



E-ISSN: 2278-4136
P-ISSN: 2349-8234
JPP 2017; 6(6): 1917-1922
Received: 04-09-2017
Accepted: 05-10-2017

Amit Kumar Singh
Department of Botany, Uday
Pratap Autonomous College,
Varanasi, Uttar Pradesh, India

Maneesh Kumar Singh
Department of Horticulture,
Uday Pratap Autonomous
College, Varanasi, Uttar
Pradesh, India

Vineet Singh
Department of Horticulture,
Uday Pratap Autonomous
College, Varanasi, Uttar
Pradesh, India

Rajeev Singh
Deptt. of Agril. Economics,
N.D.U.A. & T. Kumarganj,
Faizabad, Uttar Pradesh, India

Tushar Raghuvanshi
Deptt. of Agril. Extension, Sam
Higginbottom Institute of
Agriculture, Technology and
Sciences, Uttar Pradesh, India

Chandan Singh
Deptt. of Soil Science & Agril.
Chemistry, N.D.U.A. & T.
Kumarganj, Faizabad Uttar
Pradesh, India

Correspondence
Rajeev Singh
Deptt. of Agril. Economics,
N.D.U.A. & T. Kumarganj,
Faizabad, Uttar Pradesh, India

Debilitation in tomato (*Solanum lycopersicum* L.) as result of heat stress

Amit Kumar Singh, Maneesh Kumar Singh, Vineet Singh, Rajeev Singh, Tushar Raghuvanshi and Chandan Singh

Abstract

High temperatures cause an array of morpho-anatomical, physiological and biochemical changes in tomato plants, which affect plant growth and development and may lead to a radical reduction in economic yield. The adverse effects of heat stress on tomato can be mitigated by developing crop plants with improved thermotolerance using various genetic approaches. Heat stress affects tomato plant growth throughout its ontogeny, though heat-threshold level varies considerably at different developmental stages. For instance, during seed germination, high temperature may slow down or totally inhibit germination, depending on tomato plant species and the intensity of the stress. At later stages, high temperature may adversely affect photosynthesis, respiration, water relations and membrane stability, and also modulate levels of metabolites. In order to cope with heat stress, plants implement various mechanisms, including maintenance of membrane stability, scavenging of ROS, production of antioxidants, accumulation and adjustment of compatible solutes. The objective of our study was to collect and elaborate the work done by different scientists at different levels and approaches to create heat tolerance in tomato crop.

Keywords: Heat stress, High temperature, morphological, biochemical, physiological.

Introduction

Plant growth and development is reliant upon the temperature surrounding to it, each species and plants has a specific temperature range represented by a minimum, maximum, and optimum. These values were summarized by Hatfield *et al.* (2008, 2011) [20-21] for a number of different species typical of seed and fruit production. Variation in developmental processes lies at the core of functional differences in plant genotypes and species growing under different environmental conditions. Environmental stresses have inconstant effects on different organs and tissues within a plant, and as such, molecular, cellular and morphological responses to stress vary among tissues, and throughout developmental life time of a plant. The range in developmental processes across genotypes, and the ability of a plant of a given genotype to dynamically shifting these developmental progressions in response to the environment is the key to plant success in natural and agricultural settings (Nicotra *et al.*, 2010) [40]. The expected alterations in temperature over the next 30-50 years are envisaged to be in the range of 2-3 °C (IPCC) (2007). Heat waves or extreme temperature events are projected to become more intense, more frequent, and last longer than what is being currently observed in recent years (Meehl *et al.*, 2007) [35].

Table 1: Physiological disorders of vegetable crops caused by high temperatures

S. No.	Crop	Disorder	Aggravating factor
1	Asparagus	High fiber in stalks and spheres	High temperature
2	Asparagus	Feathering and lateral branch growth	Temperature more than 32°C, especially if picking frequency is not increased
3	Bean	Higher fiber in pods	High temperature
4	Carrot	Low carotene content	Temperature <10 °C or >20 °C
5	Cauliflower	Blindness, buttoning, riceyness	Temperature fluctuation
6	Cauliflower, Broccoli	Hollow stem, leafy heads, no heads, bracting	High temperature
7	Cole crops and lettuce	Tip burn	Drought, combined with high temperature, high respiration
8	Tomato, pepper, watermelon	Blossom end rot	High temperature, especially if combined with drought and high transpiration.

