.

[48] Yuan, X.K. and Yang, Z.Q. 2018. The effect of endogenous hormones on plant morphology and fruit quality of tomato under difference between day and night temperature. Hortic Sci. 45: 131–138.

[49] Xiao, F., Yang, Z., Han, W., Li, Y., Qiu, Y., Sun, Q. and Zhang, F. 2017. Effects of day and night temperature on photosynthesis, antioxidant enzyme activities, and endogenous hormones in tomato leaves during the flowering stage. J. Hortic. Sci. Biotechnol. 6:1-10.

[50] Mirza, H., Kamrun, N., Mahabub, A., Rajib, R. and Masayuki, F. 2013. Physiological, biochemical and molecular mechanisms of heat stress tolerance in plants. Int. J. Mol. Sci. 14: 9643-9684.

[51] Alsamir, M., Ahmad, N.M., Keitel, C., Mahmood, T., and Trethowan, R. 2017. Identification of high-temperature tolerant and agronomically viable tomato (*Solanum lycopersicum*) genotypes from a diverse germplasm collection. Adv. Crop Sci. Technol. 5(4): 299-309.

[52] Adams, S.R., Cockshull, K.E. and Cave, C.R.J. 2001. Effect of temperature on the development of tomato fruits. Ann. Bot. 88: 869-877.

[53] Aguayo, E. and Artes, A. 2004. Quality of fresh-cut tomato as affected by type of cut, packaging, temperature and storage time. Eur. Food Res. Technol. 219 (5): 492-499.

[54] Aronson, E.L. and Menulty, S.G. 2009. Appropriate experimental ecosystem warning methods by ecosystem, objective and practicality. Agric. Forest Meteorol. 149:1791–1799.
[55] Khanal, B. 2012. Effect of day and night temperature on pollen characteristics, fruit quality and storability of tomato. M.Sc. thesis. Norwagian Institute of Life sciences, Norway, 46p.
[56] Gómez, R., Costa, J, Amo, M., Alvarruiz, A., Picazo, M. and Pardo, J.E 2001. Physicochemical and colorimetric evaluation of local varieties of tomato grown in SE Spain. J. Sci. Food Agric. 81 (11): 1101-1105.
[57] Moraru, C., Logendra, L., Lee, T.C. and Janes, H. 2004. Characteristics of 10 processing tomato cultivars grown hydroponically for the NASA Advanced Life Support (ALS) Program. J. Food Composition Anal., 17(2): 141-154.
[58] Anza, M., Riga, P. and Garbisu, C. 2006. Effects of variety and growth season on the organoleptic and nutritional quality of hydroponically grown tomato. J. Food Qual., 29 (1): 16-37.
[59] Beckles, D.M. 2012. Factors affecting the postharvest soluble solids and sugar content of tomato (*Solanum lycopersicum* L.) fruit. Postharvest Biol. Technol., 63 (1): 129-140.
[60] Gautier, H., Buret, M., Grasselly, D. and Causse, M. 2005. Fruit load or fruit position alters response to temperature and subsequently cherry tomato quality. J. Sci. Food Agric., 85 (6): 1009-1016.
[61] Oms-oliu, G., Hertog, M.L.A.T.M., van DePoel, B., Ampofo-asiama, J., Geeraerd, A.H. and Nicolaï, B.M. 2011. Metabolic characterization of tomato fruit during preharvest development, ripening, and postharvest shelf-life. Postharvest Biol. Technol., 62 (1): 7-16.
[62] Weerakkody, W. 2003. Nutritional value of fresh leafy vegetables as affected by pre-harvest factors. 511-515 pp.
[63] Yuan, X.K. 2016. Effect of day/night temperature difference on chlorophyll content, photosynthesis and fluorescence parameters of tomato at fruit stage. Photosynthetica. 54 (3): 475-477.

Publication History
Received 03.07.2020
Revised 17.07.2020
Accepted 19.07.2020
Online 30.07.2020