Heat Tolerance in Tomato

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Abstract: High temperature is the prevalent characteristic of subtropical and tropical regions and higher temperature has become an important limiting element for tomato production and yield. Although, tomato crops exhibit anatomical, morphological, physiological, phonological, and molecular responses to tackle with heat stress, but their reproductive stage and yields are extremely influenced by the high temperature. Various QTL's, heat shock proteins, and genes were detected in terms of heat resistance in tomato however a few stress-resistant tomato varieties are developed through traditional breeding ways. This is because the complicatedness of heat resistant characteristics that may be handled by the activity of different genes whose expression patterns are induced by several environmental elements. Furthermore, resistance to heat stress is developmentally regulated, stage-special event and resistance at one step of crop improvement is sometimes not related to resistance at other growth steps. Therefore, to produce of tomato under heat stress successfully, resistance may be required at whole imperative steps of crop growth such as germination of seed, reproductive and vegetative steps. Recently, various molecular and classical markers for heat resistance were screened and MAS (Marker-Assisted Selection) may be applied to improve tolerance of tomato to heat stress via biotechnological and molecular methods. To study heat tolerance in tomato appropriately, this paper will be an appropriate material and will assist for future studies.

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1. Introduction

Tomato (*Lycopersicon esculentum* Mill.) is usually a fruit but it is sometimes called as a vegetable and vastly grown in the world and forms an imperative industry for agriculture. Throughout the world, after potato, it is mostly used as a second vegetable (FAOSTAT, 2005) and is definitely the most prominent garden plant. Tomatoes are consumed straightly as a raw vegetable or combined with other various food items such as tomatoes that are completely peeled, paste, diced products and diverse sorts of juice, soups and sauces (Foolad, 2007). In various parts of the world, tomatoes are an imperative section of a variant and balanced diet (Willcox et al., 2003). Tomato does not have a higher rate in nutrition value; one average tomato that is fresh (135gm) prepares vitamin C (47 percent RDA), vitamin A (22 percent RDA), and 25 calories energy. In the USA diet, for instance, tomato is the first among all vegetables and fruits as a rich origin of minerals and vitamins (Rick, 1980) and antioxidants that are phenolic (Vinson et al., 1998). Moreover, tomatoes which are fresh are the wealthy origins of the antioxidant lycopene (Nguyen and Schwartz, 1999) that preserves cells of plants from oxidants which have been related to cancer (Giovannucci, 1999).

Tomato crops are developed in vast sorts of environments with diverse climatic in the universe from the tropical areas to some degrees of the Arctic Circle. The biggest tomato producing nations involve China, USA, India, Turkey, Egypt, Italy, Spain, Brazil, Iran, Mexico, Canada, Greece and Russia (FAOSTAT, 2005). Although tomato has a good potential to be cultivated every location in the universe but it confronts lots of abiotic stress and high temperature is a crucial problem nowadays. According to the Intergovernmental Panel on Climatic Change (IPCC), in each decade, worldwide average temperature will be enhanced by 0.3°C (Jones et al., 1999) and reached to around 1°C and 3°C higher than the current temperature by the years of 2025 and 2100, respectively and led to warming of the globe. AVDRC proposed that "in environments that are tropical, high temperature situations are sometimes common during the growing season and with climatic alteration, tomato plants in this region will be issued to enhanced temperature stress". Climatic analysis in areas in which tomato is grown proposes that temperatures are enhancing and the intensity and quantity of above-normal temperature will rise in the next decades (Bell et al., 2000). In this condition, tomato production that is resistant to heat is extremely required.

Heat stress is identified as the enhancement in temperature below a threshold level for some time is enough to prompt irreversible harm to crop growth and improvement. As a whole, a temporary increase in temperature 10°–15°C above normal, can lead to heat stress or shock (Wahid et al., 2007). Heat resistance refers to the capability of the crop to develop and create economic production in high temperatures.

However, heat stress because of high temperatures is an important problem to plant yield throughout the world (Hall, 2001). Heat stress has been considered as one of the most imperative prompt of alteration in biochemical, morphology, and physiology facets of crops that decreases normal growth in diverse plants, involving tomato (Thomas and Prasad, 2003; Wahid et al., 2007). When temperature is up, injury of cellules and death may happen within minutes that could be related to a disturbance of cellular structure (Schoffl et al., 1999). When temperature is optimum, damages or death may happen after long term exposure. Direct damages can be happened in high temperatures such as denaturation and aggregation of protein, and enhanced membrane lipids liquidity. Indirect or slower heat damages can be occurred in terms of enzymes inactivation in chloroplast and mitochondria, limitation in of protein production, degradation of protein and loss of integrity of membrane (Howarth, 2005). Furthermore, in tomato, high temperatures can lead to remarkable losses in its yield because of the diminished fruit set, small size, and fruits low quality (Stevens and Rudich, 1978). Heat stress before anthesis period is linked with developmental alterations in the anthers, especially disorders in epidermis and endothecium, shortage in stromium opening and poor formation of pollen (Sato et al., 2002). Hazra et al. (2007) clarified that, in tomato, the signals which cause fruit set failure at high temperatures involves bud drop, abnormal flower growth, poor pollen creation, poor inflorescence and viability, abortion of ovule and reduced carbohydrate existence. Moreover, marked prohibition of photosynthesis happens at temperatures above average, causing remarkable decrease in yield. Intense heat stress (45°C, 20 min) in tomato that is mature-green leads to programmed cell death (PCD) in terms of fragmentation of DNA, cytochrome c release, and activity of special enzymes which are caspase-like (Qu et al., 2009). It is properly detected that reproductive organs of crops have higher susceptibility to heat stress in comparison with vegetative organs (Ruan et al., 2010; Zinn et al., 2010).

