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Breeding Tomato (*Lycopersicon esculentum* Mill.) Resistant to High Temperature Stress

Pranab Hazra[1*] • Samsul Haque Ansary[2] • Debasis Sikder[1] • K. V. Peter[3]

[1] Department of Vegetable crops, Bidhan Chandra Krishi Viswavidyalaya, Mohanpur-741252, West Bengal, India
[2] KRIBCO, Purulia, West Bengal, India
[3] Department of Vegetable Science, Kerala Agricultural University, Trissur, Kerala, India
***Corresponding author*: * hazrap@rediffmail.com**

ABSTRACT

The evidence of global warming has increased interest in the cause of yield declines at temperatures only slightly above optimal in many crops including tomato. It has been well documented that heat stress can occur in tomato at mean daily temperatures of 28-29ºC, which are just a few degrees above the optimum temperature range of 21-24ºC. Such moderately elevated temperature stress may not disrupt biochemical reactions fundamental for normal cell functioning but may reduce fruit set as a common response to such elevated temperatures. This review article highlights different adverse effects of heat/high temperature and gene action governing various characters under high temperature conditions and breeding methods for the development of heat resistant tomato varieties.

Keywords: breeding method, genetic control, heat tolerance, reproductive characters

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INTRODUCTION

The evidence of global warming has increased the interest in the cause of yield declines at temperatures only slightly above optimal in many crops such as rice (Baker and Allen 1993), groundnut (Vara Prasad *et al*. 1999), cowpea (Craufurd *et al*. 1998), tomato (Peet *et al*. 1998), and others. Above optimal temperatures can shorten the crop life period and markedly hasten flowering and ripening of fruits in tomato (Ansary 2006). Analysis of recent climate trends (Bell *et al*. 2000) suggests that temperatures in tomato production areas worldwide are already rising, and the frequency and severity of episodes of above optimal temperatures will increase in the coming decades. Tomatoes are grown widely in tropical and sub-tropical regions where they often experience high temperatures during fruit set. It has been well documented that heat stress can occur at mean daily temperatures of 28-29ºC, which are just a few degrees above the optimum temperature range of 21-24ºC. Such moderately elevated temperature stress may not disrupt biochemical reactions fundamental for normal cell functioning since the temperatures are still in the range that a tomato plant would grow normally, although reduced fruit set is the common response to such elevated temperatures mainly due to different reproductive malfunctioning. This situation necessitates orientation of a research programme for the development of tomato varieties tolerant to high temperature stress.

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Invited Review

OPTIMUM TEMPERATURE FOR PROPER GROWTH OF TOMATO

Night-time temperature

Influence of comparatively low night temperature of 13ºC for proper fruit set in tomato had been recorded much earlier and this phenomenon was termed thermoperiodism. Later it had been well documented through studies in the phytotron that a reduction in night temperature in the range of 15º-20ºC markedly increased the biological and comercial yield in tomato (Went 1950; Charles and Harris 1972).

Daily mean temperature

Peet *et al.* (1997) demonstrated that daily mean temperature is more critical than night-time temperature *per se* and at a daily mean temperature of 29ºC, fruit number, fruit weight per plant and seed number per fruit decreased markedly compared with those at 25ºC. Average night temperature of 19.2ºC in the spring-summer season remained just below the upper critical limit of 15ºC to 20ºC as suggested by Went (1950) however, a huge reduction in fruit set in this season under an average daily mean temperature of 26.8ºC supported the proposition of mean daily temperature being more critical than actual night temperature for fruit set in tomato (Ansary 2006). The optimal daily mean temperature for net assimilation rate in tomato is between 25º and 30ºC (Khavari-Nejad 1980), and optimal daily mean temperatures for fruit set and satisfactory fruit yield of tomato have been reported as 21º-24ºC (Geisenberg and Stewart 1986), 22º-25ºC (Peet and Bartholomew 1996), 22º-26ºC (Sato *et al.* 2000), 21.3ºC with an average day/night temperature of 27.3ºC/15.1ºC (Ansary 2006) and 26.3°/15.6°C (Dhankar *et al.* 2001).

HEAT TOLERANCE

The ability of a plant to survive acute thermal stress is one way to define heat stress resistance and a more useful definition agronomically is the maintenance of yield when exposed to stress (Mahan *et al.* 1995). In that sense, heat tolerance of tomato is determined by the ability of a plant to set fruits at high temperature. Heat tolerance in tomato is regarded as a genetically controlled attribute of the plant because of significant genotype-environment interaction for this character (Rudich *et al.* 1977; Palta *et al.* 1979). However, most researchers have concluded that poor fruit set at high temperatures in tomato could not be attributed to a single factor (Rudich *et al.* 1977; Kuo *et al.* 1979) hence, most authorities considered it as a complex trait (Berry and Gould 1979; El Ahmadi and Stevens 1979b; Prendergast 1982).

HIGH TEMPERATURE STRESS FOR TOMATO

Tomato is an example of a species with well documented but not well understood sensitivity to high temperatures (Picken 1984). It was documented much earlier that although tomato plant can grow under a wide range of temperatures, fruit production was limited by high daytime temperatures above 32ºC and especially, by high night-time temperatures above 21ºC (Moore and Thomas 1952). Reports of high temperature stress causing marked reduction in anthesis, blossom drop and fruit set for tomato are 30ºC and 45ºC (Iwahori and Takahashi 1963), as little as 4 hours exposure to 40ºC during flowering (Bar-Tsur 1977), above 26º/20ºC day/night and severely above 35º/26ºC day/night (El Ahmadi 1977), day temperature above 32ºC during summer (Kalloo 1988), 35º/23ºC day/night (Abdul-Baki and Stommel 1995), at 35º/30ºC (Lohar and Peat 1998), at 32º/26ºC day/night temperature (Sato *et al.* 2000), 38°/22°C day/night (Dhankar *et al.* 2001) and at an average of 34.3ºC/19.2ºC day/night temperature, average daily mean temperature being 26.8ºC (Ansary 2006). However, plants are most sensitive to moderately elevated temperature of 32/26ºC day/night 7-15 days before anthesis, although stress relief for at least 3 hour post-anthesis increases fruit set, assuming pollen develops under non-stressed conditions (Sato *et al.* 2002).