(Source: Spaldon *et al.*, 2015) [57]

Tomato is one of the most significant vegetable ever used all over the world belongs to the family Solanaceae. Requirements of tomato crop are relatively cool, dry climate for high yield and best quality. However, it can be grown to a wide range of climatic conditions from temperate to hot and humid tropical. The most favourable temperature for most varieties lies stuck between 21 and 24°C. The plants can endure ranges of temperatures, but the plant tissues are damaged below 10°C and above 38°C. Tomato plants respond to temperature deviation during the growth cycle, for seed germination seedling growth, flower and fruit set fruit quality. If cool or hot climatic spells continue during flowering, production of pollen will be low. This will influence fruit formation (Wahid, *et al.* 2007) [1-63-64]. This assessment accentuates on tomato plant responses and adaptations to heat stress at the whole plant, cellular and sub cellular levels, forbearance mechanisms and strategies for heritable enhancement of tomato crop with heat stress tolerance. For the tomato crop the range of temperature requirements at different stages was suggested by Naika, *et al.* (2005) [39] (Table 1).

Table 1: Requirements of temperature at different stages of tomato crop

Stage	Temperature (°C)		
	Min.	Optimum range	Max.
Seed germination	11	16-29	34
Seedling growth	18	21-24	32
Fruit set	18	20-24	30
Red colour development	10	20-24	30

Debilitation due to heat stress in tomato

Morphological symptoms

In tomato, reproductive processes adversely affected by high temperature, including meiosis in both male and female organs, pollen germination and pollen tube growth, ovule viability, stigmatic and style positions, number of pollen grains retained by the stigma, fertilization and post-fertilization processes, growth of the endosperm, proembryo and fertilized embryo (for a review see (Foolad, 2005) [16]. Most noticeable effect of high temperatures on reproductive processes in tomato is the production of an exerted style (i.e., stigma is elongated beyond the anther cone), which may prevent self-pollination. At high temperature Poor fruit set has also been associated with low levels of carbohydrates and growth regulators released in plant sink tissues (Kinet and Peet, 1997) [27]. Growth chamber and greenhouse studies suggest that high temperature is most deleterious when flowers are first visible and sensitivity continues for 10–15 days. Reproductive phases most sensitive to high temperature are gametogenesis (8–9 days before anthesis) and fertilization (1–3 days after anthesis) in various plants (Foolad, 2005) [16]. Both male and female gametophytes are sensitive to high temperature and response varies with genotype; however, ovules are generally less heat sensitive than pollen (Peet and Willits, 1998) [41-42]. Reproductive processes are markedly affected by high temperatures in most plants, which ultimately affect fertilization and post-fertilization processes leading to reduced crop yield. Heat stress destructively affects the vegetative growth and reproductive development of the tomato plants which ultimately reduces yield and quality of tomato fruit. High temperature decreased the leaf area, foliar curling, yellowing and stunting of the plants (Gomez *et al.* 2004, Abdelmageed, *et al.* 2009) [17, 3]. Total flower bud and flower production, mainly at the first four russes, may be a

reliable criterion of heat tolerance selection. Reproductive processes in tomato crop are extremely susceptible to high temperature than the vegetative ones. (Lahar, and Peat, 1998 [28], Abdelmageed, *et al.* 2003 [2], Alsdon, *et al.* 2006) [28, 2, 4]. Mean temperature of 29 °C causes, fruit number, fruit weight per plant and seed number per fruit markedly decreased as compared with those at 25 °C. Peet *et al.* (1998) [41-42] and Sato *et al.* (2000) [51] concluded that mutilation of pollen and anther development by elevated temperature contributes to decreased fruit set in tomato. Simple sugars are the principal metabolic substrates can be used by germinating pollen (Stanley, 1971) [59]. Speranza *et al.* (1997) [58] observed that starch reserves stored during pollen development give rise to carbohydrates at maturity. According to Pacini (1996), during pollen development soluble carbohydrates of sporophytic origin may be consumed, polymerized or be transformed into other molecules. Mature tomato pollen grain of is starchless (Buchmann, 1986) [6]. However, amylolytic activity, accompanied by a decreased starch concentration and an increased soluble sugar concentration, detected in developing tomato anthers (Bhadula and Sawhney, 1989) [5]. Bhadula and Sawhney (1989) [5] concluded that a deficiency in carbohydrate metabolism in the tomato anther which leads to abnormal pollen development. Saini (1997) [45] observed that stress-induced arrest of male gametophyte development is preceded by disturbances in carbohydrate metabolism and distribution within anthers. Affected pollen grains failed to accumulate starch, which is a major constituent of fertile grass pollen. In tomato, the failure of viable pollen grain production under high temperature conditions may also be associated with stalled sugar metabolism. Tomato plants can develop an acclimated mechanism in opposition to super optimal thermal stress caused at 35°C, temperature well above the optimal growth temperature, this acclimated method in tomato plants appear to consist of the addition of phenolic compounds as a feasible form of adapting to this stress. It can be possible, by manipulating characters concerned with the bioactivity of phenolic compounds, to make active acclimated mechanisms in plants under stress caused by temperature (Rivero, *et al.*, 2001) [44]. The metabolism of phenolic compounds as well includes the performance of oxidative enzymes as, Peroxidase and Polyphenol oxidase that catalyse the oxidation of phenols to quinones.