Crop species have different susceptibility in reaction to abiotic stress. Medium temperature for growth and reproduction is markedly different between crop species and their lines (Bohnert et al., 1995). However, in some occasions, tomato crops demonstrate special HSPs for presenting resistance to heat stress. The resistance is dedicated by HSPs which causes to promoted physiological parameters including photosynthesis, better use of water and nutrient, and integrity of membrane (Camejo et al., 2005; Ahn and Zimmerman, 2006; Momcilovic and Ristic, 2007). Such developments cause tomato growth to be feasible in heat stress situation. However, all of the lines within species have different abilities in tolerance to the heat stress but there are severe differences between and within species that provide chances to promote tomato tolerance to heat stress via genetic instruments. Vegetative and reproductive developments in tomatoes are intensively manipulated by temperature or various environmental elements (Abdalla and Verkerk, 1968).

Various endeavors to promote tomato heat-resistant lines through traditional plant breeding methods have become prosperous (Ehlers and Hall, 1998; Camejo et al., 2005). But conventional breeding ways prepare low information on the locations of chromosomes that control complicated characteristics, the contemporary impacts of every chromosomal location on other characteristics (Epistasis, Pleiotropy or Linkage), or the genetic origin of such yield related characteristics due to dominance or over-dominance nature (Semel et al., 2006). If there is merely phenotype analysis, selection by conventional breeding instruments is hard when there are huge interactions between genotype and environment. There is no trustworthy field screening method that can be applied year by year or race by race (Kamel et al., 2010). Nevertheless, progressive methods of genetic engineering and molecular breeding have prepared further instruments that could be used to promote tomato with developed tolerance to heat. Molecular markers are used for both evaluating diversity of genes in germplasm collections and detecting varieties within population. Kantety et al. (1995) exhibited that ISSR method was capable to distinguish variations among inbred lines that are closely related and also individual population. Thin ISSR is very helpful to study genotypes of tomato. One technique to simplify polygenic characteristics' selection and breeding is to detect traits of interest through genetic markers. DNA markers have eased QTL (quantitative trait locus) mapping researches in populations which are segregated and exhibited certain genomic locations resulted from wild germplasm which have good potential to promote characteristics that are related to fruit (Gur and Zamir, 2004). Discovering of RAPD markers on tomato's genome map is advantageous to develop programs for breeding plants. It provides the easiest and most rapid technique for distinguishing a huge number of genome markers (Edwards et al., 1992). Michelmore et al. (1991) promoted the bulked segregant analysis of F_2 crops as an easier alternative method to analysis of isogenic line where the greatest and lowest extremes of the F_2 population are bulked for the improvement of RAPD and SSR molecular markers required for QTL-assisted selection. ISSR markers have already found to be highly variable, require less time, money and labor than other ways and have the capability to be inherited (Wolfe and Liston, 1998). However, to make sure that this strategy is successful, endeavors of crop physiologists, breeders and biologists are crucial (Wahid et al., 2007).

This review paper concentrates on responses of tomato to high temperature stress at the whole organs of crop, cellular and sub-cellular levels, mechanisms and methods of resistance for genetic development of tomato with resistance to heat stress that will be a substantial material for more studies.

2. Threshold levels of heat-stress in tomato

A threshold temperature can be defined as value of daily average temperature in which a decrease in crop growth starts. Upper and lowermost developmental threshold temperatures have been detected for various crop genotypes in laboratory and field via controlled experiments. A less developmental threshold or an origin temperature is one below which growth of plant stops. At the same time, an overhead developmental threshold is the temperature above which growth ceases. Identifying a steady overhead threshold temperature is hard as the crop behavior may be different depending on other environmental situations (Miller et al., 2001). In tomato, for instance, when the environment temperature is higher than 35°C, its germination, seedling and vegetative stage, flowering and fruit set and ripening phase of fruit are inappropriately impacted (Miller et al., 2001). In general, basis and overhead threshold temperatures are varied in various crops which belong to diverse environments. However, Camejo et al. (2005) clarified that 30°C as overhead threshold temperature in emergence phase is harmful for tomato. Therefore, it is extremely favorable to estimate threshold temperatures for various steps of tomato crops to hinder harms by adverse temperatures in the crop ontogeny.

3. Reactions of tomato to heat stress

3.1. Anatomical and morphological reactions of tomato

In tropic climates, extra radiation and great temperatures are sometimes the most prohibiting elements that affect plant development and final yield. Greater temperatures can lead to remarkable pre- and post-harvest harms, involving burning of twigs and leaves, leaves sunburns, stems and branches, senility of leaf and abscission, prohibition in the development of shoot and root, discoloration of fruit, and diminished production (Guilioni et al., 1997; Ismail and Hall, 1999; Vollenweider and Gunthardt-Goerg, 2005). Abdelmageed and Gruda (2009) perceived that morphological traits including fruits and flowers number per crop, percentage of fruit fresh weight and set were diverse in heat resistant and heat susceptible tomato lines and the outcomes were differed in field and glasshouse environments in 11 lines of tomato. There were vast levels of differentiations between the diverse varieties in their flowers number in glasshouse. ‘CLN-1-0-3’ created the greatest flowers number in each plant, but ‘Omdurman’ and ‘UC-82-B’ generated the lowermost numbers. Such impressiveness of high temperature is basically because of the reduction in bud or flower production and drop of flower. This outcome was similar to that of El-Ahmadi and Stevens (1979) where heat susceptible cultivar created only dropped flowers at high temperature. Fruits number in each plant was high in ‘CLN-16-B’and ‘CLN-1-0-3’ but ‘CLN-26-D’, ‘Summerset’ and ‘UC-82-B’ had an average fruits number per crop, but the other lines had a few fruits in glasshouse. In contrast, under open field environments, the fruits number was ‘zero’ in the heat susceptible line ‘UC-82-B’ and the heat resistant line ‘Summerset’ yielded the biggest fruits number. Concerning percentage of fruit set; there were marked variations between the various lines. ‘Summerset’ presented the greatest percentage of fruit set, but ‘UC-82-B’ the heat susceptible variety had no fruits. Other lines generated low and ‘CLN-1-0-3’ was average. Percentage of fruit set exhibited a similar result as in the fruits number per crop. Satti and Abdalla (1984) and Dane et al. (1991) perceived the same outcomes in their own trials. In fruit fresh weight estimation, ‘Summerset’ demonstrated the greatest fruit weight and this is followed by ‘Drd-85-F_1’, ‘Omdurman’, ‘Kervic-F_1’ and ‘Maverick-F_1’, while the other lines were either medium or low. This finding proves previous discoveries of El-Ahmadi and Stevens (1979), Sato et al. (2000) and Abdelmageed and Gruda (2009).

