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Review

SOME ASPECT RELATED TO HEAT TOLERANCE IN TOMATO (*Solanum lycopersicum* L.)

Reseña bibliográfica

Aspectos relacionados con el estrés de calor en tomate (*Solanum lycopersicum* L.)

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ABSTRACT. Although tomato plants can grow in a wide range of climatic conditions, their vegetative and reproductive growth is severely impaired at high temperatures, resulting in reduced yield and fruit quality. This high-temperature sensitivity is particularly important in areas with tropical or subtropical climates. In such environments, heat stress may become a major limiting factor for tomatoe production. This work was focused in explain different aspect related to heat stress tolerance at cellular and whole plant levels, difficulties on the quantification of stress tolerance, as well as the necessity on an understanding of the physiological mechanisms and genetic basis for thermotolerance in order to achievement progress in tomato plant breeding.

RESUMEN. Aunque el tomate puede crecer en un amplio rango de condiciones climáticas, su crecimiento vegetativo y reproductivo se ve seriamente afectado en condiciones de temperaturas altas, resultando en una reducción del rendimiento y de la calidad del fruto. Estas condiciones son importantes, fundamentalmente, en ambientes tropicales y subtropicales, donde el estrés es un factor limitante en la producción de tomate. En este trabajo se exponen los principales aspectos relacionados con la tolerancia al calor en el cultivo a nivel celular, morfoagronómico y de planta completa; las dificultades en la cuantificación de la tolerancia a este estrés, así como la necesidad de conocer los mecanismos fisiológicos y las bases genéticas de la termotolerancia con vistas a lograr progresos en el mejoramiento genético del cultivo.

Key words: stress, fruit set, plant breeding, heat tolerance, tomato

Palabras clave: estrés, fructificación, mejora genética, tolerancia al calor, tomate

INTRODUCTION

Tomato (*Solanum lycopersicum* L.) after potato (*Solanum tuberosum* L.) is the most consumed vegetable due to its high fruit value in terms of versatility, both for fresh consumption and diversity of its processed fruits (1).

Although tomato plants can grow in a wide range of climatic conditions, their vegetative and reproductive growth is severely affected under high temperature conditions, causing serious damage to their reproductive structures, which consequently brings fruit set deficiency and decreases production (2, 3, 4); therefore, it constitutes one of the most important factors causing low tomato production in tropical environments (5, 6, 7, 8). Such damage is usually greater when environmental temperature exceeds 35 °C (2, 3, 9, 10). This sensitivity to high temperatures is particularly important in tropical or subtropical climate areas, where heat stress may become a limiting factor for tomato field production (11).

Every year, high temperatures and the increased frequency, magnitude and intensity of heat waves cause considerable economic losses (12, 13, 14). As a result of global warming, average temperature is estimated to rise between 3 and 6 °C for the year 2100, which would cause serious economic

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damage to the crop if considering that tomato fruiting decreases significantly when temperature increases a little (2). This effect gets worse if temperature rises coincide with rainy periods, increasing pest occurrence, mainly when the crop grows in the open air (15 16).

One of the most important indicators of tomato heat tolerance at plant level is its ability of fruiting or fruit setting under stressful environments, so that those varieties with greater fruiting capacity under high temperature and humidity are best suited for tomato production in the tropics (15, 17, 18, 19, 20); thus, any method used for screening tomato accessions should be associated with it.

In general, genetic breeding can be an economically viable solution for tomato production under high temperature conditions; however, some progress in these programs depends on the understanding of physiological mechanisms and genetic bases of heat stress tolerance at the cellular and whole plant levels. At present, there is available information on the knowledge of physiological and metabolic aspects of heat stress tolerance in plants (4); nevertheless, research studies on the genetic and breeding characterization for stressful conditions have been somewhat limited, although some efforts have been recently made in this way (6, 9, 11, 20, 21, 22).

Quantification of tomato heat tolerance has serious difficulties; firstly, its direct selection under field conditions is generally difficult, due to the presence of other adverse environmental factors affecting the accuracy and repeatability of these trials (21, 23, 24, 25, 26). Besides, stress tolerance in a specific plant developing stage does not always correlate with tolerance in other developing stages (9, 11, 25, 27); hence, a better understanding of physiological and developing aspects under stressful conditions will enable a better understanding of genetic basis of plant stress tolerance.

Recent advances in molecular techniques, including genetic transformation, expression analysis and quantitative trait loci analysis (QTLs), have helped understand the biochemical and molecular bases of plant stress tolerance (19, 28, 29, 30, 31). These advances are expected to contribute significantly to plant development with heat tolerance in the near future (7, 11, 21).

It is known that tomato (*Solanum lycopersicum* L.) is moderately susceptible to various abiotic factors including high temperatures. However, among related species, there are wild species with a useful source of genetic variation, which has been widely employed in breeding programs to improve agronomically desirable characteristics and to characterize genetic-physiological bases of heat tolerance and develop heat tolerant plants. This review discusses agronomic and physiological aspects related to heat tolerance in the crop; it also presents recent advances in genetic aspects related to breeding for these conditions.