ADVERSE EFFECT OF HIGH TEMPERATURE

Temperature is a crucial factor for fruit set in tomato and the rates of many physiological processes of tomato plants are determined by temperature. The vegetative and reproductive responses of tomato are strongly modified by temperature alone or in conjunction with other environmental factors like light, nutrition and moisture (Abdalla and Verkerk 1968). The critical pre-anthesis high temperature stress was associated with developmental changes in anther, most strikingly, irregularities in the epidermis and endothesium, lack of opening of the stomium, and poor pollen formation (Sato *et al.* 2002). Several manifestations causing failure of tomato fruit set at high temperatures have been documented:

1) **Bud drop**: At high temperatures, abscissic acid formation increases and flowers tend to drop before pollination which varied between 10.0% in the heat tolerant cultivar Hotset and 66.2% in the most heat sensitive cultivar Hosen-Eilon at 33.0ºC/23.0ºC day/night temperature (Levy *et al.* 1978) and between 28.6% in the heat tolerant line CLN R (selection from CLN line from AVRDC) and 68.7% in the most heat susceptible local cultivar Patharkutchi in the wide array of 38 materials under study at an average of 34.3ºC/19.2ºC day/night temperature (Ansary 2006). El-Ahmadi and Stevens (1979a) also recorded bud drop at 38ºC/27ºC day/night temperature studying with six high temperature tolerant cultivars viz., Saladette, PI 262934, BL 6807, S 6916, CIAS161 and VF36. Generally when flowers abort at elevated temperatures, it is interpreted as an indication that the plant is under carbohydrate stress, and source-sink relations are disturbed (Seginer *et al.* 1994; Bertin 1995). However, differences between tomato cultivars in rates of abscission under moderately elevated temperatures of 32/28ºC day/night may be genetic, rather than resulting from lowered carbohydrate availability (Peet *et al.* 1998; Sato *et al.* 2002). Ueda *et al.* (1996) suggested that the increased abscission was due to changes in sugar metabolism and increased cellulose activity in the abscission zone.
2) **Undeveloped flowers**: The optimum relative humidity for tomato pollination is generally thought to be 50-70%. Three tomato cultivars NC8288, FM-9 and FL 7156 differing in heat tolerance were exposed to mild heat stress (31/25 vs. 28/22ºC) at three relative humidity levels (30, 60, 90%) in controlled environmental chambers and the treatments represented vapour pressure deficits (VPD) ranging from 0.38 to 2.70 averaged over a 24 hour period. The percentage of undeveloped flowers and pollen germination were most sensitive to high temperature at high humidity conditions (Peet *et al.* 2003).
3) **Persistent flower and calyx**: Flowers or calyces may remain persistent on the plant for a long time but fertilization is not rendered to fruit-set due to high temperature (Abdalla and Verkerk 1968; Lohar and Peat 1998).
4) **Splitting of antheridial cone**: Sometimes due to excessive heat stress, the cone-shaped anthers burst open and become out of reach to the stigma head (Levy *et al.* 1978; Hanna and Hernandez 1982; Ansary 2006) however, splitting of antheridial cone is genotype-dependent (Phookan *et al.* 1997; Ansary 2006).
5) **Lack of anther dehiscence**: Pollens fail to liberate from the anthers under high temperatures 38ºC/27ºC day/night (El-Ahmadi and Stevens 1979a) and 32ºC/26ºC day/night (Sato *et al.* 2000). High temperature stress 7-15 days before anthesis mostly affect anther development, especially in tissues with important roles in pollen development and release, such as the tapetum, stomium

and/or circular cell clusters and cultivar differences in pollen release and germination under heat stress are the most important factors determining their ability to set fruit (Sato *et al.* 2000). Failure of anther dehiscence may also be caused because the endothecial layer is not thickened enough at high temperatures (Rudich *et al.* 1977).