Under high temperatures, alterations in tomato anatomy were not explored in detail and a little information was accessible. In general, it is obvious that high temperature influences markedly plants anatomy at the tissue, cellular, and sub-cellular levels. The additional impacts of all these alterations in high temperature stress can lead to crop low growth and yield (Wahid et al., 2007). In all plant organs, there is a common trend of closure of stomata and loss of curtailed water, diminished size of cell, enhanced densities of stomata, and higher root and shoot’s xylem vessels (Anon et al., 2004). The tomato flower happens in the three patterns that are organizational and flowers that are simple appear as well as branched and simple cymes. Flowers number that appears in inflorescence is based on environmental elements including temperature (David et al., 1996).

3.2. Reactions of tomato in reproductive stage

Camejo et al. (2005) claimed that the medium temperatures for tomato plantation during the photoperiod are between 25°C and 30°C and during the dark period is 20°C. However, only 2-4°C rise in optimal temperature improperly influenced gamete development and prohibited the capability of pollinated flowers into seeded fruits and therefore diminished crops yields (Peet et al., 1997; Sato et al., 2001; Firon et al., 2006). Recently, Miller et al. (2001)

clarified that heat stress higher than 35°C became a major blockade element for germination of seed, vegetative growth and seedling, flowering stage, fruit set and ripening in tomato. Peet et al. (1997) claimed that heat stress inappropriately impacts meiosis and germination in pollen, development of ovule and improvement and viability of embryo. Foolad (2005) also mentioned that meiosis in male and female organs, germination of pollen and development of pollen tube, viability of ovule, style and stigmatic situations, pollen grains number that are maintained by the stigma, fertilization and post-fertilization trends, endosperm development, pre-embryo and fertilized embryo influenced improperly by high temperature in tomato. Moreover, the most outstanding impact of high temperatures on reproductive stages in tomato is the production of an exserted style (i.e., stigma is elongated beyond the anther cone), that may hinder self-pollination. Critical period of susceptibility to optimize high temperature (32°/26°C) is 7 to 15 days before anthesis (Sato et al., 2002). High temperatures also participated in development of floral bud which caused to abortion of flower. Pollen grains numbers that created by the heat resistant varieties stayed more than susceptible lines (Abdelmageed et al., 2003).

Pollen viability and production are so susceptible to small rises in temperature higher than the medium (Thomas and Prasad, 2003). A decrease in generation of pollen, release, viability, germination capability, fruit set, and production in tomato at temperatures above medium levels has mentioned by various scientists (Peet et al., 1997; Sato et al., 2000; Pressman et al., 2002). Pollen viability germination and percentage capability decreased markedly in moderate and high temperature environments. It was mentioned that pollen grains which are germinated diminished 13 times when the temperature enhanced gradually from optimum (Pressman et al., 2002). Both the pollen germination and release capability in high temperature are imperative elements to identify the capability of fruit set. This is because a fail in pollen germination or release can hinder creation of fruit set even the pollen is viable (Sato et al., 2000). Pollination, growth of pollen tube and fertilization, and pollen germination must take place prosperously for good fruit set (Kinet and Peet, 1997). The fruit set decline under optimum high temperature stress is mainly because of a decrease in release and viability of pollen but not in generation of pollen (Sato et al., 2006) formerly, Sato et al. (2000) did not detect marked linkage among produced pollen grains number and fruit set. Eventually, they finalized that both pollen release and viability are the most imperative elements that effect fruit set in high temperature condition. Pressman et al. (2002) claimed that the impact of heat stress on viability of pollen was linked with metabolism of carbohydrate during growth of anther. Under medium temperature, in pollen, concentration of soluble sugar enhanced slightly. Consistent high temperature hindered concentration of starch to be increased and caused soluble sugar content in mature pollen to be reduced. These probably lead to a reduction in livability of pollen. Poor fruit set has also been related to low amount of carbohydrates and growth regulators distributed in sink tissues of plant at high temperature (Kinet and Peet, 1997). Growth chamber and trainings of greenhouse propose that when flowers are first visible high temperature is most detrimental and susceptibility goes on for 10 to 15 days. Release of pollen and capability of germination can be a suitable standard for identifying crop reaction to high temperature and this is applied as a standard for selection in programs for breeding to choose heat resistant varieties (Comlekcioglu and Soylu, 2010).

