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

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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 13°C for proper fruit set in tomato had been recorded much earlier and this phenomenon was termed thermodormancy. Later, it had been well documented through studies in the phytotron that a reduction in night temperature in the range of 15°-20°C markedly increased the biological and commercial 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 29°C, fruit number, fruit weight per plant and seed number per fruit decreased markedly compared with those at 25°C. Average night temperature of 19.2°C in the spring-summer season remained just below the upper critical limit of 15°C to 20°C as suggested by Went (1950) however, a huge reduction in fruit set in this season under an average daily mean temperature of 26.8°C 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 25° and 30°C (Khavari-Nejad 1980), and optimal daily mean temperatures for fruit set and satisfactory fruit yield of tomato have been reported as 21°-24°C (Geisenberg and Stewart 1986), 22°-25°C (Peet and Bartholomew 1996), 22°-26°C (Sato et al. 2000), 21.3°C with an average day/night temperature of 27.3°C/15.1°C (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, many authorities considered it as a complex trait (Berry and Gould 1979; El Ahmad 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 than although tomato plant can grow under a wide range of temperatures, fruit production was limited by high daytime temperatures above 32°C and especially by high night-time temperatures above 21°C (Moore and Thomas 1952). Reports of high temperature stress causing marked reduction in anthesis, blossom drop and fruit set for tomato are 30°C and 45°C (Iwahori and Takahashi 1963), as little as 4 hour exposure to 40°C during flowering (Bar-Tsur 1977), above 26°/20°C day/night and severely above 35°/26°C day/night (El Ahmad 1977), day temperature above 32°C during summer (Kaloo 1988), 35°/23°C day/night (Abdul-Baki and Stommel 1995), at 35°/30°C (Lohar and Peat 1998), at 32°/26°C day/night temperature (Sato et al. 2000), 38°/22°C day/night (Dhankar et al. 2001) and at an average of 34.3°/19.2°C day/night temperature, average daily mean temperature being 26.8°C (Ansary 2006). However, plants are most sensitive to moderately elevated temperature of 32/26°C 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 endothecium, lack of opening of the stamium, 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, abscisic 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 33.0°C/23.0°C 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 34.3°C/19.2°C day/night temperature (Ansary 2006). El-Ahmad and Stevens (1979a) also recorded bud drop at 38°C/27°C 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 (Segner et al. 1994; Bertin 1995). However, differences between tomato cultivars in rates of abscission under moderately elevated temperatures of 32/28°C 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 of NC8288, FM-9 and FL 7156 differing in heat tolerance were exposed to mild heat stress (31/25 vs. 28/22°C) 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. 1998)

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; Hana and Hernandez 1982; Ansary 2006) however, splitting of antheridial cone is genotype-dependent (Phoikan 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-Ahmad 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 endothelial 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 (Leyv 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 antherial 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 o- vules 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 tempera- ture stress (Abdul-Ikki 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-Ahamadi 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 38.27°C day/night (El-Ahamadi and Stevens 1979a) and to 24.4% from 66.9% at 34.5°C/19.2°C 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 characteris- tics.

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; Mathuvel 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 for- mation:** 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 pol- len production:** Starch reserves stored during pollen development give rise to soluble sugars at maturity and deficiency in carbohydrate metabolism in the tomato an- thers resulting in decreased starch concentration in pol- len grains leads to abnormal pollen development under high temperature (Bhadula and Sawhney 1989; Press- man et al. 2002; Firon et al. 2006). However, total soluble protein 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:** Un- developed flowers remaining on the plant without deve- loping further under high temperature stress is related to reduced carbohydrate availability for the development of the fruits (Sato et al. 1999, 2001, 2004).

22) **Reduced total soluble protein content:** Heat suscepti- bility 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:** De- velopmental abnormalities in male and female repro- ductive 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 (Kinnet and Peet 1997).

24) **Reduction in fruit size and seeds/fruit:** At high tempe- ratures, fewer ovules are fertilized and consequently the number of seeds/fruit is reduced considerably with a re- duction of fruit size (El-Ahamdi and Stevens 1979a; An- sary 2006).