6) **Poor pollen production**: Flowers are produced without proper development of male or female parts under high temperatures (Lohar and Peat 1998) although Sato *et al.* (2000) suggested that the number of pollen grains produced, photosynthesis and night respiration did not limit fruit set under chronic, mild heat stress; rather pollen release and germination under heat stress are the most important factors determining their ability to set fruit.
7) **Pollen sterility**: High temperature leads to reduction of pollen fertility and such pollen is unable to fertilize (Levy *et al.* 1978; Ansary 2006).
8) **Embryo sac degeneration**: The embryo sac may degenerate due to high temperatures causing no fruit set (Iwahori 1966).
9) **Browning and drying of stigma**: The stigma head is dried and becomes brown due to desiccation at high temperatures (Iwahori 1966; Abdalla and Verkerk 1968; Ansary 2006).
10) **Reduction in stigma receptivity**: Stigma receptivity is reduced drastically due to high temperature stress (Charles and Harris 1972).
11) **Style elongation**: High temperature leads to protrusion of the style over the antheridial cone and becomes out of reach of the anthers causing a drastic reduction of fruit set (Rick and Dempsey 1969; Charles and Harris 1972; El-Ahamadi 1977; Rudich *et al.* 1977; Hanna *et al.* 1983; Berry and Rafiqueuddin 1988; Lohar and Peat 1998; Ansary 2006).
12) **Under-developed ovary**: High temperature affects the formation of the ovary and most of the time viable ovules are not produced in these ovaries (Hanna and Hernandez 1982).
13) **Poor fertilization**: Sometimes pollen germination may take place but fertilization of gametes is greatly reduced due to the prevalence of high temperatures (Johnson and Hall 1952; Iwahori 1966).
14) **Slow pollen tube growth**: Pollen may germinate over the stigma head but growth of the pollen tube is so slow that flowers senesce before the pollen tube can reach the ovary (Iwahori 1967; Dempsey 1970; Levy *et al.* 1978).
15) **Poor pollen viability**: Pollen viability is drastically reduced due to desiccation at high temperatures (Abdalla and Verkerk 1968; Arora 1977; Rudich *et al.* 1977; Levy *et al.* 1978; Iapichino and Loy 1987; Schoper *et al.* 1987; Ansary 2006) however, response of pollen to high temperature stress was genotype-dependent and not a general predictor of fruit set under high temperature stress (Abdul-Baki and Stommel 1995).
16) **Poor pollen germination**: Pollen germination is very much reduced under high temperatures (Iwahori 1967; Rick and Dempsey 1969; Charles and Harris 1972; El-Ahmadi and Stevens 1979a; Peet *et al.* 2003; Ansary 2006). At high temperature stress mean *in vitro* pollen germination was reduced even in the heat tolerant cultivars/lines compared to normal growing condition drastically to 17.1% from 49.5% at 38/27ºC day/night (El-Ahmadi and Stevens 1979a) and to 24.4% from 66.9% at 34.3ºC/19.2ºC day/night (Ansary 2006). However, Charles and Harris (1972) and Rudich *et al.* (1977) concluded that tomato cultivar variability in pollen germination was not correlated with their heat setting characteristics.
17) **Poor ovule viability**: Viability of ovules is also drastically reduced due to high temperature stress (Iwahori 1965; Abdalla and Verkerk 1968; El-Ahamadi 1977; El-Ahamadi and Stevens 1979a; Muthuvel *et al.* 2001).
18) **Ovule abortion and endosperm degeneration**: Due to high temperature, formation of the ovule in the ovary is greatly hampered leading to low fertility and sometimes the endosperm become degenerated (Iwahori 1966).
19) **Disruption in meiosis and prevention of pollen formation**: At high temperature, meiotic cell division is hindered and due to incomplete meiosis, formation of gametes is hampered (Johnson and Hall 1952; Iwahori 1965).
20) **Hindered sugar metabolism and failure of viable pollen production**: Starch reserves stored during pollen development give rise to soluble sugars at maturity and deficiency in carbohydrate metabolism in the tomato anthers resulting in decreased starch concentration in pollen grains leads to abnormal pollen development under high temperature (Bhadula and Sawhney 1989; Pressman *et al.* 2002; Firon *et al.* 2006), and carbohydrate content of developing and mature tomato pollen grains may be an important factor in determining pollen viability (Firon *et al.* 2006).
21) **Reduced carbohydrate availability for the fruits**: Undeveloped flowers remaining on the plant without developing further under high temperature stress is related to reduced carbohydrate availability for the development of the fruits (Sato *et al.* 2001, 2004).
22) **Reduced total soluble protein content**: Heat susceptibility is related to a decrease in total soluble protein content in heat-susceptible genotypes with the heat stress compared to the heat resistant genotypes (Camejo and Torres 2001).
23) **Developmental abnormalities and poor fruit set**: Developmental abnormalities in male and female reproductive tissues reduced the supply of photosynthates and poor production of growth regulators in sink tissues have been cited as explanations for poor fruit set in tomatoes at high temperatures (Kinet and Peet 1997).
24) **Reduction in fruit size and seeds/fruit**: At high temperatures, fewer ovules are fertilized and consequently the number of seeds/fruit is reduced considerably with a reduction of fruit size (El-Ahmadi and Stevens 1979a; Ansary 2006).
25) **Inhibition of pathogen induced resistance mechanisms**: Heat shock inhibits pathogen induced resistance mechanisms in plant hosts and induce susceptibility of tomato to root knot nematode caused by *Meloidogyne incognita* (Zacheo *et al.* 1995) and to *Ralstonia solanacearum* (Kuun *et al.* 2001).

PHYSIOLOGICAL MANIFESTATIONS RELATED TO HIGH TEMPERATURE STRESS

Oxidative metabolism and enzyme systems

Heat stress affected different forms of oxidative metabolism of tomato plants at 35°C for 30 days causing a decrease in shoot weight; accumulation of H_2O_2 in the leaf by inhibiting the ascorbate/glutathione cycle initially and then provoked an oxidative burst; increased superoxide dismutase (SOD) activity; decreased activities of different enzymes such as catalase (CAT), guaiacol peroxidase (GPX), ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR) and glutathione reductase (GR) which are associated with detoxifying H_2O_2; and increased levels of antioxidant compounds, like ascorbate (AsA), dehydroascorbate (DHA), oxidized glutathione (GSSG) and reduced glutathione (GSH) content (Rivero *et al.* 2004). Heat stress at 35ºC and above induces the accumulation of soluble phenolics in the tomato plant by activating their biosysthesis as well as inhibiting their oxidation and cause i) decrease in shoot weight, ii) reduced Fe uptake iii) highest phenylalanine ammonia-lyase (PAL) activity, iii) boosted superoxide dismutase (SOD) activity, iv) depressed activities of Fe-chelate reductase (FeCH-R), aconitase (Aco), guaiacol peroxidase (GPX), catalase (CAT) activity and iii) lowest peroxidase and polyphenol oxidase activity (Rivero *et al.* 2001, 2003a, 2003b). High Fe-superoxide dismutase (FeSOD) activity in the plants under heat or cold stress could be explained by a defensive response to heat or cold stress (Rivero *et al.* 2003b). Feussner *et al.* (1997) suggested that in plants, as in yeast, a certain subfamily of ubiquitin-conjugating enzyme (UBC) is specially involved in the proteolytic degradation of abnormal proteins as a result of heat and other stress after isolating a clone of a UBC from a lamda-ZAP cDNA library generated from mRNA of tomato cells grown in suspension for 3 days. The open reading frame, LeUBC1, encodes a polypeptide with a predicted molecular mass of 21370 Da, as confirmed by bacterial over-expression and SDS-PAGE and increase in LeUBC1 mRNA was detectable in response to heat shock.

Link *et al.* (2002) suggested that activation of 50 kDa mitogen-activated protein (MAP) kinase possibly regulate the heat stress response in tomato. Application of heat stress in a naturally occurring temperature resulted in a fast and transient activation of 50 kDa mitogen-activated protein (MAP) kinase both in photoautotrophic cell suspension culture and in leaves of mature plants. The heat activation of the MAP kinase was calcium dependent. The specific phosphorylation of tomato heat stress transcription factor HsfA3 by a purified preparation of the heat activated MAP kinase supports a physiological role of the identified kinase activity in transducing the heat stress signal.