GENERAL FEATURES

Considering the main abiotic stress forms to which plants are exposed in nature, heat stress has an independent mode of action on plant cell physiology and metabolism. Although it often gets worse by additional abiotic stresses, such as drought and salt stress, it is important to disentangle the independent action and biological effects of high temperatures, in order to alleviate the combined abiotic stress effects. Susceptibility to high temperatures affects vegetative and reproductive development and varies with plant developing stage. Effects observed depend on species and genotypes, with plentiful inter- and intraspecific variations (32, 33).

Therefore, in response to heat stress, plants show different morphological adaptations, including short-term mechanisms of avoidance or acclimatization involving leaf orientation, cooling, and transpiration or changing membrane lipid composition (9).

Initial exposure to a moderately high temperature provides plant tolerance to a normally lethal temperature. This phenomenon is called acquired thermotolerance (34). Even when plants grow in their natural area, they may experience high temperatures or diurnal fluctuations that would be lethal in the absence of this rapid acclimatization. Therefore, the acquisition of thermotolerance may reflect a more general mechanism involving metabolic homeostasis (35). However, just a limited number of factors responsible for plant thermotolerance development have been defined, due to such character complexity (35).

Thermotolerance is an essential component of acclimatization in different organisms, including plants. Generally, it is divided into acquired thermotolerance (ability to acquire tolerance to lethal temperatures) and basal thermotolerance (ability to survive at temperatures above the optimal for growth) (36). The ability to acquire thermotolerance is by increasing protective gene expression, prior to stress exposure. A prolonged exposure period to a moderately high temperature is as harmful as the brief exposure to extreme temperatures (37, 38).

There are four important effects under high temperature stress conditions (39):

- Differentiated response of reaction rates due to its activation energy differences
- Protein denaturation and aggregation
- Membrane lipid hyper-fluidity
- Direct chemical decomposition

It has been pointed out that thermotolerance development should moderate different types of damage and toxic effects caused by high temperatures, through protective factor induction limiting damage size or by activating plant recovery processes against damage, although these mechanisms are not necessarily mutually exclusive (23, 40).

TOMATO MORPHOAGRONOMIC RESPONSE TO HIGH TEMPERATURES

The first plant response to high temperature stress impact results in a developing stage reduction, besides decreasing its organ size and finally its yield (11). Plants can only develop within their thermal thresholds, or minimum and maximum temperatures, varying according to each species, and they reach the highest development under optimal temperature conditions (17, 41, 42, 43). It has been shown that temperature increases are associated with pre- and postharvest as burns and abscission of leaves, branches and stems, leaf senescence reducing root growth, flower abortions and fruit drop, discoloration and yield reduction (9).

High temperatures affect tomato plant development, causing serious damage to reproductive structures, which consequently brings fruit set deficiency and decreases production (2, 44); hence, it constitutes one of the most important factors provoking low tomato production under tropical environments (15, 41, 45).

Average optimum crop temperature is between 21 and 24 °C (9), depending on plant developmental stage, but temperatures only a few degrees above the optimal range may reduce fruit production and seed formation (10, 17, 41). Thus, average daytime temperatures exceeding 32 °C and average night temperatures above 21 °C decrease tomato production (8, 9). As in other crops, tomato reproductive organs are generally more heat sensitive than vegetative organs (4, 46, 47, 48).

Temperature increase affects almost all tomato pollen developing stages, both in female and male organs; however, the greatest effect undoubtedly occurs at the meiotic phase, in which either viability or the amount of pollen produced is quite difficult (2, 4, 41, 43, 49); this aspect has been previously stated in numerous studies (42, 43, 49), where it has been reported that when pollen is produced at temperatures above 35 °C, its viability is reduced, but this answer varies from one cultivar to another (4, 11, 17).

Therefore, the critical period of tomato plant development in the presence of high temperatures is from 8 to 13 days prior to anthesis, which is associated with changes in its anther development, epidermal and endothecial irregularities, and poor pollen formation (41, 43), microsporogenesis being greater affected than megasporogenesis (50). During pollen development, soluble carbohydrates present in spores may be immediately consumed or polymerized and transformed into other molecules, so that in the presence of heat stress, a starch concentration reduced three days before anthesis decreases sugar concentration in mature pollen grains, which may lead to a pollen viability reduction (43, 49, 50, 51).

An adverse effect on pollen tube growth, egg viability, stigma positions, pollen germination and its fertility, endosperm formation and embryo development is also attributed to high temperatures, causing fewer fruits per plant (43). Similarly, they can affect stigma receptivity and cause fruiting failure (5, 18) as well as increased tomato fruit parthenocarpy (2, 8).

Not every accession presents fruiting or fruit set failures by gametophyte formation disturbances, some plants reach a great vegetative development, but the number of clusters and flowers per cluster is reduced or they do not even appear; likewise, maximum fruit number may also decrease, increasing the risk of malformations (19, 52). Several authors have reported the presence of flower malformations that may cause antheridal cone rupture, so that anthers are separated from the style, which thereby hinders pollen arrival to the stigma, provoking floral abortions (8, 43, 50).

Another phenomenon caused by high temperatures is stigmatic exertion, provoked by stamen growth, as the pistil has shown to poorly respond to environmental variations (44). This phenomenon is associated with fruit set failure, since it is difficult for the pollen to reach the stigma, and it gets worse when high temperatures are joined with low illumination (44). Moreover, floral abscissions increase and many flowers have parthenocarpic fruits (10, 42), a fact that strongly correlates with style exertion, so that no fruits are produced when the style is more than 1 mm outside the antheridal cone (10, 17). In this environment, fruiting percentage, fruit number and its mass, and seed content are further reduced (17, 18, 45, 49, 53).

