Genetic Enhancement of Tomato Crop for Abiotic Stress Tolerance

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Abstract

India being the second largest producer of tomato will still fall short of the country's requirement. The main concern is the decreasing productivity due to negative effects of environmental stresses. Production of tomato is subjected to many abiotic stresses, mainly heat and drought. In order to sustain tomato production with present day challenges, we need to have a thorough knowledge of the plant's reaction toward the stress and develop sufficient genetically enhanced varieties or hybrids which are tolerant and capable of mitigating the stress. Here we have made an attempt to address the challenge thrown to the breeders by the changing climatic scenario.

11.1 Introduction

Tomato occupies a significant position in world vegetable production due to its worldwide consumption. World's acreage of tomato is 43 lakh ha with a productivity of 33.5 tha^{-1}, while in India, it is cultivated in 6.34 lakh ha, with a productivity of 19.33 tha^{-1} (FAO STAT 2010). Changing climatic scenario has resulted in marginal increase/decrease in temperature regimes affecting the normal growing environment of an already adapted cultivar(s) of important vegetable crops. Abiotic stress is the primary cause of crop loss worldwide, reducing average yields for most major crop plants by more than 50% (Boyer 1982; Bray et al. 2000). Abiotic stress leads to a series of morphological, physiological, biochemical, and molecular changes that adversely affect plant growth and productivity (Wang et al. 2001). To maintain growth and productivity, plants must adapt to stress conditions and exercise specific tolerance mechanisms. Plant modification for enhanced tolerance is mostly based on the manipulation of genes that protect and maintain the function and structure of cellular components. Sources of genetic tolerance (or resistance) to different abiotic stresses are found within the related wild species, including *L. chilense, L. peruvianum, L. pennellii, L. pimpinellifolium, L. hirsutum, L. cheesmanii, L. chmielewskii,* and *L. parviflorum* (Foolad 2005). Progress in developing heat-tolerant cultivars has been hindered by the complexity of

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the trait and its low heritability values (Scott et al. 1986; Villareal and Lai 1979). For successful tomato production under environmental stress, tolerance may be needed at all major stages of plant development, including seed germination, the vegetative stage, flowering and fruiting.

Drought is the single most important factor affecting world food security and the catalyst of the great famines of the past (Schonfeld et al. 1988). Drought, defined as the occurrence of a substantial water deficit in the soil or atmosphere, is an increasingly important constraint to crop productivity and yield stability worldwide (Ceccarelli and Grando 1996). At present, an unsustainable 70% of the world's water is used for agriculture. By 2025, it is expected that most Asian countries will join those that already have water shortages. Uncertainties over global warming raise further concerns; thus, it has become a major target of plant research (Sharma and Lavanya 2002).

11.2 Effect of Temperature on Yield and Quality of Tomato

High temperature stress can be caused due to high maximum and/or minimum temperature. Tomato has a base temperature for vegetative development when growth commences, and an optimum temperature when the plant growth reaches the peak of the sigmoid curve. Any change in temperature above or below this optimum temperature will directly and negatively reflect on plant growth. Optimal mean daily temperatures for tomato are between 21°C and 24°C. Tomato is particularly sensitive to short periods of hot temperatures if they coincide with critical stages of the crop development depending on developmental stage (Geisenberg and Stewart 1986; Haque et al. 1999; Araki et al. 2000). Temperature fluctuation of only a few degrees above optimal can reduce fruit production and seed set (Peet et al. 1997). Apart from day temperature, night temperature also plays a crucial role in fruit yield and quality (Iwahori and Takahashi 1964; Abdalla and Verkerk 1968; Rudich et al. 1977; Levy et al. 1978; El Ahmadi and Stevens 1979; Kuo et al. 1979; Hanna and Hernandez 1982). As tomato cultivation is taken all round the year and in arid regions, development of cultivars with improved fruit set under high temperatures is the need of the hour for crop production in regions where the temperature during part of the growing season reaches 35^{0}C or higher (Johnson and Hall 1953; Iwahori 1965, 1966; Stevens and Rudich 1978). Heat stress at vegetative and reproductive stages of the plant ultimately reduces yield and fruit quality (Charles and Harris 1972; Rudich et al. 1977; El Ahmadi and Stevens 1979; Hanna and Hernandez 1982; Yakir et al. 1984; Berry and Uddin 1988;Abdul-Baki 1991; Dane et al. 1991; Wessel-Beaver and Scott 1992).