3.3. Phenological reactions of tomato

Heat stress can induce changes in crops directly such as existing physiological trends or indirect like changes of developmental patterns. These reactions may be different in one phenological step to one other (Weaich et al., 1996). Moreover, stress resistance is adjusted extensionally, stage-special event; resistance at one step of crop growth cannot be linked to resistance at other growth steps. For instance, in tomato, although crops are susceptible to high temperatures at entire ontogeny of crop, fruit set and flowering are highly susceptible steps; fruit set is slightly influenced by temperatures above 20°/26° C day/night and is intensely impacted by above 26°/35°C (Berry and Rafique-Uddin, 1988). Perception of alterations in phenology of crop in reaction to heat stress can disclose a proper understanding of the crop and stress atmosphere interactions. Diverse phonological steps are different in their susceptibility to high temperature, but this is based on species and varieties (Wollenweber et al., 2003; Howarth, 2005). In the growth step, when crop is under stress the intensity of feasible harms is experienced by plant. It is unknown whether damaging influences of heat episodes are cumulative that occur at various developmental steps (Wollenweber et al., 2003).

Alsadon et al. (2006) perceived remarkable variations in heat resistance in twenty tomato lines at diverse steps of growth. At the vegetative step, the remarkable greatest average values for EC (electrical conductivity) were detected in Edkawi variety (63.12 µmho/cm) and this is followed by Pakmore VF, Castle Rock, Chico, Pakmore and Tnshet Star, respectively. They also identified that these lines had higher susceptibility to heat stress at vegetative step, in contrast, the marked lowermost average value for EC was distinguished in Pearson, Super Strain-B, Queen, VFN-8 and Strain-B varieties, which indicate that these lines had the best function and were resistant to heat stress at vegetative step. The other nine genotypes exhibited average mean values for EC were detected to be mildly resistant to heat stress. In the next step, heat susceptible varieties presented the greatest average values and heat resistant varieties had the lowermost average values. The rest varieties, that demonstrated average values for EC, were noticed to be moderately resistant to heat stress. In the fruiting step, those varieties that had the greatest EC average values were detected to be rather susceptible to heat stress. In contrast, those varieties that had the lowermost EC values were noticed as the best heat resistant varieties and the rest varieties, that showed medium values, were noticed to be moderately resistant to heat stress. The same findings were perceived by Saadella et al. (1990), Kuo et al. (1993) and Ismail and Hall (1999) in cowpea and wheat.

3.4. Physiological reactions of tomato

Physiologists and geneticists express that most stress resistant characteristics are complicated and handled by rather than one gene and impacted highly by different environments (Blum, 1988). In tomato crop water relations, concentration of compatible osmolytes, cell membrane thermo integrity, photosynthesis, and alterations in hormones are important physiological reactions to heat stress.

3.4.1. Waters relations

Crop water situation is an imperative variable under changing environmental temperatures (Mazorra et al., 2002). Heat stress, in tomato, disturbed hydraulic conductivity of root and the leaf water relationships (Morales et al., 2003). During daytime, increased transpiration affects water deficit in crops, prompting a reduction in potentiality of water and causing disturbance of lots of physiological parameters (Tsukaguchi et al., 2003). High temperatures can prompt crops to face more loss of water during daytime compared to nighttime (Wahid et al., 2007).

3.4.2. Compatible osmolytes accumulation

An important adaptive system in lots of crops developed under abiotic stresses, involving salinity, lack of water and severe temperatures, is cumulating of organic compounds that have low molecular mass, commonly called compatible osmolytes (Hare et al., 1998; Sakamoto and Murata, 2002). Under stress, various crop species may cumulate different varieties of osmolytes including sugar alcohols (polyols), and sugars, quaternary and tertiary ammonium, proline, and tertiary sulphonium compounds (Sairam and Tyagi, 2004). In high temperature conditions, fruit set reduced in tomato crops because of the disturbance in metabolism of sugar and transport of proline during the narrow window of male reproductive growth (Sato et al., 2006). To summarize, due to remarkable functions of osmolytes in reaction to environmental stresses in crops, (e.g., heat) resistance may be increased by enhanced cumulating of solutes that are compatible via conventional crop breeding, MAS (marker-assisted selection) or GE (genetic engineering) techniques (Ashraf and Foolad, 2007).

3.4.3. Photosynthesis

Changes in several photosynthetic approaches in heat stress are proper indexes of thermo resistance of the crop as they are correlated with growth. When photosynthesis is limited, crop development can be prohibited at high temperatures. Photochemical responses in thylakoid lamellae and metabolism of carbon in chloroplast stroma have been proposed as the primitive areas of damage at high temperatures (Wise et al., 2004). Rising leaf temperatures and density of photosynthetic photon flux affect thermo resistance adjustments of PSII, displaying their potentials to optimize photosynthesis in different environmental situations since the overhead thermal ranges do not exceed (Salvucci and Crafts-Brandner, 2004; Marchand et al., 2005). In tomato varieties that had different capacities to thermo resistance in enhanced chlorophyll a: b proportion and diminished chlorophyll, carotenoids proportion were perceived in the resistant varieties in high temperatures, showing that these alterations were linked to tomato’s thermo resistance (Camejo et al., 2005; Wahid and Ghazanfar, 2006). Moreover, in high temperatures, reduction in chlorophyll a and b was rather proved in progressed in comparison with developing leaves (Karim et al., 1997, 1999). These impacts on photosynthetic machinery or chlorophyll were proposed to be related to the creation of active oxygen species (Camejo et al., 2006; Guo et al., 2006). PSII is intensely thermo labile and its function is highly diminished or relatively halted in high temperatures (Bukhov et al., 1999; Camejo et al., 2005) that may be because of the exclusivity of thylakoid membranes wherever PSII is situated (Mcdonald and Paulsen, 1997). Heat shock decreases the number of photosynthetic pigments (Todorov et al., 2003), rubisco binding proteins (RBP), soluble proteins, and large and small subunits (SS) of rubisco in darkness but enhances them in light, exhibiting their functions as HSPs and chaperones (Kepova et al., 2005). Photosynthesis is detected as a physiological index that is highly susceptible to high temperatures, and a rise in the content of atmospheric CO_2 will make temperature to be enhanced and this may present a remarkable effect on the yield and distribution of lots of crop genotypes in the future (Wahid et al., 2007).