One of the most important indicators of crop heat tolerance is the ability of fruiting at high night temperatures, in such a way that those varieties showing greater fruiting capacity under low temperature and high humidity conditions are the most suitable for tomato production in the tropics (15, 17, 42, 49).

Fruit number per plant is one of the main yield components and it is correlated with it and fruit set; hence, the significance of this indicator has been highlighted when selecting to increase tomato yields in summer seedings, which is very helpful in identifying heat tolerant cultivars (45).

Within this context, breeded tomato varieties in temperate areas often have fruit set failures when grown in tropical areas, mainly during summer season (45); thus, it is necessary to have a breeding program with the objective of obtaining varieties that develop under these conditions and provide, if possible, a series of favorable characteristics, such as higher pollen dehiscence, higher stamen opening and pollen sack, no stigma exertion, well-organized and normal endothecium, no anther cone crack, a large seed number per fruit to measure gamete viability, high pollen and egg viability, high pollen tube growth rate, which undoubtedly will alleviate harmful effects of high temperatures during out-of-season tomato production in the tropics (6, 15, 17, 43).

Although poor fruit set is the worst effect of high temperatures on tomatoes, there are other not less important damages in mature fruits, which are more prone to infections and cracks; they are soft fruits and have little commercial value (44, 45).

PHYSIOLOGICAL AND BIOCHEMICAL ASPECTS OF HEAT TOLERANCE

Most organisms, including plants, are constantly exposed to sudden temperature changes that can cause short-term or chronic stresses. It is considered that heat stress occurs when temperature increases above the physiological optimum and may cause several plant injuries depending on the intensity (temperature in degrees), length and increased temperature rate. Severe cell damage can occur within a few minutes at very high temperatures, and even cause plant cell death, due to a collapse of cellular organization. In moderately high temperatures, injuries and cell death are mostly dependent on long-term exposure.

In general, high temperatures interfere with normal cell homeostasis by changing membrane fluidity and permeability (54) in protein folding and photosynthetic activity period (40, 55, 56, 57, 58, 59) in metabolic pathways (57, 60). At a whole plant level, there is a general tendency to reduce cell size, close stomata and reduce water loss, while chloroplast subcellular changes lead to a significant photosynthetic deterioration (61).

Thus, the loss of enzyme activity is due to the weakening of electrostatic and hydrophobic interactions that stabilize its native configuration, so that heat tolerant species have many high temperature resistant enzymes and vice versa (2, 4, 48).

Heat produces adverse effects on primary photochemical reactions; there is evidence that Rubisco and other enzymes from carbon metabolism are affected by stress, light and other environmental factors, being capable of increasing plant heat tolerance (31, 32, 58, 61). Under these conditions, photosystem II activity (PSII) may be inhibited, which is the highest heat sensitive of the electron transport chain, so that photosynthesis can be completely inhibited by high temperatures before another symptom is detected (54, 59, 62).

That is why several studies suggest that photosynthesis is the most affected physiological process by high temperatures and its damage depends on chloroplast stability to maintain active photosynthetic reactions and chlorophyll synthesis rate (59, 63, 64).

High temperatures also affect carbohydrate metabolism, considering this character as a plant strategy to tolerate environmental stress (65, 66). Besides, these conditions decrease chlorophyll fluorescence and cause cytoplasm changes, affecting the structure of proteins or other polymers, such as DNA (deoxyribonucleic acid) or RNA (ribonucleic acid) (57, 61).

Environmental stresses, in general, can distort normal cell metabolism and affect the balance of free radical production, lowering plant photosynthetic capacity (32, 58), so that there is evidence that high temperature-acclimated plants are associated with oxidative stress by increasing antioxidant system expression (38, 61), then enzyme activity changes appear under these conditions, such as peroxidases (Prx), catalases (CAT), superoxide dismutases (SOD) and ascorbate oxidases (AO) (19, 50, 67).

In fact, it has been suggested that these enzymes are vital for the survival of aerobic organisms, since they may prevent membrane peroxidation and other types of damage, which are necessary to plant defense mechanism; hence, they are important as high temperature tolerance indicators (67, 68).

Antioxidant system is not the only one affected by temperature increases; in fact, under these conditions, other systems as carbonic anhydrase (CA), esterase (Est), acid phosphatase (Aps), amylase (Amy), aspartate amino transferase (Got), phenyl amino lyase (PAL), formiate dehydrogenase (FdH), polygalacturonases and dehydrogenases are generally changed (69, 70). Several studies have noted how usefulness it is to evaluate these enzymes as plant heat tolerance indicators (69, 70, 71); however, the most widely used method to estimate plant cellular thermotolerance is undoubtedly cell viability, which evaluates mitochondrial electron transport chain based on the principle of reducing tetrazolium salt to formazan by the action of dehydrogenase respiratory enzymes (71).