11.2.1 Germination

Several factors may contribute to reduced set fruit under high temperatures and can be considered as potential selection criteria. Heat stress adversely affects critical steps in the life cycle of a tomato plant. Higher temperatures during seed germination reduces the number of days taken for germination, thereby inhibiting stratification (pre chilling effects). Though not much work has been done in this aspect to see the result of such early emergence, this is one such delayed effect where the response by the plant is after the conclusion of the stimulus. It is one of the most noticeable changes caused by increase in temperature in the life cycle.

11.2.2 Vegetative Stage

Higher growth temperatures result in shorter crop production times, i.e., number of days to harvest (DTH), but with smaller fruit and lower yield (Rylski 1979a, b; Sawheny and Polowick 1985). Differences in temperature during vegetative growth influence the rate of development and timing to first flower. Hurd and Cooper (1970), Grimstad (1995), and Sauser (1998) reported that application of a short 2-week chilling temperature prior to anthesis delayed crop development but resulted in larger individual fruit size. Abdalla and Verkerk (1968) showed set fruit could be severely inhibited by short- and long-term exposure to temperatures in excess of 30°C in certain cultivars (El Ahmadi and Stevens 1979). Other research indicated that the duration, magnitude, and timing of short-term temperature pulses during the growing season influenced fruit development time (Adams and Valdés 2002), firmness, and yield (Mulholland et al. 2003).

Nonreproductive processes affected by high temperature are photosynthetic efficiency (Bar-Tsur et al. 1985; Dinar and Rudich 1985), increase in rate of transpiration, assimilate translocation (Tanaka et al. 1974; Went and Hull 1949), mesophyll resistance (Stevens and Rudich 1978), disorganization of cellular membranes like the thylakoid membrane wherein the photosystem II complexes are located (the most heat-sensitive part of the photosynthetic membrane (Santarius and Weis 1988; Weis and Berry 1988), Rubisco, and other enzymes which participate in carbon metabolism, changes in viscosity levels in the protoplasm and electrolyte leakage from the leaves (Shen and Li 1982) have been observed in response to high temperatures).

At higher temperatures, trusses appear faster (Adams et al. 2001a), and therefore, initially, there are more fruits on a plant at a higher temperature. These will grow at the expense of vegetative growth but may also cause a delay in the growth of newly set fruit and might even lead to flower or fruit abortion (De Koning 1989), as developing and flowering trusses are weaker sinks than fruiting trusses (Ho and Hewitt 1986).

11.2.3 Reproductive Stage

Flowering is the most sensitive stage affected by high temperature. At vegetative stage, the factors that are affected by increase in temperature include reduced flower production (Iwahori and Takahashi 1964; Iwahori 1965, 1966; Sugiyama et al. 1966), reduction in pollen production, reduced ovule and pollen viability, failure of fertilization due to decreases in pollen germination, and pollen tube elongation (Iwahori 1966; Weaver and Timm 1989; Peet et al. 1997; Sato et al. 2000; Pressman et al. 2002; Thomas and Prasad 2003), Splitting of the antheridial cone, stigma, and stylar exsertion is also reported (Rudich et al. 1977; Levy et al. 1978; El Ahmadi and Stevens 1979a). Heat stress not only affected the male gametes and its germination but also adversely affected the ovule development, viability, and development of the embryo (Peet et al. 1988); high temperatures directly cause dehydration of stigma which in turn inhibits pollination. An increase of 2–4°C from the optimal temperature adversely affected gamete development and inhibited the ability of pollinated flowers into seeded fruits and thus reduced crop yields (Peet et al. 1997; Sato et al. 2001; Firon et al. 2006). A brief period of 40°C for 3–4 h 8–9 days before anthesis and 1–3 days after anthesis affected meiosis and fertilization (Iwahori and Takahashi 1964; Iwahori 1965, 1966; Sugiyama et al. 1966). Critical period of sensitivity to moderate high temperature (32/26°C) is 7–15 days before anthesis (Sato et al. 2002). The reduction of set fruit under moderately high temperature stress is mostly due to a reduction in pollen release and viability but not in pollen production (Sato et al. 2006). The numbers of pollen grains produced by the heat-tolerant genotypes were higher than those of sensitive genotypes (Abdelmageed et al. 2003), and this criterion can be used for selection of heat-tolerant lines from a germplasm collection.