Physiological responses to heat stress

Plants acquire various mechanisms to ensure survival under elevated temperatures. High temperatures affect several physiological processes dealing finally with yield reduction. Physiological and biochemical processes affected by temperature are photosynthetic enzyme activity; membrane integrity, photophosphorylation and electron transport in chloroplast, stomatal conductance to CO₂ diffusion and photo assimilate translocation (Dinar and Rudich, 1985) [13]. Heat shock can be used as control of some plant diseases as alternative for chemical control of vegetable seeds diseases (Jahn *et al.*, 2000) [23], as well as for post-harvest, to improve the quality of vegetables (Loaiza-Velarde *et al.*, 2001) [30]. Temperature affects growth and development of vegetables in terms of seed germination, development of economic parts, flowering, pollination, fruit set, quality of produce, seed production, seed storage, seed dormancy and occurrence of disease and pests (Sing, S.P., 1997) [56]. Significant inhibition of photosynthesis occurs at temperature above the optimum level, resulting in significant loss of

potential productivity (Salvucci and Crafts-Brandner 2004) [48]. Plant water eminence is the most crucial variable under changing ambient temperatures (Mazorra *et al.*, 2002) [33]. In general, plants have a propensity to maintain steady tissue water status regardless of temperature when moisture is plenty; however, at high temperatures severely harm this tendency when water is limiting (Machado and Paulsen, 2001) [31]. Under field conditions, high temperature stress is frequently associated with reduced water availability (Simoes-Araujo *et al.*, 2003) [55]. In tomato heat stress disconcerted the relations of leaf water and root hydraulic conductivity (Morales *et al.*, 2003) [38]. In general, during daytime rate of transpiration induces water deficiency in plants, causing decreased water potential which leading to perturbation of many physiological processes (Tsukaguchi *et al.*, 2003) [61]. High temperatures seem to cause water loss in plants more during daytime than night time.

The adaptive mechanism in many plants grown under extreme temperatures is accumulation of certain organic compounds of low molecular mass referred to as compatible osmolytes (Hare *et al.*, 1998; Sakamoto and Murata, 2002) [19, 47]. Under high temperature stress, different plant species may accumulate a variety of osmolytes such as sugars and sugar alcohols (polyols), proline, tertiary and quaternary ammonium compounds, and tertiary sulphonium compounds (Sairam and Tyagi, 2004) [46]. Accumulation of such solutes may contribute to enhanced high temperature stress tolerance of plants. Glycinebetaine (GB), an amphoteric quaternary amine, plays an important role as a compatible solute in plants under various stresses under high temperature (Sakamoto and Murata, 2002) [47]. In assessing the functional significance of accumulation of compatible solutes, it is suggested that proline or GB synthesis may buffer cellular redox potential under heat and other environmental stresses (Wahid and Close, 2007) [1-63-64]. Under high temperatures, fruit set in tomato plants failed due to the disruption of sugar metabolism and proline transport during the narrow window of male reproductive development (Sato *et al.*, 2006) [52-53].