On the other hand, a wide range of metabolites capable of mitigating deleterious effects of oxidative stress has been identified, which go along with many hostile environmental conditions, such as heat stress. Osmoprotectants as proline, glycine-betaine, polyamines, malondialdehyde, trehalose, mannitol, ethylene, salicylic and jasmonic acids and comoglutation antioxidants, ascorbate and tocopherols are included in this group, which act as osmotic solutes, increasing cell osmotic potential (36, 57, 72, 73). Similarly, it is said that several plant growth regulators, such as abscisic acid (ABA), salicylic acid (SA), ethylene, cytokinins, auxins and brassinosteroids play an important role in plant thermotolerance (40, 74, 75, 76).

At gene level, abiotic stresses can cause genetic rearrangements, because cells exposed to stress affect methylation patterns altering heterochromatin, resulting in gene expression changes. Additionally, transposon demethylation can encourage active tramposaze expression and lead to mobile and non-mobile genetic element transposition, which have a variety of effects, among which are: gene activation or deactivation, gene portion capture, gene activity co-suppression and transcription reduction; therefore, gene rearrangements resulting from stress can be a major source of genetic variation (23, 50). Likewise, there is a decrease of certain neutral sugar concentration, such as galactose, changes in fruit peel color, effects on internal chlorophyll degradation, inactivation of many types of proteins resulting in damage followed by attack of proteases, injuries and nucleic acid mutations (50, 51, 61, 77), and lycopene synthesis (7).

In tomato crop, it was reported that temperature presented a change in oxygen uptake and respiratory coefficient, as well as an increased dehydrogenase activity, so that sub-lethal temperatures cause serious damages to the functional activity of respiratory system. In fact, according to these authors, respiratory process rearrangement seems to be a necessary element, because certain amounts of energy are required to reach a greater heat tolerance; therefore, a close relationship between thermotolerance level and gas exchange by plant breathing (9, 61).

Concerning pollen grain and anther development, imbalances of proline, polyamine and carbohydrate contents were observed in short-term and long-term heat stress treatment at 32-36 °C associated with fruiting failures (49, 78), whereas temperatures of 38 °C reduce pollen germination and tube growth, due to less contents of spermidine and spermine and soluble sugars, a poor starch assimilation in pollen grain formation and its maturity (25, 43, 49). Consequently, differences among cultivars may also be associated with certain ability to regulate these metabolic and/or physiological pathways. In fact, it has been shown that heat tolerant tomato lines are able to keep unchanged carbohydrate content, besides an adequate pollen grain development, even when exposed to prolonged high temperature regimes (59, 79).

Other results have indicated that at 35 °C, phenol concentration increases in plants, by activating its biosynthesis and inhibiting oxidation as well as decreasing Prx, Cat, Guayacol peroxidase, ascorbate peroxidase (APrx), dehydroascorbate reductase, gluatation reductase (GR) and polyphenol oxidase (PPO) activities (27, 67, 70).

Also, greater accumulation of hydrogen peroxide and increases in PAL, SOD and antioxidant compound (ascorbate, dehydroascorbate, reduced and oxidized glutathione) activities has been found, as well as inhibition of ascorbate/glutathione cycle and oxidative cleavage (67).

In this regard, it should be noted that drought studies in the crop suggest SOD activity as screening tool to develop drought tolerant tomato varieties and to other environmental stresses (80).

In brief, plants are often subjected to unfavorable conditions for its optimal functioning caused by the environment; these stresses have a great selective pressure on plants throughout their evolution, which has provoked plant adaptation to the environment by natural selection mechanisms.

CELL MEMBRANE AND ITS ROLE IN THERMOTOLERANCE

Physiological mechanisms related to high temperature damages occur at the structural organization level, so that its symptoms are mainly associated with the loss of membrane integrity, causing injures to primary photosynthetic process, changes in phosphorylation, thylakoid structure, lipid bilayer phase composition and protein denaturation; therefore, membranes are the most affected by this stress and considered the primary heat damage site (2, 13, 60).

Indeed, membranes show a fine molecular arrangement capable of selectively capturing some substances in relation to others, to receive, translate and amplify signals, regulate the flow vectorially and the concentration of various substances through pump systems and carriers, as well as to provide specific ion channels with physiologically-regulated flow doors and to have a complex membrane potential arrangement (81), so that their loss of integrity results in the cell membrane rupture, structural damages, increased permeability and electrolyte efflux, reducing photosynthetic and mitochondrial activity (37, 68).

Plant tolerance ability to high temperatures involves a series of reactions and complex mechanisms, cell membrane being one of the main components of thermotolerance, thereby, a good heat tolerance indicator (68). Effects caused by high temperatures may be determined by cell membrane thermostability technique (CMT), which has been widely used to evaluate the behavior of plants subjected to these stresses in various crops and to quantify the acquired thermotolerance level in plants (68, 82, 83, 84, 85).

CMT method is based on electrolyte diffusion from leaf tissue cell to aqueous medium. In the presence of heat temperature stress, membrane permeability increases; thus, the amount of electrolytes outflowing because of cell damage may be measured by electrical conductivity of the solution and expressed in percentages, which enables its interpretation (82, 83). Several studies have suggested the efficacy of this technique to detect the genetic variability for heat tolerance in tomato (6, 86).

Some authors suggest that the ability of some plants to tolerate high temperatures is closely correlated with their genetic potential for this feature (68, 82). Several investigations report that CMT under high temperatures is controlled by a reduced group of genes; genetic variability has also been found in different crops, suggesting that this character could be used as a selection criterion to search for stress-tolerant materials (68, 81).