11.2.4 Fruit/Yield

Plants exposed to a fluctuating temperature regime often suffer no overall loss of yield when compared with those grown in a constant regime having the same mean temperature (Hurd and Graves 1984; Khayat et al. 1985; de Koning 1988, 1990). However, fluctuation in temperature may affect the pattern of crop yield as the rate of developmental events such as fruit maturation and volume is determined largely by temperature (Hurd and Graves 1985). Elevated temperature often increases the fruit growth rate, but it has a greater effect in hastening maturity, and as a result, the response of the plant is exhibited by compensating the final mean weight of tomato fruits (Hurd and Graves 1985; Sawhney and Polowick 1985).

Furthermore, temperature extremes can inhibit the ripening process (Lurie et al. 1996; Adams et al. 2001). Due to an increasing need to be able to schedule the crops with precision to meet stringent retail demands, heat stress acts as a constraint for continuity of high-quality product output to the market by a farmer.

11.3 Genetic Resources for Stress Tolerance

Efforts to introduce heat tolerance to the heat-sensitive commercial cultivars have prompted interest in developing criteria for evaluating germplasm from domesticated and wild species for heat tolerance. Identification of genetic resources with stress tolerance is a prerequisite for a sound breeding program in evolving stress-tolerant varieties/hybrids.

Tomato	Fla. 7156, Fla. 7771, Fla. 7776, CL-5915, CLN-1621 F, Red Cherry, Nagcarlan, Beaverlodge-6804 & 6806, *L. esculentum* var. *cerasiforme* (PI 190256), Fresh Market 9, Saladette, Processor 40, Solar Set, CLN5915-206, CLN2498D, CLN2413D, CLN2366A & CLN2123C

11.4 Biochemical Parameters of Abiotic Stress

The quality of the harvested fruit is of major concern to growers because fruit is graded according to external attractiveness (e.g., color, size, shape, and skin defects) or internal characteristics such as taste and texture (Guichard et al. 2001; Shi et al. 2002). Gautier et al. (2005) reported decreases in sugar and lycopene content in cherry tomato when fruit temperatures were increased by approximately 1 °C following fruit set through harvest under high fruit load. However, the majority of studies on the influence of temperature on fruit quality parameters have focused on postharvest fruit ripening (e.g., Dalal et al. 1968, Lurie et al. 1996). The rate of starch biosynthesis, which influences sink-strength, and thus final fruit size and yield, is potentially at its highest levels the first 10–35 d following fruit set (Ho 1996; Walker et al. 1978). Temperature changes during this time may also affect fruit maturation and growth by influencing regulation of the enzyme's acid invertase and sucrose synthase or cell expansion and division (Guichard et al. 2001; Ho and Hewitt 1986) and regulation of sugar transport into the fruit (Ho 1996).

11.4.1 Effect of Drought on Yield and Quality of Tomato

Tomato plant is sensitive to water deficits during and immediately after transplanting, at flowering stage, and during fruit development (Doorenbos and Kassam 1979). Water consumption remains constant until the onset of ripening after which, in determinate varieties, it decreases (Rudich and Luchinsky 1986). The growing season can be divided into 5 stages, viz, germination, vegetative growth stage, reproductive stage, fruit development and ripening stage.

The first organ/system to be affected by drought is the root system, wherein the root tips are the actual sensors of stress. Evidence leading to prove that the root tip experiences a loss in turgor much earlier than the root (Zhang et al. 1987). Production of ramified root system under drought is important to aboveground dry mass, and the plant species or varieties of a species show great differences in the production of roots (Jaleel et al. 2009). Tomato plants tend to show denser root system at soil water potentials which are slightly less than field capacity (Miche-lakis and Chartzoulakis 1988). The importance of root systems in acquiring water has long been recognized. The relative root growth may undergo enhancement, which facilitates the capacity of the root system to extract more water from deeper soil layers. Samuel and Paliwal (1994) observed that the water-stressed plants (tomato cv.PKM-1) showed a drastic reduction in tissue water content compared with the control plants.