3.4.4. Cell membrane thermo stability

Maintained role of cellular membranes under stress is fundamental for trends like respiration and photosynthesis (Blum, 1988). Heat stress fastens the kinetic energy and motion of molecules in membranes which lose chemical bonds in biological membranes molecules. This causes the biological membranes' lipid bilayer to be rather liquid by either proteins denaturation or a rise in fatty acids that are unsaturated (Savchenko et al., 2002). The stability and roles of biological membranes are susceptible to high temperature, as heat stress changes membrane proteins' tertiary and quaternary structures. These changes increase the penetrance of membranes, as obvious from enhanced loss of electrolytes. The enhanced solute leakage, as a symptom of diminished cell membrane thermo stability (CMT), has long been applied as an indirect estimation of heat-stress resistance in different crop species, involving potato and tomato (Chen et al., 1982), soybean (Martineau et al., 1979), cotton (Ashraf et al., 1994), cowpea (Ismail and Hall, 1999), wheat (Blum et al., 2001), sorghum (Marcum, 1998), and barley (Wahid and Shabbir, 2005).

3.4.5. Alterations in hormone

Crops have the capability to monitor and adjust to inappropriate environmental situations, although the adaptability or tolerance degree to special stresses differs between species and genotypes. Hormones have an imperative function in this issue. Under heat stress condition, hormonal homeostasis, stability, content, biosynthesis and compartmentalization are changed (Maestri et al., 2002). Stress hormones such as abscisic acid (ABA) and ethylene (C_2H_4), are included in the regulation of various physiological properties by performing as signal molecules. Diverse environmental stresses, such as high temperature, leads to enhanced ABA levels (Larkindale and Huang, 2005). Other researches also propose that various HSPs (e.g., HSP70) induction by ABA can be one system whereby it confers thermo resistance (Pareek et al., 1998). Another kind of hormone, brassinosteroids have already been presented to confer thermo resistance to oilseed rape (*Brassica napus*) and tomato, but not to cereals (Dhaubhadel et al., 1999). The potential functions of other phytohormones in tomato for thermo resistance are unclear yet.

3.5. Molecular reactions of tomato

Tomato exhibits molecular reactions to heat stress by creating heat shock proteins.

3.5.1. Heat shock proteins

Production and cumulating of special proteins are inquired when heat stress is rapid and these proteins are identified as HSPs. Enhanced production of HSPs happens when crops experience either sudden or slow rise in temperature (Nakamoto and Hiyama, 1999; Schoffl et al., 1999). HSPs induction seems to be a worldwide reaction to temperature stress, being perceived in various organisms from bacteria to human (Vierling, 1991). In semiarid and arid areas, crops can produce and cumulate remarkable levels of HSPs. Under cyclic or developmental control, certain HSPs can also be expressed in various cells (Hopf et al., 1992). In this regard, HSPs expression is limited to certain steps of growth, including germination, embryogenesis, growth of pollen, and maturation of fruit (Prasinos et al., 2005). Three sorts of proteins, as detected by molecular weight, account for most HSPs, viz., HSP90, HSP70 and less molecular weight proteins of 15–30 kDa. The ratios of these protein sorts vary between crop species (Feussner et al., 1997). In reaction to high temperatures, special HSPs have been distinguished in various crop species. For instance, HSP68, that is located in mitochondria and usually expressed incorporately, was detected to have enhanced expression under heat stress in barley, tomato, maize, potato, and soybean cells (Neumann et al., 1993). The gene for a nuclear-encoded HSP, Hsa32, that encode a 32 kDa protein, has been cloned in tomato (Liu et al., 2006). Immune-localization researches have identified that HSPs naturally link to specific cellular structures, like chloroplasts, cell wall, mitochondria, and ribosomes (Nieto-Sotelo et al., 2002; Yang et al., 2006). In tomato crops which suffer from heat stress, HSPs gather into a granular structure in the cytoplasm, probably preserving the protein bioproduction machinery (Miroshnichenko et al., 2005). Presence of HSPs can hinder other proteins denaturation that can be impacted by high temperature. The conformational dynamism and aggregate state of small HSPs may be vital for their roles in thermo-protection of crop cells from harmful influences of heat stress (Sch¨offl et al., 1999; Iba, 2002). The specific significance of small HSPs in crops is proposed by their abnormal diversity and abundance. The capability of small HSPs to gather into heat shock granules (HSGs) and their decomposition is a prerequisite for crops cells survival under constant stress environments at sub-lethal temperatures (Miroshnichenko et al., 2005). LMW-HSPs may have structural functions in stability of cell membrane. LMW-HSPs localization in chloroplast membranes proposed that these proteins preserved the PSII from improper impacts of heat stress and played a function in transport of photosynthetic electron (Barua et al., 2003). Recently, in tomato, dual function of LMW HSP21 has been expressed as conserving PSII from oxidative harm and taking part in fruit color alteration during storage at low temperatures (Neta-Sharir et al., 2005).

4. QTLs for heat tolerant in tomato

In tomato, while substantial endeavors have been appropriated to the detection and mapping of QTLs conferring resistance to environmental stresses including drought, low temperatures, and salinity less mapping study has been performed on high temperatures (Foolad, 2005). Kadirvel (2010) showed an AVDRC report regarding two QTLs for heat resistant in tomato in chromosome 6 and 12. They exhibited that in Chromosome 6 the QTL is TES0111-SLM6-5; LOD score is 2.3; Variance10.6%; Additive influence 9.12; Donor CLN1621L and in chromosome 12 the QTL is SLM12-31-SLM12-50; LOD score is 2.6; Variance 13.0%; Additive influence 5.81; Donor CLN1621L. However, it seems that in tomato less improvement has been done in breeding and detection of QTLs for heat resistance than breeding for resistance to any other environmental stresses. This scenario proposed to a greater importance on breeding and detection of QTLs for heat resistance in tomato.