This idea confirms that selection effectiveness for a particular trait, specifically CMT, depends on the relative magnitude of phenotypic and genotypic differences within a population, so considering that there are very few studies and selection progress based on this criterion (87).

A high correlation was determined between thermostability measurements of cell membrane during the vegetative stage and early reproductive stage under controlled conditions. This suggests that the proper use of CMT method at the vegetative phase can be very useful to identify high temperature tolerant genotypes during early growth stages, so that it could be a good selection criterion for heat tolerant genotypes, since it includes plant genetic variability (68, 81).

HEAT SHOCK PROTEINS (HSP) AND ITS ROLE IN THERMOTOLERANCE

Heat shock response is associated with the synthesis of a particular group of proteins called heat shock proteins (HSP), resulting from gene *hs* transcription. These proteins are synthesized when the synthesis of most normal proteins is repressed (88, 89, 90). The induction of these proteins increases plant thermotolerance, allowing the tissues to be exposed to temperatures that were previously considered lethal; however, the exact role of HSPs in thermotolerance remains uncertain (91).

HSPs are involved in protein folding; for example, aggregated or misfolded protein recovery is an activity that explains their role in thermal stress. HSPs may also play a role in the growth and development under normal environmental conditions (92). Its rapid accumulation in sensitive organs can play an important role in protecting cell metabolic apparatus; therefore, it acts as a key factor in plant adaptation and survival under heat stress conditions (9, 91).

Plant response to heat stress is characterized by the synthesis of six kinds of preserved proteins, which are named according to their molecular mass: HSP100, HSP90, HSP70, HSP60, sHSP (low molecular mass protein) and HSP8.5 (ubiquitin group) (93). sHSP has a molecular mass ranging from 15 to 30kDa, which can be roughly divided into at least six families encoding for several proteins located in the cytosol, nucleus or different organelles (chloroplasts, mitochondria and endoplasmic reticulum) (40, 91, 94).

In higher plants, HSPs are usually induced at 38-40 °C (70) and seems to increase excessively at a temperature, which is often between 10 and 15 °C above the normal organism growth temperature. Surpassing that temperature, total protein synthesis decreases abruptly and only HSP proteins are synthesized (61, 95).

In general, HSPs have important functions like “chaperone” proteins, in addition to their functions in protein folding after translation and in protein transformation to carrier structures in the membrane, they are deeply involved in high temperature resistance and in other kinds of stress (51, 70, 89, 90, 96, 97). It has been demonstrated that HSPs produced during stress remain in the cell several hours thereafter and that tissues which are previously given a thermal shock and synthesize HSPs can survive after a subsequent heat treatment while in other cases it can be lethal (61, 90, 97), indicating the presence of HSPs is essential for thermotolerance (51, 86, 89).

Some HSPs are not only of heat stress, they have been induced by other stimuli, such as water, salinity and low temperature stresses; also ethanol, ethylene, dinitrophenol, arsenite compounds and other chemical agents are highlighted as well as in the presence of abscisic, jasmonic and salicylic acids (27, 70, 98).

HSPs may play a specific role in changing or keeping proteins, preventing its denaturation and restorative function, as part of their physiological response to various environmental stresses.

That is why HSPs play a fundamental role in protecting proteins and cell membranes against irreversible damages caused by stress. It has been shown that they are involved in generating heat tolerance, which probably takes place by protecting essential enzymes and nucleic acids from heat denaturation. Without this protection, nucleic acids could be divided by specific metal ions entering the cytoplasm from outside (or from the vacuole) as membranes become more permeable (91). HSPs are highly preserved in all organisms and play an essential role in cell function (23, 40, 50).

In many plant species, there is a positive relationship between HSPs and cell membrane thermal stability, efficient use of water and photosynthesis, as well as heat tolerance in the whole plant (9, 51, 90, 99). Additionally, these proteins have been linked to reactive oxygen species (ROS), which confirms the hypothesis that during plant evolution, they are able to suppress ROS or use them as HSP-inducing molecular signals (96).

In this regard, it has been noted that the best acclimation occurs when high temperature stress occurs gradually rather than a sudden temperature change (38). In fact, there is evidence to show that HSPs increase survival to oxidative stress (9, 50, 91), suggesting the existence of a communication between HPS expression and oxidative stimulus, which can be the basis for a cross tolerance between these kinds of stress. Furthermore, HSP genes (hsp17, hsp83, hsp101, etc.) can be induced by ROS, H_2O_2 (100).

In tomato crop, there are different proteins induced by heat treatments to leaves, flowers and fruits, within which lies HSP21, also called TOM111 and LeHSP23.8 (101), located in the chloroplast and mitochondria respectively, and chaperone proteins have been identified in HSP70 and HSP90 classes (90).

The role of HSP100 have been studied in response to heat stress, demonstrating that a wide range of species synthesize proteins of about 100kDa constitutively in the presence of heat stress, which are involved in thermotolerance of organisms (102). These proteins play important cellular functions as “chaperone”, including survival under stress conditions (49, 102).

It is suggested that HSP100 are required for survival during short periods of time at extreme temperatures, helping prevent protein aggregation and/or denaturation at high temperatures; therefore, limiting cell damages induced by heat (49, 50, 70). In the crop, it has been proved that HSP101 transcript levels increase in mature pollen grains as a response to heat stress, improving grain thermotolerance (49).