Tomato cultivar resistant to root knot nematode (*Meloidogyne incognita*), VFN8 showed a temporary break of resistance under high temperature of 30ºC and above with an optimum at 34ºC. Heat induced susceptibility is associated with a reduced hypersensitive reaction, and that there is a correlation between hypersensitivity and reduced peroxide activity and lignin levels in the roots because of partial blocking of lignification at high temperature stress (Zacheo *et al.* 1995). Heat shock pulse induce significant accumulation of heat shock protein (Hsp70/Hsc70) which protect the pathogen (*Ralstonia solanacearum*)-activated phenylpropanoid pathway (PAL2-GUS activity, PAL (phenylalanine ammonia lyase) enzyme activity, lignin deposition), thus inhibits pathogen-induced resistance mechanisms in incompatible plant hosts, leaving the plant vulnerable to pathogen attack (Kuun *et al.* 2001).

Photosynthesis

Net photosynthesis in tomato was greatest at 28/20ºC day/night temperature in 12 hour photoperiod and transpiration was positively correlated with net photosynthesis but there was no consistent relationship between net photosynthesis and dark respiration (Jun *et al.* 1990). Heckathorn *et al.* (1998) reported that photosystemII electron transport of tomato plants was disturbed by stress of 42ºC for 6 hours and exposure of continuous mild heat stress (32-34º/22-26ºC day/night) may not have been high enough to depress photosynthesis. Feller *et al.* (1998), however, reported that Rubisco activity was inhibited via Rubisco activase inhibition under moderately high temperatures, 30 and 35ºC in cotton and wheat, respectively. In fact, photosynthetic rates under mild heat stress of 32/26ºC tended to be a little lower than under 28/22ºC in all the five lines, FLA 7156, Fresh Market 9, NC 8288, Piedmont and TH 318 differing in heat tolerance (Sato *et al.* 2000). High temperature stress reduced photosynthesis more in the heat-sensitive than in the heat-tolerant line 'Saladette' (Bar-Tsur 1977). In agreement to this findings, Jun *et al.* (1990) also reported that heat tolerant cultivar 'Moneymaker' showed the highest rate of net photosynthesis at high temperature regime of 33/20ºC day/night compared to the heat susceptible cultivar 'Roma'. This reduction in the CO_2 assimilation rate observed in the heat-sensitive cultivar 'Campbell-28' was generated by manipulating the Calvin cycle and also in the functioning of PSII while no changes in these parameters were observed in the thermotolerant genotype 'Nagcarlang' after the stress was imposed, and injury to the plasmalemma caused by heat stress was evident only in the heat-sensitive genotype (Camejo *et al.* 2005). Brazaityte (1999) also recorded that when daily irradiance was sufficient, the photosynthesis intensity as measured by CO_2 metabolism in the leaf chamber of some hybrids was limited by high temperatures above 35°C. Heat led to a sun-type adaptation response of the photosynthesis pigment apparatus for the heat-tolerant genotype and thus an increase in the chlorophyll *a*/*b* ratio and a decrease in the chlorophyll/carotenoid ratio were shown in the heat-tolerant genotype under stress (Camejo *et al.* 2005). It was recorded earlier that the heat-tolerant cultivar 'Shuki' is a better biomass or carbohydrate producer than the non-heat-tolerant cultivar 'Sataan' (Nkansah and Ito 1994). Carbohydrate metabolism and/or translocation may also explain high temperature effects observed during the post-anthesis period. Pollen tube elongation has a high energy requirement. It was observed in kiwifruit that starch reserves in stylar tissue gradually disappeared and carbohydrate secretion occurred as the pollen tube passed through the pistil Gonzalez *et al.* (1996) which suggests that pollen tube elongation relies on carbohydrate supplies secreted by the pistil. A short period of relief from high temperature stress of 32/26ºC increased fruit set which might have happened due to increased availability of carbohydrates for pollen tube elongation effecting fertilization (Sato *et al.* 2002).

Pollen development

In tomato, meiosis in both mega and microspore mother cells, which took place 8-9 days before anthesis, was very sensitive to high temperature (Iwahori 1965, 1966) however, microsporogenesis was more sensitive to moderately elevated temperatures of 32/26ºC day/night than megasporegenesis and post-anthesis process (Peet *et al.* 1998; Firon *et al.* 2006). Microspore meiosis takes place about 9 days before anthesis (Picken 1984), and differentiation of stomium, tapetum, middle layers and endothecium occurs before meiosis (Goldberg *et al.* 1993). Differentiation process of those organs are sensitive to high temperature stress affecting pollen viability and release adversely since stomium is important for anther dehiscence (Koltunow *et al.* 1990) and the tapetum, middle layers and endothecium supply carbohydrate for pollen development. Pollens grains develop in the anther and are initially surrounded by the tapetum layer which mediates growth and nutrition, mainly in the form of sugars (Pacini 1996). The sugars are absorbed through the apoplast and may be either metabolized immediately, or stored as starch in amyloplasts. Pacini and Viegi (1995) have shown in tomato that starch is stored in amyloplasts during development but the mature pollen grains are starchless. It was also concluded from an ultra-structural study of pollen development in tomato, that starch is synthesized in the early stage of pollen development but it is missing in the mature pollen grain (Polowick and Sawhney 1993). High temperature stress has great influence on pollen sugars. The major effect of continuous exposure of the plants to high temperatures (32/26ºC day/night) on pollen development is a decrease in starch concentration 3 day before anthesis, which results in a decreased sugar concentration in the mature pollen grains (Pressman *et al.* 2002). In all the heat sensitive cultivars, the heat stress (32º/26ºC day/night in green house) caused a marked reduction in starch concentration in the developing pollen grains at 3 days before anthesis, and a parallel decrease in the total soluble sugar concentration in the mature pollen, where as in the heat tolerant cultivars, starch accumulation at 3 days before anthesis and soluble sugar concentration at anthesis were not affected by heat stress which indicate that the carbohydrate content of developing and mature pollen grains may be an important factor in determining pollen quality, and suggest that heat tolerant cultivars have a mechanism for maintaining the appropriate carbohydrate content under heat stress (Firon *et al.* 2006). Such changes were associated with inhibition of acid invertase and starch synthase while ADP-glucose pyrophosphorylase were not affected by the heat stress (Sheoran and Saini 1996). Aloni *et al.* (2001) concluded that inability to metabolize sucrose to hexoses might be the key factor causing pollen malfunction under high temperature stress. Impaired biosynthesis of polyamines like spermidine and spermine contents in pollen particularly due to the low activity of *S*-adenosylmethionine decarboxylase (SAMDC), probably due to impaired protein synthesis or functional enzyme formation, is the major cause for the poor performance of tomato pollen at high temperatures while arginine decarboxylase activity is little influenced by high temperature stress (Song *et al*. 2002).