5. Molecular markers and classical genetic markers for heat tolerant tomato

To define, any characteristic which is expressed in multifold forms and inherited in a simple Mendelian fashion can be regarded and applied as a genetic marker. In tomato, there are more than 1300 morphological, physiological (e.g., male sterility, fruit abscission, fruit ripening), and disease tolerance genes (Kalloo, 1991) of them less than 400 have been mapped (Mutschler et al., 1987; Tanksley, 1993; Chetelat, 2002). The genetic markers' second generation, isozymes have been famous in 1970s and early 1980s. In tomato, 41 isozymic genes that correspond to 15 separate enzymatic responses have been detected, among them 36 have been mapped onto the 12 tomato chromosomes (Tanksley, 1993; Tanksley and Bernatzky, 1987). Despite their huge benefits, isozyme markers are so restricted in number and sometimes are not polymorphic between lines which are highly-related (Foolad et al., 1993; Tanksley and Orton, 1983).

With the arrival of DNA marker technique in 1980s (Botstein et al., 1980) and early 1990s, lots of restrictions linked to isozyme and morphological markers were conquered and genetic mapping entered to a new exciting and developed era with the promise to remarkably enhanced efficiency of crop breeding and genetics study. A DNA marker is usually branched from a small area of DNA that exhibits sequence polymorphism between individuals within or between species. DNA markers, that are phenotypically neutral and identically unrestricted in number, have permitted scanning of whole genome and assigning landmarks in high density on each chromosome in lots of crop species, involving tomato. During the past two decades, several sorts of molecular markers have been improved and progressed, like, but not restricted to, randomly amplified polymorphic DNAs (RAPDs) (Williams et al., 1990), simple sequence repeats (SSRs or microsatellites) (He et al., 2003; Tautz, 1989), amplified fragment length polymorphisms (AFLPs) (Vos et al., 1995), cleaved amplified polymorphic sequences (CAPS) (Konieczny and Ausubel, 1993), restriction fragment length polymorphisms (RFLPs) (Botstein et al., 1980), variable number of tandem repeats (VNTRs or minisatellites) (Jeffreys et al., 1985), sequence characterized amplified regions (SCARs) (Paran and Michelmore, 1993), expressed sequence tags (ESTs) (Adams et al., 1991), conserved ortholog sets (COS) (Fulton et al., 2002), single-strand conformation polymorphisms (SSCPs) (Orita et al., 1989), insertion deletions (InDels), and single nucleotide polymorphisms (SNPs) (Landegren et al., 1998). Kamel et al. (2010) secluded DNA from the two contrasting parents, LSSS1 as a heat resistant parent and Super Strain B as a heat susceptible parent, their subsequent F_1 and DNA bulks of the resistant and susceptible groups of F_2 segregating population were experimented against 10 preselected primers. All of the primers had polymorphisms with the genotypes studied. Primers A16 and Z13 presented 2 positive molecular markers that were only detected in the resistant parent (LSSS1), F_1 and the resistant F_2 bulk with 100 bp molecular sizes for primers A16 and 500 bp for primer Z13, while they were absent in the susceptible parent (Super Strain B) and the susceeptible F_2 bulk. In contrast, primers C02, C03, C05, C08, C14 and C15 demonstrated 8 molecular markers that were detected only in the susceptible F_2 bulk with 500 bp molecular size and 1500 bp for primer C02, 1750 bp and750 bp for primer C03, 2400 bp for primer C05, 550 bp for primer C08, 400 bp for primer C14 and 650 bp for primer C15. Zhang et al. (1994) and Mackay and Caligari (2000) claimed that analysis of RAPD that is mixed with BSA has been applied to screen for markers associated with genes of interest. Furthermore, Lin et al. (2006) detected 14 random amplified polymorphic DNA (RAPD) markers associated with heat resistance characteristics in tomatoes under heat stress with the use of the bulked segregant analysis. Various RAPD markers were unique to one special characteristic, and the rest were related to two characteristics while several markers demonstrate one polymorphic band and the others two polymorphic band. They also made use of 22 genetic markers as indirect selection linked to morphological traits and exhibited polymorphic bands, 13 were special to the susceptible parent i.e. C09 marker presented 1.5 kb for high number of flower and 1.0 kb for low number of fruit; D06 marker's 0.3 kb for high number of fruit and 1.0 kb for low number of flower; D11 marker's 0.3 kb for high number of flower and 0.3 kb for high fruit weight ; D12 marker's 1.0 kb for high number of flower; K06 marker's 1.1 kb for high number of flower and 1.3Kb for low number of fruit; K14 marker's 0.5 kb for high number of flower; P06 marker's 0.5 kb for high yield ; X01marker's 0.4 kb for high fruit weight and 0.7 kb for low number of flower while 9 were specific to the resistant parent, like D08 marker's 1.0 kb for low number of flower; K02 marker's 1.6 kb for low number of flower and 0.5 kb for low number of fruit; K08 marker's 0.6 kb for low number of flower; K20 marker's 0.9 kb for low fruit weight; P08 marker's 1.2 kb for low number of flower and 0.8Kb for low yield; S13 marker's 1.2 kb for low weight of fruit and 1.3 kb for low weight of fruit. Kamel et al. (2010) also detected that 844A as a primer presented as positive molecular marker that was only distinguished in the resistant parent (LSSS1), F_1 and the resistant F_2 bulk with 650 bp molecular sizes. These findings were similar to those of Lin et al. (2010) who made use of 160 F_2 tomato crops segregating population to detect ISSR markers that were related to fruit characteristics in the tomato which exposed to high temperatures. Lin et al. (2010) screened 100 ISSR-PCR primers in the parents and 51 were identified to be polymorphic and of them 42 markers were segregated in a Mendelian fashion. The greatest (14) and lowermost (3) band numbers were created by primers 884 and 814, respectively. Lin et al. (2010) created 127 AFLP bands with fragment sizes that ranged from 50 to 500 bp with the use of 2 ECoRIMseI primer pair combinations. Of these, 50 polymorphic bands with an average number of 25 bands per primer pair were disclosed. Among detected 50 polymorphic fragments, 26 AFLP loci were identified to be associated with the genetic map. Mansour et al. (2009) detected differentiations in tomato varieties that were grown under heat stress and distinguished only 15 ISSR (814, 844A, 844B, 17898A, 17898B, 17899A, 17899B, HB8-15) and 20 RAPD (P1-20) primers that could distinguish intra-specific differentiations.