25) **Inhibition of pathogen induced resistance mecha- nisms:** 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 solana- cearum (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 H2O2 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 H2O2; and increased levels of antioxidan-t compounds, like ascorbate (AsA), dehydroascorbate (DHA), oxidized glutathione (GSSG) and reduced glutathi- one (GSH) content (Rivero et al. 2004). Heat stress at 35°C and above induces the accumulation of soluble phenolics in the tomato plant by activating their biosynthesis 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 dismu- tase (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,
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). FeSOD activity was positively correlated with net photosynthesis but there was a decrease in the chlorophyll a/b ratio and a decrease in the chlorophyll/carotenoid ratio were shown in the heat-stressed plants (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 stigmas and stamen tissue gradually disappear. Thus, 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, microprosperogenesis was more sensitive to moderately elevated temperatures of 32/26ºC day/night than megasporegenESIS 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 stigmata, 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 stigmata 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 Vieggi (1995) have shown in tomato that starch is stored in amyloplasts during development but the mature pollen grains are starchless. It was 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 decreased availability of carbohydrates for pollen tube elongation (Pressman et al. 2002). In all the heat sensitive cultivars, the heat stress (32ºC6ºC 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 in the mature pollen grains 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 stigmas and stamen tissue gradually disappear. Thus, increased availability of carbohydrates for pollen tube elongation effecting fertilization (Sato et al. 2002).

**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 photosystem II 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 tolerance could be correlated at high photosynthesis at 30ºC day/night compared to the heat susceptible cultivar ‘Roma’. This reduction in the CO2 assimilation rate observed in the heat-sensitive cultivar ‘Campbell-28’ was generated from mRNA of tomato cells grown in a poly peptide 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 peroxidase 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 (Ralsstonia 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).

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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 reproductive 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 deterioration 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 40°C, there was no disappearance of green surface colour with no significant C₃H₄ 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 delaying 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 a shorter period of days 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; Rafiuddin et al. 2001). Studies reported a negative correlation between proline content and yield of fruits. When plants of the wild Nagcarlan (Lycopersicon esculentum var. cerasi-forme) were exposed to different temperatures of 40, 45, 50, 55 and 60°C for 90 min before germination and 30 and 35°C for 60, 90, 120 and 180 min at germination in vitro and the greatest differentiation in pollen germination was noted after treatments of 45°C for 90 min before germination and of 35°C for 60 and 90 min at germination which opened up the possibility for gametophytic selection of high temperature tolerant genotypes for biomass at high temperature 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).

**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, 0.44 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 (Rajadhav et al. 1996), release of number of pollen grains (Satô 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 of the wild Nagcarlan (Lycopersicon esculentum var. cerasi-forme) were exposed to different temperatures of 40, 45, 50, 55 and 60°C for 90 min before germination and 30 and 35°C for 60, 90, 120 and 180 min at germination in vitro and the greatest differentiation in pollen germination was noted after treatments of 45°C for 90 min before germination and of 35°C for 60 and 90 min at germination which opened up the possibility for gametophytic selection of high temperature tolerant genotypes for biomass at high temperature 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 (Satô 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 ex-
Programmes. Characterized before using them in combination breeding, mit of heat tolerance in heat-tolerant lines should be fully understood to improve heat tolerance and 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).

**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; Rajiadhab 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 (Rajiadhab 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 characters under high temperatures (Ansary 2006). However, several reports discussing 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 exertion 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 (Villarel 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 heterothallic genotypes under high temperature conditions (Table 1).