Amendments in various photosynthetic attributes under heat stress are good indicators of thermotolerance of the plant show correlations with growth. Any constraint in photosynthesis can limit plant growth at high temperatures. Photochemical reactions in thylakoid lamellae and carbon metabolism in the stroma of chloroplast have been suggested as the primary sites of injury at high temperatures (Wise *et al.*, 2004) [66]. Chlorophyll fluorescence, the ratio of variable fluorescence to maximum fluorescence (Fv/Fm), and the base fluorescence (F0) are physiological parameters that have been shown to correlate with heat tolerance (Yamada *et al.*, 1996) [68]. Increasing leaf temperatures and photosynthetic photon flux density influence thermotolerance adjustments of PSII, indicating their potential to optimise photosynthesis under varying environmental conditions as long as the upper thermal limits do not exceed (Salvucci and Crafts-Brandner, 2004b; Marchand *et al.*, 2005) [49, 32]. In tomato genotypes differing in their capacity for thermotolerance, an increased chlorophyll a:b ratio and a decreased chlorophyll:carotenoids ratio were observed in the tolerant genotypes under high temperatures, indicating that these changes were related to thermotolerance of tomato (Camejo *et al.*, 2005; Wahid and Ghazanfar, 2006) [9, 65]. Furthermore, under high temperatures, degradation of chlorophyll a and b was more pronounced in developed compared to developing leaves (Karim *et al.*, 1997, 1999) [24-25]. Such effects on chlorophyll or photosynthetic apparatus were suggested to be associated with the production of active

oxygen species (Camejo *et al.*, 2006; Guo *et al.*, 2006) [8, 18]. PSII is highly thermolabile, and its activity is greatly reduced or even partially stopped under high temperatures (Bukhov *et al.*, 1999; Camejo *et al.*, 2005) [7, 9], which may be due to the properties of thylakoid membranes where PSII is located (McDonald and Paulsen, 1997) [34]. Heat stress may 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 center (Fig. 1) (De Ronde *et al.*, 2004) [12]. Heat stress causes dissociation of manganese (Mn)-stabilizing 33-kDa protein at PSII reaction center complex followed by the release of Mn atoms (Yamane *et al.*, 1998) [69]. Heat stress may also impair other parts of the reaction center, e.g., the D1 and/or the D2 proteins (De Las Rivas and Barber, 1997) [11].

High temperature influences the photosynthetic capacity of C3 plants more strongly than in C4 plants. It alters the energy distribution and changes the activities of carbon metabolism enzymes, particularly the rubisco, thereby altering the rate of RuBP regeneration by the disruption of electron transport and inactivation of the oxygen evolving enzymes of PSII (Salvucci and Crafts-Brandner, 2004b) [49]. Heat shock reduces the amount of photosynthetic pigments (Todorov *et al.*, 2003) [60], soluble proteins, rubisco binding proteins (RBP) and large- (LS) and smallsubunits (SS) of rubisco in darkness but increases them in light, indicating their roles as chaperones and HSPs (Kepova *et al.*, 2005) [26]. Moreover, under heat stress, starch or sucrose synthesis is greatly influenced as observed from reduced activities of sucrose phosphate synthase (Chaitanya *et al.*, 2001) [10], ADP glucose pyrophosphorylase and invertase (Vu *et al.*, 2001) [62]. Some hormones like brassinosteroids have recently been shown to confer thermotolerance to tomato (Wahid *et al.*, 2007) [1-63-64].

Biochemical changes

Heat stress limit several biochemical processes required for tomato plant survival. Heat stress significantly increased the chlorophyll (Chl) degradation, malondialdehyde (MDA), hydrogen peroxide (H₂O₂), proline (Pro) and glycinebetaine (GB) content, and decreased the photosynthetic pigment (Chl a and Chl b) and total soluble carbohydrate (TSC) content and the activities of Rubisco, carbonic anhydrase (CA), and nitrate reductase (NR). High temperature, particularly high night time temperature, limits the productivity of tomato, which is very sensitive to heat stress (Moore and Thomas (1952) [37]. High temperature impairs pollen development and pollen viability by disrupting the carbohydrate metabolism, resulting in a decrease in tomato fruit set (Pressman *et al.* (2002) [43]. Also, Heat stress disturbs proline translocation and hormonal balance in plants that reduce yield and fruit quality (Sato *et al.*, 2006, Sangu E., 2015) [52-53, 50]. HS markedly limits photosynthesis, respiration, water balance, and membrane stability, and also disturbs primary and secondary metabolites in plants (Hemantaranjan *et al.* 2014, Wahid *et al.*, 2007, Ding *et al.*, 2016) [22, 1-63-64, 14]. Abiotic stress leads to imbalanced generation of reactive oxygen species (ROS) that disturb metabolic homeostasis in plants, resulting in autocatalytic peroxidation of membrane lipids and pigments (Mittler *et al.*, 2012, Wahid *et al.*, 2007) [36, 1-63-64]. To counter oxidative damage, plants activate non-enzymatic and enzymatic detoxification system to maintain or reprogram the metabolic homeostasis (Mittler *et al.*, 2012) [36]. The antioxidant enzymes, such as catalase (CAT), peroxidase (POD), superoxide dismutase (SOD), and ascorbate peroxidase (APX), as well as other macromolecules, such as proline

(Pro), glycinebetaine (GB), carbohydrates play a key role in plants in coping with abiotic stress.