The most obvious morphological effect is growth inhibition, i.e., reduction in vegetative growth, in particular shoot growth. Leaf growth is generally more sensitive than the root growth. In contrary to root, reduced leaf expansion, accelerating senescence, and abscission of the older leaves are beneficial to plants under water-deficit condition, as less leaf area is exposed resulting in reduced transpiration (Shinohara et al. 1995). Water deficit leads to decrease in the number of flowers and consequently the number of fruit and ultimately to less marketable yield (Losada and Rincaon 1994; Colla et al. 1999; Rahman et al. 1999; Veit-Kohler et al. 1999). Reduction in the size of the fruit is also observed in tomato (Adams 1990).

It has been observed that irrigation at reproductive and fruit development stages led to a 120% increase in yield (Rudich et al. 1977). A range between 300 and 400 mm of irrigation is essential for good fruit (Silva and Marouelli 1996) and between 400 and 600 mm during 90–120 days of the plant life cycle (Doorenbos and Kassam 1979).

In a situation where water deficit becomes too intense or prolonged, plants can wilt, cells can undergo shrinkage, and this may lead to mechanical constraint on cellular membranes. The strain on membrane is one of the severe effects of drought implicated on plant physiology (Shilpi and Narendra 2005).

The highest demand for water in tomato plant is during flowering (Doorenbos and Kassam 1979). Regular irrigation is vital for optimum yield (Helyes et al. 1999). Ripening is the most sensitive stage and any heterogeneous distribution of irrigation leads to fruit cracking (Losada and Rincaon 1994). Lapushner et al. (1986) observed that the fruit weight of tomato was reduced by water stress.

Blossom-end rot (BER) of tomatoes is a common problem occurring under conditions of water stress and heavy fruit load (Hodges and Steinegger 1991). It appears as brown to black lathery spots of the underside/blossom end of the fruit of tomatoes which eventually leads to decay of fruits (Sanders et al. 1989). Even a temporary water stress during early fruit enlargement can cause BER because the fruits are the last to receive adequate calcium (Hodges and Steinegger 1991). Reid et al. (1996) observed a greater incidence of internal blackening and BER, and lower concentration of calcium, in nonirrigated plants than that of irrigated plants. Calcium movement in the roots depends mainly on soil moisture.

11.4.2 Biochemical Parameters

Consumer acceptance being the ultimate goal of a breeding program, tomato breeders have to constantly try not only to increase the yield potential of their hybrids or varieties but also have to retain and improve the flavor component of the fruit under drought conditions (Stevens et al. 1977).

Certain metabolic processes are triggered in response to stress, which increase the net solute concentration in the cell, thereby helping the movement of water into the leaf resulting in increased leaf turgor. Large numbers of compounds are synthesized, which play a key role in maintaining the osmotic equilibrium and in the protection of membranes as well as macromolecules. These compounds include proline, glutamate, glycine betaine, carnitine, mannitol, sorbitol, fructans, polyols, trehalose, sucrose, oligosaccharides, and inorganic ions like K+. These compounds help the cells to maintain their hydrated state and therefore function to provide resistance against drought and cellular dehydration (Hoekstra et al. 2001; Ramanjulu and Bartels 2002).

Quality of the fruit in terms of total soluble solids, acidity (May 1993; Shinohara et al. 1995; Colla et al. 1999; Veit-Kohler et al. 1999), viscosity, and vitamin C is improved by water deficit (Rudich et al. 1977; Veit-Kohler et al. 1999; Zushi and Matsuzoe 1998). Though high sugar content in tomato is a desirable character which can be achieved by decreased irrigation (Imada et al. 1989; Veit-Kohler et al. 1999), on the contrary the overall yield is drastically reduced. A decrease up to 20% irrigation or even lesser percentage of irrigation shows significant improvement in tomato fruit flavor components (Veit-Kohler et al. 1999). Accelerated development of color and increased amount of beta-carotene content in cherry tomato due to water deficit is observed. Water deficit leads to reduction in tomato fruit size (Adams 1990), thereby reducing the locular size and the capacity of the fruit to accumulate acids and sugars, which eventually leads to poor flavor (Stevens et al. 1977).