6. Marker-assisted selection (MAS) for heat tolerance in tomato

Marker-Assisted Selection is defined as a selection for a characteristic that depend on the genotype of an associated marker more than the characteristic itself. In essence, a marker that is associated can be applied as a criterion for selecting indirectly. The potential of MAS as an instrument for plant progress has been vastly investigated (Tanksley et al., 1989; Ribaut et al., 2002; Servin et al., 2004). Despite the utility of MAS for manipulating single-gene characteristics is straightforward and has been properly documented, its usefulness for complicated characteristics has also been distinguished (Stuber and Edward, 1986; Edwards and Johnson, 1994; Eathington et al., 1997; Schneider et al., 1997; Knapp, 1998; Toojinda et al., 1998; Stuber et al., 1999; Zhu et al., 1999; Hospital et al., 2000; Bouchez et al., 2002; Tar'an et al., 2003; Zhou et al., 2003; Jiang et al., 2004). However, it should be understood that MAS for polygenic characteristic progress is in its primary step and transitory process and the field is on the verge of producing convincing outcomes. Based on most simulation studies and empirical outcomes, it seems that characteristic heritability (h^2) and the number-of-QTLs are the most imperative elements impacting the impressiveness of MAS. MAS seems to be most useful for characteristics with low h^2 (0.1–0.3) and that are handled by rather small numbers of QTLs with huge impacts. In general, it is accepted that in most cases, for a trait that has a low-heritability, MAS will have better selection outcomes than selection of phenotypic (Stuber et al., 1999). Previous researches presented that heat resistance exhibits low heritability so that MAS can be applied for producing of heat resistant tomato. The stages are needed for the progress of markers to be used in MAS and various benefits of MAS are expressed in a review by Collard et al. (2005). Polymorphism level that is distinguished in molecular marker followed by the use of marker-assisted selection (MAS) has been certified to be proper alternative way of the agronomic selection, where it provides crop breeders with environmental-independent genetic markers for certain economic characteristics.

7. Development of heat-stress tolerance of tomato

Under agricultural systems, crops adaptation or their resistance to environmental stresses can be manipulated by different methods. Generally, the negative influences of abiotic stresses on agricultural yield are diminished by a composition of genetic development and cultural practices (Wahid et al., 2007). Genetic improvement involves progress of varieties that can resist to environmental stresses and generate economic yield. However, genetic progress of crops for stress resistance is an economically constant solution for generation of plants in stressful conditions (Blum, 1988). The relatives of the planted tomato have certified to be valuable origines of favorable genes for better genetic development (Rick, 1986) and prosperous inter-generic crosses have also been made among planted tomato and its nearly related Solanum species (Rick, 1960; Stoeva and zagorska, 1987; Wann and Johnson, 1963). Hybrid lines also seemed to have a proper performance consistency especially under stress than optimal growing environments (Yordanov, 1983). Both traditional and hybrid breeding ways, that benefit of additively acting genes and genetic interactions, should be useful in tomato heat resistance breeding. In favor of hybrid breeding, around 1/3 of the diallel hybrid progenies from the foregoing study had better fruit set than the better heat resistant parents (AVDRC, 1988). In another related study, crosses among heat resistant stocks were better in fruit setting capability and yield than their crosses with heat susceptible parents from the diallel test (Opena et al., 1987).

Adjustment or alterations in cultural practices, like the time of planting, crop density, and management of soil and irrigation can reduce stress impacts, for instance Hanna et al. (1997) identified development and yield reactions of heat resistant tomatoes to depth of transplant, daily irrigation time and color of polyethylene mulch. They cultivated five-week-old tomato seedlings to a depth of 15.0 cm and perceived remarkable rise in marketable yield but mean fruit mass was not affected by transplant depth, in contrast, crop dry mass was markedly enhanced by deeper transplanting. Irrigation in morning enhanced the marketable and total yields, average fruit mass in 1994, and dry mass of crop in 1995. White-surface mulch had the same impact on fruit mass and yield. They finalized that a rise in yield of heat resistant tomatoes can be performed by deeper transplanting, irrigation in morning, making use of white-surface polyethylene mulch, or a mixture of all three. Practically, to be prosperous in developing agricultural yield in stress conditions, both genetic progress and adjustment in cultural practices must be done simultaneously (Wahid et al., 2007). In below, a summary of such endeavors and improvements is discussed and demonstrated.