Besides tissue dehydration, heat stress induces oxidative stress. That are, generation and reactions of activated oxygen species (AOS) including singlet oxygen (1O_2), superoxide radical (O_2^-), hydrogen peroxide (H_2O_2) and hydroxyl radical (OH^-) are symptoms of cellular injury due to high temperature (Liu and Huang, 2000) [29]. AOS cause the autocatalytic peroxidation of membrane lipids and pigments which leading to loss of membrane semi-permeability and modifying its functions (Xu *et al.*, 2006) [67]. Superoxide radical is regularly synthesized in the chloroplast and mitochondrion and some quantities are also produced in microbodies. The scavenging of O_2^- by superoxide dismutase (SOD) results in the production of H_2O_2 , which is removed by APX or CAT. Though, both O_2^- and H_2O_2 are not as toxic as the OH^- , but it is formed by the combination of O_2^- and H_2O_2 in the presence of trace amounts of Fe^{2+} and Fe^{3+} through the Haber–Weiss reaction. The OH^- can damage chlorophyll, protein, DNA, lipids and other important macromolecules, thus fatally affecting plant metabolism and limiting growth and yield (Sairam and Tyagi, 2004) [46]. Plants have developed a series of both enzymatic and non-enzymatic detoxification systems to counteract AOS, so protecting cells from oxidative damage (Sairam and Tyagi, 2004) [46].

It is observed that, over expression of SOD in plants affect a number of physiological phenomena, which include the removal of H_2O_2 , oxidation of toxic reductants, biosynthesis and degradation of lignin in cell walls, auxin catabolism, defensive responses to wounding, defence against pathogen or insect attack, and some respiratory processes (Scandalios, 1993) [54]. Expression and activation of APX is related to the appearance of physiological injuries caused in plants by thermal stress (Mazorra *et al.*, 2002) [33]. Decrease in antioxidant activity in stressed tissues that result in higher levels of AOS which may contribute to injury (Fadzillah *et al.*, 1996) [15]. Protection against oxidative stress is an important component in determining the survival of a plant under heat stress.