11.4.3 Selection of Genotypes for Water Stress Tolerance

Tissue tolerance to severe dehydration is not common in crop plants but is found in species native to extremely dry environments (Ingram and Bartels 1996). Selection of genotypes for drought tolerance in water-limited environments can result in populations or species with suites of traits that improve their relative fitness in response to drought (Dudley 1996; McKay et al. 2001, 2003; Chaves et al. 2003; Juenger et al. 2005). Such traits, including acclimation responses, can improve tolerance of tissue desiccation allowing leaves to persist and function longer into drought periods or improve avoidance of water loss, allowing leaves to maintain high water potential during drought (Ludlow 1989; Kramer and Boyer 1995).

High yield potential under drought stress is the target of crop breeding. In many cases, high yield potential can contribute to yield in moderate stress environment (Blum 1996).

Genetic variability for drought tolerance in *Solanum lycopersicum* is limited and inadequate. Direct selection in the field is not always possible because uncontrollable environmental factors, such as variations in rainfall, interactions with extreme temperatures, and variations in salinity and nutrient availability, adversely affect the precision and repeatability of such trials (Richards 1996). There is no reliable field screening technique that could be used year after year and generation after generation. Selection and breeding for drought tolerance is also difficult because tolerance is a developmentally regulated, stage-specific phenomenon (Ludlow and Muchow 1990; Richards 1996).

The best source of resistance is from other species in the genus Solanum. In the Tomato Genetics Resource Center (TGRC) at the University of California, Davis has assembled a set of the putatively stress-tolerant tomato germplasm that includes accessions of *S. cheesmanii*, *S. chilense*, *S. lycopersicum*, *S. lycopersicum* var. *cerasiforme*, *S. pennellii*, *S. peruvianum, and S. pimpinellifolium*, *S. chilense*, and *S. pennelli* are indigenous to arid and semiarid environments of South America. Both species produce small green fruit and have an indeterminate growth habit. *S. chilense* is adapted to desert areas of northern Chile and often found in areas where no other vegetation grows (Rick 1973; Maldonado et al. 2003) *S. chilense* has finely divided leaves and well-developed root system (Sánchez Peña 1999). *S. chilense* has a longer primary root and more extensive secondary root system than cultivated tomato (O'Connell et al. 2007). Drought tests show that *S. chilense* is five times more tolerant of wilting than cultivated tomato. S. pennellii has the ability to increase its water use efficiency under drought conditions unlike the cultivated *S. lycopersicum* (O'Connell et al. 2007). It has thick, round waxy leaves and is known to produce acyl-sugars in its trichomes, and its leaves are able to take up dew (Rick 1973). Studies comparing drought response in S. pennellii, a self-incompatible species from the driest environments, to *S. lycopersicum*, the self-compatible cultivated tomato, have shown that S. pennellii had higher water use efficiency (WUE) both in water-stressed and nonstressed conditions (Kebede et al. 1994; Martin et al. 1999). Interestingly, *S. pennellii* and *S. lycopersicum* had similar night time stomatal opening when well watered (Caird et al. 2007a, b). *Solanum pennellii* also reduced leaf conductance (g) more rapidly in response to drought, allowing it to maintain higher leaf water potential (Ψ l) compared to *S. lycopersicum* (Torrecillas et al. 1995). The differential drought responses of *S. pennellii* and *S. lycopersicum* suggest that adaptation to diverse habitats may have played a role in speciation processes in wild tomatoes (Schluter 2001; Levin 2005; Nakazato et al. 2008). Indeed local adaptation to habitat water availability has been shown in other herbaceous species. In studies of sapphire rock cress and dandelion, populations from drier environments had a higher WUE than populations from wetter conditions in common garden experiments (McKay et al. 2001; Brock and Galen 2005). These differences in intrinsic, drought-related traits suggest there may be differences in physiological responses to drought among populations when habitats differ in water availability. An advanced drought-tolerant line (RF4A) has been developed at Indian Institute of Horticultural Research by interspecific hybridization with *S. pennellii*.