7.1. Traditional breeding strategies

Traditional breeding of heat resistant crops basically based on selection and a common technique of selecting crops for heat stress resistance has been to grow breeding materials in a hot target production environment and detect individuals/lines with higher yield (Ehlers and Hall, 1998). A proposed method has been detected in selection criteria during early steps of crop growth that can be linked to heat resistance during reproductive steps. In tomato, a potent positive correlation has been perceived between yield and fruit set under high temperature. Therefore, estimation of germplasm to detect sources of heat resistance has regularly been performed by screening for fruit set under high temperature (Berry and Rafique-Uddin, 1988). Among various other characteristics that are influenced by high temperature, the non-reproductive trends involve efficiency of photosynthesis, assimilate translocation, mesophyll tolerance, and cellular membranes disorganization (Chen et al., 1982). Breeding to develop such characteristics under high temperatures can lead to improvement of varieties with heat resistance approaches. Various other concerns when applying conventional breeding protocols to promote heat resistant crops are as follows:

-Detection of genetic resources with heat resistance approaches. In lots of crop species, for instance tomatoes and soybeans, restricted genetic differentiations exist within the cultivated species necessitating detection and use of wild accessions (Foolad, 2005).

-In different crop species, heat resistance is sometimes linked to various unfavorable agronomical or horticultural traits. In tomato, for instance, two unfavorable traits generally perceived in heat resistant lines are small fruit and limited foliar canopy (Scott et al., 1997).

-The small fruit production is mostly because of improper impacts of high temperature on the creation of auxins in the fruit and the poor canopy is for the sake of the highly reproductive nature of the heat resistant varieties (Scott et al., 1997).

Heat resistance breeding is yet in its primitive step and needs more attention in comparison with the past. Unfortunately, the literature has partially less information on breeding for heat resistance in various plant species. However, although all the complicatedness of heat resistance and hardships confronted during transfer of resistance, various heat resistant inbred lines and hybrid varieties with commercial acceptability have been improved and released in tomato (Scott et al., 1986; Scott et al., 1995).

7.2. Molecular and biotechnological strategies

Recent genetic researches and endeavors to convince high-temperature resistance of crops with the use of conventional protocols and transgenic attributes have vastly detected that crop heat stress resistance is a polygenic characteristic. Various ingredients of resistance, handled by various sets of genes, are vital for heat resistance at various steps of crop growth or in diverse tissues (Howarth, 2005; Bohnert et al., 2006). Therefore, the use of genetic stocks with diverse levels of heat resistance, co-segregation and correlation analyses, molecular biology methods and molecular markers to detect resistance, QTLs are promising attributes to dissect the genetic source of thermo-resistance (Maestri et al., 2002). Recently, biotechnology has assisted substantially to a proper understanding of the genetic source of heat resistance. For instance, various genes which are responsible for inducing the HSPs synthesis, have been detected and secluded in diverse crop species, involving maize and tomato (Liu et al., 2006; Sun et al., 2006; Momcilovic and Ristic, 2007). It has also been exhibited that tomato MT-sHSP has a molecular chaperone role in vitro (Liu and Shono, 1999) and recently it has been presented that MT-sHSP gene shows thermo-resistance in transformed tobacco with the tomato MT-sHSP gene (Sanmiya et al., 2004) at the crop level. Experimental data gained from transgenic, reverse-genetics and mutation attributes in non-cereal species prove causal involvement of HSPs in thermo-resistance in crops (Queitsch et al., 2000).

7.3. Induction of heat resistance of Tomato

Though genetic methods may be advantageous in the production of heat resistant crops, it is probable that the recently produced crops are yielded low in comparison with near-isogenic heat susceptible crops. Therefore, substantial attention has been devoted to the induction of heat resistance in existing high-yielding varieties. Among the various techniques to achieve this target, foliar application of, or pre-sowing seed treatment with, low concentrations of inorganic salts, osmoprotectants, signaling molecules (e.g., growth hormones) and oxidants (e.g., H_2O_2) as well as preconditioning of crops are common attributes. Preconditioned tomato crops presented better osmotic adjustment by keeping the osmotic potential and stomatal conductance and better development than non-conditioned crops (Morales et al., 2003). Similarly, heat acclimated, in comparison with non-acclimated, turf grass leaves revealed higher thermo-stability, lower lipid peroxidation product malondialdehyde (MDA) and lower harm to chloroplast in exposure to heat stress (Xu et al., 2006). In tomato, it was exhibited that heat treatment administered to crops prior to chilling stress resulted in diminished incidence and intensity of chilling injury in fruit and other organs (Whitaker, 1994). Therefore, to promote heat resistant tomato crop, alternative methods to genetic means would involve pre-treatment of crops or seeds with heat stress or certain mineral or organic compounds. The success of such method, however, based on tomato plant and genotypes and must be studied on case basis.

8. Conclusions and future prospects

Already substantial improvement has been performed in tomato research, involving development of molecular markers, mapping of specific genes and QTLs, comparative analysis of different characters, fine-mapping and map-based cloning of genes and genome sequencing and organization. Molecular mapping can be applied as criteria for indirect selection and tomato improvement. However, little information is available for the use of markers in tomato breeding especially for the development of complex characteristics like heat resistance. However, depending on the most recent discoveries and research progresses, it is clear that the future of routine application of markers in heat resistant tomato breeding is prospective. But the most imperative problem is the improvement of appropriate markers for the breeding programs. PCR based molecular markers that can distinguish polymorphism between closely related genotypes can be used in marker-assisted breeding for heat resistant tomato. Furthermore, the complete sequencing of the tomato genome will assist to progress sequence-based high-resolving markers. This will make MAS as a routine procedure in tomato breeding programs especially for improvement of many complicated characteristics. For complex traits i.e. heat resistance obtaining a reliable phenotypic data for QTL mapping may not be proper on the other hand, partitioning of the total genetic variation for heat resistant characteristic into its physiological and developmental components would lead to detection of QTLs for individual components that may be more useful. The importance of such progresses is well distinguished by the geneticists and plant breeders and lots of research programs have commenced such activities. As heat resistant tomato is a demandable criterion in tropical and subtropical environment in future, a combination of traditional breeding protocols and marker assisted breeding will become a routine procedure for heat resistant tomato production.

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