References

1. A Wahid, S Gelani, M Ashraf, MR Foolad. Environmental and Experimental Botany. 2007; 61:199-223.
2. Abdelmageed AH, N Gruda, B Geyer. Effect of high temperature and heat shock on tomato (*Lycopersicon esculentum* M.) genotypes under controlled conditions. Conference on International Agricultural Research for Development. Deutscher Tropentag, Göttingen, 2003, 8-10.
3. Abdelmageed AHA, N Gruda, MMA El-Balla. Performance of Different Tomato Genotypes in the Arid Tropics of Sudan during the Summer Season. I. Vegetative Growth. J. Agri. Rural Develop. Tropics and Subtropics. 2009; 110(2):137-145.
4. Alsadon AA, MA Wab-alah, SO Khalil. *In vitro* Evaluation of Heat Stress Tolerance in Some Tomato Cultivars. J. King Saud Univ. 2006; 19(1):13-24.
5. Bhadula SK, Sawhney VK. Amylolytic activity and carbohydrate levels during the stamen ontogeny of a male fertile, and a 'gibberellin sensitive' male sterile mutant of tomato (*Lycopersicon esculentum*). Journal of Experimental Botany. 1989; 40:789-794.
6. Buchmann SL. Vibratile pollination in *Solanum* and *Lycopersicon*: a look at pollen chemistry. In: D'Arely WG, ed. Solanaceae, biology and systematics New York: Columbia University Press, 1986, 237-252.
7. Bukhov NG, Wiese C, Neimanis S, Heber U. Heat sensitivity of chloroplasts and leaves: leakage of protons from thylakoids and reversible activation of cyclic electron transport. Photosyn. Res. 1999; 59:81-93.
8. Camejo D, Jim'enez A, Alarc'on JJ, Torres W, G'omez JM, Sevilla F. Changes in photosynthetic parameters and antioxidant activities following heat-shock treatment in tomato plants. Funct. Plant Biol. 2006; 33:177-187.
9. Camejo D, Rodr'iguez P, Morales MA, Dell'amico JM, Torrecillas A, Alarc'on JJ. High temperature effects on photosynthetic activity of two tomato cultivars with different heat susceptibility. J. Plant Physiol. 2005; 162:281-289.
10. Chaitanya KV, Sundar D, Reddy AR. Mulberry leaf metabolism under high temperature stress. Biol. Plant. 2001; 44:379-384.
11. De Las Rivas J, Barber J. Structure and thermal stability of photosystem II reaction centers studied by infrared spectroscopy. Biochemistry. 1997; 36:8897-8903.
12. De Ronde JAD, Cress WA, Kruger GHJ, Strasser RJ, Staden JV. Photosynthetic response of transgenic soybean plants containing and Arabidopsis P5CR gene, during heat and drought stress. J. Plant Physiol. 2004; 61:1211-1244.
13. Dinar M, Rudich. Effect of heat stress on assimilates partition in tomato. Ann. Bot. 1985; 56:239-249.
14. Ding X, Jiang Y, Hao T, Jin H, Zhang H, He L, *et al.* Effects of heat shock on photosynthetic properties, antioxidant enzyme activity, and downy mildew of cucumber (*Cucumis sativus* L.). PLOS ONE, DOI:10.1371/journal.pone.0152429. 2016.
15. Fadzillah NM, Gill V, Finch RP, Burdon RH. Chilling, oxidative stress and antioxidant responses in shoot cultures of rice. Planta. 1996; 199:552-556.
16. Foolad MR. Breeding for abiotic stress tolerances in tomato. In: Ashraf, M., Harris, P.J.C. (Eds.), Abiotic Stresses: Plant Resistance Through Breeding and Molecular Approaches. The Haworth Press Inc., New York, USA, 2005, 613-684.
17. Gomez O, M Pinon, Y Martinez, M Quinones, D Fonesca, H Laterrot. Breeding for resistance to begomovirus in tropic-adapted tomato genotypes; Plant Breeding. 2004; 123:275-279.
18. Guo YP, Zhou HF, Zhang LC. Photosynthetic characteristics and protective mechanisms against photooxidation during high temperature stress in two citrus species. Sci. Hort. 2006; 108:260-267.
19. Hare PD, Cress WA, Staden JV. Dissecting the roles of osmolytes accumulation during stress. Plant Cell Environ. 1998; 21:535-553.
20. Hatfield JL, Boote KJ, Fay P, Hahn L, Izaurralde RC, Kimball BA, *et al.* Agriculture In: The Effects of Climate Change on Agriculture, Land Resources, Water Resources, and Biodiversity in the United States, 2008.
21. Hatfield JL, Boote KJ, Kimball BA, Ziska LH, Izaurralde RC, Ort D, *et al.* Climate impacts on agriculture: implications for crop production. Agron. J. 2011; 103:351-370.
22. Hemantaranjan A, Bhanu AN, Singh MN, Yadav DK, Patel PK, Singh R, Katiyar D. Heat stress responses and thermotolerance. Adv Plants Agri Res. 2014; 3:1-10.
23. Jahn M, E Nega, S Werner. Pilzbefall an gemüsesaatgut: Verträglichkeit und Wirkung der Heißwasserbehandlung.