Hormonal factors

Different hormonal factors are also related to high temperature stress. Auxin and gibberellic acid content were reduced in plants in the glasshouse under high temperatures with an increase in proline content (Muthuvel *et al*. 1999). Auxin production is reduced with a simultaneous high level of abscissic acid in the plant at high temperatures, which favours premature senescence and abscission of reproducetive organs (Iwahori 1967; Levy *et al*. 1978; El-Ahmadi and Stevens 1979a). High temperature stress also suppresses ethylene production (Johjima 1995; Inaba *et al*. 1996; Lurie *et al*. 1996) causing impaired ripening of fruits.

Fruit ripening

High temperature inhibits fruit ripening and fruit colour deteriorates by inhibiting the accumulation of ripening-related mRNAs and ripening processes that depend on continuous protein synthesis, ethylene production, high respiration rate, reduction in carotene synthesis, lycopene accumulation, and cell-wall dissolution, which are all diminished under high temperatures, i.e. 32°C and above (Johjima 1995; Inaba *et al*. 1996; Lurie *et al*. 1996) and at 40ºC, there was no disappearance of green surface colour with no significant C_2H_4 production (Inaba *et al*. 1996). Uneven ripening and softness are also two major defects caused due to high temperature stress (Adams and Valdes 2002; Mulholland *et al*. 2003). Masarirambi *et al*. (1996) also found that tomato fruit ripening was reversibly inhibited at high temperatures due to less production of ethylene, and by increasing the duration of ethylene/high temperature treatment to 48 or 72 h at 35° or 40°C inhibited subsequent red colour development at 20°C, while prior exposure to 30°C stimulated colour development, which suggested that tomatoes were affected by ethylene at high temperatures, but were slow to respond in terms of colour development until transferred to a lower temperature. Similarly, El-Otmani (1995) suggested that exposing tomato fruits to a short period of high temperatures delayed subsequent fruit ripening without affecting the quality.

Fruit quality characters

Of the five climatic factors recorded, temperature was predominantly implicated in affecting tomato fruit quality and the fruits that matured during summer under high temperatures showed a higher accumulation of organic and ascorbic acid with the shortening of crop duration while the fruits that matured during winter to spring under optimum temperature conditions were firmer, had higher soluble sugars, and a longer growing period for consumption, marketing and transportation, fruits should be harvested around 1000°C days from flowering to maturation (Islam and Khan 2000). From a detailed study employing 44 genotypes it was recorded that total soluble solids (TSS) and total sugar content of the fruits was not much affected by high temperature stress, mean ascorbic acid content in fruits was reduced from 24.39 mg/100 g in autumn-winter to 20.35 mg/100 g in the fruits produced in spring-summer and mean lycopene content in the fruits was reduced from 2.45 mg/100 g fresh in autumn-winter to 2.02 mg/100 g in spring-summer under high temperature condition (Ansary 2006).

GENETIC VARIABILITY AND SELECTION INDICES FOR TOLERANCE TO HIGH TEMPERATURE

Different studies recorded wide variability among the different genotypes for important characters viz., the number of aborted fruits, the number of ripened fruits per plant, mature fruit weight, soluble solids content, fruit firmness and colour, etc. under high temperatures linking depicting tolerance to high temperature enabling selection of lines with high fruit-set character under high temperature conditions (Noda and Machado 1992; Giordano *et al*. 2005; Brar *et al*. 2005; Ansary 2006). Heritability estimates play an important role in predicting genetic gain by selection of superior segregates or progenies. High and medium to high heritability at high temperature was recorded for a number of flowers (El Ahmadi and Stevens 1979a; El-Hassan 1985) and stigma exertion (El-Ahmadi and Stevens 1979a). However, Villareal and Lai (1979) reported that heat tolerance exhibited low heritability and that expression of genes for heat tolerance was influenced by the environmental conditions, particularly temperature and atmospheric humidity because some accessions which appeared heat-tolerant in one trial were not as heat-tolerant in another trial.

Narrow-sense heritability for fruit set traits were low, 0.31 for percentage of fruit set; 0.28 for mean fruit number per cluster; and 0.53 for flower number per cluster (Hanson *et al*. 2002) and in conformity to these findings narrow-sense heritability in another study recorded were 0.63 for pollen viability, 0.46 for pollen germination, 0.44 for flower/cluster, 0.54 for fruit set/cluster, 0.37 for fruits/plant (Ansary 2006) while a high heritability estimate in a limited sense was recorded for fruit characters under high temperature condition in other investigations (Sherif and Hussein 1992; Grilli *et al*. 2003).

Different sets of correlations and path analyses in several studies suggested a different set of characters as important selection indices for high temperature tolerant genotypes viz., stigma position (Rick and Dempsey 1969), fruit setting score and fruit development (Raijadhav *et al*. 1996), release of number of pollen grains (Sato *et al*. 2000), pollen viability (Silva *et al*. 2000), flowers per plant, fruits per plant, yield per plant, proline content, auxin and gibberellin levels (Muthuvel *et al*. 2000), fruits/plant, fruits/cluster, percent fruit set and pollen viability (Dhankar *et al*. 2001), flower trusses/plant, flower truss, pollen viability and pollen germination percentage (Ansary 2006). Fruit yield under high temperatures is negatively correlated with cell membrane injury as depicted by electrical conductivity (Dhankar *et al*. 2001). Pollens of the tomato cultivar Campbell 28 and the wild Nagcarlan (*Lycopersicon esculentum* var. *cerasiforme*) were exposed to different temperatures of 40, 45, 50, 55 and 60ºC for 90 min before germination and 30 and 35ºC for 60, 90, 120 and 180 min at germination *in vitro* and the greatest differentiation in pollen germination was noted after treatments of 45ºC for 90 min before germination and of 35ºC for 60 and 90 min at germination which opened up the possibility for gametophytic selection of high temperature and the establishment of screening method against heat stress (Alvarez *et al*. 1994). High temperature and the plants produced as a result of the pollination with heated pollen were more heat resistant in comparison with those produced by pollination with normal pollen (Graty *et al*. 1996). Anyway, it emerged beyond doubt that for many species like tomato, that reproductive processes appear to be much more sensitive to temperature stress than vegetative growth (Sato *et al*. 2002) and for this reason, the top three characters that contribute to maximum genetic divergence in high temperature growing conditions are pollen germination, style length and pollen viability (Ansary 2006).