<table>
<thead>
<tr>
<th>Heat tolerant genotypes</th>
<th>Reference</th>
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<tbody>
<tr>
<td>OK-7-2, OK-7-3</td>
<td>Amuti 1971</td>
</tr>
<tr>
<td>Punjab Tropic, Marzano, Avalanche, P-4</td>
<td>Nandpur et al. 1975</td>
</tr>
<tr>
<td>Nagarcarlang, Breeding line 165</td>
<td>Shelby 1975</td>
</tr>
<tr>
<td>Chico III, Merit, C 28, Red Rock</td>
<td>Stoner and Otto 1975</td>
</tr>
<tr>
<td>Saladette, BL 6807, PI 262934, CIAS 161</td>
<td>Bar Tsur 1977; El-Ahmadi 1977</td>
</tr>
<tr>
<td>Nagarcarlang</td>
<td>Villarel and Lai 1979</td>
</tr>
<tr>
<td>Vivid, Pink Vogue, VF 10, CR 1324, VF 145 F5, 598891 (USA); KF 1738, Ventura PS (Hungary); Delta 10, State Farm Favourite (USSR)</td>
<td>Ivkin and Popova 1978</td>
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<tr>
<th>Table 1 Reaction of different tomato genotypes to heat stress</th>
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<tr>
<td>Heat tolerant genotypes</td>
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<tr>
<td>-------------------------</td>
</tr>
<tr>
<td>AU 165, Nagarcarlang</td>
</tr>
<tr>
<td>L 125, L 226, L 232, L 2972, L 3690</td>
</tr>
<tr>
<td>L. pimpinellifolium</td>
</tr>
<tr>
<td>HS-102 Volgogradskii 5/95</td>
</tr>
<tr>
<td>BL 6807, S 6916, CL 9-0-0-1, Saladette</td>
</tr>
<tr>
<td>Caro Red, Vitamin</td>
</tr>
<tr>
<td>Saladette</td>
</tr>
<tr>
<td>Cold set, Hot set, Early Subarctic</td>
</tr>
<tr>
<td>200, 202, 178 D</td>
</tr>
<tr>
<td>Pelican, Tropic, Caraiabe, Savarian, L 567, L 569, L 571, L 573</td>
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<tr>
<td>Salyut, Belosnezzika</td>
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<tr>
<td>Kross 525, Veeroma, Olimpiets</td>
</tr>
<tr>
<td>S 6916, Saladette, CL 1, Burgess</td>
</tr>
<tr>
<td>L 72, HC 108</td>
</tr>
<tr>
<td>Nistru, Fakel</td>
</tr>
<tr>
<td>CL 5915, 222 D4 0-4-0, CL 5915-229, D4 1-5-0, CL 5915-299, D4 1-1-0</td>
</tr>
<tr>
<td>L. glandulosum, L. pimpinellifolium, L. esculentum var. cerasiforme</td>
</tr>
<tr>
<td>Saladette, Ohio 7663, BL 6807, Chico III</td>
</tr>
<tr>
<td>Solar Set</td>
</tr>
<tr>
<td>Likurich, Meridian, Nistru, Victorina</td>
</tr>
<tr>
<td>Taichung Asveg 4 (F1 hybrid)</td>
</tr>
<tr>
<td>Swift, AC 362</td>
</tr>
<tr>
<td>3-31A-B1-2B, S111, B200</td>
</tr>
<tr>
<td>Shuki</td>
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<tr>
<td>Moneymaker and Red Cherry</td>
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<tr>
<td>Neptune</td>
</tr>
<tr>
<td>HTT 29, HTT 34, HTT 62, HTT 95 BT 1</td>
</tr>
<tr>
<td>Nagarcarlang, Mex-12, P1410 and L10-3</td>
</tr>
<tr>
<td>LE 1253, LE 1258, LE 1259 and LE 1265</td>
</tr>
<tr>
<td>CL 5915</td>
</tr>
<tr>
<td>Amalia, Nagarcarlang</td>
</tr>
<tr>
<td>EC339356 and EC339357, and Selection-7 and -18</td>
</tr>
<tr>
<td>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</td>
</tr>
<tr>
<td>FLA 7156</td>
</tr>
<tr>
<td>Amalia</td>
</tr>
<tr>
<td>Sonali, Hotsat, Kewalo, Saladette, NDTV-60,</td>
</tr>
<tr>
<td>Viradoro, Santa Clara</td>
</tr>
<tr>
<td>UC-82B, N-SummerSet</td>
</tr>
<tr>
<td>Nagarcarlang</td>
</tr>
<tr>
<td>CLN B, CLN R (selection from CLN lines from AVRDC)</td>
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</table>
ritabilities for most of the characters which implies that single plant selection in the F2 for heat tolerance will not be effective and the F2 lines derived from heat-tolerant F2 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 normal conditions (Hallauer et al. 2002; Ansary 2005) implied that single plant selection in the F2 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 F3 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 (Bear 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-INDUCTIBLE 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 tomato (LeDS2) with the same desiccation-specific expression in leaves and organ specific expression in flowers and organ specific expression in flowers and tomato (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 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 6°C and 25°C. At higher temperatures, 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, specifically 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-port 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 e-xists in the tomato genome as shown by Southern blot. Song et al. (2006) identified a heat inducible filamentation temperature-sensitive H (fthS) like gene from tomato. Because the protein structure was highly homologous to Arabidopsis AtfHs6, the cloned tomato fthS 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, stigmata, 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 biometric 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 (Crone and Borman 2006).