- Gemüse. 2000; 3:17-19.
24. Karim MA, Fracheboud Y, Stamp P. Heat tolerance of maize with reference of some physiological characteristics. *Ann. Bangladesh Agri.* 1997; 7:27-33.
 25. Karim MA, Fracheboud Y, Stamp P. Photosynthetic activity of developing leaves is less affected by heat stress than that of developed leaves. *Physiol. Plant.* 1999; 105:685-693.
 26. Kepova KD, Holzer R, Stoilova LS, Feller U. Heat stress effects on ribulose-1, 5-bisphosphate carboxylase/oxygenase, Rubisco binding protein and Rubisco activase in wheat leaves. *Biol. Plant.* 2005; 49:521-525.
 27. Kinet JM, Peet MM. Tomato. In: Wien, H.C. (Ed.), *The Physiology of Vegetable Crops*. CAB International, Wallingford, UK, 1997, 207-258.
 28. Lahar DP, WE Peat. *Flora Characteristics of Heat-tolerant and Heat-sensitive Tomato (Lycopersicon esculentum Mill.) Cultivars at High Temperature*. Scientia Horticulturae. 1998; 73:53-60.
 29. Liu X, Huang B. Heat stress injury in relation to membrane lipid peroxidation in creeping bent grass. *Crop Sci.* 2000; 40:503-510.
 30. Loaiza-Velarde JG, FA Tomas-Barbera, ME Salveit. Heat shocks applied either before or after wounding reduce browning of lettuce leaf tissue. *J. Amer. Soc. Hort. Sci.* 2001; 122(6):873-877.
 31. Machado S, Paulsen GM. Combined effects of drought and high temperature on water relations of wheat and sorghum. *Plant Soil*, 2001, 233.
 32. Marchand FL, Mertens S, Kockelbergh F, Beyens L, Nijs I. Performance of high arctic tundra plants improved during but deteriorated after exposure to a simulated extreme temperature event. *Global Change Biol.* 2005; 11:2078-2089.
 33. Mazorra LM, Nunez M, Echerarria E, Coll F, S´anchez-Blanco MJ. Influence of brassinosteroids and antioxidant enzymes activity in tomato under different temperatures. *Plant Biol.* 2002; 45:593-596.
 34. McDonald GK, Paulsen GM. High temperature effects on photosynthesis and water relations of grain legumes. *Plant Soil.* 1997; 196:47-58.
 35. Meehl GA. *Global Climate Projections*. In: *Climate Change: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press, Cambridge, 2007.
 36. Mittler R, Finka A, Goloubinoff P. How do plants feel the heat? *Trends in Biochemical Science.* 2012; 37:118-125.
 37. Moore EL, Thomas WO. Some effects of shading and parachlorophenoxy acetic acid on fruitfulness of tomatoes. *Proceedings of the American Society for Horticultural Science.* 1952; 60:289-294.
 38. Morales D, Rodríguez P, Dell´amico J, Nicolás E, Torrecillas A, S´anchez-Blanco MJ. High-temperature preconditioning and thermal shock imposition affects water relations, gas exchange and root hydraulic conductivity in tomato. *Biol. Plant.* 2003; 47:203-208.
 39. Naika S, Juede J, Goffau M, Hilmi M, Dam V. *Cultivation of Tomato Production, processing and marketing*, Agromisa/ CTA. Revised edition, Agrodok-series, 2005, 17.
 40. Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, *et al.* Plant phenotypic plasticity in a changing climate. *Trends Plant Sci.* 2010; 15:684-692.
 41. Peet MM, Sato S, Gardner RG. Comparing heat stress effects on male-fertile and male-sterile tomatoes. *Plant, Cell and Environment.* 1998; 21:225-231.
 42. Peet MM, Willits DH. The effect of night temperature on greenhouse grown tomato yields in warm climate. *Agric. Forest Meteorol.* 1998; 92:191-202.
 43. Pressman E, Peet MM, Pharr DM. The effect of heat stress on tomato pollen characteristics is associated with changes in carbohydrate concentration in the developing anthers. *Ann Bot* 2002; 90:631-636.
 44. Rivero RM, JM Ruiz, PC Garc´ia, LR L´opezLefebvre, E Sanchez, L Romero. Resistance to cold and heat stress: accumulation of phenolic compounds in tomato and watermelon plants. *Plant Sci.* 2001; 106:315-321.
 45. Saini HS. Effects of water stress on male gametophyte development in plants. *Sexual Plant Reproduction.* 1997; 10:67-73.
 46. Sairam RK, Tyagi A. Physiology and molecular biology of salinity stress tolerance in plants. *Curr. Sci.* 2004; 86:407-421.
 47. Sakamoto A, Murata N. The role of glycine betaine in the protection of plants from stress: clues from transgenic plants. *Plant Cell Environ.* 2002; 25:163-171.
 48. Salvucci ME, Crafts-Brandner SJ. Relationship between the heat tolerance of photosynthesis and the thermal stability of rubisco activase in plants from contrasting thermal environments. *Plant Physiol.* 2004a; 134:1460-1470.
 49. Salvucci ME, Crafts-Brandner SJ. Inhibition of photosynthesis by heat stress: the activation state of Rubisco as a limiting factor in photosynthesis. *Physiol. Plant.* 2004b; 120:179-186.
 50. Sangu E, Tibazarwa FI, Nyomora A, Symonds RC. Expression of genes for the biosynthesis of compatible solutes during pollen development under heat stress in tomato (*Solanum lycopersicum*). *Journal of Plant Physiology.* 2015; 178:10-16.
 51. Sato S, Peet MM, Thomas JF. Physiological factors limit fruit set of tomato (*Lycopersicon esculentum* Mill.) under chronic high temperature stress. *Plant, Cell and Environment.* 2000; 23:719-726.
 52. Sato S, Kamiyama M, Iwata T, Makita N, Furukawa H, Ikeda H. Moderate increase of daily mean temperature adversely affects fruit set of *Lycopersicon esculentum* by disrupting specific physiological processes in male reproductive development. *Ann Bot.* 2006; 97:731-738.
 53. Sato S, Kamiyama M, Iwata T, Makita N, Furukawa H, Ikeda H. Moderate increase of mean daily temperature adversely affects fruit set of *Lycopersicon esculentum* by disrupting specific physiological processes in male reproductive development. *Ann. Bot.* 2006; 97:731-738.
 54. Scandalios JG. Oxygen stress and superoxide dismutases. *Plant Physiol.* 1993; 101:7-12.
 55. Simoes-Araujo JL, Rumjanek NG, Margis-Pinheiro M. Small heat shock proteins genes are differentially expressed in distinct varieties of common bean. *Braz. J. Plant Physiol.* 2003; 15:33-41.
 56. Sing SP. *Principles of vegetable production*, first edition, Agrotech. Publishing Academy. Udaipur, 1997, 60-80.
 57. Spaldon S, Samnotra RK, Chopra Sandeep. *Climate resilient technologies to meet the challenges in vegetable production.* 2015; 3(2):28-47.
 58. Speranza A, Calzoni GL, Pacini E. Occurrence of mono- or disaccharides and polysaccharide reserves in mature pollen grains. *Sexual Plant Reproduction.* 1997; 10:110-