TRANSCRIPTION FACTORS INVOLVED IN HEAT TOLERANCE

HSP gene transcription and other genes related with plant adaptations to stress are controlled by regulatory proteins called heat shock factors (HSF), which are located at the cytoplasm in an inactive state (91, 103, 104). It has been determined at times that HSFs constitutive expression increases basal thermotolerance without affecting acquired or induced thermotolerance; thus, they are considered transcriptional heat shock activators (43, 90, 91, 94, 103). HSF are classified into three classes, according to their structural differences and binding sites (HsfA as HsfA1 and HsfA2; HsfB which includes HsfB1 in tomato and HsfC) (56, 105).

Generally, the first stage of abiotic stress response is stress signal perception by cell wall receivers, followed by transduction involving second messengers, such as cytosolic Ca^{2+}, ABA and kinases, leading to activate specific transcription factors and *cis*-acting elements (25, 75).

Transcription factors (TF) play a central role when preparing environmental response and plant morphogenetic program. They are *trans*-acting proteins, capable of recognizing specific DNA sequence targets (*cis* elements) located in regions promoting certain genes. The regulation of gene expression is largely governed by TF interaction with this kind of *cis* elements, inducing or suppressing various signal transduction pathways through domino effect (23, 25).

In plants, numerous genes encoding TFs have been identified and characterized. Vegetable TFs are classified into families and subfamilies, according to the degree of amino acid sequence preservation, size and coding gene structural composition. However, in plants, not more than 10 % of these sequences have been isolated and studied reliably, assigning TF function to encoded proteins. Furthermore, it should be noted that similarity between proteins of organisms belonging to different kingdoms does not necessarily imply they are involved in regulating the same events (23, 25, 40).

Regarding strategies where TFs have been overexpressed, ectopically expressed, or silenced, it was observed that transforming plants showed altered responses to environmental conditions, either by the action of biotic factors or abiotic ones (105, 106). In some cases, doubling or tripling genes encoding protein type WRKY caused the lack of response in silenced mutants. In others, plants with improved responses to different types of stress were obtained, so confirming the hypothesis that transcription factors act simultaneously in different signaling pathways (23, 94).

The use of inducible promoters to replace constitutive ones presents a viable choice. When modifying appropriate factors, morphology and development process become indistinguishable from non-transformed control plants, achieving good tolerance levels (107).

For tomato crop, HsfA1 proved to act as heat stress response regulator. Its suppression reduces strongly tomato plant ability to survive at high temperatures (4, 90, 108). Both in *Arabidopsis* and tomato, HsfA2 accumulate at quite high levels after multiple cycles of PCR and recovery (43, 109).

Regarding tomato, *LeFAD3* gene overexpression (desaturated omega-3 acid) has shown to increase cold tolerance in transgenic plants (110). Similarly occurs with saturated omega-3 acid overexpression (*FAD3, FAD7*) (111). On the contrary, *LeFAD3* suppression increases fatty acid saturation, alleviates photosystem II photoinhibition and increases heat stress tolerance (57). Likewise, it has been shown that *Spodoptera frugiperda* expression (J.E. Smith) *SfIAP*, a family inhibitor of apoptosis-related proteins in transgenic tomato plants confer abiotic stress tolerance, such as heat and salinity (112).

Another group of proteins involved in plant tolerance to abiotic stress are kinase MAPK (*mitogen-activated protein kinase*). It is stated that under several stress conditions, MAPK cascade is activated in plants (113), so that by handling this kinase expression in transgenic tomato plants, tolerance to various abiotic stresses could be higher (25).

HEAT TOLERANCE GENETICS IN TOMATO

It is desirable to develop heat tolerant tomato cultivars for its production in tropical regions where temperatures reach 35 °C.

However, tomato breeding for heat stress is a difficult task, partly due to the complexity of characteristics associated with heat tolerance and partly because of a low-to-moderate heritability of these characters (9, 11).

Another disadvantage is that heat tolerant lines tend to produce smaller fruits than those that are commercially acceptable with poor canopy (9, 11, 43). That is why to overcome these obstacles, it is recommended to use, in different breeding programs, those genotypes able to bear fruit at high temperatures, which must be crossed with large and vigorous fruit genotypes (7, 11).

Several studies on fruit set inheritance have been made, as this is one of the most affected characters under high temperature conditions. It was reported that this trait inheritance is dominant at high temperatures, with additive effects and moderate heritability (h^2) (11, 15, 19). Results of heritability indicate that a high homozygosis degree is needed to predict selection progress in tomato crosses, in order to obtain tolerant varieties to this abiotic stress by crossing, so that selection will be effective if performed in more advanced generations[A] (>F5) (15).

In a diallelic analysis using several heat tolerant and susceptible tomato genotypes, it was determined that pollen fertility and fruit production at high temperatures mainly showed an additive genetic control (11, 114).

High heritability values were obtained in thermostability studies of cell membrane and viability by TTC reduction in the crop[A], indicating that these characters have little environmental impact. Dominance and epistasis effects were detected, although phenotypic variance portion was also significant, due to additive variance that could be exploited in breeding programs of the species.