Sources of resistance to drought have been reported in several accessions of wild taxa which includes LA0429 (*S. cheesmaniae* Ecuador), LA1401 (*S. cheesmaniae* Ecuador), LA3661 (*S. chmielewskii* Peru), LA2680 (*S. chmielewskii* Peru), LA1334 (*S. lycopersicum* var. *cerasiforme* Peru), LA1421 (*S. lycopersicum* var. *cerasiforme*), LA2133 (*S. neorickii* Ecuador), LA3657 (*S. neorickii* Peru), LA1335 (*S. pimpinellifolium* Peru), LA1416 (*S. pimpinellifolium* Ecuador), and RF4A (*S. pennellii* derived, IIHR, India).

11.4.4 Water Management

On an average, water use efficiency in the existing irrigation project in India is only about 40%. A bulk of water meant for agricultural use in fact does not benefit crops. With better water management, if the efficiency is improved to the level of 60%, it will allow an additional 8 million hectare of land under irrigation with the existing irrigation facilities alone in India (Bhagavantha-goudra 2000). The quality of tomato can be enhanced, and water can be saved by using well-managed drip irrigation system (Rudich et al. 1977). Water requirement of tomato changes according to the stage of the crop; therefore, an irrigation regime ideal for tomato should be arrived at to meet the demand of water by the plant.

11.5 Conclusion and Future Prospects

To address the impact of heat stress (Ainsworth et al. 2008), breeding new cultivars with enhanced adaptation to high temperatures will help farmers grow crops in stressful environments of the twenty-first century. Low heritability values, complexity of the trait, and environmental factors such as relative humidity are a few constrains encountered in developing tolerant lines (Scott et al. 1986; Villareal and Lai 1979; Abdalla and Verkerk 1968) through conventional breeding. Genetic resources and breeding methods combining conventional and molecular tools (including the transgenic approach) are needed to develop such cultivars. However, as indicated by Bonhert et al. (2006), abiotic stresses such as temperature extremes, water scarcity, and ion toxicity (e.g., salinity and heavy metals) are difficult to dissect because defense responses to abiotic factors require regulatory changes to the activation of multiple genes and pathways. Nevertheless, recent advances in genomic research addresses this problem in a more integrated manner with the multigenicity of the plant abiotic stress response.

Drought stress is an important area with respect to increase in plant productivity. Therefore, the basic understanding of the mechanisms underlying the functioning of physiological, biochemical, and molecular aspects is important for the development of tolerant tomato plants. Accumulating evidence suggests that plant response to drought stress is controlled by more than one gene and is highly influenced by environmental variation (Ceccarelli and Grando 1996; Richards 1996). A deeper understanding of the transcription factors regulating these genes, the products of the major stress responsive genes, and cross talk between different signaling components should remain an area of intense research in future. Transfer and utilization of genes from these drought resistant species will enhance tolerance of tomato cultivars to dry conditions, although wide crosses with *S. pennellii* produce fertile progenies, *S. chilense* is cross incompatible with *S. lycopersicum*, and embryo rescue through tissue culture is required to produce progeny plants. The knowledge generated through these studies should be utilized in making transgenic plants that would be able to tolerate stress condition without showing any growth and yield penalty. Therefore, it is desirable that appropriate stress-inducible promoters should drive the stress genes as well as transcription factors, which will minimize their expression under a nonstressed condition, thereby reducing yield loss. The product of these genes should also be targeted to the desired tissue as well as cellular location to control the timing as well as intensity of expression. Attempts should be made to design suitable vectors for stacking relevant genes of one pathway or complementary pathways to develop durable tolerance. These genes should preferably be driven by a stress-inducible promoter to have maximal beneficial effects. Additionally, due importance should be laid on the physiological parameters such as the relative content of different ions present in the soil as well as the water status of the crop in designing transgenic plants for the future.

The ultimate goal is to develop plants with improved water use efficiency, resulting in crops that could significantly increase their yield and alleviate an increasingly imminent threat of food scarcity. Drought stress tolerance can not only improve the productivity of the land already in use but may also permit the exploitation of cultivable land with limited water supplies and in areas where cultivation was not practiced. Research is in progress to identify the genetic factors underlying drought tolerance in *S. chilense* and *S. pennellii* and to transfer these factors into cultivated tomatoes.

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