115.

59. Stanley RG. Pollen chemistry and tube growth. In: Heslop-Harrison J, ed. Pollen: development and physiology London: Butterworths, 1971, 131-155.
60. Todorov DT, Karanov EN, Smith AR, Hall MA. Chlorophyllase activity and chlorophyll content in wild type and *eti 5* mutant of *Arabidopsis thaliana* subjected to low and high temperatures. Biol. Plant. 2003; 46:633-636.
61. Tsukaguchi T, Kawamitsu Y, Takeda H, Suzuki K, Egawa Y. Water status of flower buds and leaves as affected by high temperature in heat tolerant and heat-sensitive cultivars of snap bean (*Phaseolus vulgaris* L.). Plant Prod. Sci. 2003; 6:4-27.
62. Vu JCV, Gesch RW, Pennanen AH, Allen LHJ, Boote KJ, Bowes G. Soybean photosynthesis, Rubisco and carbohydrate enzymes function at supra-optimal temperatures in elevated CO₂. J. Plant Physiol. 2001; 158:295-307.
63. Wahid A, Gelani S, Ashraf M, Foolad MR. Heat tolerance in plants: An overview. Environmental and Experimental Botany. 2007; 61:199-223.
64. Wahid A, Close TJ. Expression of dehydrins under heat stress and their relationship with water relations of sugarcane leaves. Biol. Plant. 2007; 51:104-109.
65. Wahid A, Ghazanfar A. Possible involvement of some secondary metabolites in salt tolerance of sugarcane. J. Plant Physiol. 2006; 163:723-730.
66. Wise RR, Olson AJ, Schrader SM, Sharkey TD. Electron transport is the functional limitation of photosynthesis in field-grown Pima cotton plants at high temperature. Plant Cell Environ. 2004; 27:717-724.
67. Xu S, Li J, Zhang X, Wei H, Cui L. Effects of heat acclimation pretreatment on changes of membrane lipid peroxidation, antioxidant metabolites, and ultrastructure of chloroplasts in two cool-season turfgrass species under heat stress. Environ. Exp. Bot. 2006; 56:274-285.
68. Yamada M, Hidaka T, Fukamachi H. Heat tolerance in leaves of tropical fruit crops as measured by chlorophyll fluorescence. Sci. Hortic. 1996; 67:39-48.
69. Yamane Y, Kashino Y, Koike H, Satoh K. Effects of high temperatures on the photosynthetic systems in spinach: oxygen-evolving activities, fluorescence characteristics and the denaturation process. Photosynth. Res. 1998; 57:51-59.