[A] Florido, M. Bases genéticas de la tolerancia del tomate a estrés abióticos. Informe final de proyecto PNCT, no. 0800129, Inst. INCA, MES, 2012, p. 62.

The existence of additive and dominance effects on character expression suggests that one part of genotypic variation is heritable and not the other one, thus, these methods can be effective when screening accessions in a germplasm bank, when selecting lines to obtain heat tolerant hybrids, and in programs to obtain new varieties related to parent selection for crossings and to selection in advanced generations (F_5-F_7), when lines have a high homozygosis degree.

Including these characters in genetic breeding can complement empirical methods and so increase selection efficiency, ensuring heat tolerant genes that might be lost by traditional procedures, involving a large number of plants when selecting characters that generally have low heritabilities (13, 21, 115).

The advantage of dominant nature of fruit set ability is that F_1 hybrids can be obtained between heat tolerant and susceptible parents. In this approach, shortcomings of heat tolerant parents, such as disease susceptibility, small fruit and poor foliage cover could be at least partially improved with heat sensitive cultivars used for hybrid production (2, 21, 116).

Despite difficulties encountered when transferring heat tolerance characteristics in tomato, several hybrid cultivars and breeded lines with heat tolerance and acceptable horticultural characteristics have been developed and released (9, 11, 53, 117). Small fruit size has been overcome with F_1 hybrid production obtained by crossing heat tolerant cultivars having small fruits with susceptible lines having very large fruits. The use of these hybrid cultivars has increased tomato production in tropical and subtropical areas (2, 11, 53). However, there are a few reports on heat tolerant tomato cultivars developed through traditional protocols.

In general, information about the genetic basis of heat tolerance is scarce, due to its multigenic nature, although it is thought that the use of traditional protocols in the crop along with molecular biology techniques, including the technology of molecular markers and genetic transformation will lead to characterize and/or develop breeded heat tolerant plants.

BREEDING FOR HEAT TOLERANCE

Tomato breeding for heat tolerance can be an economically viable solution for production under stress conditions (9, 43). Breeding progress in this regard depends on the understanding of physiological mechanisms and genetic basis of stress tolerance at the cellular, molecular and whole plant levels of the crop.

Researches show that most tests performed to evaluate crop tolerance to high temperature stress are complex, controlled by more than one gene and highly influenced by environmental variations (2, 9, 11, 15). That is why quantification of tolerance often has serious difficulties.

Direct selection under field conditions is hard, because environmental factors are hardly controlled and affect the accuracy and repeatability of these tests. Sometimes high temperature conditions cannot be guaranteed in the field, besides stress tolerance is regulated by development, specifically in each stage; therefore, tolerance at a particular stage of plant development might not be correlated with tolerance in another developing stage (118). In fact, it has been shown that the most sensitive tomato stages to heat are flowering and fruit set, they being poorly affected when day/night temperatures are above 26/20 °C, but severely affected when they exceed 35/26 °C (119).

Therefore, a separate study of genetic-physiological and developmental components could provide a better understanding of plant response to heat stress and enable plant development with stress tolerance throughout their life cycle (9, 118).

A commonly used method for selecting plants with heat tolerance has been to breeded plant materials under production environments and to identify individuals or lines with great potential yield. However, under such conditions, the presence of other stresses, such as pests, has made the selection process very difficult, mainly during reproductive stage. Identifying a selection criterion during the early stages of plant development would be ideal, which could be correlated with tolerance during reproductive stage. Unfortunately, these criteria are not easily identified (9).

A major challenge in traditional breeding for heat tolerance is to identify reliable detection methods and effective selection criteria to enable detecting heat tolerant plants. In some plant species, such as tomato, there is a strong positive correlation between fruit set and yield under high temperature conditions. Therefore, evaluating germplasm to identify heat tolerance sources has been regularly carried out by detecting fruit set under high temperature conditions (9, 11, 119).

There are two useful biotechnology tools for studying and breeding heat tolerance in plants: molecular marker-assisted selection (MAS) and genetic transformation (Figure). The use of these tools has greatly contributed to a better understanding of genetic and biochemical bases of stress tolerance in plants and, in some cases, they have led to plant development with increased stress tolerance. Due to the complexity of abiotic stress tolerance and the difficulty of phenotypic selection, MAS has been considered an effective tool in this regard (1, 9).