SCREENING OF THE GENOTYPES FOR HEAT TOLERANCE

Heat tolerant genotypes possess an inherent ability to set fruits under high temperatures but obviously to a lesser extent, decreasing by 60 to 83% at a day/night temperature of 40º/25ºC (Cheema *et al.* 1993), 45% to 65% at a day/night temperature of 35º/23ºC (Abdul-Baki and Stommel 1995) and 40 to 45% at a day/night temperature of 34.3ºC/19.2ºC (Ansary 2006). Great variation exists among genotypes in their ability to flower and set fruit under high temperatures. Some genotypes set fruit, produce normal flowers, show high photosynthetic activity and better pollen germination under high temperature conditions (**Table 1**).

Table 1 Reaction of different tomato genotypes to heat stress

Heat tolerant genotypes	Reference
OK-7-2, OK-7-3	Amuti 1971
Punjab Tropic, Marzano, Avalanche, P-4	Nandpuri *et al.* 1975
Nagcarlang, Breeding line 165	Shelby 1975
Chico III, Merit, C 28, Red Rock	Stoner and Otto 1975
Saladette, BL 6807, PI 262934, CIAS 161	Bar Tsur 1977; El-Ahmadi 1977
Nagcarlang	Villareal and Lai 1979
Vivid, Pink Vogue, VF 10, CR 1324, VF 145 F5, 598891 (USA); KFh 1738, Ventura PS (Hungary; Delta 10, State Farm Favourite (USSR)	Ivakin and Popova 1978
AU 165, Nagcarlang	Shelby *et al.* 1978
L 125, L 226, L 232, L 2972, L 3690	Villareal *et al.* 1978
L. pimpinnellifolium	Villareal and Lai 1979
HS-102	Arora *et al.* 1981
Volgogradishii 5/95	Ivakin 1981
BL 6807, S 6916, CL 9-0-0-1, Saladette	Hanna and Hernandez 1982
Caro Red, Vitamin	Kalyagina and Pugachev 1982
Saladette	Shen and Li 1982
Cold set, Hot set, Early Subarctic	Tarakanov and Andreeva 1982
200, 202, 178 D	Alpatev *et al.* 1983
Pelican, Tropic, Caraibe, Savarian, L 567, L 569, L 571, L 573	Hernandez *et al.* 1983
Salyut, Belosnezhka	Dobrenkova and Lukyanenko 1984
Kross 525, Veeroma, Olimpiets	Tkacheva 1984
S 6916, Saladette, CL1, Burgess	Byari 1985
L 72, HC 108	Gomez *et al.* 1985
Nistru, Fakel	Kravchenko *et al.* 1987
CL 5915, 222 D4 0-4-0, CL 5915-229, D4 1-5-0, CL 5915-299, D4 –1-1-0	Sajjapongse 1987
L. glandulosum, *L. pimpinnellifolium, L. esculentum* var. *cerasiformae*	Paskal and Kravchenko 1987
Saladette, Ohio 7663, BL 6807, Chico III	Berry and Rafiqueuddin 1988
Solar Set	Scott *et al.* 1989
Likurich, Meridian, Nistru, Victorina	Kireeva *et al.* 1989
Taichung Asveg 4 (F1 hybrid)	Lin and Hong 1989
Swift, AC 362	Reddy *et al.* 1989
3-31A-B1-2B, S111, B200	Santipracha 1994
Shuki	Nkansah and Ito 1994
Moneymaker and Red Cherry	Johjima 1995
Neptune	Scott *et al.* 1995
HTT 29, HTT 34, HTT 62, HTT 95	Mohamed 1997
BT 1	Phookan *et al.* 1997
Nagcarlang, Mex-12, P1410 and L10-3	Florido *et al.* 1999
LE 1253, LE 1258, LE 1259 and LE 1265	Muthuvel *et al.* 2000
CL 5915	Silva *et al.* 2000; Hanson *et al.* 2002
Amalia, Nagcarlang	Camejo and Torres 2001
EC339356 and EC339357, and Selection-7 and -18	Dhankar and Dhankar 2002
L 3960, LE 79, SEL.120, L-4139, CL-32-0-19-0-0, CL-143-0-4-B-0-0, CL-143-0-10-3 , L-125	Patgaonkar *et al.* 2003
FLA 7156	Sato *et al.* 2000, 2004
Amalia	Alvarez *et al.* 2004
Sonali, Hotset, Kewalo, Saladette, NDTVR-60	Nainar *et al.* 2004
Viradoro, Santa Clara	Giordano *et al.* 2005
UC-82B, N-SummerSet	Brar *et al.* 2005
Nagcarlang	Camejo *et al.* 2005
CLN B, CLN R (selection from CLN lines from AVRDC)	Ansary 2006

GENETIC CONTROL OF IMPORTANT CHARACTERS UNDER HIGH TEMPERATURE STRESS

The genetics of fruit set at high temperature in tomato is not clearly understood however, prominent genotype × environment interaction and variation in character expression in genetic populations under high temperatures in different studies suggest the involvement of polygenes in the control of heat tolerance in tomato (Rick and Dempsey 1969; El-Ahmadi and Stevens 1979b; Raijadhav *et al.* 1996; Dhankar *et al.* 2002; Grilli *et al* 2003; Ansary 2006). The importance of dominance gene action for different characters influencing heat tolerance viz., flower/truss, fruit set/truss, flower drop/truss, pollen viability, pollen germination, fruits/plant and fruit weight has been recorded in different studies (Raijadhav *et al.* 1996; Dhankar and Dhankar 2002; Ansary 2006) and at the same time, conditioning of over-dominance for flower cluster/plant and pollen viability (Ansary 2006) and yield/plant (El-Ahmadi and Stevens 1979b) at high temperatures amply suggested the importance of a non-additive genetic system for the expression of the characters influencing heat tolerance. On the other hand there are reports on the preponderance of additive gene action for flower drop (Hanna *et al.* 1983) and percent fruit set (El-Ahmadi and Stevens 1979a) at high temperatures which also deserves due attention during framing of breeding strategies.