The tomato MT-shHSP 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-shHSP 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-shHSP gene to study the role of MT-shHSP gene in imparting tolerance to high temperature to the vegetative part an dit awas assumed that MT-shHSP gene is just not expressed by plants under has shock, but has a u-
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 exertion, substantial pollen production, adequate pollen viability and release from anther and fruit set would be essential to enhance tomato heat tolerance. None 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 concurrently 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 F2 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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REFERENCES

Abdalla AA, Verkerk K (1968) Growth, flowering and fruit-set of the tomato at high temperature. The Netherlands Journal of Agricultural Science 16, 71-76
Bar Tsur A (1977) High temperature effects on gas exchange characteristics, flowering and fruit-set in tomatoes. MS Thesis, Hebrew University of Jerusalem, Israel, 250 pp
Berry SZ, Rafiqueuddin M (1988) Effect of high temperature on fruit set in tomato cultivars and selected germplasm. Cultivus Tomo- päicales 22, 13-17
Canepa JM, Torres W (2001) High temperature effect on pollen (Lycopersicon esculentum) pigment and protein content and cellular viability. Cultivos Tropicales 46, 716B
Charles WB, Harris RE (1972) Tomato fruit set at high and low temperature. Canadian Journal of Plant Science 52, 497
Dhankar SK, Dhankhar BS, Sharma NK (2001) Correlation and path analysis in tomato under normal and high temperature conditions. Haryana Journal of Horticultural Science 30, 89-92
Dhankhar SK, Dhankhar BS (2002) Gene action for fruit yield in tomato at high temperature conditions. Haryana Journal of Horticultural Science 31, 221-223
Dhankhar SK, Dhankhar BS, Dudi BS (2002) Inheritance of number of flowers per cluster at high temperature in tomato. Haryana Journal of Horticultural Science 31, 97-99
Dobrenkova LG, Lukyanenko AN (1984) Influence of high temperature on physiological characteristics of tomato flowers. Russians inveni vivulissa 137, 5-6
El-Ahmad AB (1977) Genetic and Physiology of High Temperature Fruit Set in the Tomato. PhD Thesis, University of California, Davis, CA, USA
El Ahmadi AB, Stevens MA (1979a) Responses of heat tolerant tomatoes to
high temperature. *Journal of the American Society for Horticultural Science* 104, 686-691

El-Tabbaddou AB, Stevens MA (1979b) Genetics of high temperature fruit set in tomato. *Journal of the American Society for Horticultural Science* 104, 691-696


Gomez O, Depestrre T, Hernandez JC, Baldy B (1985) Tomato breeding in Cuba. *Ciencia y Tecnica en la Agricultura, Hortaliizas, Papa, Granos Fibra* s 6, 63-70


Hanson PM, Chen JT, Kuo G (2002) Gene action and heritability of high temperature fruit set in tomato line CL5915. *HortScience* 37, 172-175


Iwahori S (1965) High temperature injuries in tomato. *Vegetation and reproduction of tomato with special reference to the abnormalities caused by high temperature. Journal of the Japanese Society for Horticultural Science* 34, 3-41