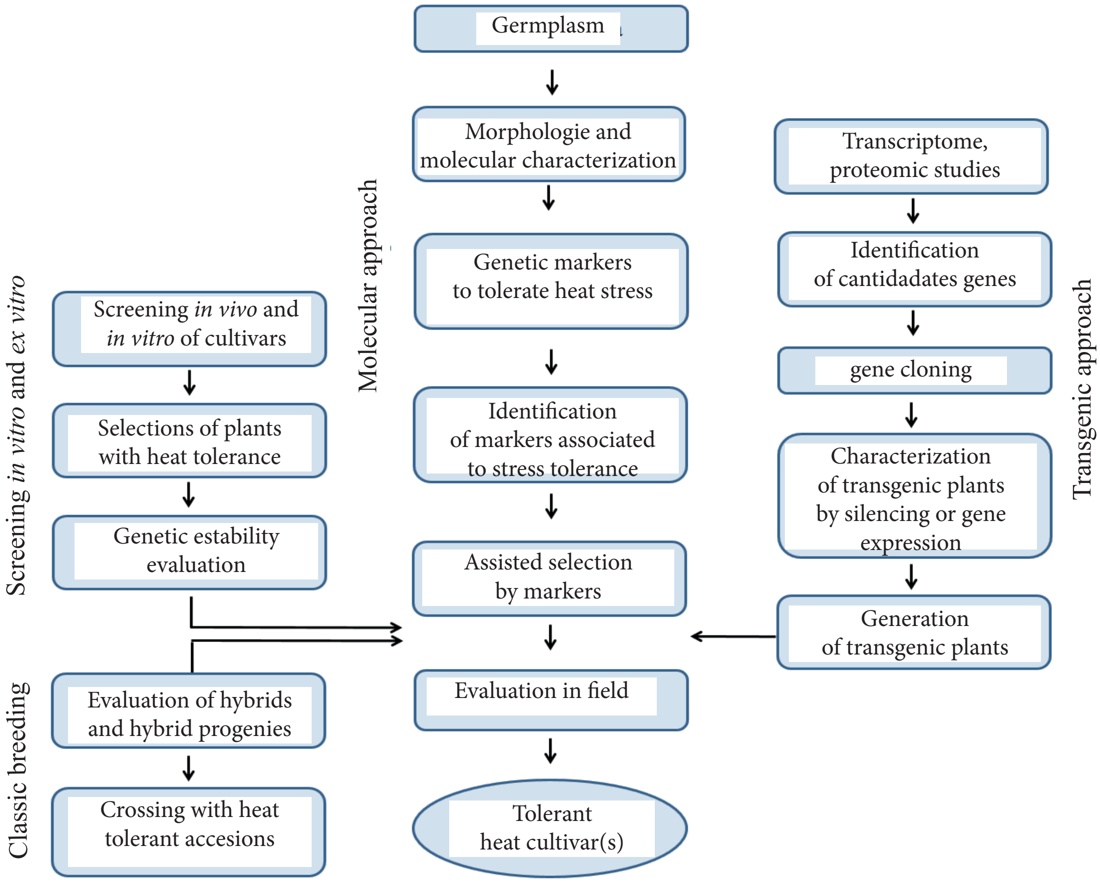
Nevertheless, the use of these tools requires that genetic markers are associated with genes or QTLs affecting plant tolerance to stress or individual components contributing to it (59, 120, 121).

Many researchers have made a lot of efforts in different crops, in order to identify genetic markers associated with different environmental stresses, mainly extreme temperatures, salinity and drought (9); however, only a few research studies have been conducted to identify genetic markers associated with heat tolerance.

That is why understanding heat tolerance mechanisms is important to design breeding strategies in various crops including tomato (25, 103, 122, 123). So far, few tools have been reported in tomato to improve environmental stress tolerance. Figure 1 shows a scheme that can be used for this purpose in tomato by combining classical and biotechnological tools (25).

It should be noted that gene overexpression and/or silencing by genetic engineering encoding osmoprotectants, ion or antioxidant enzyme transporters in tomato represent a step towards increasing heat tolerance in the crop.

Unfortunately, further progress in this sense depends on future genes that would be discovered by proteomic and transcriptome studies, which may lead to a more complete



Modified of Pandey (25)

Summary of strategies used in tomato breeding for heat tolerance

understanding of physiological processes involved in such response, as well as to determine which promoters or transcription factors will be the most appropriate in genetic transformation techniques. Knowing the genetic-physiological bases of heat tolerance together with genetic transformation techniques will enable to increase heat tolerance in tomato cultivars (9, 25).

In short, genetic breeding aimed at obtaining lines, hybrids or varieties with adaptability to high temperatures is still in its early stage and deserves more attention than it has been in the past. However, despite all the complexity of heat tolerance and difficulties encountered during tolerance transfer, some commercially accepted inbred lines and hybrid cultivars have been developed and released in tomato (117).

However, to speed such advances, the main areas of prior attention in the future should be: the design and/or development of accurate selection procedures, identification and characterization of genetic resources under high temperature conditions, discerning the genetic basis of heat tolerance at each stage of plant development, the development and screening of large breeding populations to enable gene transfer into commercial cultivars (9, 11, 85).

The use of advanced molecular biology techniques could lead to breeded heat tolerant plants.

FINAL CONSIDERATIONS

Genetic resources available for heat tolerance have been identified among *Solanum* species, *Lycopersicon* section. Its morphological and physiological components have been solved and its genetic basis determined at the whole plant level. In recent years, many breeding lines and crops have been developed with a high fruit set ability under heat tolerance conditions. Many of these lines also show undesirable horticultural characteristics, particularly small fruit size, low yield, poor foliage cover and articulated pedicel. However, years of research on tomato crop and efforts in this regard have resulted in the development of new high-yielding breeding lines and medium-sized hybrid cultivars, high fruit set capacity and other agronomically desirable attributes related to this abiotic stress. However, little research has been done on the basis of HTA molecular genetics in tomato. This research line as well as an investigation on the relationship between high temperature tolerance during different plant developing stages should be strengthened.

Consequently, a successful future tomato breeder will be the one who is able to combine three components of modern tomato breeding: the art of traditional plant breeding and introgress wild species genes as well as the access and use of genes from other species through recombinant DNA techniques, which will lead to search for more challenging and exciting results than those that have been so far achieved.

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