Hanson *et al.* (2002), in studies with the heat tolerant parent CL5915 for fruit set and fruit yield recorded complete dominance with the involvement of some epistatic component for heat tolerance while incomplete dominance in the direction of increasing fruit set percentage at high temperatures emerged from another investigation (Grilli *et al.* 2003). In yet other investigation, fruit set in four out of six "heat tolerant" × "heat tolerant" cross combinations indicated the possible involvement of epistatic components of genetic variance for the expression of characters under high temperatures (Ansary 2006). However, several reports depicting the involvement of partial dominance for the control of fruit set components under heat stress (Shelby *et al.* 1978; El-Ahmadi and Stevens 1979a; Opena *et al.* 1989; Ansary 2006) indicate the possibility of developing heat-tolerant genotypes through a combination breeding approach, i.e. hybridization between selected parents followed by selection to develop a suitable line.

The position of the stigma, which is directly related to fruit set in high temperatures is determined by few genes but influenced by environmental factors particularly temperature and atmospheric humidity (Rick and Dempsey 1969), and El-Ahmadi and Stevens (1979a) suggested that, since the genetic variance for stigma exsertion is largely additive (Chen and Tanksley 2004), selection for low stigma protrusion could be effective and rapid. High temperature not only has a direct effect on tomato plants, but also enhances their disease tolerance (Sato *et al* 2004).

FRAMING OF BREEDING STRATEGY

The physiological causes of fruit set reduction in heat-tolerant lines must be understood to improve heat tolerance and to address those constraints though breeding. The upper limit of heat tolerance in heat-tolerant lines should be fully characterized before using them in combination breeding programmes.

Different researchers suggested different breeding methods like, reciprocal recurrent selection (Villareal and Lai 1979), recurrent selection followed by modified single seed descent (El-Hassan 1985), simple selection, hybridization and recurrent selection (Dhankar *et al.* 2002), pure line and hybrid breeding (Cheema *et al.* 2003) and pedigree method of breeding (Alvarez *et al.* 1994) for the improvement of heat tolerant attributes in tomato. However, the major hindrance for realizing genetic gain is the revelation of low heritabilities for most of the characters which implies that single plant selection in the F_2 for heat tolerance will not be effective and the F_3 lines derived from heat-tolerant F_2 may not necessarily be heat-tolerant which is probably due in part to a reduction in dominance effects associated with increased inbreeding (Hallauer and Miranda 1981). Low- and medium-range narrow sense heritability for flower/cluster, pollen germination, percentage of fruit set and fruits/plant under high temperatures (Hanson *et al.* 2002; Ansary 2006) implied that single plant selection in the F_2 for heat-tolerance from crosses involving a heat-tolerant genotype like CL5915 will not be effective and that selection should be based on replicated family testing in the F_3 and later generations (Hanson *et al.* 2002). On the other hand, a high heritability estimate in a limited sense emanating from another investigation suggested that the selection of individuals based on evaluation of characters can be efficient (Grilli *et al.* 2003). Such variation might have happened due to different set of genotypes under study and variation in the environmental exposure hence, the resistant lines must be tested in as many environmental conditions as possible to determine their range of adaptation (Villareal and Lai 1979).

Good cross combinations showing heat tolerance involved one parent with high GCA and the other with poor GCA effects (Brar *et al.* 2005) and in agreement with this finding a heat tolerant cultivar L72 was earlier developed by selecting for heat tolerance among progeny from the cross between heat-tolerant genotype 'Summertime' and heat susceptible genotype 'Campbell 28' (Gomez *et al.* 1988). However, with a view to overwhelming importance of dominance genetic variance for the conditioning of different fruit set characters under high temperatures and because of large negative genetic correlation between heat tolerance and fruit size (Wessel-Beaver and Scott 1992) heterosis breeding to develop heat tolerant hybrids possessing better fruit size and quality may be the best strategy (Cheema *et al.* 2003; Ansary 2006).

HEAT-INDUCIBLE GENE, HEAT SHOCK PROTEIN AND TRANSGENIC TOMATO

The drought-inducible DS2 genes of potatoes are members of the ASR (abscisic acid, stress and ripening) gene family and DNA and RNA gel blot analysis revealed the presence of a gene highly homologous to the potato gene StDS2 in tomato (LeDS2) with the same desiccation-specific expression in leaves and organ specific expression in flowers and green fruits which also suggests a narrow species-specificity and late evolution of the DS2-type genes within the family Solanaceae (Doczi *et al.* 2005).

Heat shock response is universal and many heat shock protein (Hsp) genes are highly conserved in all organisms and characteristics of such genes identified in tomato are reviewed. Sun *et al.* (1996) obtained a heat shock gene from tomato, hsc70 genomic clone (Lehsc70-3; *L. esculentum* heat shock cognate 70-3) by screening a genomic library with the tomato Lehsc70-2 cDNA. Two restriction fragments of 2.6 and 5.0 kb, which compose the Lehsc70-3 gene, were subcloned into pBluescriptIIKS+ and analysed. Transcript mapping reveals that the mature Lehsc70-3 mRNA contains a 122-nt 5′ untranslated region (UTR), a coding region of 1956 nt corresponding to a polypeptide of 651 amino acids, an intron of 717 nt and a 3′ UTR. High temperature treatment (37°C) caused a two-fold increase in the level of Lehsc70-3 mRNA. However, Lehsc70-3 mRNA was expressed at substantial levels in the vegetative tissues of tomato plant, suggesting a general function of this hsc70 gene in tomato. Kuun *et al.* (2001) also reported that heat shock pulse induce the accumulation of heat shock proteins, specially the 70-kDa heat shock protein (Hsp70-inducible/Hsc70-constitutive). Small heat shock proteins (sHsps) are the major family of Hsp induced by heat stress in plants. Approximately 1.9 kb of Lehsp23.8 5′-flanking sequence was isolated from tomato genome and by using the β-glucuronidase (GUS) reported gene system, the developmental and tissue specific expression of the GUS gene controlled by Lehsp23.8 promoter was characterized in transgenic tomato plant (Yi *et al.* 2006). Liu *et al.* (2006) re-ported a novel Hsp gene, Hsa32, which encodes a heat shock associated 32 kDa protein. Hsa32 cDNA was isolated from a subtractive library prepared from tomato heat shock induced versus control mRNA and unlike the multigene families of many well characterized Hsps, only one copy of Hsa32 exists in the tomato genome as shown by Southern blot. Sun *et al.* (2006) identified a heat inducible filamentation temperature-sensitive H (ftsH) like gene from tomato. Because the protein structure was highly homologous to *Arabidopsis* AtFtsH6, the cloned tomato ftsH like cDNA was named LeftsH6. No LeftsH6 expression was detected after cold, salt, drought or light stress challenges. Heat shock elements (HSEs) were identified in the 5′-flanking sequence of LeftsH6, which specially bound heat shock factor (HSF) HsfA2 from tomato as determined by electrophoretic mobility shift assay (EMSA) analysis. Subsequently, transgenic tobacco plants carrying the GUS gene driven by the LeftsH6 promoter were generated. High levels of heat induced GUS staining were detected in the leaves, roots and flowers of the transgenic plants. The ovaries, stigmas, anthers, and sepals in the flowers at various developmental stages as well as the pollen grains of mature anthers showed strong heat induced GUS staining.

Expression of heat shock protein (Hsp family) is increased as evidenced by increased accumulation of class I and II sHSP mRNAs in tomato fruits following treatments by methyl jasmonate and methyl salicylate (Ding *et al.* 2001). The effect of salicylic acid on the expression of 70 kDa heat shock proteins (Hsp70/Hsc70) in tomato under normal and elevated temperatures were investigated using biometabolic labeling and Western blotting and its relation to membrane integrity was considered. A dose and time dependent influence was observed, where short exposure to high levels of salicylic acid potentiated heat-induced Hsp70/Hsc70 accumulation, while longer exposure to moderate to high levels of salicylic acid first induced Hsp70/Hsc70 and thereafter suppressed heat shock protein induction (Cronje and Borman 2006).

The tomato MT-sHSP gene, which expresses a small heat shock protein was introduced under the control of the 35S promoter into tobacco (*Nicotiana tabacum*), to examine the thermo-tolerance of the transformed plants. Irrespective of the orientation, sense or antisense, of the gene, the transgenic plants exhibited a normal morphology and growth rate in the vegetative growth stage. When 4-week-old seedlings were exposed to sudden heat stress, the sense plants which over-expressed the MT-sHSP gene exhibited thermotolerance, whereas the antisense plants in which the expression of the gene is suppressed exhibited susceptibility (Sanmiya 2004). Transgenic tomato line was also developed that over-expressed tomato MT-sHSP gene to study the role of MT-sHSP gene in imparting tolerance to high temperature to the vegetative part an dit aws assumed that MT-sHSP gene is just not expressed by plants under has shock, but has a unique function involved in thermotolerance (Nautiyal *et al.* 2005). Tomato plants tolerant to high temperature stress have also been developed with a transgenic heat shock factor (the HSF gene). Tomato plants from cultivar MP-1 were transformed with a chimeric 35S::AtHSF-GUS gene (containing the heat shock factor from *Arabidopsis thaliana*, AtHSF, fused to GUS and driven by the 35S promoter) and the transgenic plants were more resistant to both high and low temperature stress (Lurie *et al.* 2003). Hence, constitutive expression of the AtHSF-GUS gene improves resistance to both high and low temperature stresses. The heat shock protein (HSP21) plays a role in plant development under normal growth conditions, in addition to its protective effect under stress conditions (Neta *et al.* 2005).

CONCLUSIONS AND PERSPECTIVES

Poor fruit set of tomato induced by high temperature stress is a major cause of low yield in the tropical and subtropical part of tomato growing areas of the world. Development of heat tolerant tomato lines has been a major objective in tomato breeding and biotechnology particularly in the perspective of global warming causing yield declines in many crops including tomato at temperatures only slightly above optimal. Although, heat stress causes reduced yield in tomato mainly by affecting male gametophyte development yet the heat tolerant genotypes do not respond to high temperature in a single general pattern. Several characteristics viz., high number of flowers per plant, absence of stigma exsertion, substantial pollen production, adequate pollen viability and release from anther and fruit set would be essential for optimum heat tolerance. A line that possesses all the model traits should perform exceptionally well at high temperature however, carbohydrate imbalance and disturbed microsporogenesis which are the underlying cause of poor pollen viability and pollen release and concomitantly poor fruit set must be properly addressed to frame the breeding strategy. At the same time, 8-13 days before anthesis, the most sensitive period to moderately elevated temperature stress must have the focus while screening or developing the heat tolerant lines. The heat tolerant lines must be retested in as many environmental conditions as possible to determine their range of adaptation before employing in the breeding programme. The physiological causes for fruit set reduction in heat-tolerant lines must be understood to improve heat tolerance and to address those constraints through breeding.

It would be more effective if selection for high temperature tolerant lines is based on the replicated family testing in the F_2 and other advanced generations. In conventional breeding approaches, hybrids specifically targeted for high temperature tolerance offer the best chance of overcoming the constraints related to elevated temperature condition. Different molecular breeding approaches e.g. QTLs related to heat tolerance, molecular markers in the quantification of heat tolerance, isolation and characterization of the genes encoding novel heat-shock proteins open new vistas in enhancing thermotolerance in tomato through biotechnological interventions.

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